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Size-dependency in hydraulic and photosynthetic properties of three *Acer* species having different maximum sizes

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Abstract Recent studies suggest that physiological traits can be affected by tree size due to stronger hydraulic limitation in taller trees. As trees vary greatly in size, both within and among species, the adaptive responses to hydraulic limitation may be different among species with different maximum sizes. To investigate this, we explored size-dependency in photosynthetic and hydraulic parameters of three *Acer* species (*Acer mono* Maxim., *Acer amoenum* Carr and *Acer japonicum* Thunb.) using trees of various sizes under well-lit conditions. Leaf stomatal conductance of the *Acer* species decreased with tree size, implying that water supply to leaves decreases as trees grow. In contrast, content of nitrogen increased with tree size, which may compensate for the decrease in stomatal conductance to maintain the photosynthetic rate. Although the increase in nitrogen and leaf mass per area were larger in species with larger statures, the size-dependency in stomatal conductance was not different among species, and photosynthetic rate and hydraulic conductance were maintained in the three *Acer* species. Therefore, we suggest that hydraulic limitation on gas exchange does not necessarily depend on the maximum height of the species and that maintenance of photosynthesis and hydraulic properties is a fundamental physiological process during tree growth.

Keywords Hydraulic conductance · Nitrogen content · Ontogenetic change · Scaling · Water potential

Introduction

Trees vary greatly in size, both within and among species. It has been suggested that taller trees experience increased hydraulic stress in drawing water from soil into their canopies (Midgley 2003). In tall canopy trees, increasing path length may increase hydraulic resistance, which could reduce stomatal conductance and then photosynthesis (Ryan and Yoder 1997; Barnard and Ryan 2003). Because such reductions in photosynthetic rate would eventually limit tree growth, this mechanism, which is called the “hydraulic limitation hypothesis”, has received attention as an explanation for the limitation to tree height as well as the size-dependent change in physiological processes in trees.

Although many studies have tested hydraulic limitation in trees thus far, it is not well understood how hydraulic limitation differs among species. Recently, Ryan et al. (2006) reviewed 51 studies that tested hydraulic limitation and found that hydraulic limitation on gas exchange often occurs in taller trees but is not universal (Ryan et al. 2006). Hydraulic limitation could have a strong influence on limiting height growth in the tallest known trees on earth, *Sequoia sempervirens* (Koch et al. 2004). Koch et al. (2004) found vertical gradients in physiological and morphological traits of *S. sempervirens* and estimated a maximum tree height of 122–130 m, which is similar to the tallest record in the past. However, most species are more limited in height, to approximately 20–50 m, and vary widely in their maximum height. Since the hydraulic limitation hypothesis focuses on only the size-dependent limitation within species, another intricacy arises when comparisons are made among species with different potential maximum sizes.

Hydraulic limitation could be compensated for by size-dependent structural or anatomical changes, such as a decrease in the ratio of leaf area to sapwood area (McDowell et al. 2002) or an increase in the allocation in fine roots (Magnani et al. 2000) in taller trees. This may lead to differences in the extent of hydraulic limitation

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among species. McDowell et al. (2002) demonstrated that the size-dependent decrease in the ratio of leaf area to sapwood area was smaller in taller species, suggesting that trees that are able to maintain a high ratio of leaf area to sapwood area are able to grow to greater final heights. However, few studies have tested the variability in hydraulic limitation among species with different maximum heights.

Elucidating differences in hydraulic limitation among species may help us to understand the size-dependent variations in photosynthetic rate of trees. Many studies have investigated the patterns of photosynthetic rate with increasing size and have revealed that the extent of ontogenetic change in photosynthetic rate depends on the species. For example, net photosynthesis per unit leaf area decreased with increased age in *Picea abies* and *Pinus aristata*, while it increased in *Larix laricina* and *Quercus rubra* (Bond 2000). Thomas and Winner (2002) indicated that ontogenetic decreases in photosynthetic capacity per unit leaf area (A_{area}) are found most commonly among conifers, whereas increases in A_{area} are generally found among broad-leaved deciduous trees. Generally, leaf nitrogen is a limiting factor for photosynthetic capacity, because a large amount of nitrogen is invested in photosynthetic enzymes (Evans 1989). However, for tall canopy trees, water use in leaves is also suggested to have strong influence on the photosynthetic rate (Brodribb et al. 2002; Santiago et al. 2004). Therefore, hydraulic properties, as well as leaf nitrogen, may play an important role in determining the photosynthetic rate as trees grow.

