

## Sap flow in trembling aspen: implications for stomatal responses to vapor pressure deficit

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**Summary** We monitored sap flow and estimated diurnal changes in transpiration rates of two trembling aspen (*Populus tremuloides* Michx.) stands, located in the southern boreal forest and aspen parkland of Saskatchewan, Canada. In both stands during the peak growing season (June and July), sap flow during the day (0700–1700 h local time) increased linearly with vapor pressure deficit (VPD) from 0 to about 1 kPa, but then remained remarkably constant at VPD > 1 kPa (up to 4.8 kPa in the aspen parkland stand). The results imply an inverse relationship between stomatal conductance and VPD under well mixed conditions, for VPD > 1 kPa. We postulate that the stomata are operating to maintain leaf water potentials above a critical minimum value, which in turn places a maximum value on the rate of sap flow that can be sustained.

**Keywords:** aspen parkland, boreal forest, poplar, *Populus*, transpiration.

### Introduction

In the interior of western Canada, regional gradients in climatic moisture regimes and hydrological functioning of ecosystems appear to be closely linked to forest distribution (Hogg 1994, 1997). An understanding of the factors controlling forest transpiration is thus especially important in this region, and is critical to predicting how the productivity and hydrology of the boreal forest would respond to a warmer and drier climate. Water vapor flux from different vegetation types in the boreal forest and its control by environmental and ecophysiological factors is one of the major processes being studied in the Boreal Ecosystem–Atmosphere Study (BOREAS, see Sellers et al. 1995).

Trembling aspen (*Populus tremuloides* Michx.) is the most important deciduous tree species in the western Canadian boreal forest, commonly growing in pure stands, or in mixed stands with white spruce (*Picea glauca* (Moench) Voss) and other boreal conifers (Peterson and Peterson 1992). In a previous study (Hogg et al. 1997), we collaborated with other BOREAS researchers to examine transpiration rates at the BOREAS Old Aspen site, located in the southern Canadian boreal forest in Prince Albert National Park, Saskatchewan. Transpiration of aspen was measured by two sap flow methods (heat pulse and constant power), alongside tower-based eddy

correlation measurements above and below the aspen canopy (Black et al. 1996). Scaling up the sap flow rates determined by the heat pulse method to the stand level yielded values that were similar to those obtained by the tower-based measurements. All three methods showed a linear increase in midday aspen transpiration with increasing vapor pressure deficit (VPD) up to about 1 kPa, beyond which transpiration was relatively constant (VPD 1–2.5 kPa). When taken together with the aerodynamic characteristics of the site, the observed responses indicated significant reductions in canopy conductance when VPD was high (Blanken et al. 1997).

Trembling aspen is also the predominant tree species in the aspen parkland, a vegetation zone that represents a transition between the boreal forest and the prairies to the south (Bird 1961). Although little is known about the ecophysiological functioning of aspen in this climatically warmer and drier vegetation zone, it may provide an analog of the responses of the southern boreal forest to possible climate change (Hogg and Hurdle 1995).

In the present study, we monitored diurnal changes in sap flow and transpiration at a site in the aspen parkland (parkland site), located 100 km due south of the BOREAS Old Aspen site (boreal site). The first objective was to determine relative transpiration responses to VPD at the parkland site, and to make comparisons with similar measurements made at the boreal site. Specifically, we tested the hypothesis that aspen transpiration during the day is insensitive to VPD beyond a threshold value of 1 kPa, even at the high values of VPD that can occur at the parkland site (4.8 kPa in the present study). The second objective was to use the results to develop a simple relationship between VPD and stomatal conductance in aspen, as a contribution to understanding the causes of low forest productivity in the aspen parkland zone.

### Materials and methods

#### Description of study sites

The study was conducted in two trembling aspen stands located in central Saskatchewan, Canada. The boreal site is located in the southern boreal forest of Prince Albert National Park (53°38' N, 106°12' W, elevation 600 m). The parkland site is in Batoche National Historic Park (52°44' N, 106°09' W,

elevation 500 m), located midway between Saskatoon and Prince Albert. The parkland site is a Canadian Forest Service research site that forms part of the Boreal Forest Transect Case Study (Price and Apps 1995).

The two sites differ in climate, vegetation, tree growth form and productivity (see Hogg and Hurdle 1995). Based on the 1951–1980 climate normals (Environment Canada 1982), the parkland site receives less precipitation (375 mm year<sup>-1</sup> at Rosthern, 52°40' N, 106°20' W) than the boreal site (462 mm year<sup>-1</sup> at Waskesui Lake, 53°55' N, 106°05' W). Mean growing season temperatures (May to September) are 14.5 °C at the parkland site and 12.5 °C at the boreal site.

The vegetation of the boreal site consists of an extensive, even-aged stand of trembling aspen, 70–80 years old and 18–22 m tall. The understory is dominated by beaked hazelnut (*Corylus cornuta* Marsh.) about 2 m tall. The stand is relatively homogeneous except for a few small openings and occasional patches of balsam poplar (*Populus balsamifera* L.). The site is gently rolling and generally well drained, with a predominantly clay loam soil texture.

