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Hydraulic adjustment of maple saplings to canopy gap formation

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Abstract The leaf-specific hydraulic conductivity (K_L) of plant stems can control leaf water supply. This property is influenced by variation in leaf/sapwood area ratio (A_L/A_S) and the specific hydraulic conductivity of xylem tissue (K_S). In environments with high atmospheric vapor pressure deficit (VPD), K_L may increase to support higher transpiration rates. We predicted that saplings of *Acer rubrum* and *A. pensylvanicum* grown in forest canopy gaps, under high light and VPD, would have higher K_L and lower A_L/A_S than similar sized saplings in the understory. Leaf-specific hydraulic conductivity and K_S increased with sapling size for both species. In *A. rubrum*, K_S did not differ between the two environments but lower A_L/A_S ($P = 0.05$, ANCOVA) led to higher K_L for gap-grown saplings ($P < 0.05$, ANCOVA). In *A. pensylvanicum*, neither K_S, A_L/A_S, nor K_L differed between environments. In a second experiment, we examined the impact of sapling size on the water relations and carbon assimilation of *A. pensylvanicum*. Maximum stomatal conductance for *A. pensylvanicum* increased with K_L ($r^2 = 0.75$, $P < 0.05$). A hypothetical large *A. pensylvanicum* sapling (2 m tall) had 2.4 times higher K_L and 22 times greater daily carbon assimilation than a small (1 m tall) sapling. Size-related hydraulic limitations in *A. pensylvanicum* caused a 68% reduction in daily carbon assimilation in small saplings. Mid-day water potential increased with *A. pensylvanicum* sapling size ($r^2 = 0.69$, $P < 0.05$). Calculations indicated that small *A. pensylvanicum* saplings (low K_L) could not transpire at the rate of large saplings (high K_L) without reaching theoretical thresholds for xylem embolism induction. The coordination between K_L and stomatal conductance in saplings may prevent xylem water potential from reaching levels that cause embolism but also limits transpiration. The K_S of the xylem did not vary across environments, suggesting that altering biomass allocation is the primary mechanism of increasing K_L. However, the ability to alter aboveground biomass allocation in response to canopy gaps is species-specific. As a result of the increase in K_L and K_S with sapling size for both species, hydraulic limitation of water flux may impose a greater restriction on daily carbon assimilation for small saplings in the gap environment.

Key words Hydraulic conductivity · Biomass allocation · Transpiration · *Acer rubrum* · *Acer pensylvanicum*

Introduction

The water potential gradient in plants and the ability to supply leaves with water are influenced by the leaf-specific hydraulic conductivity of stems (K_L, Zimmermann 1983; Tyree and Ewers 1991). Leaf-specific hydraulic conductivity may vary in response to atmospheric humidity in order to maintain leaf water supply. High K_L permits increased transpiration without an increase in the water potential gradient between leaves and the soil (Zimmermann 1983; Tyree and Ewers 1991). This may be adaptive in environments with high atmospheric vapor pressure deficit (VPD). Leaf-specific hydraulic conductivity is affected by the relative allocation to conducting and leaf tissues and the intrinsic capacity of the conducting tissue to move water. For the shoot, K_L and its components can be expressed as:

$$K_L = K_H/A_L = (K_H/A_S)/(A_L/A_S) \tag{1}$$

where K_H is the mass flow of water through the stem per unit pressure and time, and A_L and A_S are the leaf area and cross-sectional stem sapwood area, respectively (Tyree and Ewers 1991). The intrinsic capacity of the conducting tissue, or specific hydraulic conductivity (K_S)

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is represented by K_H/A_S, and the contribution of biomass allocation to K_L is represented by the leaf/sapwood area ratio (A_L/A_S).

The specific hydraulic conductivity of a stem (K_S) increases with the fourth power of the radius of the conducting elements in the sapwood as described by the Hägen-Poiseuille Law (Zimmermann 1983). There is interspecific variation in xylary element radius (Carlquist 1988) and thus K_S (Zimmermann 1978, 1983). However there is little evidence that growth environment directly affects K_S (Margolis et al. 1995). Because average xylary element diameter increases with stem diameter, K_S is strongly size-dependent (Ewers and Zimmermann 1984a, b; Gartner 1995). Unlike K_S, A_L/A_S responds to the growth environment but is relatively size independent (Zimmermann 1983; Margolis et al. 1995).

There is broad variation in A_L/A_S among species (Margolis et al. 1995) and among conspecifics growing in different environments (Gower et al. 1987; Callaway et al. 1994; Margolis et al. 1995; Mencucinni and Grace 1995). This variation may be caused by differences in atmospheric humidity during growth. By combining Darcy's law and the Penman-Montieth equation, Whitehead et al. (1984) derived an equation relating A_L/A_S of trees to atmospheric humidity. Their equation states:

$$A_L/A_S = (K_S \times \Delta\Psi)/(C \times l \times D \times g) \qquad (2)$$

where K_S is specific hydraulic conductivity, $\Delta\Psi$ is the water potential difference between the soil and the leaves, C is a constant that includes temperature- and pressure-dependent physical properties of water and air, l is tree height, D is the VPD, and g is the average leaf conductance in the crown. Thus A_L/A_S is positively related to the conducting capacity of the stem and water potential difference ($K_S \times \Delta\Psi$) and inversely related to evaporative demand and transpiration rate (constant $\times\ l \times D \times g$). Based on this relationship A_L/A_S is expected to decrease with increasing VPD (Whitehead et al. 1984; Mencuccini and Grace 1995) thus increasing K_L.