This study aims to clarify the differences in hydraulic and photosynthetic properties among species with different maximum heights. We used three *Acer* species, *Acer mono* Maxim., *Acer amoenum* Carr and *Acer japonicum* Thunb. *A. mono* and *A. amoenum* are canopy species, while *A. japonicum* is a sub-canopy species. These species are all shade-tolerant, but *A. mono* is less shade-tolerant than the other two species. We selected trees of these *Acer* species that were under well-lit conditions, in order to compare them by focusing on differences in both tree height and asymptotic height of the species. The following questions were addressed in this study: (1) is hydraulic limitation associated with the maximum height of species? and (2) does the size-dependency of leaf photosynthetic and hydraulic traits (i.e., leaf gas exchange, water potential, and nitrogen content) differ among the species? In order to test the above two questions, we measured the photosynthetic and hydraulic properties of *A. amoenum* and *A. japonicum* to build upon the previously published work on *A. mono* by Nabeshima and Hiura (2004).

Methods

Study sites and plant materials

The study site is a deciduous broad-leaved forest stand in Tomakomai Experimental Forest (TOEF, 42°40' N,

141°36' E). Annual precipitation at TOEF is 1,177 mm year⁻¹, and the precipitation in summer is 182 mm month⁻¹. The summer and winter mean temperatures are 17°C and -4°C, respectively. The topsoil of the study site is very shallow, and the volcanic deposits of Mt. Tarumae, which erupted in 1667 and 1739, are approximately 2 m thick (Shibata et al. 1998).

The dominant species at the study site are *A. mono*, *A. amoenum*, *Cercidiphyllum japonicum* Sieb. et Zucc., *Ostrya japonica* Sarg., *Prunus ssiori* F.Schmidt, and *Quercus crispula* Blume (Hiura et al. 1998). *A. mono* and *A. amoenum* are late-successional species (Kikuzawa 1983; Koike 1988), and saplings of these species are generally more abundant under closed canopies than in gaps (Abe et al. 1995). *A. japonicum* is also shade-tolerant, but is a sub-canopy species. The three *Acer* species are all shade-tolerant; however, the amount of extension growth in *A. amoenum* and *A. japonicum* is smaller and the growth modes are more shade-tolerant than in *A. mono* (Sakai 1987, 1990). We estimated maximum heights of each species by an equation in Thomas (1996), using diameter at breast height (with a precision of 0.1 cm) and height (with a precision of 1 cm) data measured in TOEF during 1998 to 2004.

$$H = H_{\text{max}}[1 - \exp(-a\text{DBH}^b)], \quad (1)$$

where H is tree height, H_{max} is asymptotic height, DBH is diameter at breast height, and a and b are constants. The estimated asymptotic heights are 22.16 m (*A. mono*), 19.91 m (*A. amoenum*), and 16.85 m (*A. japonicum*), (Fig. 1).

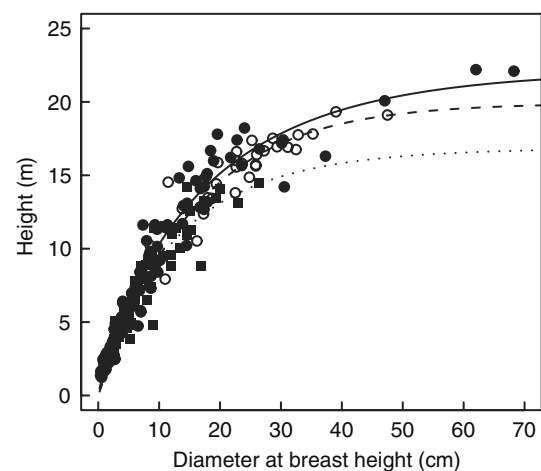


Fig. 1 Relationship between diameter at breast height (DBH) and tree height (H) of *A. mono* (filled circles), *A. amoenum* (open circles) and *A. japonicum* (filled squares) in TOEF. Fitted curves were estimated by Eq. 2 in Thomas (1996): $H = 22.16 [1 - \exp(-0.0833\text{DBH}^{0.875})]$ ($R^2 = 0.96$, $n = 120$) for *A. mono* (solid line); $H = 19.91 [1 - \exp(-0.0614\text{DBH}^{1.021})]$ ($R^2 = 0.93$, $n = 36$) for *A. amoenum* (dashed line); and $H = 16.85 [1 - \exp(-0.1027\text{DBH}^{0.896})]$ ($R^2 = 0.89$, $n = 60$) for *A. japonicum* (dotted line)

