Temperature, light and leaf hydraulic conductance of little-leaf linden (*Tilia cordata*) in a mixed forest canopy

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Received May 8, 2006; accepted June 19, 2006; published online February 1, 2007

**Summary** Response of whole-leaf hydraulic conductance (*G*\(_{L}\)) in little-leaf linden (*Tilia cordata* Mill.) to temperature and photosynthetic photon flux (*Q*\(_{P}\)) was estimated by the evapotranspirative flux method under natural conditions in a mixed forest canopy. Mean midday *G*\(_{L}\) in the lower- and upper-crown foliage was 1.14 and 3.06 mmol m\(^{-2}\) s\(^{-1}\) MPa\(^{-1}\), respectively. Over the study period, leaf temperature (*T*\(_{L}\)) explained about 67% of the variation in *G*\(_{L}\), and *Q*\(_{P}\) explained about 10%. Leaf water potential and crown position also affected *G*\(_{L}\) significantly. About a third of the temperature effect was attributable to changes in viscosity of water, and two thirds to changes in protoplast permeability (i.e., symplastic conductance). Leaf hydraulic conductance was highly sensitive to changes in *Q*\(_{P}\) when *Q*\(_{P}\) was less than 200 µmol m\(^{-2}\) s\(^{-1}\), and *G*\(_{L}\) sensitivity decreased with increasing irradiance. Sensitivity of *G*\(_{L}\) to variation in *T*\(_{L}\) increased consistently with increasing temperature in the range of 16 to 29 °C. There were positive interactions between temperature and light in their effects on *G*\(_{L}\): the light response was more pronounced at higher leaf temperatures. Because of frequent rains during the study period, the trees experienced no soil water deficit, and, within the range experienced, soil water potential had no effect on *G*\(_{L}\). Leaf hydraulic conductance exhibited a seasonal pattern that could be explained primarily by temporal variability in mean air temperature and irradiance, in addition to which an age-related trend (*P* < 0.001) of increasing *G*\(_{L}\) from the end of June to the beginning of August was observed.

**Keywords:** evaporative flux method, leaf temperature, photosynthetic photon flux density, seasonal trend, within-crown variability.

**Introduction**

Water flow through the soil–plant–atmosphere continuum has important implications for leaf water supply and plant performance. However, there are still gaps in our knowledge of the mechanisms determining leaf water balance. Evidence of the paramount role of leaves in the regulation of whole-tree liquid phase conductance has accumulated during the last decade, but little is known about the microhydrological processes that continuously occur inside the leaf (Sack and Tyree 2005).

Plants may be considered as a water-conducting interface between the soil and the atmosphere that consist of foliage and root, each with a high hydraulic resistance, connected by stem, a water conducting pathway with an intrinsically low resistance (Salleo and Nardini 2005). Leaves account for 50–90% of the hydraulic resistance to water flow through the shoots of woody plants (Yang and Tyree 1994, Nardini and Salleo 2000, Nardini 2001) and, thus, form a substantial part of the hydraulic resistance in whole plants. For many species over a range of life forms, leaves, including petioles, contribute 30% or more of the plant total hydraulic resistance (Becker et al. 1999, Sack et al. 2003a, Gyenge et al. 2005, Sack and Holbrook 2006, Salleo and Söber 2001, Brodribb et al. 2005, Franks 2006, Sack and Holbrook 2006). Therefore, changes in leaf hydraulic conductance (*G*\(_{L}\)) should have a significant impact on stomatal behavior. The concept that photosynthesis may be limited by leaf hydraulic properties is of particular importance, because it provides new insights into the factors controlling plant productivity and growth. Studies performed with woody species from different phylogenetic groups have confirmed a close relationship between *G*\(_{L}\) and photosynthetic capacity (Aasamaa and Söber 2001, Brodribb et al. 2005, Franks 2006, Sack and Holbrook 2006).

