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Tree transpiration varies spatially in response to atmospheric but not edaphic conditions

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Summary

1. Measuring transpiration simultaneously in time and space can establish a better understanding of how to mechanistically scale spatiotemporal values.

2. This study tested the following predictions to falsify a tree hydraulic hypothesis of spatial variation in transpiration: (i) stands with larger trees will a have longer range and greater sill and nugget at a given vapour pressure deficit (D); (ii) the range, sill and nugget will decline faster with increasing D with larger trees; and (iii) soil moisture, texture and/or N levels will be correlated with transpiration.

3. We used cyclic sampling to efficiently collect spatial sap flux data from 144 trees in two forested stands in northern Wisconsin: an Aspen-dominated stand with small trees and a Maple–Pine-dominated stand with larger trees.

4. In the Maple stand, the range of spatial autocorrelation in half-hourly transpiration dropped from 80 to 20 m with increased D, whereas in the Aspen stand the range dropped from 55 to 35 m with a similar increase in D.

5. Differences in the range of spatial autocorrelation at a given D were driven by sapwood area, which is a function of tree size.

6. These results show that species and tree size as well as individual tree hydraulics drive spatial variability in transpiration with little additional variation explained by the measured edaphic conditions.

7. Scaling from individual tree transpiration to the landscape in time and space should incorporate atmospheric drivers in time and investigate other potential drivers of tree size in space such as light competition.

Key-words: geostatistics, scaling, sapflux, plant hydraulics, vapour pressure deficit

Introduction

Most ecological processes occur in patches or are distributed along gradients, and this non-stochastic distribution violates the assumptions of classical statistics (Robertson 1987; Legendre & Fortin 1989; Legendre 1993). Legendre (1993) suggests that spatial or temporal autocorrelation in ecosystem properties promotes diversity of species and functional traits, and that small scales will exhibit autocorrelation, whereas larger scales will exhibit trends. This property of temporal and spatial autocorrelation has been observed at practically all scales (Legendre 1993) from microbe (Franklin *et al.* 2002) to landscape (Bishop, Schroder & Colby 2003) and forms an important foundation of the structure of ecological communities (Reiners & Driese 2004). Recent work on tree transpiration suggests spatial properties are connected to drivers in time (Adelman, Ewers & Mackay 2008; Loranty *et al.* 2008) but has not tested how these connections may change with different stand types. This study compares the spatial dynamics in tree transpiration of two stands varying in species composition and structure.

Tree transpiration, because it can be estimated continuously via sapflux (Granier 1987), scaled between stems and leaves with allometrics (Wullschleger, Meinzer & Vertessy 1998), and has a relatively well-understood mechanistic basis (Sperry *et al.* 2002), serves as an excellent venue for quantifying connections between temporal and spatial controls over ecosystem patchiness. Transpiration varies over a diurnal cycle that is driven by vapour pressure deficit (D), due to tree

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hydraulic responses and photosynthetically active radiation (Q_0) at a particular soil moisture content (Whitehead *et al.* 1996; Hinckley *et al.* 1998). Stomatal conductance responds to the rate of water loss at the leaf level and is limited by the product of hydraulic conductivity (k) and the water potential gradient (Ψ) between leaves and soil (Franks, Drake & Froend 2007). This limitation results in a saturating relationship between transpiration and D due to hydraulic stress with trees having a larger initial stomatal conductance declining faster (Oren *et al.* 1999; Ewers *et al.* 2005). Hydraulic stress in trees is further increased by coarser soil texture (Hacke *et al.* 2000), increased soil N (Ewers, Oren & Sperry 2000) and decreased light conditions in the canopy (Schäfer, Oren & Tenhunen 2000).

Recent work has shown that transpiration demonstrates spatial autocorrelation that is driven temporally by D (Adelman, Ewers & Mackay 2008; Loranty *et al.* 2008). The most relevant spatial parameters within each range of temporal environmental drivers (e.g. low D or high D) are the range that is the distance of spatial autocorrelation, sill that is the maximum spatial variation and the nugget the minimum spatial variation. As predicted from a plant hydraulics hypothesis of spatial variation in time driven by D (Adelman, Ewers & Mackay 2008; Loranty *et al.* 2008), when D is low, trees are not hydraulically stressed and most trees' stomatal conductance is high, the range is relatively long and the sill and nugget are low. When D is high, most trees are hydraulically stressed, and so individual tree variability in stomatal response leads to a shorter range and larger sill and nugget. No studies have tried to expand the predictions of the hydraulic hypothesis of these temporal (response to D) and spatial (change in range, sill or nugget with increasing D) patterns to edaphic conditions other than soil moisture or have attempted to predict how changing patterns of trees size will influence the rate of change in the spatial patterns.

We compared two stands in northern Wisconsin to test the relationship between edaphic conditions and spatiotemporal patterns of transpiration across varying species composition and stand structure. One stand had a forested wetland dominated by alder (*Alnus incana* L. Moench) that transitioned into an upland with trembling aspen (*Populus tremuloides* Michx) whereas the other stand was a mix of much larger sugar maple (*Acer saccharum* Marsh) and red pine (*Pinus resinosa* Ait). We predict that the (i) stand with larger trees will a have longer range and greater sill and nugget at a given D; (ii) the range, sill and nugget will decline faster with increasing D in the stand with large trees; and (iii) soil moisture, texture and/or N levels will be correlated with transpiration within a stand.