The parkland site is in one of the few remaining areas of native aspen parkland. The terrain is rolling and underlain by stabilized sand dunes. The vegetation is heterogeneous, ranging from open native grassland with small stunted clones of aspen to more sheltered lowland forests of aspen and balsam poplar with an understory of red osier dogwood (*Cornus stolonifera* Michx.). Trees are stunted in relation to diameter, and are often crooked, leaning, or forked, with heights ranging from < 5 to 15 m (see Hogg and Hurdle 1995). Within the aspen stands, trees from two or more age classes are usually found (maximum age about 85 years). Dense bands of beaked hazelnut occur on north and east facing slopes, but in most upland areas, the forest understory consists of sparse grasses, herbs and low shrubs (e.g., saskatoon berry, *Amelanchier alnifolia* Nutt.; choke-cherry, *Prunus virginiana* L.; and prickly rose, *Rosa acicularis* Lindl.).

#### Sap flow by heat pulse method

Aspen clones (patches of genetically identical trees) were readily distinguishable because of differences in bark characteristics and phenology. At the boreal site, sap flow was monitored on six aspen trees in two adjacent clones from late May to October 1994. At the parkland site (Batoche), sap flow was monitored on twelve aspen trees in three clones from late May to October of both 1994 and 1995. Sap flow was determined every 3 h in 1994 (both sites) and hourly in 1995 (parkland site).

Stand characteristics of the clones monitored are shown in Table 1. At the boreal site, the aspen was relatively homogeneous but the two clones differed in leaf phenology (Hogg et al. 1997), and were thus referred to as the early-leafing and late-leafing clones (EL and LL). At the parkland site, four stations were established along a 400-m transect extending from grassland to the forest interior, and three trees were monitored each year at each station. One station was located in a small clone of stunted aspen surrounded by grassland (GL clone), two stations were located at the edge and in the

center of a large (200 × 75 m) clone in upland forest next to the grassland (UF clone), and one station was located in the center of a more mesic, lowland forest (LF clone).

Sap (water) flow was measured by the heat pulse method (Marshall 1958, Swanson 1983, 1994), using two thermocouples spaced symmetrically 0.75 cm above and below a 5-cm-long heater with a power output of 2 W cm<sup>-1</sup>. All probe elements had a diameter of 1.6 mm and holes of the same diameter were drilled using a steel template. Thermocouple depth in the sapwood was 1.5 cm for large (> 15 cm diameter) trees and 1.0 cm for smaller trees. Probes were located at a height of about 1.3 m on the north side of the tree and were thermally insulated by wrapping with white polyethylene packing material. At each station, a data logger (Model 21X, Campbell Scientific Instruments, Logan, UT, powered by batteries and a solar panel) was used to record the temperature increase at the upper ( $T_u$ ) and lower ( $T_l$ ) thermocouples 60 s after a 4-s heat pulse. On two dates of the year (DOY) in 1994 (boreal site, DOY 192 and 209; parkland site, DOY 190 and 205), one or two probes per station were removed and replaced with new probes at another location on the same tree (all probes were replaced once). In 1995, probes were replaced only as needed.

Uncorrected sap flux density ( $S$ , cm h<sup>-1</sup>) was calculated as (Marshall 1958, Hogg et al. 1997):

$$S = 4.36 \ln(T_u/T_l). \quad (1)$$

For aspen, we used a thermal conductivity of 0.38 J m<sup>-1</sup> s<sup>-1</sup> °C<sup>-1</sup>, a bulk density of 0.37 g cm<sup>-3</sup> and a gravimetric water content of 100% of actively conducting sapwood. Ideally, conditions of zero sap flow can be identified from Equation 1 when  $T_u = T_l$ , if probe spacing is exactly symmetrical and if wood heat transfer characteristics are precisely homogeneous above and below the heater. In practice, it was necessary to assume that zero sap flow occurred when the minimum value of mean  $S$  in each clone was reached (i.e., nights when VPD was near zero, excluding frost events). Thus a zero offset ( $z$ ) was applied to obtain the “zero” sap flux density ( $S'$ ), where  $S' = z + S$ . The magnitude of  $z$  was constant, and normally within  $\pm 0.5$  cm h<sup>-1</sup>; however, it was recalculated when probes were replaced.

Heat transfer theory indicates that interruption of the sap stream by probes and wounding of adjacent sapwood results in an underestimation of the true sap flux density. For our implementation, wound width was estimated to be 2.0–2.2 mm. Simulations based on a two-dimensional numerical model similar to that described by Swanson and Whitfield (1981) indicated that a correction factor ( $a$ ) of approximately 2.0 ( $\pm 15\%$ ) was warranted to obtain the actual sap flux density ( $S^*$ ), where  $S^* = aS'$ . A similar underestimation of 45% (i.e.,  $a = 1.8$ ) was observed by Cohen et al. (1981).

At each station, measurements of the wound-corrected values of sap flux density ( $S^*$ ) were multiplied by the stand sapwood area to ground area ratio (SA) to give estimates of canopy transpiration ( $E$ ). The SA was determined as the product of BA and FSA, where BA is the basal area to ground area

Table 1. Stand characteristics of aspen clones. Abbreviations are as follows: LAI = leaf area index; SA = stand sapwood area to ground area ratio; EL = early-leaving; LL = late-leaving; GL = grassland; UF = upland forest; and LF = lowland forest.

	Stand volume (m <sup>3</sup> ha <sup>-1</sup> ) <sup>1</sup>	LAI	Height (m)	Diameter (cm)	Age (year)	SA	Site type
<i>Boreal site</i>	144	2.3 <sup>2</sup>					
EL clone			18–22	21–27	70–80	0.0020	Extensive forest
LL clone			18–22	17–22	70–80	0.0032	Extensive forest
<i>Parkland site</i>	32	1.4 <sup>3</sup>					
GL clone			5	6–9	30–45	0.0009	Grassland
UF clone (edge) <sup>4</sup>			6–8	8–12	30–45	0.0010	Upland forest edge
UF clone (center) <sup>5</sup>			12–14	20–23	70–80	0.0010	Upland forest
LF clone			7–10	8–14	30–55	0.0011	Lowland forest

<sup>1</sup> Biometry surveys by Halliwell and Apps (1996).