Leaf hydraulic properties, however, are not completely understood, in part because of the extreme morpho-anatomical heterogeneity of leaves and in part because of difficulties in discriminating between liquid and gaseous water flows, vascular and extravascular compartments and apoplastic and symplastic transport pathways within the leaf (Nardini and Salleo 2005). Consequently, conflicting data have been published on the sources and partitioning of hydraulic resistance in leaves (e.g., Zwieniecki et al. 2002, Trifiló et al. 2003, Cochard et al. 2004a, Gascó et al. 2004, Sack et al. 2005). In addition to species-specific variation in the partitioning of leaf hydraulic resistance (*R*\(_{L}\) = 1/*G*\(_{L}\)), the contradictory findings arose mostly from earlier studies that have ignored the effect of light on *G*\(_{L}\). The light environment has a significant effect on the partitioning of *R*\(_{L}\) between the leaf lamina and petiole, as well as between the vascular and extravascular pathways (Nardini et al. 2005a, 2005b, Sack et al. 2005). The current consensus is that the hydraulic resistance of leaf xylem is about the same order
as that of the extravascular pathways (Gascò et al. 2004, Sack et al. 2004, 2005).

Whole-plant hydraulic conductance and that of single organs have been found to vary both diurnally (Tsuda and Tyree 2000, Brodribb and Holbrook 2004a, Lo Gullo et al. 2005, Nardini et al. 2005a) and seasonally (Brodribb and Holbrook 2003, 2005a, Aasamaa et al. 2005, Lo Gullo et al. 2005), being associated with changes in environmental conditions. The contribution of vascular versus extravascular compartments to the total hydraulic conductance may vary significantly, particularly as a result of xylem embolism. Water deficit is a primary factor affecting \( G_L \) in both trees and herbaceous species (Brodribb and Holbrook 2003, 2004b, Lo Gullo et al. 2003, Nardini et al. 2005, Salleo et al. 2003, Trifilo et al. 2003). The influence of water stress on \( G_L \) is observed at several time scales. In the short term, \( G_L \) may decline as a result of dysfunction of the vascular system caused by cavitation-induced embolism (Kikuta et al. 1997, Salleo et al. 2001, 2003, Brodribb and Holbrook 2003, 2005a, Nardini et al. 2003) or the collapse of xylem cell walls (Cochard et al. 2004b, Brodribb and Holbrook 2005b). The long-term effects of water stress on \( G_L \) are attributable to changes in the size of the xylem conduits (Nardini and Salleo 2005).

There is a growing body of evidence confirming that leaf hydraulic traits vary with light availability (Sack et al. 2005). A study of 11 temperate deciduous tree species revealed that leaf hydraulic conductance increases with increasing irradiance in six of the species tested (Tyree et al. 2005). Both experimental evidence and theoretical analysis (Tyree et al. 2005) suggest that the irradiance-dependence of \( G_L \) is consistent with an effect on extravascular tissues involving expression or activation of aquaporins. Hydraulic conductance is significantly higher in sun leaves than in shade leaves (Sack et al. 2003a), and in sun-dwelling species compared with shade-growing species (Brodribb and Holbrook 2004b). Diurnal variation in \( G_L \) is related to light availability; however, this variation is also controlled by the plant’s intrinsic circadian clock. In sunflower, \( G_L \) was 30–40% less during the dark period than during the light period (Nardini et al. 2005a).

Although dynamic viscosity of water decreases with rising temperature, the slope of the \( G_L \) response is significantly steeper than can be accounted for solely by changes in the viscosity of water (Fredeen and Sage 1999, Matzner and Comstock 2001, Sack et al. 2004). This extraviscoresponse confirms that some water in a leaf blade moves symplastically, passing through cell membranes. However, \( G_L \) may depend on biotic factors as well. Nardini et al. (2000) demonstrated that ectomycorrhizal infection increased leaf blade hydraulic conductance of seedlings of Quercus ilex L. Four different factors may affect \( G_L \): those that are attributable to changes in environmental conditions, those related to the viscosity of water and those caused by changes in the permeability of leaf cell protoplasts.

Materials and methods

Study area and sample trees

The investigation was conducted in Järvselja Experimental Forest (58°16′N, 27°20′E, 38–40 m a.s.l.), eastern Estonia, from the end of June to mid-August 2003. At the study site, mean annual precipitation is 650 mm, and the mean temperature is 17.0 °C in July and –6.7 °C in January. The growth season usually lasts 175–180 days, from mid-April to October. The annual sum of the global short-wave radiation in the region averages 3518 MJ m⁻², and the annual radiation budget is 2552 MJ m⁻² (Russak 1990). The site is a deciduous mixed forest and has a total leaf area index of about 6. The dominant species are Populus tremula L. and Betula pendula Roth in the upper-canopy layer (17–27 m) and T. cordata in the lower-canopy layer (5–18 m). Thus, the linden trees grew in shade conditions: 11–13% of the total photosynthetic photon flux (\( Q_0 \)), observable above the forest canopy, reached the upper parts of their crowns at midday in summer (Table 1). The soil is a fertile gleyed pseudosol formed on a loamy till and is characterized by a large water storage capacity (Ninemets and Kull 2001). Three neighboring linden trees 17.1–17.6 m in height, with diameters at breast height (DBH) of 13.1–14.3 cm, were selected for intensive study.