We selected various-sized trees of the three *Acer* species that were unshaded by adjacent trees and were under well-lit conditions (Table 1). Mature trees of *A. mono* and *A. amoenum* were selected at the canopy crane site in TOEF. The canopy crane site is located in a mature forest stand, and the canopy trees of *A. mono* and *A. amoenum* were close to the maximum heights. The canopy crane, which is 25 m tall with a 41.5 m jib, can approach 21 species and 183 individuals (DBH > 10 cm) (Murakami and Hiura 2003). Because this forest stand is a mature forest with some canopy gaps (Hiura et al. 1998), we can access various sizes of *A. mono* and *A. amoenum* from the canopy crane. Mature trees of *A. japonicum* were selected at a tower site in TOEF, because none of them was accessible from the canopy crane. The tower site, in which three-canopy access towers were installed, is also a mature forest stand (Oguchi et al. 2006) and is approximately 500 m away from the canopy crane site. Saplings of these *Acer* species are seldom observed in canopy gaps. To standardize light conditions among the sample trees, we selected saplings of the three *Acer* species in open sites in TOEF. The soil conditions of the canopy crane site, the other tower site and the open sites were considered to be similar because both are derived from the deep volcanic deposits of Mt. Tarumae (Shibata et al. 1998; Nabeshima and Hiura 2004).

Measurements

We measured gas exchange and water relations for *A. japonicum* and *A. amoenum* in the summers of 2003 and 2004. The dataset for *A. mono* was previously published in Nabeshima and Hiura (2004), which was measured in the summers of 2002 and 2003. To estimate hydraulic conductance of the flow path from soil to leaf, expressed on a leaf area basis (K_L , $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$), we determined transpiration rate per unit leaf area (E , $\text{mmol m}^{-2} \text{s}^{-1}$) and leaf water potential (Ψ_{leaf} , MPa) in the summer of 2003 (from mid-July to August). K_L was determined as

$$K_L = \frac{E}{\Psi_{\text{leaf}} - \Psi_{\text{soil}} - h\rho g}, \quad (2)$$

where Ψ_{soil} is the soil water potential (MPa), g is the acceleration due to gravity (9.807 m s^{-2}), ρ is the density of liquid (998 kg m^{-3} at 20°C water), and $h\rho g$ ($\text{kg m}^{-1} \text{s}^{-2} = 10^{-6} \text{ MPa}$) is the gravitational pull on a

water column of height h (m). We measured pre-dawn leaf water potential ($\Psi_{\text{pre-dawn}}$; MPa), which can be assumed to be very close to soil water potential after the gravitational component has been subtracted ($\Psi_{\text{soil}} - h\rho g$). In order to determine E , we measured stomatal conductance with steady-state porometers (LI-1600, Li-Cor, NE, USA) and re-calculated them using leaf temperature measured with an infrared thermometer (IR-TE, Chino, Tokyo, Japan) and the flow rate of dry air (Ishida et al. 1992). The equation for E was

$$E = \Delta W \left(\frac{GG_b}{G + G_b} \right), \quad (3)$$

where ΔW is the absolute difference in leaf to air vapor pressure divided by the atmospheric pressure (Pa Pa^{-1}) and G ($\text{mmol m}^{-2} \text{s}^{-1}$) is the stomatal conductance measured by steady-state porometer. G_b ($\text{mmol m}^{-2} \text{s}^{-1}$), boundary layer conductance, was estimated as

$$G_b = 0.446 \left(0.715 \left(\frac{u}{d} \right)^{0.5} \right) \left(\frac{273}{T_{\text{leaf}} + 273} \right) \left(\frac{P}{101.3} \right) 10^3, \quad (4)$$

where u is wind speed (m s^{-1}) measured by an anemometer (Wind Messe561, Empex, Tokyo, Japan), d is leaf length (m) and P is atmospheric pressure (kPa) (Percy et al. 1989; Jones 1992; Ishida et al. 1996). d for each tree was determined by measuring 20 leaves per tree. Ψ_{leaf} and Ψ_{predawn} were measured with a pressure chamber (PMS model 1003, PMS Instruments, OR, USA). Immediately after the measurement of E , we cut the twigs just below the current year's shoot to determine Ψ_{leaf} . These measurements of E and Ψ_{leaf} were conducted concurrently and three times per day for the determination of K_L (Meinzer et al. 1999), at mid-morning (07:30–10:30 hours), noon (10:30–12:30 hours) and afternoon (12:30–15:00 hours). $\Psi_{\text{pre-dawn}}$ was also determined before dawn of the same day.