<sup>2</sup> Blanken et al. (1997).

<sup>3</sup> Estimate based on litter traps.

<sup>4</sup> Excluded from 1994 analysis (problems with wounding responses).

<sup>5</sup> Excluded from 1995 analysis (problems with thermal drift).

ratio of aspen stems (at a height of 1.3 m) in one 10 × 10 m plot centered on each station, and FSA is the fraction of BA occupied by sapwood. The FSA was calculated based on two radial increment cores from each of four trees per station. The zone of active sapwood within increment cores was identified by staining with a solution of methylene blue in methyl hydrate.

#### Environmental measurements

At the boreal aspen site (1994), we measured temperature and relative humidity (at a height of 3 m) in conjunction with sap flow measurements. However, in our analysis at this site, we relied primarily on environmental measurements made by other researchers in the BOREAS experiment and by the BOREAS Automatic Meteorological Station network. These measurements were made on or near the main flux tower, located about 1 km west of our sap flow monitoring site. Vapor pressure deficit (VPD) was calculated (Jones 1992) from half-hourly averages of air temperature and vapor pressure or relative humidity at heights of 39 and 4 m. Vapor pressure deficit of the air within the aspen canopy was then estimated as the average VPD at the two heights. We also used the half-hourly measurements of above-canopy solar radiation (39 m), infrared temperature of the aspen canopy, and measurements of soil water content (0–30 cm depth) made every 1–3 days by time-domain reflectometry (TDR). Details on these measurements are provided by Black et al. (1996) and Blanken et al. (1997).

At the parkland site (Batoche), average hourly meteorological conditions were monitored from an 18-m tower (located along the 400-m transect) and at each of the four stations where sap flow was measured (growing season only). We calculated hourly VPD from in-canopy measurements of temperature and relative humidity made with a shielded Model HMP35C Vaisala probe (Vaisala Inc., Woburn, MA) at a height of 4 m in the UF (edge) clone. At this station, the aspen is relatively young and the canopy ranged in height from about 2 to 8 m. Volumetric water content of soil at 10- and 30-cm depths was monitored at each station with Colman fiberglass sensors (Soiltest,

Inc., Evanston, IL) that had been pre-calibrated in the laboratory with soil samples collected from the site. Hourly measurements of global solar radiation (Model SKS1110 silicon pyranometer, Skye Instruments, Powys, U.K.) and wind (Model 05103, R.M. Young, Traverse City, MI; at a height of 15 m, 7 m above the canopy) from the main tower were also used in the analysis. All measurements were recorded by CSI model 21X dataloggers (Campbell Scientific Instruments, Inc.).

#### Compensation for time lag between sap flow and transpiration

At the boreal aspen site in 1994, sap flow measurements showed a diurnal lag of about 1 h relative to aspen canopy transpiration, as determined by eddy correlation (Hogg et al. 1997). This was a result of diurnal changes in water storage within the tree above the point of sap flow measurement. We compensated for the lag by comparing each sap flow measurement (1-min duration) against average VPD and solar radiation for the preceding 2-h period.

At the parkland site, the mean diurnal lag of sap flow was about 0.5 h, based on its relationship with above-canopy water vapor flux measured using a low-cost eddy correlation system mounted on the tower (Hogg and Hurdle, unpublished data). We compensated for this lag by comparing each sap flow reading against the average VPD and solar radiation over the previous 1-h period.

## Results and discussion

#### Seasonal patterns of sap flow and transpiration

Changes in sap flux density ( $S'$ ) of trembling aspen are shown for the boreal and parkland sites during the 1994 growing season (Figures 1a and 1b) and for the parkland site in 1995 (Figure 1c). In each case, the increase in  $S'$  at the start of the growing season coincided with the period of rapid leaf expansion that was already occurring when probes were installed in