Leaf water relations

Foliage was sampled in the basal and top thirds of the crowns of the trees from a scaffolding tower with two platforms installed between the trees. Measurements were made around midday (1100–1300 h, Eastern European Standard Time), during the period of greatest evaporative fluxes and steepest water potential gradients in the trees. Plant water relations were studied on marked branchlets (one branchlet per crown layer), sampling two to three leaves per branchlet. Whole-leaf hydraulic conductance normalized to leaf blade area (\( G_L ; \text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1} \)) was determined by the evaporative flux method (Wullschleger et al. 1998, Brodribb and Holbrook 2003) and was calculated according to the Ohm’s law analogy:

\[
G_{L} = \frac{E}{\Delta \Psi}
\]
We measured $E$ at the leaf surface with an LI-1600M steady-state diffusion porometer (Li-Cor, Lincoln, NE). Leaf hydraulic conductance estimated in this way contains some degree of uncertainty because the porometric method tends to overestimate transpiration rate (Yang and Tyree 1994), and the estimation of $G_t$ is sensitive to any departure from steady-state flow through the leaf that might occur during natural transpiration under field conditions. Leaf temperature ($T_i$; °C) was recorded with fine copper-constantan thermocouples installed in the porometer. Immediately after $E$ measurements, the bulk leaf water potential ($\Psi_i$; MPa) was determined by the balancing pressure technique using a Scholander-type pressure chamber (resolution 0.01 MPa). Water potential in the branchlets ($\Psi_b$; MPa) was estimated by applying the method of bagged leaves (Nardini et al. 2001, Brodribb and Holbrook 2003, Sack et al. 2003b), sampling two leaves per branchlet. In the evening before each measurement day, leaves situated on the same branchlet as the leaves used for the $E$ measurements were enclosed in small minigrip bags, sealed with tape, wrapped in aluminum foil and left overnight. The water potential drop across the experimental leaf was estimated as the difference between its $\Psi_i$ and that of its matched nontranspiring (bagged) leaf, which was presumed to have equilibrated with the water potential of the branch proximal to the petiole.

Environmental characteristics

Soil water potential ($\Psi_s$; MPa) at depths of 20, 40 and 60 cm was monitored with EQ2 equitensiometers (Delta-T Devices, Cambridge, U.K.). Relative humidity of the air (%) was recorded with a HUMICAP humidity sensor (Vaisala, Vantaa, Finland), and air temperature was measured with copper-constantan thermocouples installed in the porometer. Care was taken to match cuvette conditions to ambient temperature and humidity and to hold the sensor head of the porometer horizontal during the measurements. The vapor pressure difference between the leaf intercellular spaces and the bulk air (VPD), serving as an estimate of the atmospheric evaporative demand, was calculated from the saturation vapor pressure at $T_i$ and the ambient vapor pressure. Photosynthetic photon flux ($Q_b$ (µmol m$^{-2}$ s$^{-1}$) was measured above the sample leaves with an LI-190S-1 quantum sensor attached to the porometer.

Data analysis

To compare the mean values of the environmental and plant characteristics in the lower- and upper-crown layers, we employed the Student’s $t$-test for independent samples. Mean leaf hydraulic conductances for the upper and lower thirds of the crown were calculated from the corresponding data subsets as the slope of the regression of transpiration rate and the water potential drop across a leaf. To analyze the effects of crown position as well as the effects of the environmental and plant variables on $G_t$, an analysis of covariance (ANCOVA) was performed. Crown position was treated as a fixed factor, and $T_i$, $Q_b$, $\Psi_i$, VPD and $\Psi_s$ were included in the model as covariates. During the analysis, the ANCOVA models were modified by removing insignificant covariates step by step from the model. Type IV sums of squares were used in the calculations. The assumptions of normality and homogeneity of variances were checked with the Kolmogorov-Smirnov $D$-statistic and the Levene test, respectively. If the assumptions were not met, a square root transformation was applied to the data. Post hoc mean comparisons were conducted using the Tukey HSD test.