In order to determine the photosynthetic capacity of each individual tree, we measured maximum net assimilation rate (A_{area} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and stomatal conductance to water vapor (G_{area} , $\text{mol m}^{-2} \text{s}^{-1}$) under saturating light ($1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$) using a portable gas exchange system (LI-6400, Li-Cor) with an LED light source (Li-6400-02B, Li-Cor). The measurements were made in the morning between 07:00 hours and 11:00 hours when leaf to air vapor pressure deficit (VPD) was small ($< 1 \text{ kPa}$). During the measurements, cuvette conditions were maintained at $21.1 \pm 1.1^\circ\text{C}$ leaf temperature, $370 \mu\text{mol mol}^{-1} \text{CO}_2$ concentration and $500 \mu\text{mol s}^{-1}$ flow rate. Measured under saturating light and small VPD, G_{area} is considered to be close to maximum stomatal conductance during the day (Nabeshima and Hiura 2004). Note that we used the value of G_{area} for the analysis of this study, not the G that was measured by steady-state porometer as we

Table 1 Size characteristics of sample trees

Species	DBH (\pm SD) (cm)	Height (\pm SD) (m)	Number of sample trees
<i>A. japonicum</i>	12.26 (\pm 4.97)	9.73 (\pm 4.98)	5
<i>A. amoenum</i>	25.87 (\pm 16.21)	13.79 (\pm 7.02)	8
<i>A. mono</i>	27.75 (\pm 24.75)	13.62 (\pm 8.55)	10

stated above. We selected three canopy leaves for each mature tree, and one to three leaves for each sapling. After the measurements, we punched out leaf discs of 1 cm diameter from these leaves to determine leaf mass per area (LMA, g m^{-2}) and leaf nitrogen content per unit leaf mass (N_{mass} , mg g^{-1}) for each leaf. Dry mass was determined after oven drying at 60°C for more than 3 days and N_{mass} was determined with a C/N analyzer (SUMIGRAPH NC-900, Shimadzu, Osaka, Japan).

Data analysis

The measured values, A_{area} , G_{area} , N_{area} ($N_{\text{area}} = N_{\text{mass}} \times \text{LMA}$) and Ψ_{predawn} , for each leaf were averaged for each tree. E and Ψ_{leaf} for each leaf were averaged for each time (mid-morning, noon and afternoon), and then used to determine K_L (Eq. 2). The K_L values were averaged for each tree. Minimum Ψ_{leaf} ($\min\Psi_{\text{leaf}}$) in the time course was determined for each tree. Ψ_{leaf} was also determined during the morning (Ψ_{morning}) by averaging Ψ_{leaf} in mid-morning for each tree.

Data were analyzed using linear model techniques implemented in the statistical package R (<http://www.r-project.org/>). To test the effects of tree height and species on each leaf trait (A_{area} , G_{area} , N_{area} , K_L , Ψ_{predawn} , $\min\Psi_{\text{leaf}}$, and Ψ_{morning}), we constructed statistical models. The following explanatory variables were added as factors into the models: (a) “tree height” as a continuous variable [height (m) or natural logarithms of height (m)]; (b) “species” as a categorical variable (*A. mono*, *A. amoenum*, *A. japonicum*); and (c) “tree height \times species”, which is the interaction between “tree height” and “species”. Since both categorical and continuous explanatory variables are involved, the models of this study are interpreted as an analysis of covariance in which separate slope and intercept are estimated for each level of the categorical variable (Crawley 2005). The coefficients of the models were estimated under the assumption of normal errors and constant variance. Model simplification was then conducted for each model in a stepwise algorithm to find the minimal adequate model (Crawley 2005); explanatory variables in each model were selected or deleted based on the Akaike information criterion (AIC, Akaike 1973). Through the process of model simplification, either “tree height” or “log (tree height)” was also determined, based on AIC. If “species” were selected in the minimal adequate model, each possible species combination [i.e., (*A. mono*, *A. amoenum*, *A. japonicum*), (*A. mono*, *A. amoenum* = *A. japonicum*), (*A. mono* = *A. amoenum*, *A. japonicum*), (*A. mono* = *A. japonicum*, *A. amoenum*), (*A. mono* = *A. amoenum* = *A. japonicum*)] was incorporated in the model so that we could decide which species were different from the other species. These models were then compared with each other, and a best-fit model was selected by AIC.