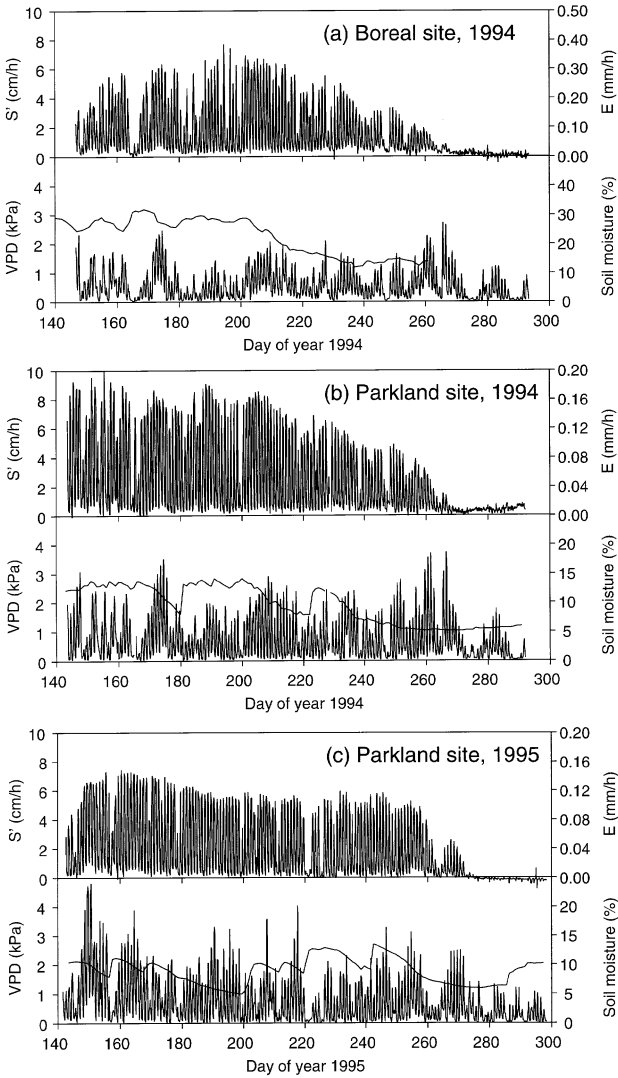


Figure 1. Seasonal changes in mean sap flux density ( $S'$ ) and estimated stand transpiration rate ( $E$ ) of trembling aspen, plotted every 3 h from late May to late October (scaling procedure between  $S'$  and  $E$  is described in text). (a) Results from the boreal aspen site in Prince Albert National Park during the 1994 BOREAS field campaign (mean of early-leaving and late-leaving clones); and (b) and (c) results from the parkland aspen site at Batoche in 1994 and 1995, respectively (mean of grassland, upland forest and lowland forest clones). Also shown are changes in vapor pressure deficit (VPD) and volumetric soil water content (data for boreal site provided by BOREAS teams TF-1 and TF-2, Black et al. 1996).

late May (DOY 142–146). The diurnal pattern of sap flow was evident throughout the summer, except on rainy, overcast days with low vapor pressure deficit (VPD) when  $S'$  was near zero. Sap flow collapsed in late September, and diurnal changes were no longer evident after leaf fall was complete, even on days with VPD > 1 kPa, indicating that transpiration through the bark was negligible relative to foliar transpiration.

The maximum volumetric soil water content at the parkland site was considerably lower (about 15%) than at the boreal site (about 30%) (Figures 1a–c) because of differences in soil

Table 2. Monthly precipitation (mm) recorded at the boreal and parkland sites, and also expressed as a percentage of the long-term average for the closest permanent weather station (Waskesui and Rosthern, Saskatchewan).

	Boreal site		Parkland site	
	1994		1994	1995
May	107 (262%)		94 (256%)	4 (11%)
June	107 (151%)		82 (145%)	56 (99%)
July	91 (112%)		115 (159%)	61 (84%)
August	22 (38%)		61 (132%)	129 (279%)
September	13 (25%)		6 (18%)	2 (6%)
May–September	340 (112%)		358 (146%)	252 (103%)

texture and water holding capacity (sand versus sandy clay loam). Precipitation was greater than normal at both sites during the 1994 growing season, especially from May to July (Table 2). In August 1994, precipitation continued to be greater than normal at the parkland site, but was only 38% of normal at the boreal site, resulting in a strong decrease in soil water content during the month. This period of soil drying coincided with a decrease in  $S'$  at the boreal site. In 1995, total precipitation during the growing season at the parkland site was near average, but May was dry and August had nearly three times the normal precipitation. In contrast to 1994,  $S'$  remained near maximum summer values until mid-September in 1995 (about DOY 256).

Estimates of canopy transpiration rate ( $E$ ) based on  $S'$  are shown in Figures 1a–c. For ease of presentation,  $E$  values are plotted based on a lumped SA of 0.0025 at the boreal site, and 0.0010 at the parkland site (cf. Table 1). Although  $S'$  was generally greater at the parkland site than at the boreal site, the much greater SA of aspen at the boreal site resulted in maximum estimated transpiration rates that were about twice (about  $0.4 \text{ mm h}^{-1}$ ) those at the parkland site (about  $0.2 \text{ mm h}^{-1}$ ).

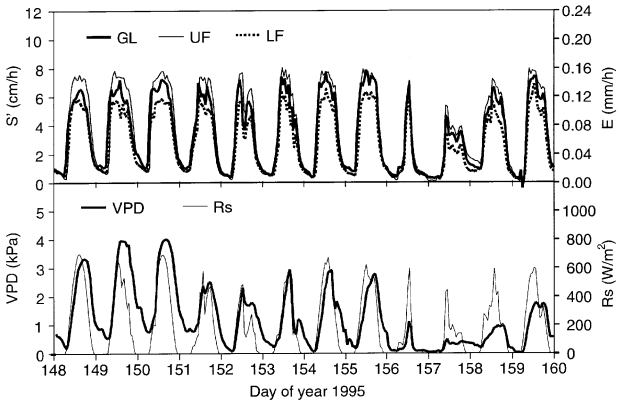


Figure 2. Sap flux densities ( $S'$ ) and estimated transpiration rates ( $E$ ) for three aspen clones (GL, UF and LF) at the parkland site during and following a hot period (May 28 to June 8, 1995). Also shown (lower graph) are accompanying changes in vapor pressure deficit (VPD, in canopy at a height of 4 m) and solar radiation ( $R_s$ , above canopy).

The magnitudes of  $S'$  and  $E$  differed among clones, but relative diurnal changes and responses to VPD were similar both at the parkland site (e.g., Figure 2) and the boreal site (Hogg et al. 1997). In the following analyses, therefore, we used the average  $S'$  and  $E$  for the clones measured at each site.

