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# Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species

B. E. EWERS,[1,2] D. S. MACKAY[3] and S. SAMANTA[4]

[1] *Department of Botany, University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA*

[2] *Corresponding author (beewers@uwyo.edu)*

[3] *Department of Geography, State University of New York at Buffalo, Buffalo, NY 14261, USA*

[4] *Department of Forest Ecology and Management, University of Wisconsin, Madison, WI 53706, USA*

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**Summary** We investigated interannual variability of canopy transpiration per unit ground area ($E_C$) and per unit leaf area ($E_L$) across seven tree species in northern Wisconsin over two years. These species have previously been shown to be sufficient to upscale stand-level transpiration to the landscape level during one growing season. Our objective was to test whether a simple plant hydraulic model could capture interannual variation in transpiration. Three species, wetland balsam fir (*Abies balsamea* (L.) Mill), basswood (*Tilia Americana* L.) and speckled alder (*Alnus rugosa* (DuRoi) Spreng), had no change in $E_C$ or $E_L$ between 2000 and 2001. Red pine (*Pinus resinosa* Ait) had a 57 and 19% increase in $E_C$ and $E_L$, respectively, and sugar maple (*Acer saccharum* Marsh) had an 83 and 41% increase in $E_C$ and $E_L$, respectively, from 2000 to 2001. Quaking aspen (*Populus tremuloides* Michx) had a 50 and 21% decrease in $E_C$ and $E_L$, respectively, from 2000 to 2001 in response to complete defoliation by forest tent caterpillar (*Malascoma distria* Hüber) and subsequent lower total leaf area index of the reflushed foliage. White cedar (*Thuja occidentalis* L.) had a 20% decrease in both $E_C$ and $E_L$ caused by lowered surface water in wetlands in 2001 because of lower precipitation and wetland flow management. Upland *A. balsamea* increased $E_L$ and $E_C$ by 55 and 53%, respectively, as a result of release from light competition of the defoliated, overstory *P. tremuloides*. We hypothesized that regardless of different drivers of interannual variability in $E_C$ and $E_L$, minimum leaf water potential would be regulated at the same value. Minimum midday water potentials were consistent over the two years within each of the seven species despite large changes in transpiration between years. This regulation was independently verified by the exponential saturation between daily $E_C$ and vapor pressure deficit ($D$) and the tradeoff between a reference canopy stomatal conductance ($G_S$) and the sensitivity of $G_S$ to $D$, indicating that trees with high $G_S$ must decrease $G_S$ in response to atmospheric drought faster than trees with low $G_S$. Our results show that models of forest canopy transpiration can be simplified by incorporating $G_S$ regulation of minimum leaf water potential for isohydric species.

*Keywords: defoliation, sap flux, water relations, water table, wetlands.*

## Introduction

Studies including more than one growing season of transpiration or evapotranspiration data are becoming increasingly common and illustrate that interannual variability in water use of ecosystems challenges models with fixed parameterizations. This variability may be attributed to functional (Jaeger and Kessler 1997, Phillips and Oren 2001) or climatic variation (Cienciala et al. 1998, Wever et al. 2002, Schwarz et al. 2004). Important contributions to functional variability include succession (Phillips and Oren 2001, Ewers et al. 2005), defoliation (Gieger and Thomas 2002) and phenology (Myneni et al. 1997). Climatic variability influences transpiration through precipitation variability causing changes in soil water content (Wever et al. 2002, Scott et al. 2004), vapor pressure deficit ($D$) and light ($Q$) seasonally and annually (Pataki and Oren 2003, Hui et al. 2003). These findings motivated us to determine what effect functional and climatic variability has on stomatal conductance control of transpiration.

As a result of atmospheric dryness or high photosynthetic rates, or both, woody plants experience water stress at high transpiration rates because of hydraulic limitations to water transport from roots to leaves (Tyree and Sperry 1989, Sperry et al. 1998). As $D$ increases, stomata close in response to decreasing leaf water potentials ($\Psi_L$) in a cue that is linked to transpiration rather than $D$ (Mott and Parkhurst 1991). Although the signal transduction mechanism and the identity of the cells receiving the signal are unknown (Salleo et al. 2001, Franks 2004), current evidence suggests that plants regulate transpiration through changes in $\Psi_L$ or leaf relative water content in response to whole-plant water status (Meinzer and Grantz 1991, Saliendra et al. 1995, Cochard et al. 1996, Nardini et al. 1996, Ewers et al. 2000, Salleo et al. 2000, Brooks et al. 2003, Franks 2004).

Such results suggest that stomatal conductance regulates transpiration (Monteith 1995) and $\Psi_L$ (Oren et al. 1999*a*) in response to $D$ to avoid potentially fatal cavitation of xylem (Tyree and Sperry 1989, Sperry et al. 1998). Regulation of $\Psi_L$ maintains a homeostasis of water in the leaves for optimal carbon uptake as a result of equilibrium between carbon uptake and soil water supply (Katul et al. 2003). This regulation is most likely the result of evolution in response to selective pressures optimizing the rate of carbon gain per water lost while restricting the rate of water loss under conditions of high atmospheric demand or low soil water supply (Raven 1993, 2002). The water supply side has been described by the following model (Whitehead and Jarvis 1981, Whitehead et al. 1984, Sperry 1995, Oren et al. 1999*a*):

$$G_S = K_S \frac{A_S}{A_L} \frac{1}{D} (\Psi_S - \Psi_L - h\rho_w g) \quad (1)$$

where $G_S$ is mean canopy stomatal conductance (mmol m$^{-2}$ s$^{-1}$), $K_S$ is whole-tree hydraulic conductance per unit sapwood area (mmol m$^{-2}$ s$^{-1}$ MPa$^{-1}$), $A_S$:$A_L$ is sapwood-to-leaf area ratio (m$^2$ m$^{-2}$), $D$ is vapor pressure deficit (mmol mmol$^{-1}$), $\Psi_S$ is soil water potential (MPa), $\Psi_L$ is leaf water potential (MPa), and $h\rho_w g$ is the gravitational pull ($g$) on the water column of density ($\rho_w$) and height ($h$). Species that maintain a minimum $\Psi_L$ in the face of soil ($\Psi_S$) or atmospheric drought ($D$) are isohydric, whereas trees that allow $\Psi_L$ to decline are anisohydric (Tardieu and Simmoneau 1998).

The response of $G_S$ to governing variables can be quantified by the following series of multiplicative functions formulated by Jarvis (1976):

$$G_S = G_{Smax} f(Q_o) f(D) f(T_A) f(\Psi_L) \quad (2)$$

where $G_{Smax}$ is maximum $G_S$, $Q_o$ is photosynthetic photon flux, and $T_A$ is air temperature. By carefully selecting subsets of data in a given range of $Q_o$, $T_A$ and soil water conditions to remove correlations between driving variables (Rayment et al. 2000), the response of $G_S$ to $D$ can be isolated and analyzed with Equation 1. We can relate $G_{Smax}$ to atmospheric conditions through its proxy $G_{Sref}$, which is $G_S$ at $D$ = 1 kPa (Ewers et al. 2001*a*). When defined in this manner, the relationship between $G_S$ and $D$ can be described as (Oren et al. 1999*a*):

$$G_S = G_{Sref} - \delta \ln D \quad (3)$$

where $-\delta$ is the sensitivity of the $G_S$ response to ln$D$ or the slope of $G_S$ versus ln$D$ ($-\delta G_S/\mathrm{dln}D$).

Across a wide range of isohydric species, and environmental conditions within those species, $-\delta$ is 0.6 $G_{Sref}$ (Oren et al. 1999*a*, 1999*b*, Ewers et al. 2001*b*, Oren et al. 2001, Wullschleger et al. 2002, Addington et al. 2004, Ewers et al. 2005). The 0.6 proportionality between $-\delta$ and $G_{Sref}$ (Equation 3) results from the regulation of minimum $\Psi_L$ to prevent excessive xylem cavitation as described by Equation 1 for isohydric plants. Complete analysis of this regulation is presented in Oren et al. 1999*a* and expanded in Ewers et al. 2005. Species or individuals with high $G_{Sref}$ have the disadvantage of a proportionally high $-\delta$ and greater absolute reduction in $G_S$ with increasing $D$, whereas species with low $G_{Sref}$ have the advantage of a low $-\delta$ and smaller absolute reduction in $G_S$ with increasing $D$. Thus, there is a tradeoff between a high $G_{Sref}$ and potentially high carbon uptake and the absolute reduction in carbon uptake that must accompany the resulting greater $G_S$ reductions in response to atmospheric drought (increasing $D$). Whether species or individuals have a high or low $G_{Sref}$, they still are isohydric if they maintain a 0.6 proportion between $-\delta$ and $G_{Sref}$. Important deviations from the 0.6 proportionality occur when (1) anisohydric species allow the minimum $\Psi_L$ to drop with increasing $D$, (2) the range of $D$ increases, or (3) the ratio of boundary layer conductance to stomatal conductance is low (Oren et al. 1999*a*). The first two conditions result in a ratio of $-\delta$ to $G_{Sref}$ that is less than 0.6 as a result of plants that have less strict regulation of $\Psi_L$ such as drought-tolerant desert species (Ogle and Reynolds 2002, Oren et al. 1999*a*) or trees that maintain a low $A_S$:$A_L$ (Ewers et al. 2005). The third condition results in a ratio of $-\delta$ to $G_{Sref}$ that is greater than 0.6 (Oren et al. 1999*a*). Because these three types of deviations from the 0.6 ratio can be successfully explained by changes to the model such as incorporation of declining $\Psi_L$ with increasing $D$, these deviations further increase confidence in the simple plant hydraulic model (Equations 1 and 3).