The components of K_L (K_S and A_L/A_S) may be controlled differentially by growth environment and size (Ewers and Zimmermann 1984a, b; Gartner 1995; Margolis et al. 1995). To determine the effects of growth environment and plant size on K_L, we compared the hydraulic properties and biomass allocation of maple saplings growing in the forest understory and under canopy gaps.

Many tree species require the high light levels of canopy gaps to reach reproductive maturity (Canham 1988). Temperature and VPD are considerably greater in gaps than in the understory (Sipe 1990; Ellsworth and Reich 1992; S.L. Naidu and E.H. DeLucia, unpublished work). Increased transpiration in response to a canopy gap will produce a greater water potential gradient. However, the incidence of xylem embolism may also increase. Saplings exposed to canopy gaps may increase transpiration, without a rise in the water potential gradient, by increasing K_L. In our first experiment we used saplings of two temperate gap-dependent species (red maple, *A. rubrum* L. and striped maple, *A. pensylvanicum* L.) to test the prediction that gap-grown saplings will have lower A_L/A_S and thus greater K_L than similar sized individuals grown in the shaded understory. In a second experiment we examined the effect of sapling size on leaf gas exchange and xylem water potential for striped maple growing in a large canopy gap. A model was used to estimate the influence of size-dependent changes in K_L on daily carbon assimilation.

Methods

Experiment 1

Species and microclimate

Measurements were made on red maple and striped maple saplings in the understory of a mixed hardwood forest (Harvard Forest, Massachusetts; 42°30′N, 72°15′W) during the summer of 1994. The dominant canopy species were *Acer rubrum* L., *Quercus rubra* L., *Fagus grandifolia* Ehrh., *Betula allegheniensis* Britton, and *Betula papyrifera* Marsh. *A. pensylvanicum* L. is common in the sub-canopy and understory. Red and striped maple co-occur across most of their ranges in eastern North America but exhibit different morphological, physiological, and life history traits. Red maple is a canopy dominant that requires several gaps to reach maturity. Striped maple is a sub-canopy species that can complete its life cycle in the understory but also responds favorably to high light conditions (Wilson and Fisher 1977; Lei and Lechowicz 1990; Sipe 1990; Sipe and Bazzaz 1994).

In the fall of 1986 seedlings (15–30 cm tall) were collected from the forest understory and planted into six paired understory plots by Sipe (1990). One year later, trees were felled over three of these plots to create large (16 × 24 m, 300 m^2) canopy gaps. Additional details of the experimental system are described elsewhere (Sipe 1990; Sipe and Bazzaz 1994, 1995). Irradiance, temperature, and VPD were highest in the center and north quadrants of these canopy gaps (Sipe 1990).

During the summer of 1994 additional environmental measurements were made in the center of one canopy gap and the adjacent understory. Air temperature and water vapor pressure were measured with a ventilated psychrometer (Model WVU-7, Delta-T Devices, Cambridge, UK). Wind speed was measured with a three-cup anemometer (Model 12102, R.M. Young Company, Traverse City, Mi., USA). Environmental data were recorded at 1-min intervals from 0800 to 1800 hours EST on three clear days (10 and 23 June and 11 July) with a CR-21X datalogger (Campbell Scientific, Logan, Utah). Canopy openness under each gap and understory plot was quantified using Solarcalc software (version 6.03, Chazdon and Field 1987) from digitized hemispherical photographs (Whitmore et al. 1993) taken in mid-July.

Hydraulic conductivity

In the summer of 1994 four to seven saplings of varying heights (50–350 cm) of each species were harvested from the center and north quadrants of each canopy gap and from the adjacent understory plots. Saplings were pooled across sites within each environment to provide 15–17 gap and understory saplings of each species. Intact saplings were brought to an air conditioned laboratory to minimize the introduction of air emboli. A 20–25 cm long segment located between the root collar and first leaf of each sapling was excised and hydraulic conductivity (K_H) was measured as in Sperry et al. (1988). Segments were cleared of air embolisms by perfusing them with a 10 mmol L^{-1} filtered (22 μm) citric acid solution under high pressure. Preliminary experiments showed that red and striped maple reached maximum volume flow rate (Q; kg s^{-1}) within 2 h of flushing at 140 kPa, so all samples were flushed for > 2 h prior to measuring hydraulic conductivity. Measurements were made at a regulated pressure of 35 kPa. After flushing, stems were exposed to the measurement pressure for another hour before data were collected. Stem efflux was collected and weighed to calculate volume flow rate.

Hydraulic conductivity (K_H; kg m MPa^{-1} s^{-1}) was expressed as the volume flow rate divided by the pressure gradient [$Q/(dP/dx)$]. Specific hydraulic conductivity (K_S; kg m^{-1} MPa^{-1} s^{-1}) was calculated as K_H divided by the sapwood area of the segment and K_L (kg m^{-1} MPa^{-1} s^{-1}) was calculated as K_H divided by the leaf area distal to the measured stem segment.

After measuring hydraulic conductivity, stems were perfused with filtered (22 μm) 0.01% basic fuchsin solution under hydrostatic pressure (*C*. 7.5 kPa) to determine the functional xylem area (= sapwood area). Dye infiltration showed that no heartwood or embolized vessels were present in the stem segments. Total leaf area (A_L), excluding the petioles, was measured to the nearest 0.1 cm^2 with a leaf area meter (LI-COR 3100, Lincoln, Neb., USA). Flow rates were corrected for differences in water viscosity associated with variation in room temperature and standardized to a temperature of 25°C.