Results

K_L remained constant from saplings to mature trees and was lower in *A. japonicum* (mean \pm SE, 1.82 ± 0.15) than in *A. amoenum* (2.47 ± 0.10) and *A. mono* (2.65 ± 0.24) (Table 2; Fig. 2a). Maximum stomatal conductance (G_{area}), which was concurrently measured with A_{area} , decreased significantly with increasing tree size and was lower in *A. japonicum* and *A. amoenum* than in *A. mono* (Table 2; Fig. 2b). $\min\Psi_{\text{leaf}}$ remained constant during ontogeny and was similar among species (Table 2; Fig. 3a). $\Psi_{\text{pre-dawn}}$ and Ψ_{leaf} during the morning were significantly decreased with increasing tree size (Table 2; Fig. 3). Ψ_{leaf} during the morning was lower in *A. japonicum* and *A. amoenum* than in *A. mono* (Table 2; Fig. 3b). $\Psi_{\text{pre-dawn}}$ was influenced by interactive effects of tree height and species (Table 2; Fig. 3a).

Maximum net assimilation rates per unit leaf area (A_{area}) remained constant during ontogeny and were lower in *A. japonicum* (mean \pm SE, 10.0 ± 0.14) and *A. amoenum* (10.3 ± 0.23) than in *A. mono* (12.0 ± 0.59) (Table 2; Fig. 4). Area-based leaf nitrogen content (N_{area}) and leaf mass per area (LMA) increased with increasing tree height (Table 2; Fig. 5a, c). N_{area} and LMA increased more markedly from saplings to mature trees for *A. mono* than for other species (Table 2; Fig. 5a). Mass-based leaf nitrogen content (N_{mass}) did not significantly depend on tree height and was marginally lower in *A. japonicum* and *A. amoenum* than in *A. mono* (Table 2; Fig. 5b).

Discussion

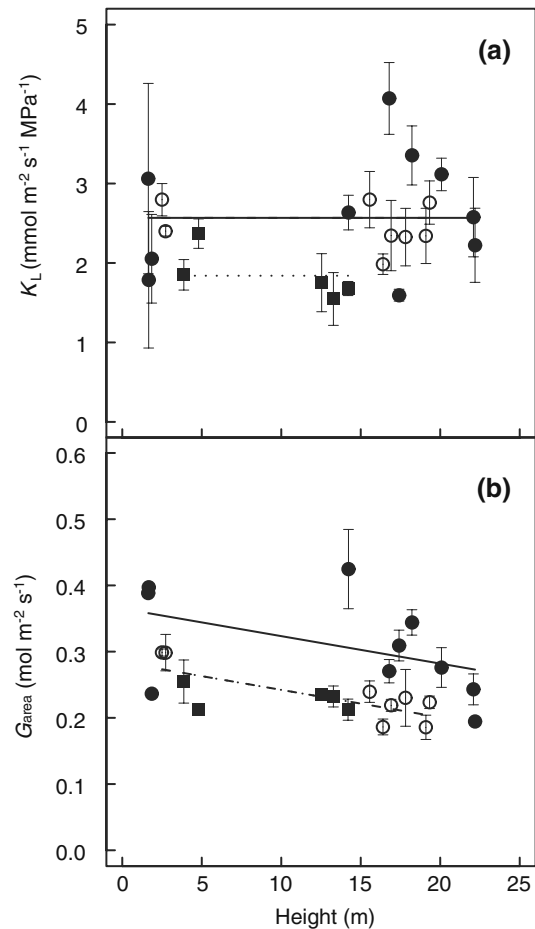
Recent studies suggest that decreased leaf-specific hydraulic conductance (K_L) due to longer path length may decrease stomatal conductance and then photosynthesis in taller trees (Hubbard et al. 1999). Although many studies showed a decline in K_L with increasing tree height (Ryan and Yoder 1997), K_L of the three *Acer* species did not decrease with tree size (Fig. 2a). Compensation mechanisms maintain homeostasis of K_L during growth (Mencuccini and Magnani 2000), such as reduction in the leaf to sapwood area ratio (McDowell et al. 2002; Mencuccini 2002) or increased allocation to fine roots (Magnani et al. 2000). Constant K_L among saplings and mature trees of the three *Acer* species suggests some compensatory mechanisms for maintaining constant K_L during growth. In this study, the differences among species in their maximum height could not be explained by differences in the size-dependency of K_L .