Materials and methods

STAND DESCRIPTIONS

The stands, hereafter referred to as Aspen and Maple for the most common species in each, are located in northern Wisconsin near Park Falls in the Chequamegon-Nicolet National Forest, *c.* 800 m south-east and north-east, for Aspen and Maple respectively, of the WLEF eddy covariance tall tower (45·945°N, 90·272°W; Bakwin *et al.* 1998; part of the Chequamegon Ecosystem Atmospher Study, ChEAS). These stands encompass the four major forest cover types that characterize the region (Burrows *et al.* 2002). The bedrock is comprised of Precambrian metamorphic and igneous rock, overlain by 8–90 m of glacial and glaciofluvial material deposited *c.* 10–12 thousand years before present. The topography is slightly rolling with an elevation range of tens of metres while outwash, pitted outwash and moraines

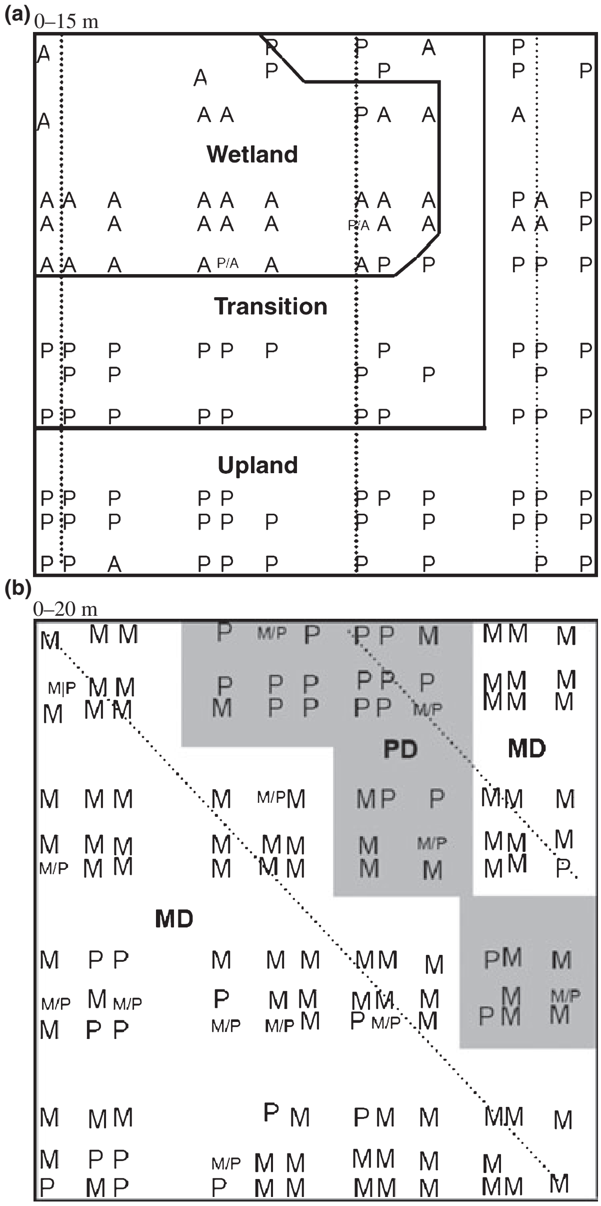

Fig. 1. Layout of tree measurements in cyclic plot designs in (a) Aspen stand and (b) Maple stand, with single letters representing the location of the sample plot centre. Soil samples were taken along each of the dotted transects. NW corner of A dominated by white cedar (*Thuja occidentalis*) not analyzed in this study, bolded MD in (b) represents the sugar maple dominated areas and the grey area represents the red pine dominated area (bolded PD). Locations with M/P or P/M are mixed red pine or sugar maple. Scales for each map are in metres.

Table 1. Comparison of soil texture and moisture in the Aspen and Maple sites

Aspen site	*n*	% Silt	% Sand	% Clay	*n*	Mean soil moisture (%) 9 June 2005	14 July 2005
W	10	23·2 (10·6) a	63·5 (11·5) a	13·3 (1·5) a	50	59·4 (21·9) a	40·4 (19·9) a
T	8	15·5 (3·8) b	72·1 (3·1) b	12·5 (1·9) a	31	19·3 (10·3) b	14·4 (8·4) b
U	18	13·8 (2·7) b	73·9 (3·5) b	12·4 (1·8) a	63	14·6 (5·6) c	10·8 (5·9) b
Maple site						4 August 2005	
MD	6	13·4 (4·6) a	74·7 (4·1) a	11·9 (1·4) a	4	17·39 (3·4) a	
PD	3	17·8 (3·1) a	69·5 (2·7) b	12·7 (1·8) b	39	15·47 (3·0) b	

Values with different letters are significantly different (α = 0·05). 9 June is a representative day and 14 July is the last and driest soil moisture taken in the Aspen site. 4 August is the only soil measurement at the Maple site. W is wetland, T is transition, U is upland areas (Fig. 1). MD is maple dominated; PD is pine-dominated areas (Fig. 2).

are the dominant geomorphic landforms. The climate is cool continental with annual precipitation of *c.* 800 mm and mean January and July temperatures of 19 °C and −12 °C respectively.

The Aspen stand (tree age = 20 years) has a soil moisture gradient from a wetland in the northwest corner to drier uplands in the other three corners (Fig. 1), although the elevational gain was only about 2 m. The drier uplands are dominated by trembling aspen (*Populus tremuloides*) whereas speckled alder (*Alnus incana*) are prevalent in the lower, poorly drained wetlands with *Sphagnum* spp. present in all hummocks. On 9 June 2005 (one of the days soil moisture measurements were made), the wetlands averaged 60%, the transition 20% and the uplands < 15% volumetric soil moisture. These results were used to divide the stand into three areas based on average soil volumetric water content values (Table 1, Fig. 1).

The Maple stand is dominated by sugar maple (*Acer saccharum*) with a swath of red pine (*Pinus resinosa*) running diagonally through the stand from the middle of the northern edge to the middle of the eastern edge. There are also a few red pines scattered throughout the rest of the stand. All of the red pines are the remnants of a plantation. Tree ages are 50 and 50–70 years for red pine and sugar maple respectively. The plot was divided into two areas (sugar maple dominated and red pine dominated) because of the distinctive patterning of the species (Fig. 1).