Biomass allocation

Each sapling was sectioned into 20- to 25-cm segments and the proximal and distal diameter of each stem segment and total stem length were recorded. The volume of bark, sapwood, and pith in each segment was estimated by multiplying the length of the segment by the average of the proximal and distal cross-sectional areas. Aboveground sapling volumes were calculated by summing the values of segments. Specific gravity (kg m^{-3}) of the wood was measured by volume displacement. Total sapwood mass was obtained by multiplying the calculated sapwood volume by its specific gravity. Leaves, stems, and branches were dried at 60°C for 48 h and then weighed. Specific leaf area (SLA; cm^2 g^{-1}) was calculated from sapling leaf area and leaf mass.

Experiment 2

Gas exchange

To determine the effect of size-dependent increases in K_L and K_S on leaf gas exchange, we measured photosynthesis and stomatal conductance of saplings of differing sizes in a canopy gap. We measured naturally-established striped maple saplings in a large gap (approximately 400 m^2) adjacent to the plots described in the first experiment. The saplings had intact leaders and varied in height from 50 to 300 cm (basal diameters 0.32–2.24 cm). A single location was chosen to minimize variation in water and nutrient availability. Gas exchange and irradiance were measured from 0800 to 1500 hours EST on July 25 and 26, with a LI-6200 (LI-COR, Lincoln, Neb., USA) closed photosynthesis system. Measurements were made using a 1-l leaf cuvette. For calculation of stomatal conductance, we assumed that all leaves were hypostomatous and had a boundary layer conductance of 1.0 mol m^{-2} s^{-1}. The saplings were in the northern half of the gap, had open canopies, and experienced similar irradiances (H. Maherali and E.H. DeLucia, personal observation; Sipe 1990). At least five times per day, two sun-exposed leaves were measured on each sapling. Data were pooled to construct composite light-response curves of photosynthetic rate and stomatal conductance for large (basal diameters 1.34–2.24 cm, > 1 m tall, $n = 8$) and small (basal diameters 0.32–1.05 cm, ≤1 m tall, $n = 10$) saplings.

Water potential and leaf nitrogen concentration measurements

To confirm that size-dependent differences in gas exchange were caused by differences in hydraulic properties, and not by differential access to soil water or nitrogen, we measured pre-dawn shoot water potential and leaf nitrogen concentration on saplings used for gas exchange measurements. Pre-dawn shoot water potential was measured on a subset of small saplings ($n = 3$) and large saplings ($n = 7$) with a pressure chamber (Plant Moisture Status Instrument Company, Corvallis, Ore., USA) between 0500 and 0600 hours EST. Midday shoot water potential was measured on the remaining small saplings ($n = 6$) and the same large saplings ($n = 8$) between 1300 and 1400 hours EST. Water potential of whole shoots or branches was measured the day after gas exchange data had been collected. Immediately after gas exchange measurements, leaves were harvested for determination of nitrogen concentration. Dried leaves (at 60°C for 48 h) were ground in a Wiley mill and acid digested (Lowther 1980). Total Kjehldahl nitrogen was measured with an autoanalyzer (Traacs 800, Bran and Leubbe, Buffalo Grove, Ill., USA).

Calculation of daily carbon assimilation

The composite response of net photosynthesis to incident irradiance and diurnal measurements of incident irradiance at sapling height on a clear day (from Sipe 1990) were incorporated into a STELLA II (version 3.05, High Performance Systems, Hanover, N.H., USA) model. This model was used to calculate diurnal photosynthesis (e.g., Forseth and Norman 1993) for a hypothetical small and large sapling growing in a canopy gap. We assumed all leaves were horizontal and received the same irradiance. Integrated daily net photosynthesis per unit leaf area was then multiplied by leaf area per sapling to yield daily carbon assimilation (g C day^{-1}) for each sapling.

We used leaf nitrogen concentration as a proxy for photosynthetic capacity (Evans 1989) and the pre-dawn water potential to estimate access to soil moisture. Percent leaf nitrogen and pre-dawn water potential did not vary with sapling size (see Results). We therefore assume that the lower photosynthetic rate at high irradiance of the small saplings resulted from hydraulic limitations. To determine the potential effect of low hydraulic conductivity on the daily carbon assimilation of a small sapling, we re-calculated daily carbon assimilation for a small sapling using the photosynthetic-light response function for a leaf on a large sapling.

Calculation of shoot water potential

Coordination between K_L and stomatal conductance may prevent saplings from transpiring at rates that induce xylem embolism. To demonstrate if this coordination occurs in striped maple, we calculated theoretical midday shoot water potentials for the representative small and large saplings and for a hypothetical small sapling transpiring at the rate of a large sapling. Shoot xylem water potential (Ψ_{SHOOT}) was calculated from transpiration per unit area (E) and K_L using the Ohm's law analogy (Tyree and Ewers 1991; Sperry et al. 1993; Sperry and Pockman 1993):

$$\Psi_{SHOOT} = -(E/K_L) + \Psi_{SOIL} \tag{3}$$

Transpiration per unit leaf area (E) was calculated from the product of leaf conductance (g_L) and the mole fraction leaf-to-air vapor pressure deficit (data not shown) (Grace 1991; Pearcy et al. 1991). Leaf conductance (g_L) was calculated from average midday stomatal conductance (g_S) measured for the large and small saplings and the boundary layer conductance (g_B). Boundary layer conductance was estimated from average wind speed and the average leaf width in the gap (Nobel 1991). Leaf-specific hydraulic conductivity was estimated using the regression equation for K_L against aboveground biomass. Soil water potential (Ψ_{SOIL}) was assumed to be −0.1 MPa. We used a path length of 1 m between the soil and the shoot for calculation of Ψ_{SHOOT}.