To explore the combined effects of current photosynthetic photon flux and leaf temperature (the two most relevant environmental factors) on the spatio-temporal variability in $G_t$ within a canopy, an empirical regression model was developed. The combination of functions giving the best fit in terms of coefficient of determination ($R^2$) and standard error of estimate (SEE) was chosen. The empirical parameters were found by multivariate optimization based on the least squares estimation procedure. Statistical relationships were considered significant if $P < 0.05$. All statistical data processing was carried out using Statistica Vers. 6.0 software (StatSoft, Inc., Tulsa, USA).

Results

Mean values of the environmental and plant characteristics re-

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Lower crown</th>
<th>Upper crown</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Environmental variables</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Photosynthetic photon flux, $Q_b$ (µmol m$^{-2}$ s$^{-1}$)</td>
<td>34 ± 4.6</td>
<td>202 ± 27.8</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Air temperature, $T_i$ (°C)</td>
<td>22.5 ± 0.38</td>
<td>23.1 ± 0.38</td>
<td>ns</td>
</tr>
<tr>
<td>Vapor pressure difference, VPD (kPa)</td>
<td>1.25 ± 0.05</td>
<td>1.35 ± 0.05</td>
<td>ns</td>
</tr>
<tr>
<td><strong>Plant characteristics</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf temperature, $T_i$ (°C)</td>
<td>22.4 ± 0.37</td>
<td>23.0 ± 0.38</td>
<td>ns</td>
</tr>
<tr>
<td>Leaf water potential, $\Psi_i$ (MPa)</td>
<td>−0.792 ± 0.017</td>
<td>−1.017 ± 0.022</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Branch water potential, $\Psi_b$ (MPa)</td>
<td>−0.520 ± 0.028</td>
<td>−0.585 ± 0.026</td>
<td>ns</td>
</tr>
<tr>
<td>Share of the total water potential drop occurring in leaves (%)</td>
<td>36.9 ± 1.03</td>
<td>42.4 ± 0.79</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
corded in a canopy of little-leaf linden in the midday period are presented in Table 1. The two canopy layers differed significantly \((P < 0.001)\) in \(Q_P\), but not in air temperature \((T_{\text{A}})\) and VPD. Because of frequent rains in Estonia during the summer months of 2003, \(\Psi_S\) of the wettest soil layer of those monitored was always above –0.017 MPa. The upper-crown foliage experienced lower \((P < 0.001)\) water potentials than the lower-crown foliage, but the mean midday \(\Psi_L\) did not drop below –1.31 and –0.96 MPa, respectively. The respective differences in \(\Psi_S\) were insignificant. Mean \(E(P < 0.001), \Delta \Psi(P < 0.001)\) and \(G_L(P < 0.05)\) differed substantially between the upper and lower thirds of the crowns (Figure 1). Transpiration rate plotted against the drop in water potential across experimental leaves is presented in Figure 2. Mean \(G_L\) for the upper-crown branches was 2.7 times higher than for the lower-crown branches, a result of the disproportionately large difference in evaporative flux compared with the driving forces in the upper- versus lower-crown foliage.

The ANCOVA revealed that leaf hydraulic conductance depended on \(T_L, \Psi_L, Q_P\) and leaf location within a crown (Table 2). Leaf temperature explained 67\%, and crown position, irradiance and leaf water potential each accounted for 9–12\% of the variation in \(G_L\) in the final model. Neither \(\Psi_S\) nor VPD had a significant effect on \(G_L\). Nevertheless, correlation analysis of the variables involved in the analysis of covariance (Table 3) revealed that VPD was strongly correlated with \(T_L\) and \(\Psi_L\) in our data set; thus, possible effects of the atmospheric evaporative demand could be hidden by the leaf factors. However, \(T_L\) and \(Q_P\) were independent of each other.