Table 2. Tree species, sapflux sample size, mean size by diameter breast height at 1·3 m (DBH) and mean sapwood area with standard errors in parentheses

	Species	*n*	DBH (cm)	Sapwood (cm^2)
Aspen stand				
W	Alder	35	5·27 (1·2)	22·8 (9·5)
	Aspen	5	6·5 (1·1)	32·9 (10·4)
T	Alder	1	6·2	30·2
	Aspen	30	9·56 (3·1)	74·0 (44·1)
U	Alder	5	4·6 (0·9)	17·1 (6·2)
	Aspen	58	8·9 (2·9)	64·3 (39·5)
Maple stand				
MD	Maple	83	22·2 (7·2)	365·38 (193·1)
	Pine	22	38·0 (7·3)	946·53 (304·3)
PD	Maple	16	26·5 (9·8)	515·85 (385·7)
	Pine	19	39·2 (7·9)	1006·71 (314·6)

W is wetland, T is transition and U is upland areas (Fig. 1). MD is sugar maple dominated; PD is pine-dominated areas of the Maple stand (Fig. 1).

SAMPLING DESIGN

A 3/7 cyclic sampling design that maximizes spatial information with a minimal number of samples (Burrows *et al.* 2002) was used to determine the location of plots. From preliminary soil moisture and basal area spatial measurements described in Loranty *et al.* (2008), the plot locations were based on a 5-m plot diameter for the Aspen stand and a 6·6-m plot diameter was chosen for the Maple stand as the trees are larger and spaced further apart. Additionally, the two sides of the Maple stand grid mirror each other to increase the number of plots in the sugar maple–red pine transition areas. Each stand has 144 plots so the Aspen stand was 120 × 120 m, and the Maple stand was 132 × 140 m (Fig. 1).

SAP FLUX MEASUREMENTS

Details of sap flux sampling are in Table 2. Transpiration per xylem areas (J_S) was measured with constant-heat sensors (Granier 1987) during June–August of 2005. One sensor pair was placed on the north side of each tree; the intra-tree scaling was from Ewers *et al.* (2002) and accounts for bark thickness, sapwood depth and radial and circumferential trends in sap flux. The largest tree in each plot was chosen for the sap flux sensor and a second if it was also dominant. Adelman, Ewers & Mackay (2008) and Loranty *et al.* (2008) justified this sampling design because tree size impacts on sap flux can still be investigated when many trees are sampled. Sap flux measurements were recorded every 30 s and averaged to 30 min values with a data logger (CR10X; Campbell Scientific, Logan, UT, USA). To include nighttime transpiration, baselines were determined from the maximum temperature difference over a week long period using the approach of Oishi, Oren & Stoy (2008). Aspen and alder were sampled in the Aspen stand as they were the dominant species in each soil moisture area (Loranty *et al.* 2008). Sugar maple and red pine were the only canopy trees throughout the Maple stand.

CALCULATION OF SAP FLUX SCALARS

Sapwood area (A_S) was calculated using DBH (diameter breast height at 1·3 m) and species-specific allometric equations derived from trees on sites of similar edaphic conditions ~10 km from the present study (Ewers *et al.* 2002). Leaf area (A_L) was calculated from allometric relationships for foliar biomass by Ter-Mikaelian & Korzukhin (1997) and specific leaf area estimated by Ewers, Mackay & Samanta (2007). Canopy transpiration per tree (E_C) is the product of A_S and

J_S. Canopy transpiration per unit leaf area (E_L) is the quotient E_C and A_L.

ATMOSPHERIC DATA

Temperature and relative humidity were measured (HMP 45C; Vaisala Oyj, Helsinki, Finland) at 2/3 (~7 m) canopy height at the Aspen stand to calculate vapour pressure deficit (D). The values for D at the Maple stand were taken from the WLEF tower data sets that can be found on the ChEAS website (http://cheas.psu.edu/); some values were gap-filled or interpolated when data were missing (Cook *et al.* 2004; Desai *et al.* 2005). Ewers *et al.* (2008) showed that stands in this area, including other aspen and sugar maple-dominated ones, 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 (slope of the two measurements was not different from 1 and the intercept was not different from 0). This also justifies an assumption of D being spatially unaffected by varying transpiration rates in each stand. The WLEF tower values for photosynthetic photon flux density (Q_0) were used for both stands.

SOIL MEASUREMENTS

Prior work in these stand types has shown that low soil moisture does not control transpiration except during times of rare drought (Mackay *et al.* 2002; Ewers, Mackay & Samanta 2007; Samanta *et al.* 2008); a condition that did not occur during this study. We thus focused our measurements on surface soil to facilitate spatial sampling and to detect excessive soil moisture that would limit tree function in the wetland areas. Soil moisture was measured with a time domain reflectometry-type probe to 6 cm (ML2× probe, HH2 moisture meter; Delta-T Devises, Cambridge, UK) at three random locations in each of the 144 plots of both stands and then averaged to obtain a plot value. The measurements were taken four times in the Aspen stand (9 June, 13 June, 12 July, 14 July 2005) and once in the Maple stand (4 August 2005). Mineral soil samples were collected with a soil corer (10 × 3·4 cm) in both stands. Soils were oven dried for 24 h at 40 °C (Robertson *et al.* 1999), and bulk density calculated. Mineral soil samples were collected at every plot in the Aspen stand and at 18 plots in the Maple stand (Fig. 1); 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, Hanau, Germany). The same subset of plots in both stands was also analyzed for soil texture (GLOBE Program 2005). The three Aspen stand transects represented the soil moisture gradient whereas the two Maple stand transects covered the areas dominated by the two different tree species.