Statistical analyses

Biomass allocation and the relationship between hydraulic properties and sapling size were described using logarithmic least squares regression ($\log Y = a \log X + b$) and tested with analysis of variance (ANOVA). All data, including linear relationships (e.g., A_L against A_S), were log-transformed to meet assumptions for ANOVA. Leaf-specific hydraulic conductivity and K_S were regressed against aboveground sapling biomass. Within a species, differences in biomass allocation and hydraulic function for saplings grown in gaps or the understory were tested using analysis of covariance (ANCOVA). Within environment differences between species were also tested with ANCOVA. Slope coefficients were tested; if no significant difference was found the interaction term was removed from the model and the intercepts were tested (Sokal and Rohlf 1995). Within species differences in SLA and sapwood specific gravity between environments were tested with a Kruskal-Wallis ANOVA. Paired samples *t*-tests were used to test for differences air temperature, VPD, wind speed, and canopy openness between gap and understory environments. Statistical analyses were done with Systat 5.2.1 for the Macintosh (Systat, Evanston Ill., USA).

Results

Experiment 1

Microclimate

Total daily irradiance on a clear day in July was 11.3 times higher in the gap than in the understory and 10.9

Table 1 Clear day or seasonal air temperature, mean irradiance (photosynthetic photon flux density, PPFD), atmospheric vapor pressure deficit (VPD), and wind speed in a large canopy gap and the adjacent understory. Clear day air temperature, VPD, and wind speed were measured simultaneously in the center of a canopy gap and the adjacent understory on 11 July 1994. Clear day total PPFD is the mean of five clear days, and seasonal irradiance and air temperatures are means of five clear days and five overcast days measured during a single season by Sipe (1990). Canopy openness was calculated from digitized hemispherical photographs taken in July 1994. All values are means ±1 SE. Significant differences ($P < 0.05$) between gap and understory environments are indicated by different capital letters

Variable	Clear Day		Seasonal	
	Gap	Understory	Gap	Understory
Air temperature (°C)	28.5 (0.24) A	22.2 (0.09) B	23.0 (1.48)[a]	20.2 (1.39)[a]
Total PPFD, (mol m^{-2} d^{-1})	24.39 (1.88)[a]	2.16 (0.08)[a]	15.76 (3.57)[a]	1.45 (1.01)[a]
VPD (diurnal range, kPa)	0.506–4.00 A	0.487–1.63 B	–	–
Canopy openness (%)	–	–	26.37 (0.84) A	13.84 (0.92) B
Wind speed (km h^{-1})	1.11 (0.12) A	1.08 (0.03) A	–	–

[a] From Sipe (1990)

Table 2 Regression equations describing biomass allocation and hydraulic relationships for *Acer pensylvanicum* and *A. rubrum*. Equations follow the form: $\log Y = a \log X + b$. All regression slopes were significantly different from zero ($P < 0.05$, ANOVA). For each species, differences between gap and understory environment were tested with analysis of covariance (ANCOVA). Within each environment, differences between species were also tested with ANCOVA. (A_L leaf area, A_S sapwood area, K_L leaf-specific hydraulic conductivity, K_S specific hydraulic conductivity, V_S sapwood volume, M_S sapwood mass, M_L leaf mass)

Y	*X*	Environment	*a*	*b*	r^2	Environment difference	Species difference
A. pensylvanicum							
A_L	A_S	Gap	1.13	4.00	0.86	ns	*
		Shade	1.05	3.71	0.91		*
K_L	Plant mass	Gap	0.34	−4.52	0.31	ns	*
		Shade	0.54	−4.85	0.85		*
K_S	Plant mass	Gap	0.26	−0.58	0.13	ns	ns
		Shade	0.56	−1.00	0.75		*
V_S	Plant mass	Gap	1.09	−6.08	0.98	ns	ns
		Shade	1.16	−6.21	0.98		ns
M_S	Plant mass	Gap	1.06	−0.40	0.97	ns	*
		Shade	1.18	−0.61	0.98		*
M_L	Plant mass	Gap	0.79	−0.32	0.95	Slope*	Slope*
		Shade	0.63	−0.28	0.95		ns
A. rubrum							
A_L	A_S	Gap	0.96	2.95	0.70	*	
		Shade	1.01	3.21	0.73		
K_L	Plant mass	Gap	0.47	−4.41	0.62	*	
		Shade	0.39	−4.52	0.72		
K_S	Plant mass	Gap	0.65	−1.26	0.64	ns	
		Shade	0.37	−0.90	0.71		
V_S	Plant mass	Gap	1.04	−6.00	0.98	ns	
		Shade	1.10	−6.08	0.98		
M_S	Plant mass	Gap	1.03	−0.29	0.98	ns	
		Shade	1.10	−0.39	0.98		
M_L	Plant mass	Gap	1.01	−0.71	0.93	Slope*	
		Shade	0.73	−0.39	0.97		

Ns non-significant, Slope * slopes significantly different $P \leq 0.05$, * intercepts significantly different $P \leq 0.05$

times higher over the season (Table 1). Clear day air temperatures, percent canopy openness, and VPD were significantly higher in the gap than in the understory ($P < 0.001$) while wind speeds were the same in both environments.

Striped maple

Leaf area increased significantly with sapwood area, but the leaf/sapwood area ratio (A_L/A_S) was the same in both environments (Fig. 1A, Table 2). The log of leaf-specific hydraulic conductivity (K_L) and specific hydraulic conductivity (K_S) for striped maple increased with the log of aboveground biomass but did not differ between environments (Fig. 1B and 1C, Table 2). With the exception of leaf mass, there was no effect of environment (gap or understory) on the size-dependent changes in aboveground biomass allocation (Table 2). Specific leaf area (gap: 346.3 ± 40.2 cm g^{-1}; understory: 542.3 ± 70.0 cm g^{-1}) did not vary with size but was higher in understory saplings than gap saplings ($P < 0.001$, Kruskal-Wallis ANOVA). Sapwood specific gravity (gap: 421.8 ± 40.0 kg m^{-3}; understory: 428.2 ± 33.7 kg m^{-3}) did not vary with size or environment.