Leaf hydraulic conductance increased with increasing temperature (Figure 3A), but the increase was significantly steeper than that of the reciprocal of the dynamic viscosity of water (Figure 3B). To separate the temperature effects on \(G_L\) caused by changes in the viscosity of water from those caused by changes in the permeability of the symplastic transport

![Figure 1. Mean transpiration rate \((E)\), water potential drop across leaves \((\Delta \Psi)\) and leaf hydraulic conductance \((G_L)\) around midday. \(n = 86\) for both crown positions. The bars indicate means ± SE.](https://academic.oup.com/treephys/article-abstract/27/5/679/1671134)

![Figure 2. Transpiration rate \((E)\) versus the drop in water potential across experimental leaves \((\Delta \Psi)\) \((n = 86\) for both crown positions).](https://academic.oup.com/treephys/article-abstract/27/5/679/1671134)

![Figure 2. Transpiration rate \((E)\) versus the drop in water potential across experimental leaves \((\Delta \Psi)\) \((n = 86\) for both crown positions).](https://academic.oup.com/treephys/article-abstract/27/5/679/1671134)

Table 2. Summary of ANCOVA of the effects of environmental and plant variables on whole-leaf hydraulic conductance around midday (1100 to 1300 h). For the whole model: \(n = 172\), multiple \(R^2 = 0.528, P < 0.001\). Abbreviations: SS, sums of squares; df, degrees of freedom; MS, mean square; \(F\), \(F\)-ratio; \(P\), statistical significance.

<table>
<thead>
<tr>
<th>Factor/ covariate</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>(F)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\Psi_L)</td>
<td>0.754</td>
<td>1</td>
<td>0.754</td>
<td>8.28</td>
<td>0.005</td>
</tr>
<tr>
<td>(Q_P)</td>
<td>0.667</td>
<td>1</td>
<td>0.667</td>
<td>7.33</td>
<td>0.007</td>
</tr>
<tr>
<td>(T_L)</td>
<td>4.327</td>
<td>1</td>
<td>4.327</td>
<td>47.53</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Crown position</td>
<td>1.156</td>
<td>2</td>
<td>0.578</td>
<td>6.35</td>
<td>0.002</td>
</tr>
<tr>
<td>Error</td>
<td>15.204</td>
<td>167</td>
<td>0.091</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3. Correlation matrix of leaf and environmental characteristics measured between 1100 and 1300 h. Abbreviations: \(Q_P\), incident photosynthetic photon flux; VPD, vapor pressure difference between the leaf intercellular spaces and the bulk air; \(\Psi_S\), water potential of the wettest soil layer; \(T_L\), leaf temperature; and \(\Psi_L\), bulk leaf water potential. \(n = 172\); statistical significance: *, \(P < 0.05\); **, \(P < 0.01\); and ***, \(P < 0.001\).

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>(Q_P)</th>
<th>VPD</th>
<th>(\Psi_S)</th>
<th>(T_L)</th>
<th>(\Psi_L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Q_P)</td>
<td>1.000</td>
<td>0.189*</td>
<td>–0.023</td>
<td>0.134</td>
<td>–0.372***</td>
</tr>
<tr>
<td>VPD</td>
<td>1.000</td>
<td></td>
<td>0.000</td>
<td>0.667***</td>
<td>–0.633***</td>
</tr>
<tr>
<td>(\Psi_S)</td>
<td></td>
<td></td>
<td>1.000</td>
<td>0.457***</td>
<td>0.003</td>
</tr>
<tr>
<td>(T_L)</td>
<td></td>
<td></td>
<td></td>
<td>1.000</td>
<td>–0.485***</td>
</tr>
<tr>
<td>(\Psi_L)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.000</td>
</tr>
</tbody>
</table>
path, we corrected the leaf hydraulic conductance values for the effects of water viscosity ($G_{LC}$) at each $T_L$ and then repeated the ANCOVA procedure. As a result of the correction for the effects of water viscosity, the relative importance of the factors changed: about 47% of the variance in $G_{LC}$ was attributable to temperature changes. The results of both the ANCOVA and the comparison of the slopes of the normalized values of water viscosity, $G_L$ and $G_{LC}$ versus $T_L$ (Figure 3B), suggested that more than two thirds of the temperature effects were related to changes in the symplastic compartment. The increase in hydraulic conductance with rising temperature suggests that leaf water supply is improved at higher temperatures. The empirical data supported this supposition: increasing temperature enhanced the water supply to leaves, resulting in a higher leaf water potential for a given transpirational water loss (Figure 4).