DATA REDUCTION

Atmospheric drivers (Q_0 and D) were both binned to smooth temporal variation (Ewers *et al.* 2007) and better quantify spatial patterns (Loranty *et al.* 2008). Two methods of binning (equal points per bin or equal sizes of bins) were tested to ensure adequate numbers of points per bin (Martin *et al.* 1997; Schäfer, Oren & Tenhunen 2000). Only the equal size bins were effective. There is typically a lag between atmospheric drivers and a tree's response to those drivers (Schulze *et al.* 1985; Phillips *et al.* 1997, 2009; Ford *et al.* 2005; Burgess & Dawson 2008). Therefore, a cross-correlation function was used to analyze the lag between transpiration and both D and Q_0 (SYSTAT 9; Systat Software, Inc., San Jose, CA, USA 1998) to verify they were the same as those found by Ewers, Mackay & Samanta (2007) for these species in nearby stands. These individual lag values were used to adjust the transpiration values vs. D and Q_0 and then the values were rebinned.

Rain days, and days with very low daily D (< 0·1 kPa; Phillips & Oren 1998), were removed from the data sets because additional errors in sap flow on such days are the result of tree transpiration, hydraulic refilling, nighttime transpiration or low D measurement uncertainty (Ewers & Oren 2000; Dawson *et al.* 2007).

GEOSTATISTICAL ANALYSES

Semi-variogram analysis was applied to J_S, E_L and E_C for all D and Q_0 bins. The interpretation of semi-variograms requires empirical models to quantify the nugget (errors/variation at distance smaller than sampled), sill (absolute amount of variation) and range (distance where point pairs are spatially independent). The range is of interest for quantifying spatial autocorrelation (Isaaks & Srivastava 1989). Both spherical and exponential models (Cressie 1993; Schabenberger & Gotway 2005) were fitted to the data with weighted regression by point-pair counts, minimizing residuals and maximizing r^2 (Legendre & Legendre 1998), using GS+ (ver. 7; Gamma Software, Plainwell, MI, USA) and SIGMAPLOT (ver. 10.0; Systat).

In both stands, the method of Adelman, Ewers & Mackay (2008) was used to exclude four outliers in the Aspen and none in the Maple stand from the spatial analyses. Because semi-variograms require second-order stationarity across a study site (Cressie 1993; Schabenberger & Gotway 2005), both stands were tested for drift and anisotropy using directional variograms (GS+; Gamma Software; Isaaks & Srivastava 1989), unpaired *t*-tests (Sigma Plot, San Jose, CA) between the different areas of the stands (Fig. 1), and manual verification of the presence of a sill (Legendre & Legendre 1998). If a significant (α = 0·05) difference was found, a normalizing value equal to the ratio of the means was applied for second-order stationarity.

Results

TRANSPIRATION IN TIME AND DRIVERS

Figure 2 illustrates J_S, E_L and E_C values of transpiration for each of the areas within the stands, averaged half-hourly, over a representative 3-day period. In the Aspen stand, upland and transition trees had higher E_C rates than wetlands (P < 0·01), wetland E_L was lowest (P < 0·05), but J_S was not different (P > 0·1). In the Maple stand, the sugar maple-dominated areas had similar J_S and E_L, but significantly lower E_C (Fig. 2; P < 0·01) than red pine-dominated areas. Within all species and spatial locations, the response to D and Q_0 was the same (data not shown). These results show that the temporal response of transpiration to D or Q_0 was not dependent on tree species or size and allows us to test the impact of tree size and species on spatial patterns.

SPATIAL PATTERNS

To test our three predictions, we first determined how the stand properties changed in space. In the Aspen stand, soil moisture and % silt and sand were significantly different in