In contrast, G_{area} of all species declined with increasing tree size (Fig. 2b). There was no difference among species in the size-dependency of G_{area} . A possible mechanism for the size-dependent decline in stomatal conductance without a decline in K_L is the avoidance of xylem cavitation and/or leaf turgor loss associated with the gravitational component of water potential. The

Table 2 Regression coefficients of photosynthetic and hydraulic parameters on tree height and tree species

Variable	Tree height	Species	Tree height × Species	Const.	R ²	F	P	AIC
A_{area} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	–	(AJ+AA)	–	12.04	0.331	11.88	0.002	13.79
G_{area} ($\text{mol m}^{-2} \text{s}^{-1}$)	–0.004	(AJ+AA)	–	0.365	0.466	10.60	<0.001	–135.48
N_{area} (g m^{-2})	0.066	(AJ)	(AJ)	1.181	0.828	22.22	<0.001	–69.67
		(AA)	(AA)					
N_{mass} (mg g^{-1})	0.084	(AJ+AA)	–	23.21	0.138	2.756	0.088	36.45
LMA (g m^{-2})	(log)	(AJ)	–23.73	45.77	0.836	23.47	<0.001	91.60
		(AA)	–14.44					
K_L ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)	–	(AJ)	–	2.568	0.208	6.77	0.017	–25.31
Ψ_{predawn} (MPa)	–0.006	(AJ+AA)	(AJ+AA)	–0.211	0.890	60.55	<0.001	–165.18
Ψ_{leaf} (MPa)	–	(AJ)	–	–1.048	–	–	–	–99.77
Ψ_{morning} (MPa)	(log)	(AJ+AA)	–	–0.435	0.347	6.84	0.005	–74.64

“Tree height × Species”, interaction between tree height and species; “const.” is constant. Coefficients in “const.” and “Tree height” indicate intercept and slope, respectively. Coefficients in “Species” and “Tree height × Species” indicate separate intercept and slope dependent on the levels of “Species”; AJ (*A. japonicum*), AA (*A. amoenum*), and AM (*A. mono*). Note that if “Species” or “Tree height × Species” is not deleted in the models, “const.” or “Tree height” indicates the coefficient of “AM” as mere a baseline of the analysis. Consequently, “Species” and “Tree height × Species” indicate how the coefficients of the other species (shown in parentheses in these columns) are higher or lower than that of “AM”. Example: “(AJ)” and “(AA)” in “Tree height × Species” of N_{area} indicates that three species are different from each other, and that the slope against “Tree height” is –0.080 lower in “AJ” and –0.053 lower in “AA” than in “AM”; and “(AJ)” in “Species” of K_L indicates that “AA” and “AM” are not different from each other and the coefficient of “AJ” is lower than that of “AM”. “+” in parentheses means that two species are not different from each other. Note that tree heights are either Tree height or log (Tree height) (shown as (log) in Table)

**Fig. 2** Relationship between (a) hydraulic conductance per unit leaf area (K_L) or (b) maximum stomatal conductance per unit leaf area (G_{area}) and tree height of *A. mono*, *A. amoenum* and *A. japonicum*. Symbols and lines are as in Fig. 1. Bars indicate standard errors ($n = 3$; but for saplings $n = 1 - 2$)

gravitational component of water potential should result in a standing xylem tension gradient of 0.01 MPa per meter increase in height (Zimmerman 1983; Bauerle et al. 1999; Koch et al. 2004), which may increase the risk of cavitation and cause a loss of turgor in taller trees (Brodribb et al. 2003). In this study, pre-dawn leaf water potential, an indicator of gravitational water potential, was lower in taller trees (Fig. 3a). Leaf water potential in the morning showed a more marked decline with increasing tree size (Fig. 3b). However, minimum leaf water potential was constant, regardless of tree size (Fig. 3a). Minimum leaf water potential is positively correlated with xylem vulnerability to cavitation and leaf turgor loss point (Sperry 1995; Brodribb et al. 2003). Given that these two properties do not change with tree size, our results suggest that decreased stomatal conductance may be a mechanism for maintaining minimum leaf water potential to avoid xylem cavitation and leaf turgor loss.

Despite the size-dependent decline in G_{area} , maximum photosynthetic rate (A_{area}) did not decrease with increasing tree size (Fig. 4). Increasing N_{area} with