Leaf hydraulic conductance exhibited a certain seasonal variability: $G_L$ increased from the end of June up to the last days of July and then began to decrease (Figure 5A). Both $T_L$ (Figure 5B) and $Q_P$ exhibited similar patterns and, thus, the temporal variation in $G_L$ could be explained by these factors. To separate the temperature- and light-dependent effects on $G_L$ and to check for a putative age-related trend involved in the temporal variation in $G_L$, we developed an empirical regression model that accounted for the combined effects of temperature and irradiance on $G_L$. Leaf hydraulic conductance increased curvilinearly with increasing $Q_P$, and the relationship was approximated by a simple power function:

$$G_L = aQ_P^b$$

(2)

where $b$ is the scaling exponent, and $a$ is a parameter depend-
ing on the shape of the relationship. Parameter \( a \) was replaced by a function of \( T_L \) and a multivariate optimization procedure was carried out. The best fit resulted from the following multiplicative function (Figure 6):

\[
G_L = 0.16 e^{0.0862T_L} Q_P^{0.180}
\]

where \( n = 172, R^2 = 0.506 \) and SEE = 1.01. Thereafter, we applied a stepwise regression procedure to the residuals of the model with \( \Psi_S \), VPD, \( \Psi_S \) of the wettest soil layer and day of year 2003 (DOY) as independent variables. The residual values depended significantly on DOY and \( \Psi_S \) (Table 4). There was a rising trend in the residual values during the study (Figure 7), indicating an increase in mean leaf hydraulic conductance, independent of \( T_L \) and irradiance, which could be related to leaf age. Figure 7 also indicates that the model accounting for the effects of \( T_L \) and \( Q_P \) tended to overestimate \( G_L \) in the first half and to underestimate \( G_L \) in the second half of the study. Because the trend in the model residuals over time was highly significant (\( P < 0.001 \)) and DOY explained 8% of the residual dispersion, DOY was included in the model to improve the fit:

\[
G_L = 3.91 \times 10^{-6} e^{0.0852T_L} Q_P^{0.179} \text{DOY}^{2.01}
\]

where \( n = 172, R^2 = 0.550 \) and SEE = 0.96.

The inclusion of DOY as an independent variable, accounting for the age-related effects on leaf hydraulic conductance, improved the fit of the model by 5%. The empirical model was used to estimate the sensitivity of \( G_L \) to changes in \( Q_P \) (Figure 8A) and \( T_L \) (Figure 8B). Leaf hydraulic conductance was highly sensitive to changes in \( Q_P \) when \( Q_P \) was < 200 \( \mu\text{mol m}^{-2} \text{s}^{-1} \), and its sensitivity decreased with increasing irradiance. The responsiveness of \( G_L \) to variations in \( T_L \) increased with increasing temperature. Over the entire study, there was an age-related trend of increasing \( G_L \) (Figure 8C).

**Discussion**

Mean \( G_L \) at midday, estimated across the whole study period, was 1.14 and 3.06 mmol m\(^{-2} \) s\(^{-1} \) MPa\(^{-1} \) for the lower and upper thirds of the crown, respectively. Single measurements of \( G_L \) on the most insolated leaves in the upper crown reached 8.72 mmol m\(^{-2} \) s\(^{-1} \) MPa\(^{-1} \). For comparison, the leaf laminae hydraulic conductance of *T. cordata* has been reported to range from 5 to 10 mmol m\(^{-2} \) s\(^{-1} \) MPa\(^{-1} \) on a seasonal scale (Aasamaa and Sõber 2005).

Whole-leaf hydraulic conductance exhibited remarkable spatial (Figure 1) and seasonal (Figure 5A) variation within the crowns of the linden trees. The differences in \( G_L \) between canopy layers paralleled the within-crown patterns of leaf diffusive conductance to water vapor reported by Sellin and Kupper (2006). Therefore, it can be concluded that the higher \( G_L \) in the upper-crown foliage compared with the lower-crown foliage is associated with higher rates of leaf gas exchange and a larger drop in water potential across a leaf (Sellin and Kupper 2006). The spatial variation in \( G_L \) in little-leaf linden (Figure 1) was induced primarily by the vertical gradient of irradiance within the canopy (Tables 1 and 2). A larger \( G_L \) for the upper-canopy foliage than for the lower-canopy foliage was ex-
Figure 8. Sensitivity of leaf hydraulic conductance ($G_L$) to the changes in (A) photosynthetic photon flux ($Q_P$) and (B) leaf temperature ($T_L$) under average environmental conditions ($T_L = 23$ °C; $Q_P = 120 \, \mu$mol m$^{-2}$ s$^{-1}$) observed within a canopy of linden trees around midday. (C) Age-related trends in $G_L$ predicted for seasonally constant mean light and temperature conditions (in the lower crown: $Q_P = 34 \, \mu$mol m$^{-2}$ s$^{-1}$, $T_L = 22.4$ °C; in the upper crown: $Q_P = 202 \, \mu$mol m$^{-2}$ s$^{-1}$, $T_L = 23.0$ °C).