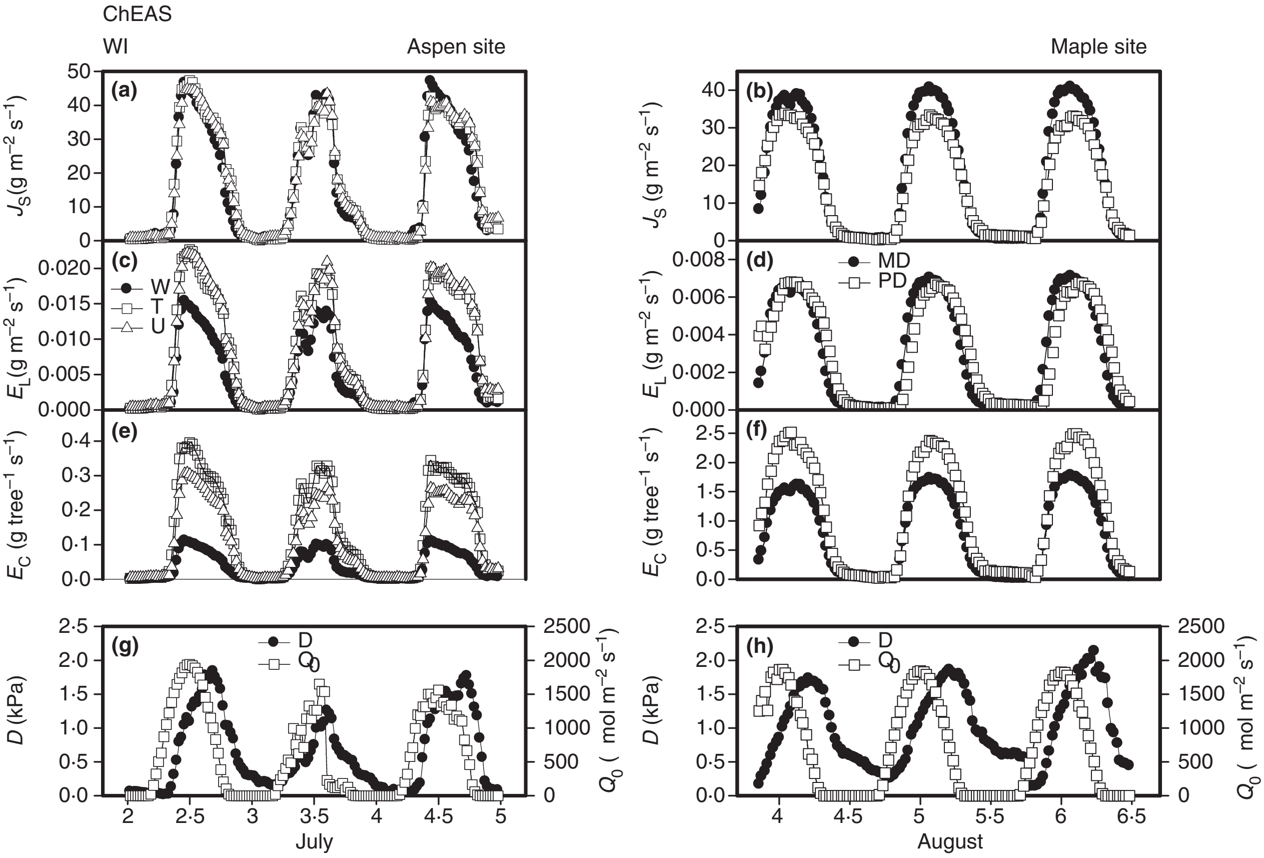

Fig. 2. (a,b) Sap flux per sapwood area (J_S), (c,d) transpiration per leaf area (E_L), (e,f) transpiration per canopy (E_C), and (g,h) vapour pressure deficit (D) and photosynthetic radiation (Q_0) for three representative days in July 2005 for the Aspen stand and in August 2005 for the Maple stand. W is wetland, T is transition and U is upland areas (Fig. 1). MD is sugar maple-dominated and PD is red pine-dominated areas (Fig. 2). Note different scales on *y*-axes on (a–f).

the wetland areas compared with the transition and upland areas; in the Maple stand sand and clay were significantly different but not % silt (Table 1). Mean E_C, E_L and DBH – but not J_S – increased from wetland to upland in the Aspen stand reflecting the change in tree size (Tables 2 and 3). The means of these four parameters were not significantly different between the upland and transition areas in this stand. A normalization factor of 3·02, equal to the ratio of the mean E_C of the upland vs. the wetland, was applied to E_C in the Aspen stand mostly reflecting the difference in alder and trembling aspen transpiration rates. The Maple stand also showed non-stationarity of means between the sugar maple and the red pine-dominated sections for E_C, J_S and DBH, but not for E_L resulting in a normalization factor of 1·37. There was no spatial autocorrelation when J_S, E_L or E_C was binned by Q_0 or time periods in either stand (data not shown).

Table 3. Average transpiration per sapwood (J_S), per leaf area (E_L) and per whole tree (E_C) at bin average 1·6–1·8 vapour pressure deficit (D) with standard errors in parentheses

	n	J_S (g m^{-2} s^{-1})	E_L (g m^{-2} s^{-1})	E_C (g tree^{-1} s^{-1})
Aspen stand				
W	40	29·14 (11·13) a	0·011 (0·008) a	0·077 (0·045) a
T	31	34·87 (12·86) a	0·017 (0·006) b	0·287 (0·238) b
U	63	33·14 (15·82) a	0·017 (0·008) b	0·231 (0·217) b
Maple stand				
MD	105	34·55 (11·66) a	0·006 (0·002) a	1·5 (0·90) a
PD	35	29·87 (12·09) a	0·006 (0·002) a	2·08 (1·03) b

For each variable, values with different letters were significantly different (α = 0·05). W is wetland, T is transition and U is upland areas (Fig. 1). MD is sugar maple dominated, PD is red pine-dominated areas (Fig. 1) and values in parentheses are 1 SE of the mean.

To test prediction 1, Fig. 3 shows the sample semi-variograms calculated at 0·6–0·8 bin average of D for all areas. The variability of J_S, E_L and E_C, at both normalized and non-normalized spatial means, is plotted against the lag distance. The range for both stands varied depending on how transpiration was expressed. In Fig. 3a–d, the range of J_S and E_L, normalized and non-normalized, is beyond the range of the area sampled because of the linear relationship. The fits for the Maple stand are weak (r^2 = 0·25–0·42) whereas the fits in the Aspen stand are quite strong (r^2 = 0·69–0·88) suggesting that tree size was playing a role in the spatial autocorrelation. The Aspen stand E_C, Fig. 3e, shows a range of *c.* 40 m and a sill of 0·0085 for normalized and not normalized, with nuggets of 0·005 and 0·0033, and r^2 = 0·69 and 0·84 for normalized and not normalized respectively. The Maple stand E_C, Fig. 3f, shows a range of 25–35 m for both, but sills of 0·23 and 0·15