Red maple

Significant positive log-log relationships between leaf area and sapwood area (Fig. 2A) and K_L and K_S with aboveground biomass (Fig. 2B and 2C) were also observed for red maple. In contrast to striped maple, K_L for red maple was higher in gap saplings than in understory saplings ($P < 0.001$, ANCOVA). Specific hydraulic conductivity was the same in both environments. Higher K_L in the gap saplings was therefore caused by lower A_L/A_S ($P = 0.05$, ANCOVA) and not to an increase in the efficiency of the sapwood, as measured by K_S. With the exception of an increase in leaf mass with

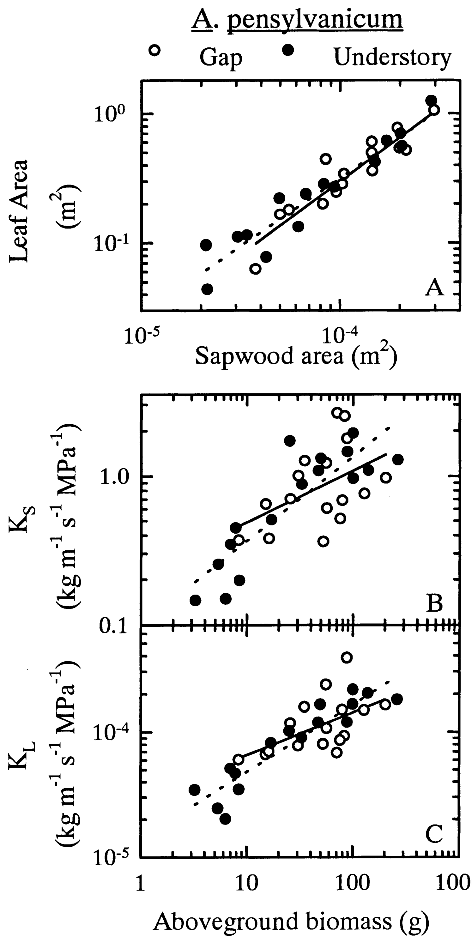

Fig. 1 **A** Sapling leaf area as a function of basal cross-sectional sapwood area, **B** specific hydraulic conductivity (K_S), and **C** leaf-specific hydraulic conductivity (K_L) as functions of aboveground biomass for *Acer pensylvanicum*. The data were fit with least squares regression and the equations are listed in Table 2. There were no significant differences in the slope or intercept of the regressions between gap and understory environments

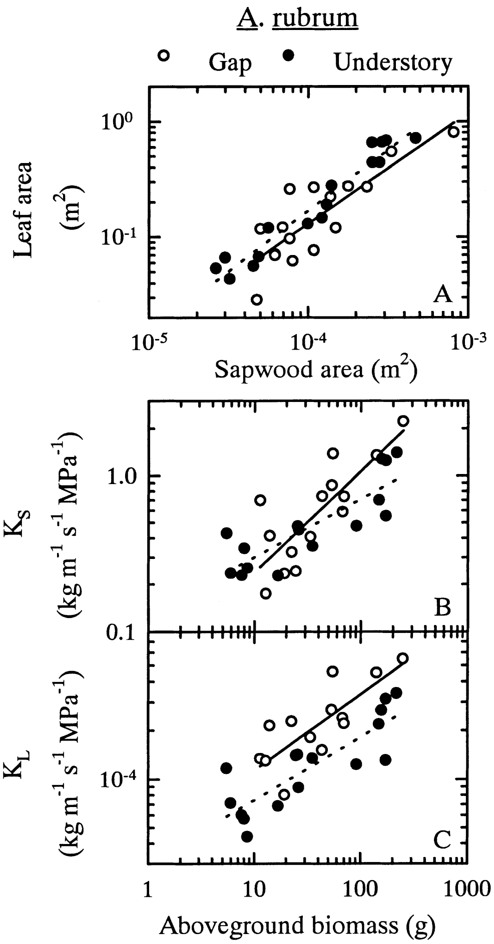

Fig. 2 **A** Sapling leaf area as a function of basal cross-sectional sapwood area, **B** specific hydraulic conductivity (K_S), and **C** leaf-specific hydraulic conductivity (K_L) as functions of aboveground biomass for *Acer rubrum*. The data were fit with least squares regression and the equations are listed in Table 2. The intercepts for leaf area vs. sapwood area and K_L vs. aboveground biomass were significantly different between gap and understory environments ($P \leq 0.05$, ANCOVA)

aboveground sapling biomass, there were no differences in aboveground biomass allocation between gap and understory environments (Table 2). Specific leaf area (gap: 225 ± 47.8 cm g^{-1}; understory: 343.8 ± 52.6 cm g^{-1}) did not vary with size and was higher in understory saplings than in gap saplings ($P < 0.0001$, Kruskal-Wallis ANOVA). Sapwood specific gravity (gap: 500.4 ± 42.7 kg m^{-3}; understory: 483.9 ± 27.2 kg m^{-3}) did not vary with size or environment.

Interspecific comparisons

Red maple in the gap and understory had higher K_L than striped maple ($P < 0.05$, ANCOVA, Table 2). Specific hydraulic conductivity was the same for both species in both environments, but A_L/A_S was lower for gap and understory-grown red maple than for striped maple ($P < 0.01$, ANCOVA, Table 2). Red maple had higher SLA and stem wood specific gravity than striped maple ($P < 0.001$, Kruskal-Wallis ANOVA).