#### Responses to VPD and solar radiation

The period chosen for the analysis of responses to VPD was May 28 to July 31 (DOY 148–212) at the parkland site and June 2 to July 31 (DOY 153–212) at the boreal site. This interval corresponded to the peak growing season period that followed spring leafing of the aspen canopy (occurring about 5 days earlier at the parkland site than at the boreal site), but before the onset of soil drying and reduced sap flow in 1994 (Figures 1a and 1b).

When estimates of daytime transpiration ( $E$ , based on  $S'$ ) were plotted against VPD, the measurements tended to plateau when VPD exceeded about 1 kPa (Figures 3a, 4a and 5a). This pattern was observed at both the boreal (1994) and parkland (1994–95) sites, and was especially evident during a hot period at the parkland site in 1995 (Figure 2), when VPD reached 4.8 kPa on two successive days (May 29–30, DOY 149 and 150). Despite the extreme conditions, maximum  $E$  was similar

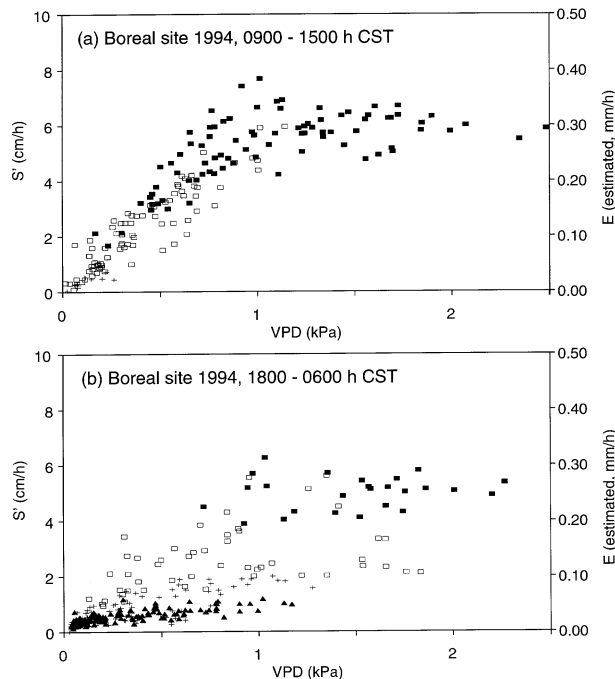


Figure 3. Sap flux density ( $S'$ , mean of two clones) and estimated transpiration rate ( $E$ ) at the boreal site in relation to mean VPD over the previous 2-h period (based on average VPD above and below the canopy, from BOREAS teams TF-1 and TF-2). Measurements made every 3 h from June 2 to July 31, 1994 (DOY 153–212) are shown separately for (a) morning to afternoon, 0900–1500 h CST, and (b) evening to dawn, 1800–0600 h CST. Symbols indicate differences in mean solar radiation ( $R_s$ ) over the previous 2-h period: (■)  $R_s > 400 \text{ W m}^{-2}$ ; (□)  $100 < R_s < 400 \text{ W m}^{-2}$ ; (+)  $0 < R_s < 100 \text{ W m}^{-2}$ ; (▲) negligible  $R_s$  (i.e., readings from  $-5$  to  $0 \text{ W m}^{-2}$ ).

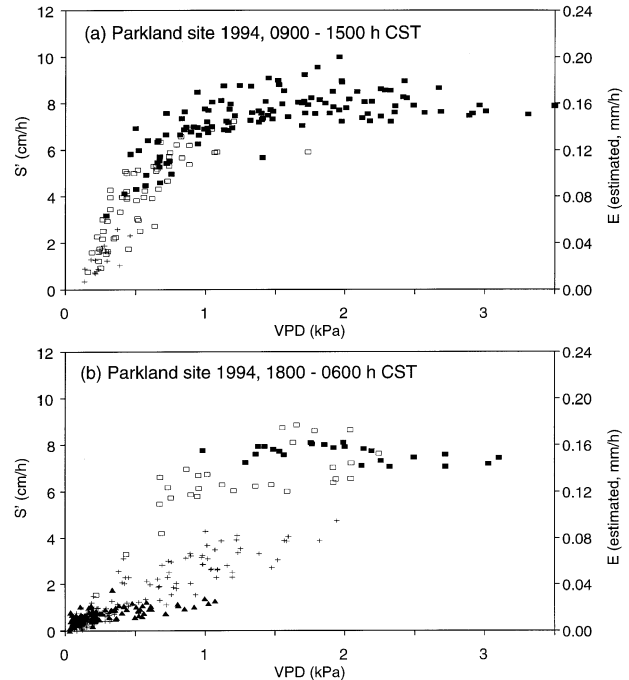


Figure 4. Sap flux density ( $S'$ , mean of three clones) and estimated transpiration rate ( $E$ ) of trembling aspen at the parkland site in relation to mean VPD (average over the previous 1-h period, within the canopy at a height of 4 m). Measurements made every 3 h from May 28 to July 31, 1994 (DOY 148–212) are shown separately for (a) 0900–1500 h CST and (b) 1800–0600 h CST. Symbols are as in Figure 3, based on mean  $R_s$  over the previous 1-h period.

to that observed on other days with much lower VPD. Soil water content (15–30 cm depth) was near field capacity on the two days with highest VPD (Figure 1c).