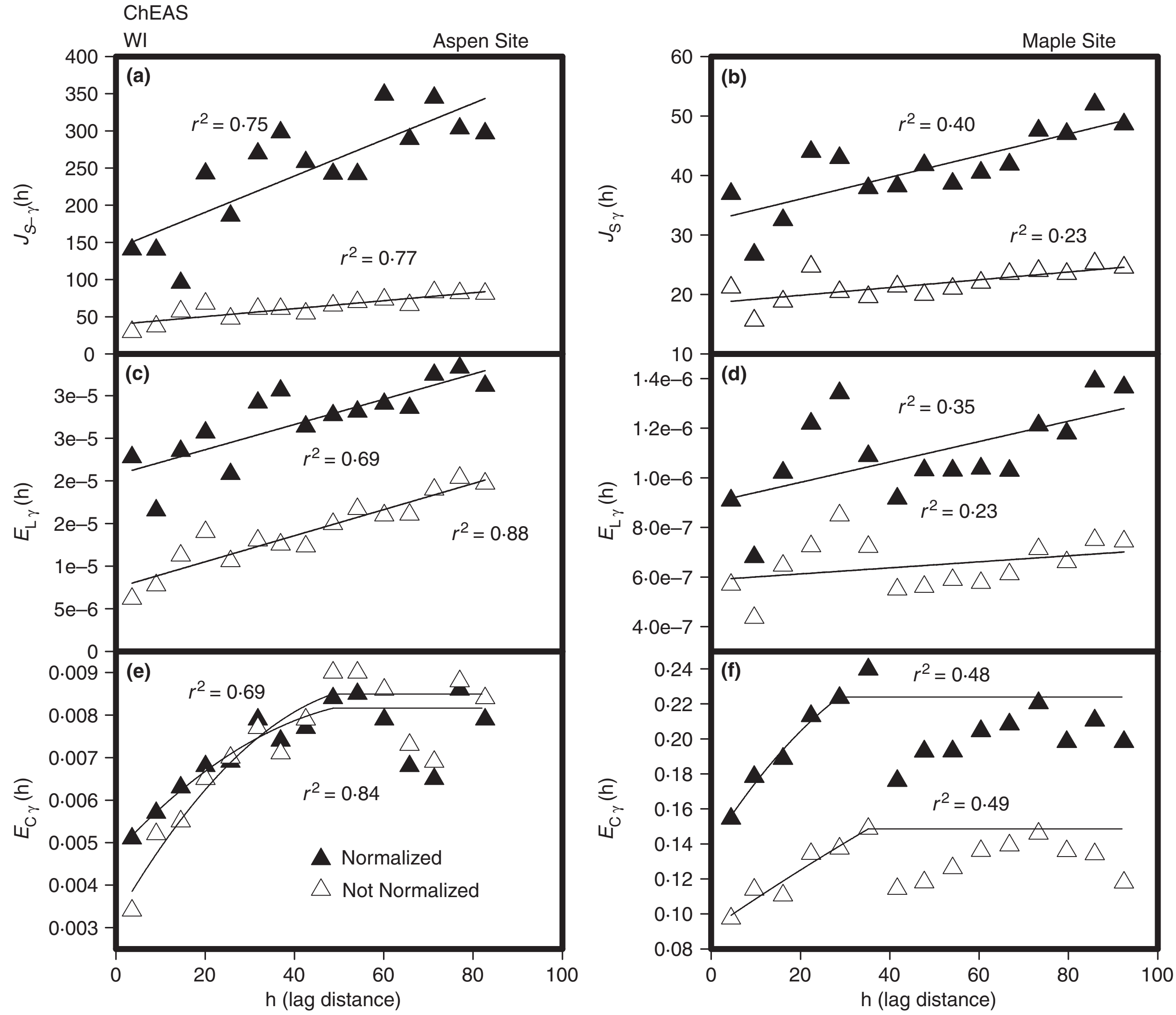

Fig. 3. (a,b) Sap flux per sapwood area (J_S), (c,d) transpiration per leaf area (E_L), and (e,f) transpiration per tree canopy (E_C) semi-variance on the *y*-axis and lag distance on the *x*-axis at the 0·6–0·8 kPa *D* bin. Normalized refers to forced stationarity of the means across the study stands and not normalized is unconverted means (Table 3). In (a–d), fitted curves are linear. In (e) and (f), a spherical model was fit to the data.

and nuggets of 0·14 and 0·09 for normalized and not normalized respectively, and the r^2 values of 0·48 and 0·49 for each are comparable. These results falsified the range part of prediction 1 but supported the nugget and sill portion. Using the normalizing factor increased the amount of variability (the sill) in both stands with a greater increase in the Maple. The range was not significantly modified. Because E_C is the most relevant to stand transpiration and shows consistent spatial autocorrelation, we focus our analyses of spatial patterns on E_C.

Figure 4 provides maps of the E_C spatial trends in both stands based on the semivariogram information. The 0·7 kPa *D* values correspond to the semivarigrams for E_C in Fig. 3 without normalization. The other panels of the figure show spatial variability in E_C with increasing *D* at 1·3 kPa *D*. The amount of variability appears visually to be greater in the Maple than the Aspen stand lending visual support to prediction 2. Figure 5 quantitatively tests prediction 2 by plotting the nugget, sill and range from each E_C semivariogram against *D* bins. All four combinations of lagging and normalizing are shown. The lagged values followed the non-lagged values very closely indicating that lagging was not necessary to estimate spatial autocorrelation. In both stands, the nugget and sill show a rise in variability as well as a plateau at the highest values. The range in Fig. 5 shows an exponential decline, indicating that E_C became more heterogeneous or patchy with increasing *D*. The Maple nugget and sill had more than 2 orders of magnitude greater variability than in the Aspen stand reflecting the higher relative differences in E_C between the stands (Table 3); further supporting prediction 2. The Maple stand had a greater rate of change of range with *D* (80–20 m over a change in *D* from 0·2 to 0·8 kPa) compared to the Aspen site (50–36 m over 0·2–1·3 kPa) supporting our second prediction.