In well-coupled plant canopies where stomata close to regulate minimum water potential (conditions that fit the unmodified forms of Equations 1 and 3), transpiration per unit leaf area ($E_L$) plateaus with increasing $D$ (Meinzer et al. 1993, Goulden and Field 1994, Martin et al. 1997, Ewers et al. 2001*b*, Ewers et al. 2002) or declines at high $D$ (Pataki et al. 2000). In plant canopies where stomata do not close quickly enough to regulate minimum water potential (e.g., *Picea mariana* (Mill.) > 70 years old (Ewers et al. 2005); *Larrea tridentata* (DC.) Cov. (Ogle and Reynolds 2002); and *Ephedra nevadensis* S. Wats. (Oren et al. 1999*a*)) $E_L$ shows a linear increase with increasing $D$ along with a corresponding reduction in the ratio between $-\delta$ and $G_{Sref}$ further suggesting that $G_S$ does not regulate $\Psi_L$ closely as $D$ increases. This behavior has been successfully modeled by allowing the minimum $\Psi_L$ to drop with increasing $D$ further supporting the overall use of Equations 1 and 3 (Ewers et al. 2005). Thus, both theory (Oren et al. 1999*a*) and empirical data (Oren et al. 1999*b*, Ewers et al. 2001*b*, Ogle and Reynolds 2002, Wullschleger et al. 2002, Addington et al. 2004, Ewers et al. 2005) support the view that the simple hydraulic model (Equations 1 and 3) can capture changes in the sensitivity of $G_S$ to $D$ whether individuals or species are isohydric or anisohydric.

To test whether a simple plant hydraulic model (Equations 1 and 3) can capture interannual differences in canopy transpiration ($E_C$), $E_L$ and $G_S$, we quantified transpiration from four stands in northern Wisconsin across two contrasting growing seasons. Over the course of the measurements, the sugar maple (*Acer saccharum* Marsh) and red pine (*Pinus resinosa* Ait) dominated stands had changes in stand development; the quaking aspen (*Populus tremuloides* Michx) dominated stand was defoliated and the white cedar (*Thuja occidentalis* L.)

dominated stand experienced a large drop in water table. Our study provides an ideal test of interannual variability due to these changes and large inherent differences between the seven tree species (other species measured include balsam fir (*Abies balsamea* (L.) Mill), basswood (*Tilia Americana* L.) and speckled alder (*Alnus rugosa* (DuRoi) Spreng.)). The seven species represent a range in leaf life span, xylem anatomy and growth rates and have been shown to be adequate to scale from stand transpiration to landscape transpiration (Mackay et al. 2002). Across these four stands, our objectives were to (1) quantify interannual variability of both dominant and subordinate species, and (2) test whether the simple plant hydraulic model can capture variability in $G_S$ response to $D$ in all species. Our hypothesis was that, across all the species and different driving forces between the two contrasting years, the 0.6 proportionality between $-\delta$ and $G_{Sref}$ will be maintained as $G_{Sref}$ varies within and between tree species.

## Methods

### *Site description*

The study was conducted in northern Wisconsin near Park Falls (46.15° N, 90.27° W) as part of the Chequamegon Ecosystem Atmosphere Study (ChEAS). The study sites were located between 3 and 10 km north of a 396-m-tall eddy covariance tower instrumented to measure energy, water and carbon exchange between the land surface and the atmosphere (Berger et al. 2001, Davis et al. 2003). The tower is located in the Chequamegon-Nicolet National Forest and four forest types (Table 1) were instrumented for transpiration studies within the adjacent Hay Creek Wildlife Management Area (Ewers et al. 2002, Mackay et al. 2002). The area is situated in the Northern Highlands physiographic province, a southern extension of the Canadian Shield. The bedrock comprises Precambrian metamorphic and igneous rock, overlain by 8–90 m of glacial and glaciofluvial material. Topography is slightly rolling, varying by at most 45 m between highest and lowest elevations in the entire study area. Outwash, pitted outwash, and moraines are the dominant geomorphic features. The growing season is short and the winters are long and cold with mean July and January temperatures of 19 and –12 °C, respectively (Fassnacht and Gower 1997). The soils are loamy sands with sandy loams below 30 cm. We verified the soil textures by standard laboratory texture analysis on soil samples from the three upland cover types (Ewers et al. 2002). The forested wetland site had continuously saturated peat soils. The water table fluctuated above and below the soil surface in the forested wetlands and was 2 m or more below the soil surface in the other forest types.

Four forest types comprise over 80% of the land surface (Burrows et al. 2002): (1) upland conifers consisting of red pine (*P. resinosa*) and jack pine (*Pinus banksiana* Lamb.) occur on excessively drained glacial outwash; (2) northern hardwood forests dominated by sugar maple (*A. sacharum*) with many other deciduous broad-leaved species, occur on finer textured moraines and drumlins; (3) aspen–fir forests occurring primarily on intermediate texture sites dominated by trembling aspen (*P. tremuloides*) and balsam fir (*A. balsamea*); and (4) forested wetlands on poorly drained lowland sites dominated by white cedar (*T. occidentalis*), balsam fir (*A. balsamea*) and speckled alder (*A. rugosa*).

The four forest types were identified through local land classification (Burrows et al. 2002, Mackay et al. 2002). We chose our sample sites for similarity in soil texture and basal area to the forest types measured by Burrows et al. (2002). Our sample species, *P. tremuloides*, *A. balsamea*, *A. saccharum*, *P. resinosa*, *A. rugosa* and *T. occidentalis*, represented 24, 13, 12, 12, 8 and 8% of the total basal area (~ 300 plots in a 2.5 km radius) around the tall tower, respectively (Burrows et al. 2002). We chose a northern hardwoods stand with a component of basswood (*T. americana*, 3% basal area) as a contrast to the dominant *A. saccharum* and to determine the extent of the difference in water use between *T. americana*'s and *A. saccharum*. Trees on the three upland sites were established about

Table 1. Specific leaf area (SLA) for each species for the years 2000 and 2001. Litterfall SLA refers to SLA of leaves and needles collected from litterfall traps at the end of the growing seasons; other values of SLA were collected during the middle of the growing season. Leaf area index calculated optically ($L_O$) and from litterfall SLA ($L_L$) are also reported, with $L_L$ conifer estimates using foliage life spans of 4, 5 and 3 years for *Pinus resinosa, Abies balsamea and Thuja occidentalis*, respectively. Values in parentheses indicate one standard error of the mean ($n$ = 20 for SLA, 4 for both $L$ measurements). Letters indicate significant differences between species within a year and an asterisk (*) indicates significant differences within a species between years ($\alpha$ = 0.05; Tukey's method).

| Stand type | Species | SLA ($m^2$ $kg^{-1}$) | | Litterfall SLA ($m^2$ $kg^{-1}$) | | $L_L$ | | $L_O$ |
|---|---|---|---|---|---|---|---|---|
| | | 2000 | 2001 | 2000 | 2001 | 2000 | 2001 | 2000 |
| Conifer | *P. resinosa* | 6.2 (0.7) a | 6.0 (0.9) a | 2.7 (0.4) a | 2.6 (0.3) a | 3.0 (1.5) a | 4.0 (1.5) a | 3.6 (0.5) a |
| Northern hardwood | *A. saccharum* | 28.7 (0.6) b | 28.5 (0.8) b | 18.1 (5.9) b | 18.2 (6.1) b | 3.5 (1.2) a | 4.6 (1.5) a | 3.8 (0.7) a |
| | *T. americana* | 34.8 (4.0) c | 32.5 (4.0) c | 21.2 (5.7) c | 21.0 (5.5) c | 0.3 (0.2) b | 0.3 (0.2) b | |
| Aspen/fir | *P. tremuloides* | 15.6 (0.7) d | 15.6 (0.7) d | 11.2 (3.2) d | 11.3 (3.4) d | 3.3 (0.5) a* | 2.1 (0.7) c | 3.5 (0.8) a |
| | *A. balsamea* | 7.6 (0.6) e | 7.4 (0.6) e | 5.6 (1.1) e | 5.8 (1.4) e | 0.6 (0.6) bc | 0.6 (0.6) bc | |
| Forest wetland | *T. plicata* | 6.0 (0.7) a | 6.2 (0.5) a | 3.7 (0.5) f | 3.7 (0.4) f | 0.4 (0.3) b | 0.4 (0.3) b | 4.1 (0.5) a |
| | *A.rugosa* | 18.9 (0.9) f | 18.7 (1.0) f | 11.8 (1.8) d | 11.9 (1.7) d | 1.2 (0.6) c | 1.2 (0.8) c | |
| | *A. balsamea* | 7.6 (0.6) e | 7.4 (0.5) e | 5.7 (1.2) e | 5.9 (1.5) e | 0.02 (0.01) d | 0.02 (0.01) d | |