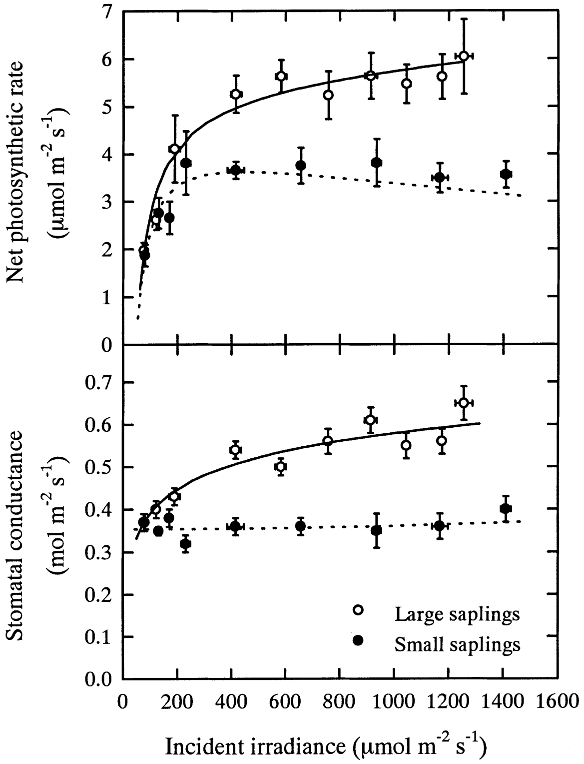

Fig. 3 The composite response of net photosynthesis (A) and stomatal conductance (g_S) to incident irradiance (I). The data are from diurnal gas exchange measurements for *A. pensylvanicum* of two different size classes growing under a canopy gap. The values for small saplings represent the mean (±1 SE) for five to ten saplings with basal diameters 0.32–1.05 cm. The values for large saplings represent the mean (±1 SE) for five to eight saplings with basal diameters 1.34–2.24 cm. Incident irradiance is plotted as the mean (±1 SE) of 100–150 μmol m^{-2} s^{-1} intervals for multiple measurements on five to ten saplings. Least squares non-linear regression equations were fit to the raw data (Tablecurve 2.11, Jandel Scientific, San Rafael, Calif., USA). The equations for small saplings are: $A = 5.24 – 237.12/I + 0.0512 (\sqrt{I})$, $r^2 = 0.53$; $g_s = 0.354 + 7.389 \times 10^{-9} I^2$, $r^2 = 0.006$. The equations for large saplings are: $A = 4.82 – 247.43/I + 0.0368 (\sqrt{I})$, $r^2 = 0.53$; $g_s = 0.012 + 0.082 \ln (I)$ $r^2 = 0.49$

Experiment 2

At irradiances greater than *c.* 400 μmol m^{-2} s^{-1}, net photosynthetic rate and stomatal conductance were greater for large than for small saplings (Fig. 3). Irradiances above 400 μmol m^{-2} s^{-1} corresponded to measurements made later in the day with higher temperatures and VPD. These conditions caused an apparent decline in net photosynthesis for small saplings. Maximum stomatal conductance for each sapling increased significantly with increasing K_L (Fig. 4, $r^2 = 0.75$, $P < 0.001$).

Daily carbon assimilation calculated for a large sapling was 22 times greater than for a small sapling (Table 3). Mean mid-day transpiration rate per unit leaf area was 34 percent higher for large than small saplings (Table 3). Leaf-specific hydraulic conductivity estimated from the regression equation of K_L against aboveground biomass (Table 2) was 2.4 times higher for a large than a small sapling (Table 3). Percent leaf nitrogen (Table 3) and pre-dawn water potential (Fig. 5) did not differ among sapling size classes. We therefore assumed all saplings had the same access to soil resources and similar photosynthetic capacities (Evans 1989). The lower net

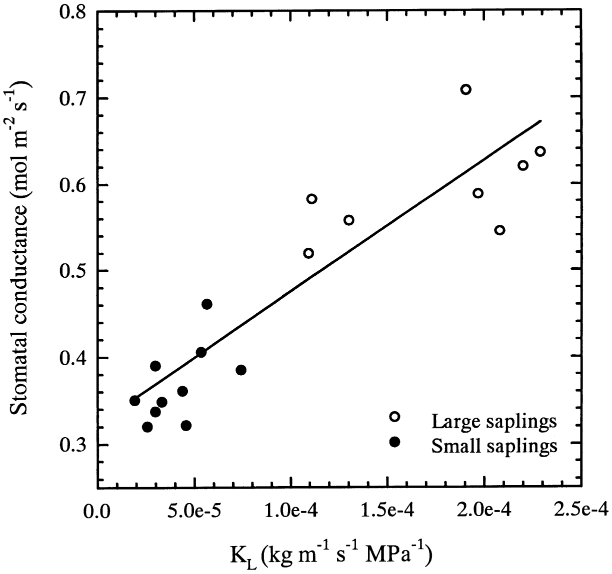

Fig. 4 Maximum stomatal conductance (g_{max}) for small (basal stem diameters: 0.32–1.05 cm; $n = 10$) and large (basal stem diameters: 1.34–2.24 cm; $n = 8$) *A. pensylvanicum* saplings growing under a canopy gap as a function of leaf-specific hydraulic conductivity (K_L). The data were fit with a least squares regression ($g_{max} = 0.32 + 1.52 \times 10^3 (K_L)$, $r^2 = 0.75$) and the slope was significantly different from zero ($P < 0.05$). Maximum stomatal conductance was measured for each sapling at irradiances greater than 800 μmol m^{-2} s^{-1} (from Fig. 3) and K_L was estimated from the following regression equation: $\log (K_L) = -4.17 + 1.61 \log$ (basal diameter), $r^2 = 0.70$