When daytime VPD was greater than 1 kPa, solar radiation flux density ( $R_s$ ) was usually  $> 400 \text{ W m}^{-2}$  at both sites (maximum  $957 \text{ W m}^{-2}$ ). Under these conditions,  $E$  was relatively insensitive to differences in either  $R_s$  or VPD (Figures 3a, 4a and 5a). However, when VPD was less than 1 kPa, there was an approximately linear relationship between  $E$  and VPD. Linear regressions between daytime  $E$  and VPD, for  $\text{VPD} < 1 \text{ kPa}$  only, resulted in  $r^2$  values ranging from 0.80 to 0.85 (Table 3).

Evening and nighttime relationships between  $E$  (or  $S'$ ) and VPD are shown in Figures 3b, 4b and 5b. All of the readings with  $R_s > 400 \text{ W m}^{-2}$  occurred at 1800 h CST and most were associated with  $\text{VPD} > 1 \text{ kPa}$ . Under these conditions (as earlier in the day),  $E$  was similar across a wide range of VPDs. Later in the day,  $E$  decreased as solar radiation declined to  $< 400 \text{ W m}^{-2}$ , even when VPD remained at high values. This finding is consistent with measurements of reduced stomatal conductance in *Populus* species at low irradiances (e.g., Ceulemans et al. 1988, McCaughey and Iacobelli 1994).

At night (with negligible  $R_s$ ), there were significant positive linear relationships between  $E$  (as estimated from  $S'$ ) and VPD (Table 3). The strongest relationship ( $r^2 = 0.80$ ) was observed at the parkland site in 1995, where sap flow showed a linear

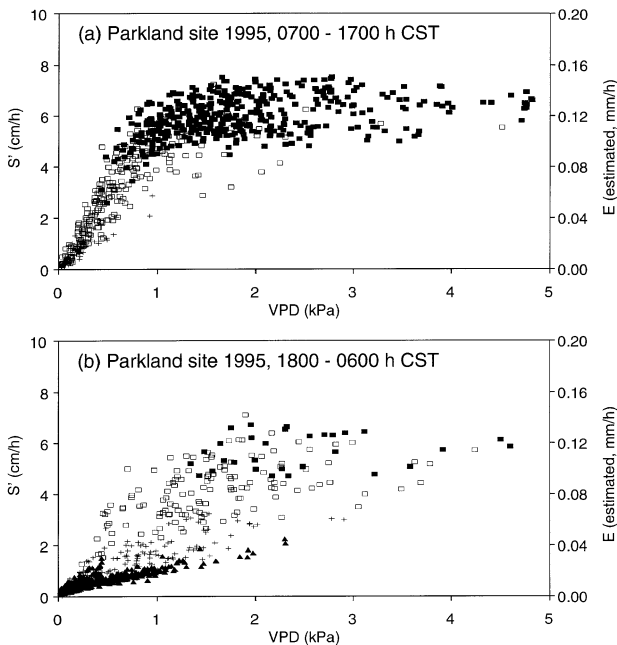


Figure 5. Hourly sap flux density ( $S'$ , mean of three clones) and estimated transpiration rate ( $E$ ) of trembling aspen at the parkland site in 1995 (DOY 148–212), in relation to mean VPD (as described for Figure 4). Measurements are shown separately for (a) morning to afternoon, 0700–1700 h CST, and (b) evening to dawn, 1800–0600 h CST. Symbols are as described in Figure 3, based on mean  $R_s$  over the previous 1-h period.

increase over the full range of nighttime VPDs observed (0–2.3 kPa, Figure 5b). Nighttime sap flow has previously been measured by the heat pulse technique, and its occurrence has been attributed to either nocturnal recharging of water in the xylem (Lopushinsky 1986, Caspari et al. 1993) or nocturnal transpiration (Green et al. 1989). Presumably, both mechanisms were operating in the present study. The use of a 0.5–1 h lag to describe the relationships between sap flow and VPD

should have removed at least some of the effect of hydraulic capacitance within the tree. However, if water recharge in the xylem is slower at night than during the day, then our estimates of  $E$  based on sap flow measurements would be greater than the actual transpiration rate (i.e., water vapor leaving the canopy).

*Inferred stomatal responses*

The tendency for daytime transpiration rates to saturate at high VPD has been previously reported in tropical rain forest (Meinzer et al. 1993, Granier et al. 1996) and in temperate forests and woodlands (e.g., Lopushinsky 1986, Price and Black 1989, Goulden and Field 1994). In forests with a high aerodynamic conductance and a low decoupling coefficient ( $\Omega$ , Jarvis and McNaughton 1986), this type of response is caused primarily by gradual stomatal closure as the VPD of ambient air (e.g., above or within canopy) increases. Under these circumstances, the vapor pressure gradient across the stomata approaches ambient VPD. Thus, canopy physiological conductance ( $g_c$ ) is similar to total conductance ( $g_t$ ), and  $g_t$  can be determined from  $E$  and ambient VPD (Köstner et al. 1992; see also Arneth et al. 1996, Granier et al. 1996):

$$g_c \approx g_t = kE/VPD, \tag{2}$$

where  $k = \rho_w G_v T_k$ ; and  $\rho_w$  (density of water) = about 1000 kg m<sup>-3</sup>,  $G_v$  (gas constant for water vapor) = 0.462 m<sup>3</sup> kPa kg<sup>-1</sup> K<sup>-1</sup>, and  $T_k$  is air temperature in K. The conversion factor,  $k$ , takes a value of about 38 at 20 °C if  $g_t$  or  $g_c$  is expressed in units of mm s<sup>-1</sup>. Estimates of stomatal conductance ( $g_s$ ) can then be obtained from  $g_c$ , where  $g_s \approx g_c/LAI$ . Reasonable estimates can be obtained from these simple relationships, but only for vegetation types with low values of  $\Omega$ . This primarily includes coniferous forests, but some deciduous forests also fall into this category; e.g.,  $\Omega = 0.2$  in a European beech (*Fagus sylvatica* L.) forest (Herbst 1995). The boreal aspen stand also had a low decoupling coefficient during the day (mean  $\Omega = 0.31$ , Blanken et al. 1997), and leaf temperatures, measured by infrared thermometry, were similar to air temperature (mean