1930 after clearcutting. The *T. occidentalis* trees in the forested wetland were about the same age. Management history of the stands, species composition and the logic behind plot sizes and tree selections are detailed in Ewers et al. 2002. Briefly, measurement plot sizes were of a 5, 10 and 6 m radius for aspen–fir, forested wetland and red pine, respectively, and the northern hardwoods plot was 20 by 40 m. The plot sizes were selected to include at least 30 trees and a range of tree sizes for detailed measurements. For each species, eight trees were selected for sap flux measurements. The trees were selected to represent the entire range of heights and diameters around the tall tower based on the data described by Burrows et al. (2002). Details of the selected trees of each species are presented in Ewers et al. (2002). A scaffolding tower of canopy height was erected in the center of each plot for canopy access and micrometerological measurements.

*Stand parameter measurements*

We measured leaf area index ($L$) optically ($L_O$) with a Li-Cor LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE) and from litterfall estimates ($L_L$). In each forest type, 16 measurements were made in a 16 m radius of a canopy access tower at the center of each plot. The location of each measurement was recorded to analyze the means and standard errors using the spatial statistics of Burrows et al. (2002). Standard field measurement methods were used to quantify $L_O$ and $L_L$ (Gower and Norman 1991, Fassnacht et al. 1994, Chen et al. 1997, Gower et al. 1999). Litterfall was collected in baskets at the same 16 sampling locations as $L_O$ (Burrows et al. 2003). Litterfall specific leaf area (SLA; ratio of leaf area to mass) was estimated from three subsamples from each litterfall basket that were scanned for leaf area and then dried to a constant mass at 65 °C and weighed. Litterfall SLA was compared with SLA measured in July based on a weighted average of three canopy layers for each tree species. Four samples from the cardinal directions were taken in the three canopy layers from each tree measured for sap flux. Tree diameters of all trees measured for sap flux were determined with diameter tape, and heights were measured with a clinometer and measuring tape to obtain angles and distances (total $n$ = 64). Data are found in Ewers et al. (2002).

Sapwood depth and bark thickness were determined from tree cores taken from the north and south sides of 14 trees of each species in each stand outside of the sap flux measurement plot, representing the range of diameter variation for each species (Ewers et al. 2002). Sapwood depth was determined visually from either coloration changes or staining with bromocresol green (Schäfer et al. 2000, Ewers et al. 2002).

Measurements of $\Psi_L$ were made in the mid-crowns on exterior foliage of three trees of each species with a pressure chamber (Model 610 PMS Instruments, Corvallis, OR). Measurements were made on two days in 2000 (predawn and midday) and nine days in 2001 (every 3 h from predawn to evening). All measurements were conducted on sunny days with midday $D$ ranging from 1.5 to 2.5 kPa. For further details see Ewers et al. (2002).

*Sap measurements and calculation of canopy transpiration*

We measured sap flux per unit conducting xylem area ($J_S$) in stem xylem of eight trees of each species at1.3 m aboveground with Granier-type sensors (Granier 1987). Many recent studies have established the need for radial and circumferential measures of $J_S$ from Granier-type sensors for appropriate tree and stand scaling (Phillips et al. 1996, Oren et al.1998, Ewers and Oren 2000, Lu et al. 2000, Lundblad et al. 2001, Ewers et al. 2002, James et al. 2002). Details of sensor-to-whole tree scaling that account for circumferential and radial trends for all the measured trees are presented in Ewers et al. (2002). Briefly, when circumferential or radial trends were significant, a weighted mean sap flux was calculated that accounted for the trends. This weighted mean sap flux was then multiplied by the sapwood area per unit ground area calculated from the diameter to sapwood depth measurements of each tree species and the plot-level diameter measurements.

Alder trees were too small for Granier-type measurements, so we used Kučera-type sensors (baby sap flux sensors, EMS, Brno, Czech Republic; Cienciala et al. 1994, Ewers and Oren 2000). These sensors estimate sap flux by maintaining a constant 4 °C difference between heated and unheated sections of the stem. The amount of heat required to maintain the temperature difference is proportional to the sap flow. The Kučera-type sensors measure the entire sap flow of the stem (for diameters between 12 and 18 mm) and need no additional scaling measurements. To avoid thermal gradients from direct radiation, all sensors were shielded with mylar.

Analyses of daily water use for both Granier- and Kučera-type sensors were performed on daily sums of $J_S$ from 0500 to 0430 h, which approximately correspond to the time of zero flow, and therefore include nighttime recharge (Phillips and Oren 1998). We calculated $E_C$ from sap flux and sapwood area per unit ground area by standard methodology (Oren et al. 1998, Ewers et al. 2002).

*Environmental measurements*

Vapor pressure deficit was calculated from relative humidity ($R_H$) and air temperature ($T_A$) measurements based on equations adapted from Goff and Gratch (1946). We measured $R_H$ and $T_A$ (Vaisala HMP 35C, Campbell Scientific, Logan, UT) at 2/3 of mean tree height by means of a scaffolding tower (sensor height/stand height, z/h = 0.79–0.83). Photosynthetic photon flux above the canopy was monitored with a quantum sensor (Li-190s, Li-Cor, Lincoln, NE) attached to the scaffolding tower in the forested wetland; $Q_o$ measurements from the larger ChEAS project were used to fill in any data gaps (Davis et al. 2003). Changes in light attenuation were estimated by application of Beer's law (Lambers et al. 1998) assuming an extinction coefficient of 0.5 for all species. Wind speed data at 2 m was utilized from the same locations. Soil volumetric water content (θ) from 0 to 30 cm was monitored continuously (CS 615, Campbell Scientific, Logan, UT) in all stands except the forested wetland because of continuous soil saturation. Soil temperature was measured in each stand at 5 cm depth with a thermistor (CS 107 probe, Campbell Scientific). Water depth measurements were made in the forested wetland with a graduated metal stick fixed to a dock. A water level measurement of zero was defined as the surface of the peat layer in between the *Sphagnum* spp. moss hummocks. The graduated stick went 50 cm below the peat layer surface; negative values thus indicate the depth of the water below the peat surface and positive values indicate the depth of water above the peat surface. Xylem flux and all environmental sensors were sampled every 30 s (CR10X, Campbell Scientific) and 30-min means were recorded.

*Defoliation*

At its peak in 2001, a large outbreak of forest tent caterpillar (*Malascoma distria* Hüber) engulfed most of northern Wisconsin (http://www.dnr.state.wi.us). This outbreak completely defoliated every individual of *P. tremuloides* in the immediate region around the WLEF TV tower, including our Hay Creek stands, as well as all trees in the Willow Creek area (WLEF and Willow Creek eddy covariance tower details in Davis et al. 2003). *Malascoma distria* is a major defoliator of deciduous trees from Louisana and Georgia into Canada. It defoliates *P. tremuloides* throughout its entire, eastern North America range. Outbreaks of *M. distria* are on about a 10-year cycle, most likely because of several insects that parasitize *M. distria* (Johnson and Lyon 1991).

*Canopy stomal conductance calculations*

Mean canopy stomatal conductance to water vapor (m $s^{-1}$) was calculated from $E_L$ and $D$ as (Monteith and Unsworth 1990):

$$G_S = \frac{K_G(T)E_L}{D} \quad (4)$$

where $K_G$ is the conductance coefficient (115.8 + 0.4236$T$; kPa $m^3$ $kg^{-1}$), which accounts for temperature effects on the psychometric constant, latent heat of vaporization, specific heat of air at constant pressure and the density of air (Phillips and Oren 1998). The $G_S$ values were converted from m $s^{-1}$ to mmol $m^{-2}$ $s^{-1}$ (cf. Pearcy et al. 1989). Equation 4 requires the following conditions (Ewers and Oren 2000): (1) $D$ is close to the leaf-to-air vapor pressure deficit, i.e., boundary layer conductance is high; (2) there is no vertical gradient in $D$ through the canopy; and (3) there is negligible water stored above the $J_S$ measurement position. To keep the measurement errors in $G_S$ (both micrometerological and sapflux) below 10%, $G_S$ was calculated only when $D \geq 0.6$ kPa (Ewers and Oren 2000).