Table 3 Comparisons of mean leaf nitrogen concentration, size, and carbon and water relations parameters for "large" (basal stem diameters: 1.34–2.24 cm; $n = 8$) and "small" (basal stem diameters: 0.32–1.05; $n = 10$) *A. pensylvanicum* saplings grown in a canopy gap. Aboveground biomass and leaf area for hypothetical large and small saplings were estimated using the respective mean basal stem diameters (*bd*) and regression equations based on destructive harvests. Calculations of daily carbon assimilation, mid-day transpiration rate, leaf-specific hydraulic conductivity, and shoot water potential are described in Methods

Parameter	Large sapling	Small sapling
Mean (± 1 SE) nitrogen concentration (%)[a]	1.89 (0.04)	1.81 (0.05)
Mean (± 1 SE) basal stem diameter (cm)	1.79 (0.12)	0.68 (0.06)
Aboveground biomass (g)[b]	127.06	9.96
Leaf area (m^2)[c]	0.7024	0.0984
Calculated daily carbon assimilation (g C d^{-1})	1.03	0.046
Calculated daily carbon assimilation without hydraulic limitation (g C d^{-1})	–	0.144
Midday transpiration rate (E; kg m^{-2} s^{-1})	1.06×10^{-4}	7.88×10^{-5}
Leaf-specific hydraulic conductivity (K_L; kg m^{-1} s^{-1} MPa^{-1})	1.57×10^{-4}	6.60×10^{-5}
Midday shoot water potential (Ψ; MPa)[d]	−0.80	−1.15
Calculated shoot water potential (MPa)[e]	−0.78	−1.29
Calculated shoot water potential developed by transpiring at the rate of a large sapling (MPa)[e]	–	−1.71

[a] No significant difference between size groups ($P > 0.05$)
[b] Estimated from the equation: biomass = 113.6 $(bd)^2$ – 175.1 (bd) + 76.5, $r^2 = 0.89$
[c] Estimated from the equation: leaf area = 0.45 $(bd)^2$ – 0.56 (bd) + 0.27, $r^2 = 0.91$
[d] Estimated from the equation: $\Psi = -1.361 + 0.3092$ (bd), $r^2 = 0.69$, from Fig. 5
[e] A path length of 1 m was assumed for this calculation

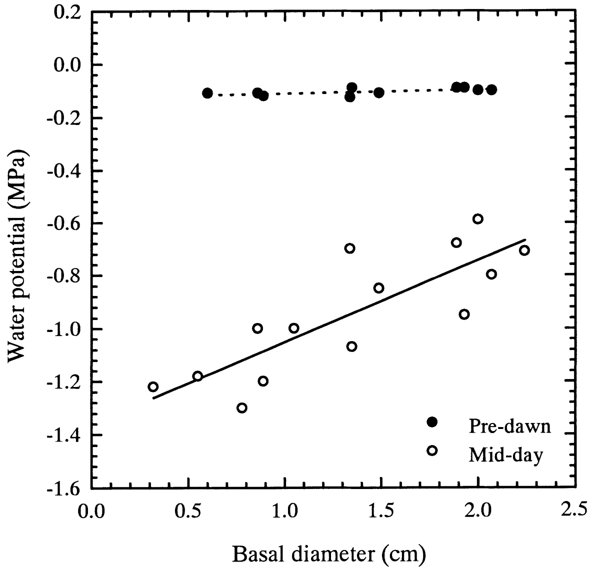

Fig. 5 Pre-dawn and midday shoot water potential (ψ) as functions of sapling basal diameter (*bd*) for *A. pensylvanicum* grown in a canopy gap. The slope for pre-dawn water potential as a function of basal diameter was not significantly different from zero ($P > 0.05$). The regression equation for midday shoot water potential vs. bd was: $\psi = -1.361 + 0.3092$ (bd), $r^2 = 0.69$. The slope was significantly different from zero ($P < 0.05$)

photosynthetic rates in the small saplings, at irradiances greater than 400 μmol m^{-2} s^{-1}, were the result of hydraulic limitation. We removed the effect of the hydraulic limitation on photosynthesis by recalculating daily C gain for a small sapling with the photosynthetic-light response function measured for a large sapling. The removal of hydraulic limitation resulted in a greater than 3-fold increase in daily carbon assimilation for a small sapling (0.046–0.144 g C day^{-1}, Table 3).

Pre-dawn shoot water potential did not vary with basal diameter for striped maple, but mid-day shoot water potential increased with basal diameter (Fig. 5, $r^2 = 0.69$, $P < 0.01$). This relationship was corroborated by calculations of shoot midday water potential (Table 3). Calculated midday shoot water potential was 0.51 MPa lower for a small sapling than for a large sapling, indicating that higher transpiration rates could be maintained by large saplings with less negative midday shoot water potential (Fig. 5, Table 3). The predicted midday shoot water potential for a small sapling, developed using the transpiration rate of a large sapling, was −1.71 MPa. This value was 0.56 MPa lower than field-measured shoot water potential for a small sapling (Table 3, Fig. 5).

Discussion

We found that the only hydraulic-related adjustment made by saplings in response to the formation of canopy gaps, where vapor pressure deficit (VPD) is higher, occurred in red maple. The specific hydraulic conductivity (K_S) of red maple xylem did not vary between gap and understory environments. However the lower A_L/A_S of gap-grown red maple saplings increased leaf-specific hydraulic conductivity (K_L) and therefore increased the intrinsic capacity to supply leaves with water relative to understory-grown saplings. In contrast K_L, K_S, and A_L/A_S did not differ between environments for striped maple.