Table 3. Linear regressions of estimated transpiration rate ( $E$ , mm h<sup>-1</sup>) in relation to VPD (kPa), based on (a) daytime (0700–1700 h CST) sap flux measurements when VPD < 1 kPa, and (b) nighttime sap flux measurements with negligible solar radiation, for the peak growing season period (dates as in Figures 3–5). All regressions are statistically significant ( $P < 0.001$ ). Also shown are preliminary estimates of  $g_c$  and  $g_s$  based on the slope (b) of the relationship between  $E$  and VPD, where  $g_c = 38b$  (Equation 2) and  $g_s = g_c/LAI$ .

Site	Year	Regression equation	$n^1$	$r^2$	estimated $g_c$	estimated $g_s$
<i>Daytime</i>						
Boreal	1994	$E = 0.301 \text{ VPD} - 0.004$	134	0.838	11.4	5.0
Parkland	1994	$E = 0.158 \text{ VPD} - 0.000$	103	0.795	6.0	4.3
Parkland	1995	$E = 0.118 \text{ VPD} - 0.001$	310	0.847	4.5	3.2
<i>Nighttime</i>						
Boreal	1994	$E = 0.032 \text{ VPD} + 0.018$	121	0.567	1.2	0.54
Parkland	1994	$E = 0.018 \text{ VPD} + 0.008$	132	0.531	0.7	0.49
Parkland	1995	$E = 0.016 \text{ VPD} + 0.006$	498	0.798	0.6	0.43

<sup>1</sup>  $n$  = Number of sap flux measurements.

absolute temperature difference of 0.7 °C during the day). This is presumably because of the small leaf size (3–4 cm in length and width) together with the flattened petioles, which promote fluttering of trembling aspen leaves, even in light breezes (see Roden and Pearcy 1993).

Based on the assumption that  $\Omega$  is low in both aspen stands examined in this study,  $g_c$  and  $g_s$  can be crudely estimated from our sap flow measurements using, for example, the slope  $b$  of regressions between  $E$  and VPD (Table 3). The small intercept values may be neglected in each of the regressions shown, because they fall within the range of error in defining zero sap flow (see Methods). Using this approach, estimated aspen  $g_c$  during the day for VPD < 1 kPa was greater (11.4 mm s<sup>-1</sup>) at the boreal site than at the parkland site (6.0 mm s<sup>-1</sup>) in 1994 (Table 3). However, the difference can be largely attributed to the greater LAI at the boreal site (2.3) compared to the parkland site (1.4); estimated  $g_s$  at the two sites (i.e.,  $g_c/\text{LAI}$ ) was similar (5.0 and 4.3 mm s<sup>-1</sup>), given the potential sources of error. Estimated values of  $g_c$  and  $g_s$  were smaller at the parkland site in 1995, presumably because of the drier soil conditions.

From Table 3, estimated nighttime  $g_s$  was near 0.5 mm s<sup>-1</sup>, or about 10–12% of the daytime  $g_s$ , at each site. However, these values may be overestimates if some of the observed sap flow was associated with nocturnal recharge of water within the stem.

Our quantitative estimates of  $g_c$  and  $g_s$  may also be affected by several sources of error. First, we have assumed that aerodynamic conductance is high relative to  $g_c$ , which may not always be the case (e.g., when wind speed is very low). Second, the most recent estimates of aspen transpiration from this site, based on eddy correlation measurements corrected for available energy (Blanken et al. 1997), are about 10–20% greater than our estimates based on sap flow. If these factors are considered, our estimates of  $g_s$  for the boreal site are comparable to the values of 4–10 mm s<sup>-1</sup> obtained by McCaughey and Iacobelli (1994) and Dang et al. (1997) for leaf-level  $g_s$  in aspen at low VPD.

Responses of  $g_c$  or  $g_s$  to environmental conditions can also be inferred from our sap flow measurements using Equation 2. However, the reliability of this approach will tend to decrease when wind speed ( $\mu$ ) and aerodynamic conductance are low, resulting in higher values of  $\Omega$  (Jarvis and McNaughton 1986). In the analysis shown for the parkland site in 1995 (Figure 6), we separately plotted the estimated conductances for  $\mu > 3 \text{ m s}^{-1}$  from those obtained when  $\mu < 3 \text{ m s}^{-1}$  (height of measurement = 15 m). The larger symbols give the range of  $R_s$  associated with each measurement, for  $\mu > 3 \text{ m s}^{-1}$  only. The conductance estimates shown are values of  $g_s$  or  $g_c$ , expressed as a proportion of their estimated value for VPD < 1 kPa (4.5 and 3.2 mm s<sup>-1</sup>, from Table 3).