*Statistical analyses*

Statistical analyses were performed in SAS (version 8.0, SAS Institute, Cary, NC). Because sap flux measurements are collected in a serial fashion, they often violate the assumption of independent errors. Therefore, we used the MIXED procedure to account for the effect of time series data on ANOVA calculations. The effect of species on daily sums of $E_C$ and $E_L$ was analyzed with day as the repeated measure. We determined the appropriate number of parameters and variance structure in repeated measures analysis that minimized the Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC; Littell et al. 1996, Ewers et al. 2002). Both of these criteria are log likelihood values penalized for the number of parameters used. Analyses of $\Psi_L$ measurements were also conducted using repeated measures analysis. Separations of species means were determined through the LSMEANS statement with the Tukey criteria in SAS. Analyses of time lags through autocorrelation and cross correlation were performed with Proc ARIMA and AUTOREG procedures in SAS. Nonlinear fits were performed with the NLMIXED procedure in SAS and Sigmaplot (version 6.0, SPSS, Chicago, IL). The following exponential saturation was used to investigate the response of daily $E_C$ to $D_Z$:

$$E_C = a(1 - e^{-bD_Z}) \quad (5)$$

where $a$ and $b$ are fitting parameters and $D_Z$ is mean daily $D$ normalized by light hours to account for day length changes within growing seasons and between studies at different latitudes (Oren et al. 1996).

A boundary line provides the best estimate of hydraulic limitation to water flux in trees because the boundary line occurs during conditions that lead to the highest $G_S$ at any given $D$ (Martin et al. 1997). These are the most appropriate conditions in which to analyze for tree species and interannual variability effects on the ratio of $-\delta$ to $G_{Sref}$ (Equation 3; Ewers et al. 2005). Variation in diurnal $G_S$ can often be explained mostly with $D$ and focusing analyses on $D$ both removes correlation among variables and allows analysis of Equations 1 and 3. By partitioning the data into categories of soil water, light and temperature, and performing a boundary line analysis on $G_S$ versus $D$ within each category, the data can be reduced to the parameters describing the relationship between $G_S$ and $D$ (Chambers et al. 1985, Pezeshki and Hinckley 1988, Schafer et al. 2000, Ewers et al. 2001*b*, Ewers et al. 2005). The boundary line was derived by: (1) partitioning the $G_S$ response to $D$ into at least five different levels of $D$; (2) calculating the mean and standard deviation of the $G_S$ data within each level of $D$; (3) removing outliers ($P < 0.05$ Dixon's test, Sokal and Rohlf 1995); and (4) selecting data above the mean plus one standard deviation of $G_S$ (Schäfer et al. 2000, Ewers et al. 2001*b*). These parameters can then be related to the categorizing variable ($D$). The resulting boundary line is then used to calculate $G_{Sref}$ and $\delta$ (Equation 3).

## Results

*Species with no interannual change in canopy transpiration*

Interannual variation in precipitation and temperature is quantified in Table 2. Of the eight sets of tree species investigated (*A. balsamea* was measured in uplands and lowlands) there was no change in SLA of growing season or litterfall leaves between years; only *P. tremuloides* had a significant decrease in $L_L$ (Table 1). Three species had no change in $E_C$ between years, whereas five species had either a significant increase or decrease (Table 3). Because *T. americana*, *A. rugosa* and lowland *A. balsamea* showed no difference in daily $E_C$, $E_L$ and $L_L$ (Tables 1, 3 and 4) with repeated measures analysis regression with $D_Z$, the regressions for all three were run for the two years combined (Figure 1; Table 4). In each case, there was no significant intercept ($P > 0.3$ for all), and the best fit was an exponential saturation (Equation 5; Table 4) and there was no systematic deviation of the residuals.

*Tree species with interannual changes in sapwood-area-based and leaf-area-based canopy transpiration*

*Acer saccharum* displayed an 83% increase in $E_C$ and a 41% increase in $E_L$ from 2000 to 2001 (Table 3), and there was an increasing but nonsignificant trend in $L_L$ (Table 1). We have no explanation for the increases in $E_L$ and $E_C$ (Figure 2) from 2000 to 2001 after analyzing stand structure (including growth), microclimate and disease and insect activity. Similar to *A. saccharum*, *P. resinosa* displayed a 57% increase in $E_C$ and a 19% increase in $E_L$ from 2000 to 2001 (Table 3), and an increasing but nonsignificant trend in $L_L$ (Table 1). *Pinus resinosa* had one of the lowest $R^2$ values for the relationship between $E_C$ and $D_Z$. An analysis of the residuals revealed that there was a distinct pattern with time (Figure 3B).

In contrast to *A. saccharum* and *P. resinosa*, *T. occidentalis* had a 20% decrease in $E_C$ and a 20% decrease in $E_L$ from 2000 to 2001 (Figure 4A; Table 3), but $L_L$ did not change between 2000 and 2001 (Table 1). To analyze the variability in $E_C$ relative to surface water height, we removed the dominate effect of $D_Z$ on $E_C$ as follows. The regression curve between $E_C$ and $D_Z$ from 2000 was used as a reference and on any day that surface water height was collected, the residual of that day compared with the 2000 regression curve was calculated. The same 2000 regression curve was also used for 2001 data so that 2001 days were calculated as the residual between the 2000 regression curve and the 2001 data. The drop in $E_C$ was well correlated *($P < 0.001$) with a drop in surface water height on the 15 days in 2000 and 13 days in 2001 when we measured surface water height in the forested wetland. The drop in water table was a result of less precipitation in 2001 and increased water flow from managed flowages in the region (J. Koch, manager of Wisconsin Dept. Nat. Res. Hay Creek Wildlife Area, personal communication).*

Like *T. occidentalis*, *P. tremuloides* had a 50% lower $E_C$ and a 21% lower $E_L$ in 2001 compared with 2000 and the decrease was a result of complete defoliation in 2001 by *M. distria*. The 36% lower value of $L_L$ after reflush in 2001 was the only significant change in $L_L$ for all species measured (Table 1). The period of actual leaf loss and subsequent reflush is depicted by the triangle in Figure 5A, which corresponds to the vertical lines in Figure 5C. There were no systematic changes in the environmental driving variables $D$, $Q_o$, and $\theta$ during the time of defoliation (Figure 5B).

Like *A. saccharum* and *P. resinosa*, upland *A. balsamea* experienced a 55% increase in $E_C$ and a 53% increase in $E_L$ from 2000 to 2001 (Table 3; Figure 6). Upland *A. balsamea* exists completely in the understory of *P. tremuloides* (height range of 2.9–5.9 and 9.0–17.8 for *A. balsamea* and *P. tremuloides*, respectively, Ewers et al. 2002). To investigate the competitive tradeoff between $E_C$ of upland *A. balsamea* and *P. tremuloides*, we analyzed the residuals of 2001 using the 2000 $E_C$ to $D_Z$ relationship (Figure 6B). The proportional changes were similar, with *A. balsamea* increasing 56% and *P. tremuloides* declining 50% (Table 3). Using the simple Beer-Lambert Law of light attenuation on the reflushed foliage estimate (Table 1) and zero foliage during the defoliation period, we found no significant ($P > 0.5$) effect of changing irradiance in 2001 on

Table 2. Precipitation during growing season (May 1–Sept. 30) and annual precipitation and mean growing season and annual temperature for the years 2000 and 2001.

| Year | Growing season precipitation (mm) | Annual precipitation (mm) | Growing season temperature (°C) | Annual temperature (°C) |
|---|---|---|---|---|
| 2000 | 490 | 830 | 15.3 | 4.1 |
| 2001 | 390 | 730 | 16.1 | 6.6 |

Table 3. Mean daily transpiration per unit leaf area ($E_L$) and canopy transpiration per unit ground area ($E_C$) and reference mean canopy stomatal conductance ($G_{Sref}$) calculated from half hourly $E_L$ values for each year of the study. Values in parentheses indicate one standard error of the mean ($n = 8$) calculated from repeated measures over each growing season. Letters indicate significant differences between species within a year and an asterisk (*) indicates significant differences within a species between years ($\alpha = 0.05$; Tukey's method).