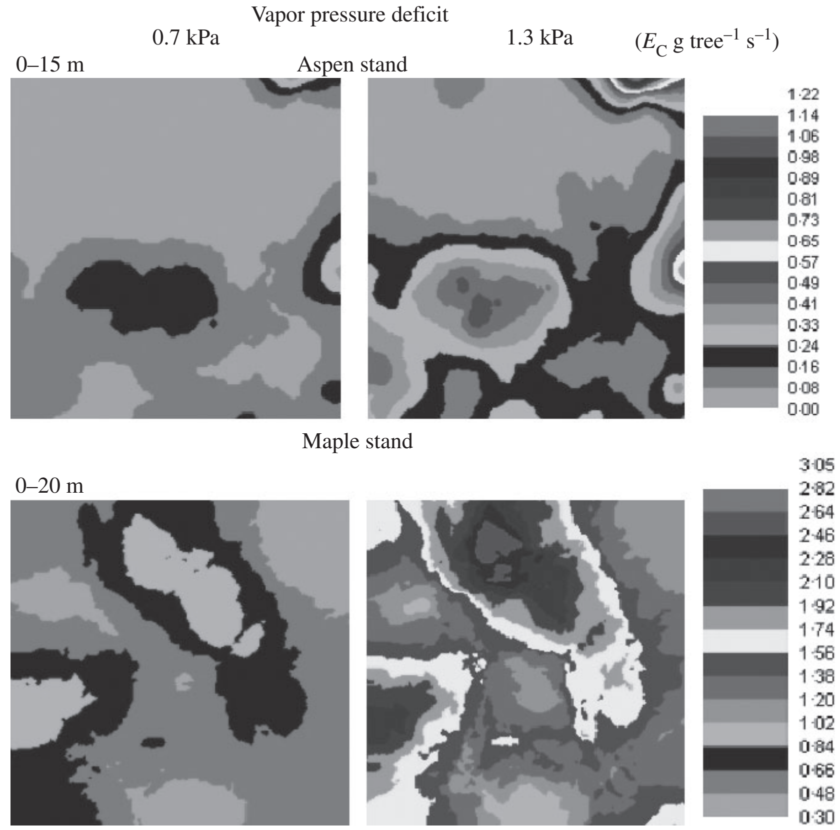

Fig. 4. Kriged maps of transpiration per canopy (E_C) for the Aspen site (top two panels) and Maple site (bottom two panels) at two different vapour pressure deficit values. Scales for each map are in metres and are directly comparable with Fig. 1.

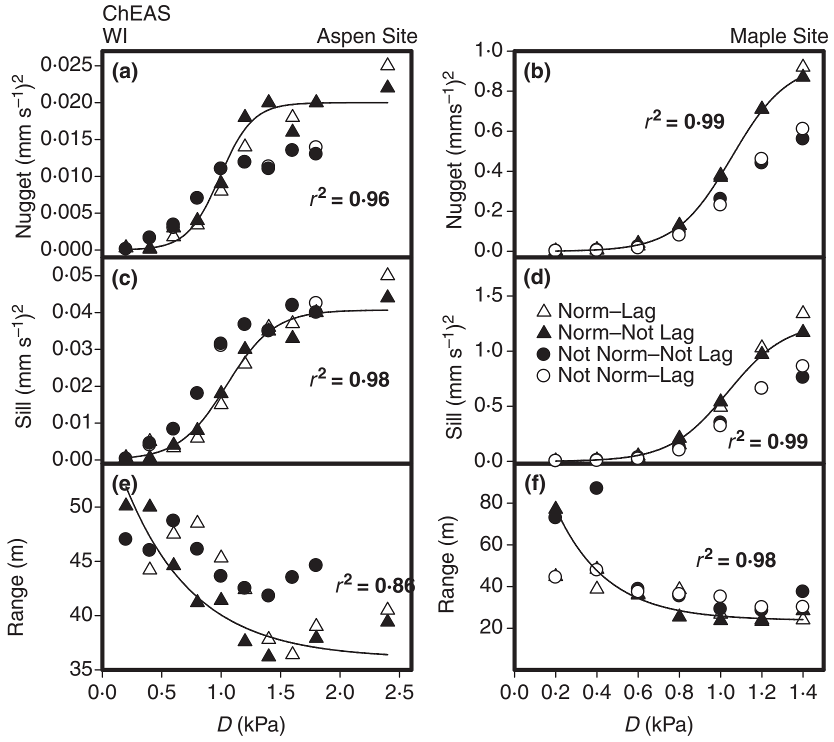

Fig. 5. (a,b) Nugget values, (c,d) sill values, and (e,f) range values of transpiration per tree canopy (E_C) across all binned vapour pressure deficit (D) values. Lag refers to the time lag between E_C and D. Note different scales on the y-axis.

EDAPHIC CONDITIONS

In the Maple stand, soil moisture showed no correlation with E_C, sapwood or DBH spatially ($P > 0{\cdot}3$ for all, data not shown), although the pine and maple areas were significantly different (Table 1). In the Aspen stand, higher rates of E_C corresponded to aspen trees and lower soil moisture (see Fig. S1) with both soil moisture and total N showing a weak inverse relationship to E_C values by species but not spatial location within species. Within a species, there was no relationship with any measured soil variable. Distance from the wetland area boundary to each tree in the other areas was calculated and plotted against E_C to explore a possible correlation with topography or wetland edge, but no correlation was found ($P > 0{\cdot}8$, data not shown). No other measured soil variable correlated to E_C, DBH or sapwood area in either stand ($P > 0{\cdot}2$, data not shown). We thus reject our third prediction.

Discussion

DRIVERS OF E_C TEMPORALLY AND SPATIALLY

D is a well-known temporal driver of transpiration and much work has supported the hypothesis that this is due to tree hydraulics (Jarvis 1980; Monteith 1995; Oren *et al.* 1999; Pataki, Oren & Smith 2000; Ewers *et al.* 2005; Ford *et al.* 2005). Our temporal data for all four species agreed with analyses by Ewers, Mackay & Samanta (2007) in time. Because neither J_S nor E_L exhibits the same amount of spatial autocorrelation as E_C (Fig. 3), sapwood area (and thus tree size reflected in diameter and sapwood area) must be driving spatial variability within a given bin of *D*. Ewers *et al.* (2002) observed in these same species that although sapwood area per ground area determines E_C, some species of trees have different relationships between size, sapwood area and transpiration rate. Pataki, Oren & Smith (2000), for example, found that aspen transpires at higher rates than other trees. Because E_C incorporates tree size using allometrics (Meinzer, Goldstein & Andrade 2001), tree diameter is an important variable for scaling (Hatton, Moore & Reece 1995), and therefore spatial heterogeneity is inherent in tree growth (Fox, Bi & Ades 2007a,b).