The capacity for hydraulic adjustment in response to a canopy gap may depend on the species' life history traits. Because of its ability to alter the pattern of aboveground biomass allocation, red maple had higher K_L in gaps than striped maple (Table 2). In previous studies in the same canopy gaps, Sipe and Bazzaz (1994, 1995) observed that red maple had higher photosynthetic rates, growth, and survival than striped maple in the north and center gap quadrants. In contrast, striped maple had greater survival and growth than red maple saplings in the southern quadrants of the canopy gap where there is no direct sunlight and VPD is lower (Sipe 1990; Sipe and Bazzaz 1995). The inability of striped maple to decrease leaf area, and thus increase K_L, upon exposure to canopy gaps may reduce its growth and survival in the most exposed gap microsites.

Sellin (1993) and Shumway et al. (1993) found that K_S for *Picea abies* L. and K_S and K_L for *Liriodendron tulipifera* L. and *Quercus rubra* L. increased in open and high-light environments. These studies, however, neglected to control for the size-dependent changes in hydraulic properties. The open-grown *P. abies* was 3 times larger than the shade-grown tree (Sellin 1993). The observed higher "effective radius" of open-grown stem wood tracheids (Sellin 1993) that led to higher K_S was because average tracheid diameter increases with increasing stem diameter (Ewers and Zimmermann 1984a, b; Gartner 1995). The experimental populations of hardwoods examined by Shumway et al. (1993) varied almost two-fold in height and we assume that the larger plants were in the high light treatment. Our results, and those of others (Ewers and Zimmermann 1984a, b; Gartner 1995), suggest that the differences in K_S between low and high light environments reported by Sellin (1993) and Shumway et al. (1993) may have been caused by differences in size rather than by environment. Our results suggest that the degree of environmental plasticity in K_S may be quite low.

Red and striped maple may be unable to increase K_S when a canopy gap forms because of increased vulnerability to xylem embolism. Specific hydraulic conductivity (K_S) increases as a function of xylem vessel frequency and diameter (Zimmermann 1983). However, wider vessels are also more vulnerable to freezing-induced xylem embolism during winter (Sperry et al. 1994). Freezing-induced xylem embolism can reduce leaf water supply or delay leaf expansion in the spring until sufficient xylem is constructed (Wang et al. 1992), potentially reducing seasonal carbon assimilation. Increasing K_L by decreasing A_L/A_S, as observed in red maple, provides a way of increasing leaf water supply without increasing susceptibility to freezing-induced embolism.

Increased sapling size was accompanied by greater K_L, increased stomatal conductance, and higher midday water potential (Figs. 4 and 5). Our calculations indicated that the shoot water potential developed by a small sapling by transpiring at the rate of a large sapling was −1.71 MPa, a value that was 0.56 MPa lower than we measured in the field (Table 3). While we did not measure the vulnerability to drought-induced xylem embolism of the small striped maple saplings, the calculated water potential surpassed the threshold of xylem embolism induction measured in similar sized *A. saccharum* branches (*c.* −1.5 MPa, Tyree et al. 1991; Tyree and Ewers 1991). Many temperate deciduous species saplings (including *Acer*) show greatly reduced stomatal conductance and transpiration at water potentials lower than −1.2 to −1.6 MPa (Ni and Pallardy 1990, 1991). Thus, a shoot water potential of −1.71 MPa is likely in excess of the threshold of xylem embolism induction in small striped maple saplings. Coordination between K_L and stomatal conductance (Meinzer and Grantz 1990) may prevent xylem water potential from reaching levels that cause embolism. This coordination also limits transpiration, and potentially carbon assimilation, of small relative to large saplings.

A limitation of this study was that we did not measure variation in root structure and function as sapling size increased. Higher in situ transpiration at higher midday shoot water potential for large saplings (Table 3) suggests that root system hydraulic conductivity, like K_L, may have also increased with sapling size. Root hydraulic properties differ from those of stems (Alder et al. 1996) so their respective effects on transpiration may also differ. Additional studies are needed to determine the impact of variation in root system hydraulic properties on transpiration.

To estimate the impact of size-related hydraulic limitation on carbon assimilation, we calculated daily carbon assimilation for a small sapling and compared it to the hypothetical daily carbon assimilation of a small sapling with the photosynthetic capacity of the "hydraulically unlimited" large sapling. Carbon assimilation for a small sapling more than tripled from 0.046 to 0.144 g C per plant per day based on the difference in photosynthetic light-response functions (Table 3). There were no differences in soil water availability and potential leaf photosynthetic capacity between sapling size groups. We conclude that the saplings with higher K_L are better able to supply leaves with water to support increased rates of gas exchange and daily carbon assimilation.

The size- and environment-driven changes in K_L observed for maples in this study may have important ecological implications for woody plant colonization and growth in canopy gaps. The increase in K_L for red maple in gaps may accelerate growth rates by reducing hydraulic limitations to carbon assimilation. In addition, the size-dependent variation in K_L observed for both species may help explain the demographics of seedlings and saplings after gap formation. Uhl et al. (1988) reported that growth was positively correlated with sapling size in a canopy gap and that individuals present in the understory prior to gap formation accounted for 83–97% of saplings in gaps of varying sizes. The greater K_L of large saplings contributes to higher rates of photosynthesis and carbon assimilation and permits increased evaporative cooling and thus lower leaf temperature for larger saplings in a gap. These benefits may contribute to the greater success of large saplings once a gap occurs.

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