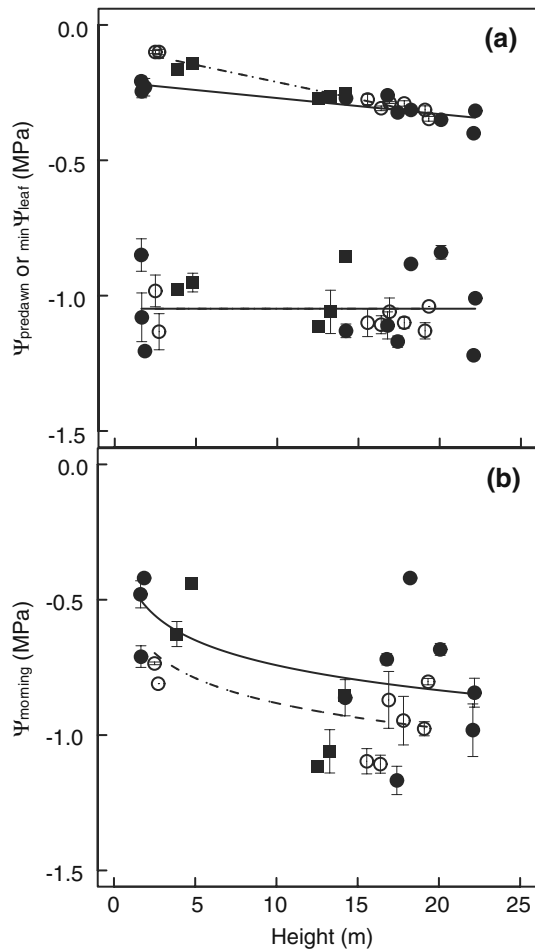


Fig. 3 Size dependency in water potentials: (a) predawn ($\Psi_{\text{predawn}} > -0.5$ MPa) and minimum ($\min\Psi_{\text{leaf}} < -0.5$ MPa) water potentials; and (b) water potential during the morning (Ψ_{morning}). Symbols and lines are as in Fig. 1. Bars indicate standard errors ($n = 3$; but for saplings $n = 1 - 2$)

increasing tree size (Fig. 5a) may contribute to maintaining photosynthetic capacity (Nabeshima and Hiura 2004). In addition, the increase of N_{area} was more marked for species with greater asymptotic height. Because constancy in A_{area} and the slope of G_{area} against tree height are similar among the species, the greater increase of N_{area} in taller species may be invested in other properties rather than photosynthetic enzymes. A possible reason for this increase of N_{area} is to strengthen leaf structure. Onoda et al. (2004) showed that early germinated *Polygonum cuspidatum* allocate more nitrogen to cell walls at the expense of Rubisco than did late germinators, suggesting a trade-off between nitrogen allocation to structural tissue versus photosynthesis. They also suggest that allocation of more nitrogen to cell walls to strengthen leaf structure in early germinated *P. cuspidatum* may have benefit for extending their leaf life span (Onoda et al. 2004). In canopy trees, wind exposure and physical abrasion are likely to be higher than in the understory, favoring tougher leaves in the canopy (Thomas and Winner

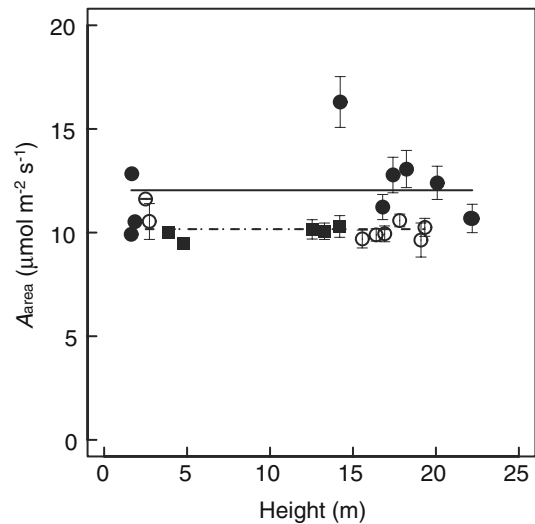


Fig. 4 Size dependency in area-based maximum net assimilation rate (A_{area}). Symbols and lines are as in Fig. 1. Bars indicate standard errors ($n = 3$; but for saplings $n = 1 - 2$)

2002). Therefore, it may be adaptive for taller canopy species to invest more N_{area} to strengthen leaf structure rather than photosynthesis as they grow.

The increased N_{area} with increasing tree size was mainly due to the increase of LMA, because LMA significantly increased with size while N_{mass} was almost constant across tree size ($N_{\text{area}} = N_{\text{mass}} \text{ LMA}$) (Table 1; Fig. 5). It is well known that LMA increases with branch or tree height (Marshall and Monserud 2003; Woodruff et al. 2004; Koch et al. 2004). LMA generally increases also with light intensity, which is often confounded with height within a forest canopy. However, LMA could be influenced only by height gradient because of the gravitational component of water potential on leaf turgor (Woodruff et al. 2004). Although some of the trees we used were in canopy gaps, and the effects of height gradient may not be separated from light intensity, the size-dependent decrease of gravitational component of water potential, $\Psi_{\text{pre-dawn}}$, could have become a driving force for increasing LMA with tree height in this study.