| Stand type | Species | $E_L$ (mm day$^{-1}$) | | $E_C$ (mm day$^{-1}$) | | $G_{Sref}$ (mmol m$^{-2}$ s$^{-1}$) | |
|---|---|---|---|---|---|---|---|
| | | 2000 | 2001 | 2000 | 2001 | 2000 | 2001 |
| Conifer | *P. resinosa* | 0.46 (0.01) a* | 0.55 (0.02) a | 1.4 (0.02) a* | 2.2 (0.09) a | 90.5 (10.1) a* | 115.2 (11.5) a |
| Northern hardwood | *A. saccharum* | 0.17 (0.01) b* | 0.24 (0.01) b | 0.6 (0.03) b* | 1.1 (0.04) b | 33.5 (2.5) b* | 51.6 (3.3) b |
| | *T. americana* | 0.70 (0.01) c | 0.70 (0.01) c | 0.2 (0.03) c | 0.2 (0.01) c | 138.5 (6.2) c | 120.7 (16.9) ad |
| Aspen/fir | *P. tremuloides* | 0.61 (0.01) d* | 0.48 (0.03) d | 2.0 (0.02) d* | 1.0 (0.05) d | 133.7 (24.8) c | 128.5 (20.6) a |
| | *A. balsamea* | 0.15 (0.01) e* | 0.23 (0.01) b | 0.09 (0.01) e* | 0.14 (0.01) e | 76.3 (5.2) d | 87.2 (6.8) c |
| Forested wetland | *T. plicata* | 0.75 (0.01) f* | 0.60 (0.01) e | 0.5 (0.02) f* | 0.4 (0.01) f | 166.5 (15.5) e* | 116.8 (14.0) a |
| | *A.rugosa* | 0.75 (0.01) f | 0.75 (0.01) f | 0.9 (0.04) g | 0.9 (0.05) d | 170.0 (20.2) e | 141.5 (19.5) d |
| | *A. balsamea* | 0.15 (0.02) b | 0.20 (0.03) b | 0.03 (0.02) h | 0.04 (0.01) g | 34.3 (2.3) b | 39.2 (3.1) e |

Table 4. Parameters from Equation 5 for the fit between $E_C$ and $D_Z$ shown in Figures 1–6. Letters indicate significant differences between species within a year and an asterisk (*) indicates significant differences within a species between years ($\alpha = 0.05$; Tukey's method). All regressions and parameters were significant ($P < 0.001$ for all); $R^2$ are shown in Figures 1–6.

| Stand type | Species | *a* | | *b* | |
|---|---|---|---|---|---|
| | | 2000 | 2001 | 2000 | 2001 |
| Conifer | *P. resinosa* | 2.5 (0.4) a* | 3.3 (0.4) a | 1.9 (0.3) a* | 2.6 (0.4) a |
| Northern hardwood | *A. saccharum* | 1.3 (0.2) b* | 2.8 (0.2) a | 2.0 (0.2) a* | 1.2 (0.2) b |
| | *T. americana* | 0.5 (0.1) c | 0.5 (0.2) b | 1.1 (0.1) b | 1.1 (0.1) b |
| Aspen/fir | *P. tremuloides* | 4.3 (0.2) d* | 2.1 (0.1) c | 1.0 (0.2) b* | 2.1 (0.3) ac |
| | *A. balsamea* | 0.1 (0.1) e | 0.2 (0.2) d | 2.0 (0.2) a | 2.0 (0.2) a |
| Forested wetland | *T. plicata* | 0.9 (0.1) f* | 0.6 (0.1) b | 1.4 (0.2) b* | 1.9 (0.2) c |
| | *A. rugosa* | 2.0 (0.1) g | 2.0 (0.1) c | 1.3 (0.1) b | 1.3 (0.1) b |
| | *A. balsamea* | 0.1 (0.1) e | 0.1 (0.1) d | 2.0 (0.2) a | 2.0 (0.2) ac |

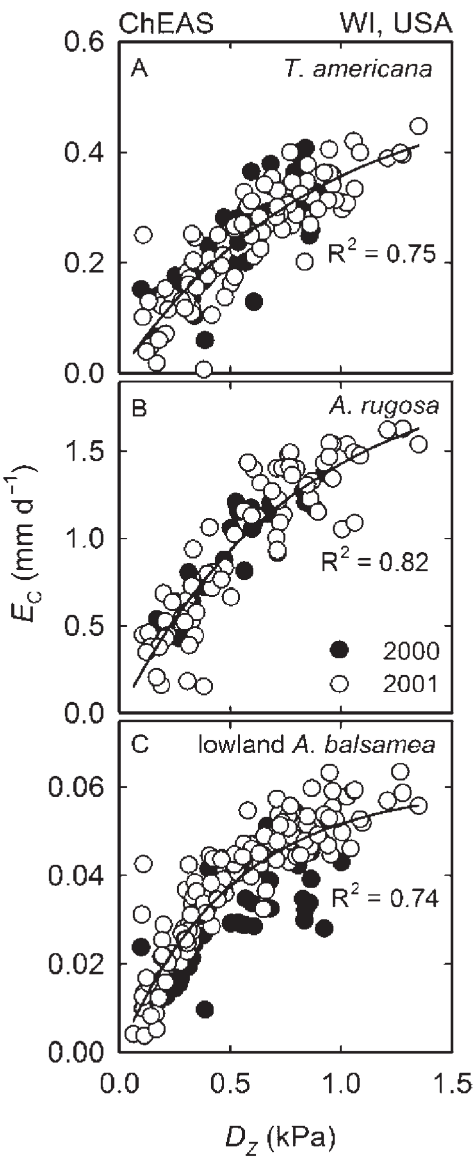


Figure 1. Relationship between mean daily vapor pressure deficit normalized by light hours ($D_Z$) and canopy transpiration ($E_C$) of (A) *T. americana*, (B) *A. rugosa* and (C) wetland *A. balsamea* over the years 2000 and 2001. Regression equations parameters are given in Table 4.

$E_C$ of *A. balsamea*. We estimated that light passing through the *P. tremuloides* canopy to upland *A. balsamea* increased 84% after the reflush in 2001 compared with 2000.

*Comparison of species effects on transpiration*

Based on a stepwise multiple regression, neither $\theta$ nor $Q_o$ significantly explained any of the intra- or interseasonal variability in $E_C$ for all seven tree species ($P > 0.2$ for both). Soil water never dropped below 0.26 $m^3\ m^{-3}$ in any of the upland stands which is above the value (~0.25 $m^3\ m^{-3}$) that triggers a reduction in transpiration based on four years of eddy covariance data from a comparator stand in the same region (Mackay et al. Water Res. Res. In Review). An exponential saturation (Equation 5) between $E_C$ and $D_Z$ was the best fit for all species in both years (Table 4; Figures 2–6). Parameter *a* from Equation 5 varied by a factor of eight, reflecting the large species effect on $E_C$ values, whereas parameter *b* varied by a factor of

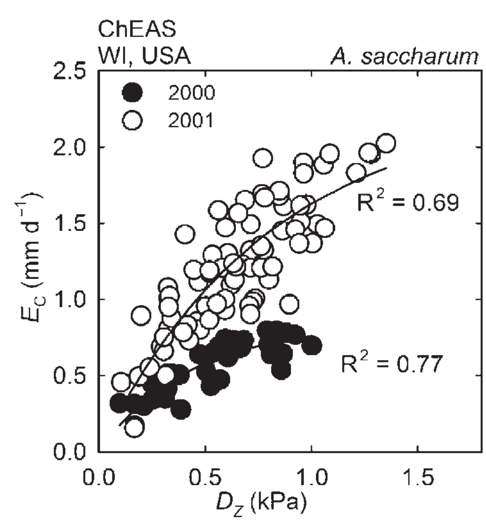


Figure 2. Relationship between mean daily vapor pressure deficit normalized by light hours ($D_Z$) and canopy transpiration ($E_C$) of *A. saccharum* over the years 2000 and 2001. Regression equations parameters are given in Table 4.

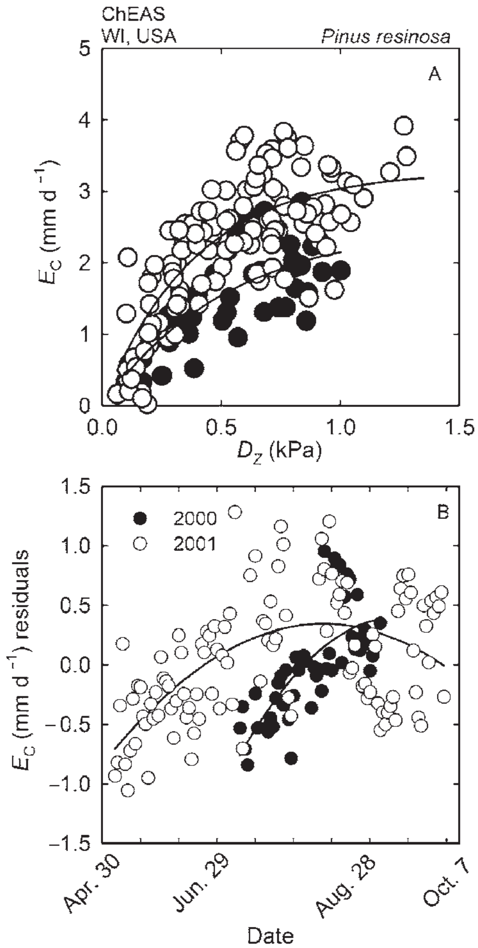


Figure 3. (A) Relationship between mean daily vapor pressure deficit normalized by light hours ($D_Z$) and canopy transpiration ($E_C$) of *P. resinosa* over the years 2000 and 2001. (B) Residuals of (A) from regression equations (Table 4) as a function of day of year.