TEMPORAL AND SPATIAL ANALYSIS OF E_C

Similar to Adelman, Ewers & Mackay (2008) and Loranty *et al.* (2008) sorting transpiration data and binning by *D* into 0·2-kPa groups was the only appropriate method. Low values of *D* increase uncertainties in tree transpiration, hydraulic refilling, nighttime transpiration or errors in low *D* measurement (Ewers & Oren 2000; Dawson *et al.* 2007). Our results showed that lagging did not influence or explain the changes in spatial autocorrelation (Fig. 5) likely because of relatively small tree size (Phillips *et al.* 2002; Ewers *et al.* 2005, 2007) and indicates that potential issues with temporal resolution in these types of sap flux sensors (Burgess & Dawson 2008; response by Phillips *et al.* 2009) are not influencing the spatial analyses.

Non-stationarity was found in both stands for more than one variable tested (DBH, E_C, J_S; Table 2). However, the causes of non-stationarity differed between the stands. A soil moisture gradient was the most likely underlying cause of the non-stationarity in the Aspen stand (see Fig. S1), which influences tree species and sizes, whereas the location of dominant tree species, and their relative sizes, was likely the underlying cause of non-stationarity in the Maple stand. Figure 5 shows that normalization increased the sill and nugget values, the variability of E_C, but did not change the range of spatial autocorrelation. These results rule out stationarity violations as an explanatory factor of the temporal changes in spatial autocorrelation.

POTENTIAL EXPLANATIONS FOR CHANGES IN SPATIAL PATTERNS

Although tree size and spacing are clearly the drivers of spatial patterns within bins of *D* at both stands (Fig. 3), tree size and spacing cannot explain the temporal changes in spatial autocorrelation with changing *D* (Fig. 5). Recent works by Adelman, Ewers & Mackay (2008) in a subalpine forest and by Loranty *et al.* (2008) modelling the spatial transpiration patterns in the Aspen stand of this study support the hypothesis that spatial changes with *D* are due to tree hydraulics. When *D* is low, trees can easily keep up with water transport demand and thus all trees have water loss rates limited solely by *D*. As *D* increases, some trees must close their stomata which results in the saturation of E_C with increasing *D* (Oren *et al.* 1999; Pataki, Oren & Smith 2000) to prevent excessive and catastrophic cavitation (Ewers, Oren & Sperry 2000; Ewers *et al.* 2005) and this has been verified for the species in this study (Ewers, Mackay & Samanta 2007). Because not all trees will have the same response to *D*, spatial autocorrelation decreases as *D* increases. Evidence now exists to support *D* as the driver of temporal variability in spatial autocorrelation of E_C from the two very different stands in this study as well as a subalpine forest in Wyoming, USA (Adelman, Ewers & Mackay 2008). Future studies should explore this mechanism beyond these forest types. For instance, once *D* is very high, most trees would have low stomatal conductance so spatial autocorrelation may increase again at higher *D* than found in these forests. However, our results rejected prediction 3 so that we rule out soil factors as driving the spatial variability at a given *D* bin. Overall our tests of the three predictions strongly support the tree hydraulics hypothesis to explain temporally varying spatial patterns in transpiration.

Loranty *et al.* (2008) has suggested that even though there was a moisture gradient across the Aspen stand, the trees were not water limited during the duration of the study. This result is supported by multiyear analysis in Mackay *et al.* (2002, 2007) showing that drought is rare in these stands and modelling work of Samanta *et al.* (2008) showing that low soil moisture limitation inclusion in mechanistic models does not improve predictive power in these stand types. Our use of shallow (6 cm) soil moisture does not attempt to explain how soil moisture deficit limits transpiration, but rather indicates how excessive soil moisture may limit transpiration. Excessive soil moisture in the Aspen stand appears to be the more important factor (see Fig. S1) and a large total N would be a strong indicator of poorly aerated soils. In northern temperate and boreal forest stands, saturated soils are common and result in well-known declines in transpiration and stomatal conductance in species that poorly respond to anaerobic conditions (Kozlowski 1984; Zhang & Davies 1987; Else *et al.* 1996) and increases in species that require flooded soils (Ewers, Mackay & Samanta 2007). Modelling studies have shown that incorporating saturated soil impacts on transpiration and stomatal conductance (Chen *et al.* 2005) and net primary productivity (Grant 2004) is crucial to increasing predictive understanding of these forest types. Our results further show that correctly modelling spatial pattern change in time also requires incorporating transpiration response to saturated soil conditions in these forest types.

In the Maple stand, most of the trees were large compared with the Aspen stand trees and may have created their own microhabitats that exist on scales smaller than that measured with soil samples (Jackson & Caldwell 1996; Young 1998; Young *et al.* 1998). The Maple stand, with its higher rates of E_C, showed a greater decrease in spatial autocorrelation as D increased and generally demonstrated higher variability, as shown by the sill and nugget (Fig. 5), than the Aspen stand. This result supports predictions 2 and 3 because the changes in spatial autocorrelation in response to D are likely due to plant hydraulic controls. Large trees have more variation in canopy conductance at a given D and thus more variation in their response to changes in D (Oren *et al.* 1999). The plantation organization of the red pines may have removed the natural spatial effect because the distribution of red pine is anthropogenic in the Maple stand.

Because tree size drives spatial autocorrelation within a given D bin, there is a need to continue to look for those environmental conditions that place the fewest limits on a tree's growth and allow for the greatest increase in sapwood area and thus E_C. We suggest as a further hypothesis that aboveground competition for light may explain the patterns of spatial variation within each stand; a previous study has shown a weak negative relationship between competing sapwood area and sap flux (Oren *et al.* 1998). Additional factors that drive tree growth and size in this region may also prove to be very useful for scaling from trees to stands and need to be identified. The approach presented here can ultimately be used to quantify temporal and spatial drivers of tree transpiration in any forest, and potentially other types of vegetation, resulting in more rigorous and effective up-scaling using testable mechanisms.

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Supporting information

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Fig. S1. Transpiration response to soil moisture and nitrogen.

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