expected, and similar differences have been observed in many plant species growing in sun-exposed versus shade conditions (Sack et al. 2003a, 2005, Brodribb and Holbrook 2004b, Nardini et al. 2005a, Tyree et al. 2005). The greater light availability in the upper canopy than in the lower canopy has consequences for both leaf vascular and extravascular compartments. In the long term, a high radiation load accompanied by large transpirational water loss has an impact on the hydraulic capacity of the leaf vein system. Leaves that have developed in a well lit environment possess a more effective vascular system that is characterized by a higher vein density, veins with larger numbers of vessels and large-diameter tracheary elements (Eschrich 1997, Nikolopoulos et al. 2002, Sack and Frole 2006). Short-term effects of changes in irradiance on $G_L$ ensue from changes in permeability of the symplastic pathway, probably related to expression or activation of plasma membrane aquaporins in bundle sheath and mesophyll cells (Henzler et al. 1999, Kaldenhoff and Eckert 1999). The results of ANCOVA (Table 2) indicated that, in little-leaf linden, both crown position (which likely reflects the long-term influences) and incident photon flux (reflecting current conditions) had a significant ($P < 0.01$) impact on $G_L$. Thus, it is probable that the light effects that we observed on hydraulic properties involved both the leaf vascular system and the permeability of the symplastic pathway.

Based on multiple sources, Sack and Holbrook (2006) stated in their review that leaf hydraulic conductance at low irradiance is, on average, 70% of the value observed at high irradiances. However, they conceded that $G_L$ is highly dynamic, the responses vary across species and $G_L$ can increase several-fold from low to full sunlight. The striking differences in $G_L$ observed within a crown of $T.$ cordata are not surprising if it is considered that the sample trees were growing in the lower canopy layer under the shade of dominant Populus tremula L. and Betula pendula Roth. trees. Most of the foliage was in dim light ($Q_P < 200 \, \mu$mol m$^{-2}$ s$^{-1}$) where small changes in irradiance were accompanied by substantial changes in $G_L$ (Figure 8A). Sack et al. (2002) measured a 4.6- to 8.8-fold increase in leaf lamina hydraulic conductance in Quercus rubra L. at irradiances above 1200 µmol m$^{-2}$ s$^{-1}$ compared with that at irradiances of less than 6 µmol m$^{-2}$ s$^{-1}$.

Ambient temperature, which determines leaf temperature, was the most important environmental factor responsible for the daily variation in $G_L$ (Table 2 and Figure 3A). Leaf temperature explained as much as 67% of the variance in $G_L$. After correcting the values of $G_L$ for the dynamic viscosity of water at each leaf temperature, the contribution of $T_L$ to the variation in leaf hydraulic conductance (i.e., $G_L$) decreased to 47%. Results of both the ANCOVA and the comparison of the slopes of the normalized values of water viscosity, $G_L$ and $G_L$ versus $T_L$ (Figure 3B), revealed an extraviscosity response, analogous to that described by other researchers (Fredeen and Sage 1999, Cochard et al. 2000, Matzner and Comstock 2001, Sack et al. 2004). The sensitivity of $G_L$ to changes in $T_L$ increased consistently with increasing temperature in the range of 16 to 29°C (Figure 8B). The data analysis suggested that about one third of the temperature effect was attributable to variation in the viscosity of water, and two thirds were related to the changes in protoplast permeability (symplastic conductance). Our results are in accordance with earlier published data, confirming that the leaf extravascular compartment is more sensitive to changes in $T_L$ than the vascular system (Matzner and Comstock 2001, Sack et al. 2004).