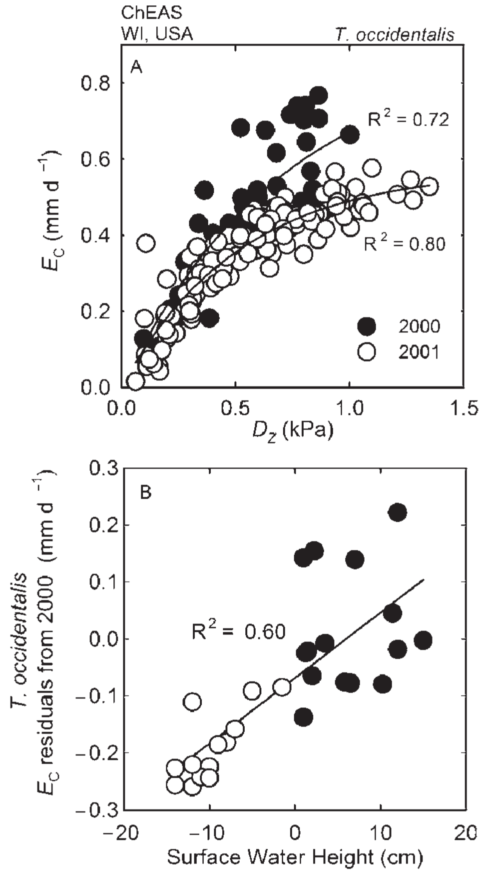


Figure 4. Relationship between mean daily vapor pressure deficit normalized by light hours ($D_Z$) and canopy transpiration ($E_C$) of *T. occidentalis* over the years 2000 and 2001. Regression parameters are shown in Table 4. (B) Relationship between residuals in (A) calculated from the year 2000 regression line and the 2000 and 2001 values and surface water height; 0 surface water height indicates the surface of the wetland peat, positive values occur when water table is above peat surface, negative below.

two, reflecting differences in the rate of curvature of the $E_C$ to $D_Z$ response (Table 4). All seven species had significantly different *a* parameters for 2000, *A. balsamea* was the same in upland and wetland. In 2001, the interannual variability in parameter *a* led to less variability among species indicating an interaction between species and interannual variability. The low impact of tree species on the *b* parameter reflected saturation of $E_C$ with increasing $D_Z$ in all species.

### *Leaf water potentials*

The large species-specific dynamics in $E_C$ and $E_L$ between 2000 and 2001 provide a rigorous test of the hypothesis that these trees maintain isohydric homeostasis of minimum $\Psi_L$ (Equations 1 and 3). We analyzed $\Psi_L$ between the two years to test if midday values were maintained in the face of drastic changes to $E_C$ and $E_L$. On all days that we measured $\Psi_L$, we found that neither midday nor predawn $\Psi_L$ differed between 2000 and 2001 in any of the seven species (Figure 7). Consistency in predawn $\Psi_L$ further supports the lack of an effect of $\theta$ on $E_C$ or $E_L$. *Populus tremuloides* showed the largest shifts in both predawn and midday mean $\Psi_L$ but neither differed significantly between 2000 and 2001 (Figure 7). Even the standard errors were similar between the two years for all species.

### *Tradeoff in canopy stomatal conductance sensitivity to vapor pressure deficit with interannual dynamics*

The simple plant hydraulic model of Equations 1 and 3 predicts that the study tree species will maintain a 0.6 ratio between $-\delta$ and $G_{Sref}$ by moving up and down a line of 0.6 slope with no intercept (Equation 3; Figure 8) in response to changes in $E_L$ (Table 3). Our results fully support these predictions. Despite large species-specific changes in $E_C$ and $E_L$ (Table 3), none of the seven tree species significantly deviated ($P > 0.4$ for all slope comparisons) from the hypothesized 0.6 ratio between $-\delta$ and $G_{Sref}$ (Figure 8). We tested the impact of canopy coupling on all species by running the analyses for understory windspeeds < 2.0 m s$^{-1}$ and > 2.0 m s$^{-1}$; there were no differences in the slopes ($P > 0.5$ for all species). Because all species maintained the 0.6 ratio between $-\delta$ and $G_{Sref}$, we can conduct

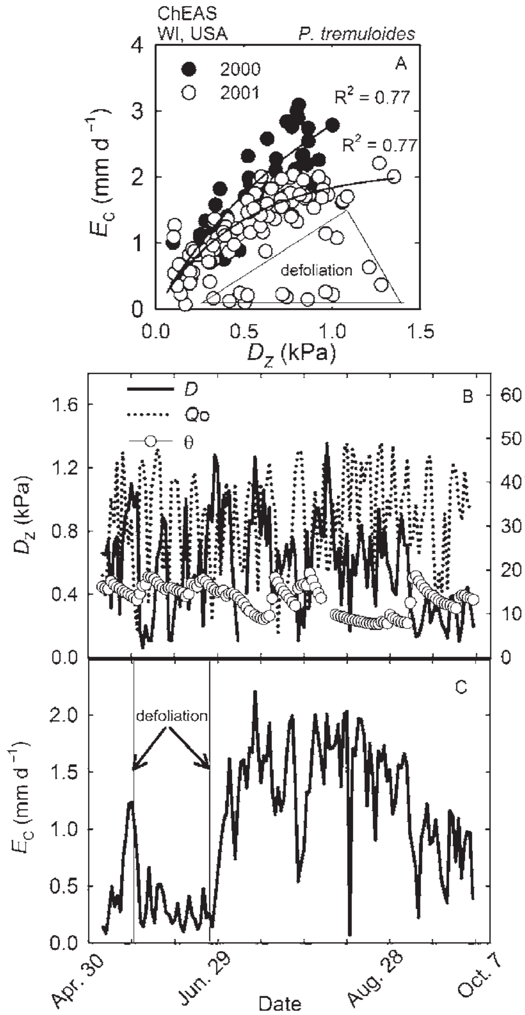


Figure 5. (A) Relationship between mean daily vapor pressure deficit normalized by light hours ($D_Z$) and canopy transpiration ($E_C$) of trembling aspen over the years 2000 and 2001; regression parameters shown in Table 4. Values within the triangle indicate the time period of complete defoliation shown in (C). (B) Mean daily volumetric soil water (θ), mean daily vapor pressure deficit normalized by light hours ($D_Z$), and daily sums of photosynthetically active radiation ($Q_o$) for the year 2001. Vertical lines indicate time periods of complete defoliation by *M. distria*. (C) Daily $E_C$ as a function of time; vertical lines indicate the period of complete defoliation.

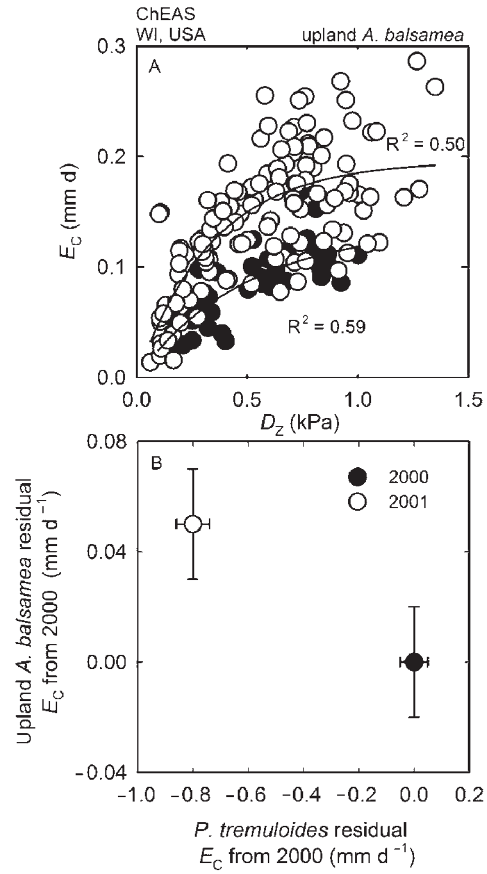


Figure 6. Relationship between mean daily vapor pressure deficit normalized by light hours ($D_Z$) and canopy transpiration ($E_C$) of upland *A. balsamea* over the years 2000 and 2001; regression parameters shown in Table 4. (B) Average residuals of $E_C$ in the year 2001 from 2000 for *P. tremuloides* and upland *A. balsamea*.

analyses on differences between years based on $G_{Sref}$ only. We found that $G_{Sref}$ followed the same statistical trends as $E_L$ in all species except *P. tremuloides* and upland *A. balsamea*. (Table 3). The lack of change in midday minimum $\Psi_L$ provides independent support for the hypothesized ratio of 0.6 between $-\delta$ and $G_{Sref}$.