For VPD > 1 kPa, there was an inverse relationship between estimated relative conductances and VPD for all daytime data (Figure 6), although for readings with  $\mu > 3 \text{ m s}^{-1}$ , the relationship between conductance and  $1/\text{VPD}$  was greater ( $r^2 = 0.86$ ;  $n = 170$ ) than for readings with  $\mu < 3 \text{ m s}^{-1}$  ( $r^2 = 0.77$ ;  $n = 241$ ). For VPD values between 0 and 1 kPa, estimates of

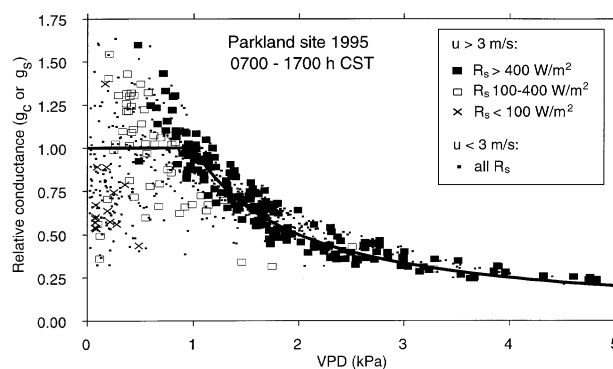


Figure 6. Responses of estimated aspen conductance ( $g_c$  or  $g_s$ ) to VPD, based on hourly daytime (0700–1700 h CST) sap flow measurements at the parkland site on 65 days in 1995 (DOY 148–212). Conductances are based on Equation 2 and are expressed as a proportion relative to the estimates in Table 3. Symbols denote average wind speeds ( $\mu$ ) and (for  $\mu > 3 \text{ m s}^{-1}$  only) solar radiation ( $R_s$ ) during the hour before each sap flow measurement. The simple inverse relationship proposed for stomatal responses to VPD under well mixed conditions during the day is also shown (see text).

relative conductance appeared to be less tightly coupled to VPD. The approximately linear relationship between  $E$  and VPD (e.g., Table 3, Figure 5a) suggests that conductances are relatively constant over this range. However, the more detailed analysis (Figure 6) showed a more complex relationship, where low values of  $R_s$  were usually associated with low VPD, but at a given  $R_s$ , conductance continued to increase as VPD decreased below 1 kPa.

Our general conclusion that gradual stomatal closure occurs at high VPD is supported by other measurements on aspen at both the leaf level (e.g., McCaughey and Iacobelli 1994, Dang et al. 1997) and canopy level (Blanken et al. 1997). Comparable responses to VPD are also evident in other types of forest (e.g., Arneth et al. 1996, Granier et al. 1996). However, our observation of a constant transpiration rate above a certain VPD threshold, and the implication that  $g_s$  varies with  $1/\text{VPD}$  under dry, well-mixed conditions, has not been reported elsewhere.

An intriguing aspect of the results is that stomata appear to maintain a relatively constant transpiration rate over a wide range of environmental conditions. This finding could be explained by leaf-level models that link stomatal responses to photosynthesis rates and environmental conditions at the leaf surface (e.g., Collatz et al. 1991). An alternative interpretation is that when VPD is high, stomata need to close sufficiently to maintain the water potential above a critical minimum threshold, below which irreversible damage might occur, e.g., by cavitation of xylem (Tyree and Sperry 1988, Sperry and Pockman 1993). Thus, the hydraulic resistance from soil to leaf may ultimately determine the maximum transpiration rate that can be sustained by the plant (Meinzer and Grantz 1990). Recent evidence suggests that this mechanism provides the best general explanation for age-related reductions in forest height growth and productivity (Gower et al. 1996, Ryan and Yoder 1997).

For this mechanism to operate in aspen, we postulate that stomatal closure occurs over a narrow range of leaf water potentials. This is true for some clones and hybrids of *Populus*, which show abrupt closure of stomata as leaf water potential is experimentally lowered below  $-2$  MPa (Ceulemans et al. 1988), but it remains to be shown that the response is similar in trembling aspen.

## Conclusions

Sap flow measurements made continuously over several weeks or more can be useful for exploring general relationships between forest canopies and changes in environmental conditions. Caution is needed in using this method for quantitative estimates of transpiration at the stand level, because of the potential for progressive wounding responses and errors associated with variation in sap flow rates within and among individual trees (see Cohen et al. 1985, Swanson 1994, Hatton et al. 1995). However, sap flow measurements have several advantages over other methods, because they provide a direct measurement of changes in transpiration at the scale of individual trees (Hogg et al. 1997).

We explored the potential of sap flow measurements as a means of inferring stomatal responses to changes in environmental conditions. Although the approach was relatively simplistic, the data provide strong evidence for an upper limit to the transpiration rate of aspen, which constrains stomatal conductance to an approximately inverse relationship with VPD. This conclusion applied equally well at both the parkland and boreal sites, despite the major differences in aspen growth form and site characteristics. However, because VPD is generally higher in the parkland, it is likely to exert a greater inhibitory effect on stomatal conductance in this region. This may partially explain why aspen productivity is lower in the parkland region than in the boreal forest.

A more powerful approach for future investigation would be to conduct simultaneous measurements made at the scale of the individual leaf (e.g., porometry and leaf water potential), branch (branch bags, see Dufrêne et al. 1993), tree (sap flow), and stand (micrometeorological methods, including eddy correlation). A study of stomatal responses to experimental manipulations such as partial removal of leaf area (Meinzer and Grantz 1990) or restriction of water flow in the xylem (Sperry and Pockman 1993) would also be useful in determining the influence of hydraulic resistance on transpiration rates in aspen and other species.

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