We demonstrated that leaf hydraulic conductance in $T.$ cordata was influenced by changes in both light availability...
and ambient temperature; however, because we gathered the data around midday when daily irradiance was highest, $T_L$ influenced leaf hydraulic conductance more than $Q_p$ (Table 2). On a diurnal scale, i.e., under conditions of changing irradiance, the contribution of light availability to variation in $G_L$ would probably be more substantial. We found positive interactions between $T_L$ and $Q_p$; the light effects on $G_L$ were more pronounced at higher leaf temperatures (Figure 6), implying that, at low $T_L$, $G_L$ remains relatively low despite sufficient irradiance incident on a leaf and may constrain stomatal conductance. Because of decreasing water viscosity and increasing symplast permeability with rising temperature, our data indicate that the water potential gradient can decrease with temperature for a given water supply to the sites of transpiration in accordance with Darcy’s law (Figure 4). Thus, stomatal limitations to gas exchange inducible by high atmospheric evaporative demand will occur more readily at lower temperatures if it is assumed that stomatal sensitivity to VPD is independent of $T_L$. Our results agree with the data of Fredeen and Sage (1999), which demonstrates a positive effect of increasing branchlet temperature on leaf water supply in *Picea glauca* (Moench) Voss.

Woody species differ greatly in vulnerability of leaves to cavitation, and leaf dehydration may trigger a decline in $G_L$, even at $\Psi_L$ values of $–0.3$ to $–0.5$ MPa (Kikuta et al. 1997, Salleo et al. 2000, Bucci et al. 2003) in some species. In little-leaf linden trees growing in relatively shady conditions, the increase in $G_L$ with decreasing $\Psi_L$ indicated that leaves did not experience conspicuous cavitation over the $\Psi_L$ range observed, even though the ANCOVA revealed a significant ($P < 0.01$) effect of $\Psi_L$ on $G_L$ (Table 2). The mean values of leaf water potential calculated across the whole study period did not exceed the apparent optimum of $\Psi_L$ for leaf conductance ($–0.80$ and $–1.10$ MPa for the lower- and upper-canopy foliage, respectively) in *T. cordata* (Sellin and Kupper 2006). In addition, there were sufficient water reserves in the soil and $\Psi_S$ did not have a significant effect on leaf water relations.

The seasonal variability in leaf hydraulic conductance observed during the study period (Figure 5A) could be explained by the similar seasonal patterns of $T_L$ (Figure 5B) and $Q_p$. However, analysis of the residuals of the empirical model developed to account for the effects of both factors revealed a trend of increasing $G_L$ over time (Figure 8C), which is probably related to leaf ontogenetic development. The hydraulic conductance of leaf laminae in *T. cordata* seedlings has been reported to increase during the first 3–4 weeks of leaf ontogeny, followed by a gradual decrease (Aasamaa and Söber 2005). The hydraulic conductance of petioles and shoot stems does not achieve its seasonal maximum before the age of 14 to 15 weeks in Estonian climatic conditions. The trend of increasing $G_L$ in our linden trees lasted for at least 11 weeks after bud break. Part of the explanation for this discrepancy may be that Aasamaa and Söber (2005) performed their experiments on seedlings grown in full sunlight, whereas our sample trees were growing in a natural forest stand in shady conditions (Table 1). It seems that, in the cool and rainy summer of 2003, under shade conditions and at low ambient temperatures, leaf maturation was slower and continued until early August. Therefore, in the year of the study, the leaves of the linden trees probably did not reach the stage when the processes of senescence (accumulation of embolism in leaf veins, formation of tyloses and decline in the permeability of membranes and cell walls; Sack and Tyree 2005) begin and lead to the onset of decreases in $G_L$.

In conclusion, leaf hydraulic conductance of little-leaf linden growing under natural conditions in a mixed forest canopy was demonstrated to depend on temperature as well as on irradiance. The spatial patterns in $G_L$ within a crown were mainly determined by light availability in the canopy. The daily variation in $G_L$ in the midday period was primarily governed by leaf temperature, which influenced both the apoplastic and symplastic compartments of the transport path. The temperature and irradiance-dependent adjustments in $G_L$ contribute to the coordination between the gaseous- and liquid-phase conductances, because well-insolated foliage, having higher leaf temperature, requires more efficient water supply to compensate for a higher rate of transpirational water loss than shaded foliage.

Acknowledgments

This study was supported by grant No. 6617 from the Estonian Science Foundation. We are grateful to Mr. Ilmar Part for language correction. Especially, we thank Lawren Sack from the University of Hawaii at Manoa for valuable suggestions and comments on the manuscript.

References