## Discussion

Despite large changes in $E_C$ and $E_L$ among many contrasting tree species, minimum $\Psi_L$ remained the same between years supporting a regulatory role of $G_S$ over minimum $\Psi_L$. This was independently confirmed by saturating relationships between $E_C$ and $D_Z$ and a measured ratio between $-\delta$ and $G_{Sref}$ that was not significantly different from 0.6 in all tree species. Our results indicate that all of the tree species we studied attempt to maintain an isohydric homeostasis of water status in the face of changing water supplies, competition, defoliation and leaf areas.

### *Dynamics in the relationship between daily canopy transpiration and vapor pressure deficit normalized by light hours*

Despite many different environmental and biological dynamics in $E_C$ and $E_L$, all species showed the same type of exponential saturation between $E_C$ and $D_Z$ (Figures 1–6; Table 4). In forest canopies where stomata close to regulate minimum $\Psi_L$, $E_C$ shows either a plateau with increasing $D$ (Meinzer et al. 1993, Goulden and Field 1994, Martin et al. 1997, Ewers et al. 2001*a*, 2001*b*, Ewers et al. 2002, Ewers et al. 2005) or even a decline at high $D$ (Pataki et al. 2000). Thus, our findings indicate that, although all seven tree species may experience interannual variability in $E_C$ and $E_L$, they do so while maintaining the homeostasis of minimum $\Psi_L$. Such relationships show that the diurnal behavior of $G_S$ response to $D$ can be inferred from

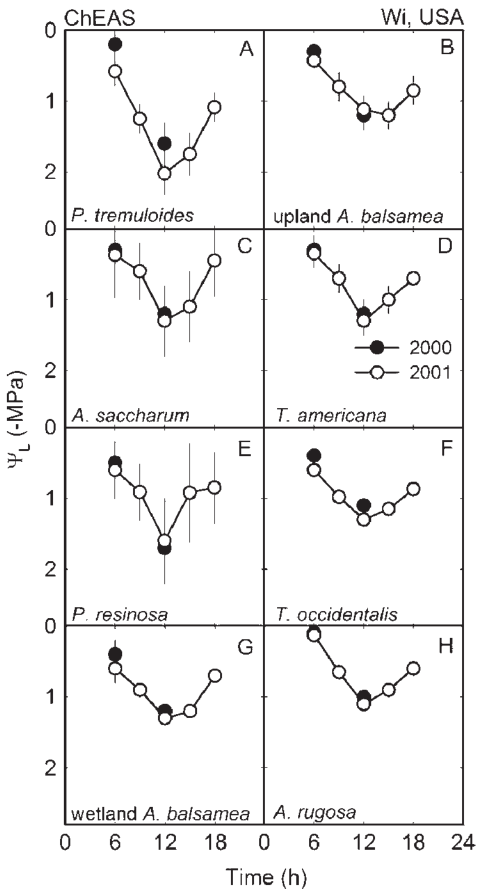


Figure 7. Relationship between leaf water potential ($\Psi_L$) and time for (A) *P. tremuloides*, (B) upland *A. balsamea*, (C) *A. saccharum*, (D) *T. americana*, (E) *P. resinosa*, (F) *T. occidentalis*, (G) wetland *A. balsamea*, and (H) *A. rugosa* on representative, full sun days in the years 2000 and 2001.

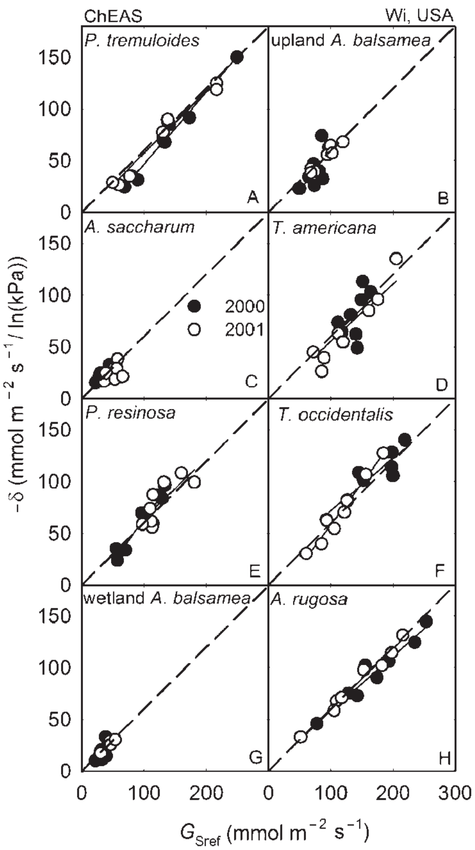


Figure 8. Relationship between mean canopy stomatal conductance at vapor pressure deficit ($D$) = 1 kPa ($G_{Sref}$) and the sensitivity of $G_{Sref}$ to $D$ ($-\delta$) for (A) *P. tremuloides*, (B) upland *A. balsamea*, (C) *A. saccharum*, (D) *T. americana*, (E) *P. resinosa*, (F) *T. occidentalis*, (G) wetland *A. balsamea* and (H) *A. rugosa.* The dotted line indicates water potential regulation as described by Equations 1 and 3.

daily $E_C$ and $E_L$ responses to $D_Z$ (Ewers et al. 2005).

We found three separate types of interannual dynamics in the relationship between $E_C$ and $D_Z$—static, increasing and decreasing. *T. americana*, wetland *A. balsamea* and *A. rugosa* had no change in mean daily $E_C$ or $E_L$ between years (Table 3) or in response to increasing $D_Z$ (Figure 1; Table 4). No particular traits of these three species separate them from the other species which showed a significant decrease or increase. Further, the dynamics of $E_C$ in *A. balsamea* changed depending on whether it was growing with defoliated *P. tremuloides* in uplands or *A. rugosa* and *T. occidentalis* in wetlands (Table 3).

*Acer saccharum*, *P. resinosa* and upland *A. balsamea* all showed significant increases in $E_C$ between 2000 and 2001 but for different reasons. Only in the case of *A. balsamea* was there a clear explanation: release from competition by the defoliated *P. tremuloides* (Figure 6). The large increases in $E_C$ and $E_L$ in *A. balsamea* from 2000 to 2001 (Table 3) suggest that it can rapidly acclimate to lack of competition despite its long leaf life span (average 5 years, maximum 16 years; Niinemets and Lukjanova 2003). Light competition is the most likely explanation because soil water did not explain the between-year differences in either $E_C$ or $E_L$.

An explanation for the increases in $E_C$ and $E_L$ from 2000 to 2001 for *A. saccharum* and *P. resinosa* is more elusive. *Acer sacchrum* could still be recovering from stand thinning in 1990. No microclimate variables could explain the difference between the years, and the lack of change in the stand competitor, *T. americana* (Figure 1), also suggests a biological rather than a stand micrometerological explanation. Using Equation 1 as a guide, $A_L$ changed in response to nonsignificant changes in $L_L$ (Table 1), whereas $A_S$ increased less than 5% between the two years, likely because of the saturating nature of the sapwood to diameter relationships in these trees (Ewers et al. 2002). Neither $\Psi_S$ nor $\Psi_L$ changed between years and tree height increases were less than 5%. Because transpiration changed without a concurrent change in either $\Psi_S$ or $\Psi_L$, $K_S$ must have changed by the same magnitude as $E_C$ (Ewers et al. 2002). Thus, changes in $K_S$ in combination with $A_L$ changes are the only biological components of Equation 1 that could explain the differences in $G_S$. We currently have no explanation for these changes, but new studies are underway to quantify the impact of vulnerability to xylem cavitation and root to leaf area ratios on $K_S$ based on vulnerability curves and a model (Sperry et al. 1998, Ewers et al. 2000).

*Pinus resinosa* also resists a clear explanation for its increase in $E_C$ and $E_L$ between 2000 and 2001. One possibility is that the stand has not yet reached peak biomass production as evidenced by the nonsignificant increase in $L_L$ (Table 1). However, $E_L$ still increased (Table 3), indicating that $L_L$ alone does not explain the increase in $E_C$. In *P. resinosa*, the dynamics with respect to the parameters of Equation 1 were similar to those of *A. saccharum*; i.e., no significant change in $A_S$, $h$, $\Psi_S$, or $\Psi_L$, whereas $K_S$ must have changed as a result of the changes in $E_C$. Furthermore, because *P. resinosa* retains foliage for about 4 years (Gower et al. 1993), two years of litterfall data are insufficient for a full interpretation of $A_L$ dynamics. Another possibility is that *P. resinosa* foliage is recovering from the regional drought in 1998. Such a response has been suggested by Burrows et al. (2003) who found net primary productivity of *P. resinosa* increased during the same two years of our study. The 4-year leaf life span of *P. resinosa* foliage suggests that any acclimations may take the entire canopy foliage about 4 years to acclimate to non-drought conditions. The two years of our study show contrasting timing but similar trends in the residual relationships with time (Figure 3B). This time trend strongly suggests a phenological trend in *P. resinosa* that occurs as a result of the three ages classes of foliage. In the spring, age classes 1–4 are present and $E_C$ rapidly increases in response to new Age 0 foliage. As Age 0 foliage $E_L$ increases to its maximum, Age 4 foliage begins to senesce in midsummer and completely senesces in fall. Such a pattern has been shown in *P. taeda*, which carries only two age classes of foliage, but nevertheless follows the overall trend shown here (Ellsworth 2000).