The increase of both LMA and N_{area} were highest in *A. mono* and lowest in *A. japonicum*. *A. mono* has not only higher asymptotic height, but also less shade tolerance than the other two species. This species grows more extensively under well-lit conditions (Sakai 1987, 1990; Uruguchi and Kubo 2005), which can provide more opportunities to grow up to the forest canopy. LMA is known to be positively correlated to leaf toughness (Reich et al. 1991), which may favor the canopy condition, as we discussed for N_{area} . Therefore, a more marked increase in LMA and N_{area} would be adaptive for *A. mono*, which may reach more often to the forest canopy than *A. amoenum* and *A. japonicum*.

In contrast to LMA and N_{area} , size-dependent decrease in G_{area} and constancy in K_L and A_{area} were

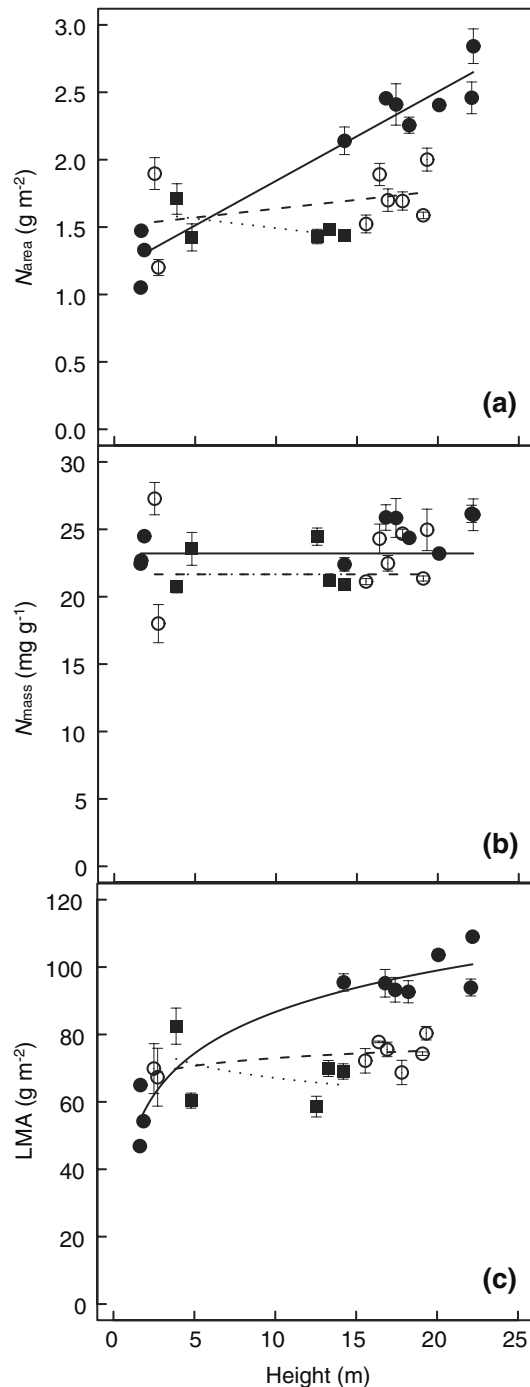


Fig. 5 Size dependency in leaf structural parameters: (a) nitrogen concentration per unit leaf area (N_{area}) (b) nitrogen content per unit leaf mass (N_{mass}), and (c) leaf mass per area (LMA). Symbols and lines are as in Fig. 1. Bars indicate standard errors ($n = 3$; but for saplings $n = 1 - 2$)

similar among the species. This indicates that hydraulic limitation to gas exchange during growth does not necessarily depend on the maximum height of the species. It is suggested that regulation of basic processes related to water and carbon economy exhibit convergence across diverse species by applying scaling factors such as size

(Meinzer 2003). In this study, photosynthetic and hydraulic properties scaling with tree height indicate functional convergence among the *Acer* species having different maximum heights.

As trees grow, the structural and functional parameters change considerably. Scaling these parameters helps us understand how trees adapt to growing tall. This study showed convergence rather than divergence in the size-dependency of hydraulic and photosynthetic properties in *Acer* species having different maximum sizes. K_L homeostasis during growth in three *Acer* species revealed that differences in their maximum height could not be explained by the size-dependency of K_L . In addition, the size-dependency of gas exchange did not depend on the maximum height of the species. The increase of N_{area} and LMA with increasing tree size, however, implies that morphological traits are more plastic than physiological traits as they grow. In contrast, the results of K_L , G_{area} , and A_{area} suggest homeostasis in hydraulic properties and photosynthesis as basic physiological processes during growth.

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