In contrast to the increases in $E_C$ of *A. saccharum*, *A. balsamea* and *P. resinosa*, *T. occidentalis* displayed a decrease in $E_C$ (Table 3) that was directly correlated with water table depth (Figure 4). The mechanism underlying this correlation has not been established. Other wetland conifers, such as *Taxodium distichum*, have been shown to be highly tolerant of flooded conditions as adults (Pezeshki and Anderson 1997, Oren et al. 2001) and *T. occidentalis* seedlings are tolerant of flooding (Collier and Boyer 1989). Many riparian and wetland species show stress effects from any deviation from normal flooding (Kozlowski and Pallardy 2002). Our data suggest that, not only is *T. occidentalis* extremely tolerant of flooding, it is obligately adapted to it. The roots of *T. occidentalis* can be found in *Sphagnum* spp. hummocks around the sites and few penetrate into the peat layer (B. Ewers, unpublished obserations). Thus, the lowering of the water table dries the roots in the upper parts of the hummocks leading to a drop in $E_C$ as a result of an increase in overall root resistance to water uptake. The roots of *A. rugosa* and *A. balsamea* in the same stand did not appear to be affected by the lower water table because their $E_C$ was the same in both years (Figure 1; Table 3). This may lead to a competitive advantage for both species when the forested wetlands are drained through drought or land management practices (Roy et al. 2000, Girardin et al. 2001). However, because *T. occidentalis* is 35% of stand $E_C$ (Ewers et al. 2002), there will be some negative feedback of lower total stand $E_C$ on water level of any draining wetlands caused by the lowering of $E_C$ from *T. occidentalis* as the water table drops.

Like *T. occidentalis*, *P. tremuloides* had a declining $E_C$ from 2000 to 2001 that was directly caused by complete defoliation by *M. distria*. After defoliation, *P. tremuloides* reflushed new leaves but the resulting leaf area was 36% less than for 2000 (Table 1). The declines in both $E_L$ and $E_C$ (Table 3) indicate that *P. tremuloides* was unable to increase its $G_S$ to acclimate to the loss of $L$ and subsequent increases in light and canopy water availability as occurs in some species (Pataki et al. 1998, Oren et al. 2001, Brooks et al. 2003). Such a response indicates that, although *P. tremuloides* may not have had the carbon reserves to replace the lost foliage entirely, it maintained leaf water status homeostasis even with less leaf area demand for water from sapwood and root area.

*Regulation of leaf water potential by canopy stomatal conductance*

Despite large species-specific changes in $E_C$ and $E_L$, the relationship between $-\delta$ and $G_{Sref}$ never significantly deviated from 0.6 (Equation 3; Figure 8), as hypothesized. The hypothesis of $\Psi_L$ regulation by $G_S$ is also supported by the consistent exponential saturation between $E_C$ and $D_Z$ among all species and years (Figures 1–6; Table 4) and the lack of difference in $\Psi_L$ between the two years (Figure 7). The relationship between these two responses has been explicitly shown across intra- and interspecific changes in $E_L$ due to $A_S$:$A_L$ dynamics in boreal forests (Ewers et al. 2005). Across an even larger range of species and across environmental conditions within species $-\delta$ is 0.6 $G_{Sref}$ indicating a broad convergence of $\Psi_L$ regulation in isohydric species (Oren et al. 1999*a*, 1999*b*, Ewers et al. 2000, Ewers et al. 2001*b*, Oren et al. 2001, Wullschleger et al. 2002, Addington et al. 2004). These studies together with our study provide substantial evidence that tree species tend to maintain a homeostasis of minimum $\Psi_L$ despite large species-specific changes in $E_C$ and $E_L$. The homeostasis of minimum $\Psi_L$ is maintained with changes in $D$ (all species), $L$ (by defoliation, *P. tremuolides*), water table (*T. occidentalis*), possibly stand development (*P. resinosa* and *A. saccharum*) and release from competition (upland *A. balsamea*).

Maintenance of the 0.6 ratio between $-\delta$ and $G_{Sref}$, means that only $G_{Sref}$ need be quantified because $G_S$ can be calculated at any $D$ value. This procedure offers a superior method to traditional $G_{Smax}$ calculations because $G_{Sref}$ is precisely defined at 1 kPa $D$, whereas $G_{Smax}$ is ill-defined owing to variations in the $D$ value at which $G_{Smax}$ is measured (Ewers et al. 2001*a*). Recent modeling work in this same northern Wisconsin region has shown the power of this approach to modeling stand transpiration (Ewers et al. 2006). Our $G_S$ values calculated from micrometerological and sap flux measurements agreed well with leaf-level stomatal conductance measurements in *A. saccharum* (Kloeppel and Abrams 1995, Raulier et al. 1999), *P. tremuloides* (Abrams 1988, Brooks et al. 1997) and *A. balsamea* (Niinemets and Lukjanova 2003). The $G_S$ values also agreed well with genus level relatives of *P. resinosa* (*Pinus taeda* L. 30–115 mmol m$^{-2}$ s$^{-1}$, Ellsworth 2000) *T. occidentalis* (*Thuja plicata* J. Donn ex D. Don 25–200 mmol m$^{-2}$ s$^{-1}$; Pepin et al. 2002, Warren et al. 2003), *A, regosa* (*Alnus* *formosa* Bong. up to 300 mmol $m^{-2}$ $s^{-1}$ Liao and Weng 2002 and *Alnus rubra* Nutt. 75–300 mmol $m^{-2}$ $s^{-1}$; Bond and Kavanaugh 1999), and *T. americana* (*Tilia cordata* Mill. 50–100 mmol $m^{-2}$ $s^{-1}$; Aasamaa et al. 2002).

Our study investigated the 0.6 ratio between $-\delta$ and $G_{Sref}$ (Equation 3) only under optimal conditions, but previous work has shown that trees merely move along the 0.6 line with changing light and soil water in *P. taeda* (Ewers et al. 2001*b*), changes in trees size in *P. tremuloides* and *P. banksiana* (Ewers et al. 2005) and changes in atmospheric $CO_2$ concentration in *Liquidambar styraciflua* L. (Wullschleger et al. 2002). Because there was insufficient data to test whether the 0.6 relationship held under low light conditions, we tested the relationship in another study using Monte Carlo simulations of model parameters and found that the set of parameters that best predicted half hourly $E_C$ fit along the 0.6 ratio between $-\delta$ and $G_{Sref}$ (Ewers et al. 2006). The ability of the model (Equations 1 and 3) to capture the regulation of $\Psi_L$ by $G_S$ at any $G_{Sref}$ means that any errors in the magnitude of $G_{Sref}$ (e.g., $L_L$ errors) will not change the interpretation of the 0.6 ratio between $-\delta$ and $G_{Sref}$.

Further evidence of the power of the simple plant hydraulic model to capture the behavior of species by Equations 1 and 3 can be found for species that do not regulate $\Psi_L$. To include these anisohydric species, the model was modified such that $\Psi_L$ is allowed to declined with a corresponding reduction in the ratio between $-\delta$ and $G_{Sref}$ (Ewers et al. 2005). Measured values of the declining ratio (as low as 0.4 in *P. mariana* (Ewers et al. 2005) and *E. nevadensis* and *L. tridentata* (Oren et al. 1999*a*)) between $-\delta$ and $G_{Sref}$ can be captured with the model by incorporating measured declines in $\Psi_L$ (Oren et al. 1999*a*, Ogle and Reynolds 2002, Ewers et al. 2005). Thus, the ability of a small and predictable change in the model to accommodate these species gives broader confidence to its overall application. The maintenance of the 0.6 ratio between $-\delta$ and $G_{Sref}$ as a result of homeostasis of minimum $\Psi_L$ also greatly simplifies models of canopy water and carbon fluxes (Ewers et al. 2006), thereby facilitating improved predictive understanding of the coupling of canopy water loss and carbon uptake (Katul et al. 2003). Application of plant hydraulics in models allows them to be grounded in mechanistic rigor while retaining the parsimony needed for larger scale modeling with sparse knowledge of individual forest stands.

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