



HAL
open science

Irradiance-induced plasticity in the hydraulic properties of saplings of different temperate broad-leaved forest tree species

Tete Severien Barigah, Tharwat Ibrahim, Aurore Bogard, Benjamin Faivre-Vuillin, Louis Lagneau, Pierre Montpied, Erwin Dreyer

► To cite this version:

Tete Severien Barigah, Tharwat Ibrahim, Aurore Bogard, Benjamin Faivre-Vuillin, Louis Lagneau, et al.. Irradiance-induced plasticity in the hydraulic properties of saplings of different temperate broad-leaved forest tree species. *Tree Physiology*, 2006, pp.1505-1516. 10.1093/treephys/26.12.1505 . hal-01189133

HAL Id: hal-01189133

<https://hal.science/hal-01189133>

Submitted on 30 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Irradiance-induced plasticity in the hydraulic properties of saplings of different temperate broad-leaved forest tree species

TÊTÈ S. BARIGAH,^{1–3} THARWAT IBRAHIM,¹ AURORE BOGARD,¹ BENJAMIN FAIVRE-VUILLIN,¹ LOUIS ANDRÉ LAGNEAU,¹ PIERRE MONTPIED¹ and ERWIN DREYER^{1,3}

¹ UMR INRA-UHP, Ecologie et Ecophysiologie Forestières, IFR 110 Génomique, Ecophysiologie et Ecologie Fonctionnelle, F 54280 Champenoux, France

² Present address: UMR INRA-UBP, Physiologie Intégrée des Arbres Fruitières et Forestiers, 234 avenue du Brézet, F 63100 Clermont-Ferrand, France

³ Corresponding authors (dreyer@nancy.inra.fr, barigah@clermont.inra.fr)

Received November 22, 2005; accepted March 21, 2006; published online September 1, 2006

Summary We assessed the irradiance-related plasticity of hydraulic architecture in saplings of *Betula pendula* Roth., a pioneer species; *Acer pseudoplatanus* L., *Fraxinus excelsior* L., *Quercus robur* L., and *Quercus petraea* Matt. Liebl. which are post-pioneer light-requiring species; and the relatively shade-tolerant *Fagus sylvatica* L. Plants were grown in pots in 36%, 16% and 4% of full sunlight. Hydraulic conductance was measured with a high-pressure flow-meter in entire, in situ root systems and in excised shoots. Leaf-specific whole-plant conductance (LSC) increased with irradiance, due, in part, to an effect of irradiance on plant size. In addition, there was a size-independent effect of irradiance on LSC due, in part, to an increase in root hydraulic conductance paralleled by an increase in root biomass scaled to leaf area. Changes in shoot conductivity also contributed to the size-independent plasticity of LSC. Vulnerability to cavitation measured in current-year twigs was much larger in shade-grown plants.

Betula pendula had the highest whole-plant, root and shoot conductances and also the greatest vulnerability to cavitation. The other species were similar in LSC, but showed some variation in root conductance scaled to biomass, with *Q. robur*, *Q. petraea* and *F. sylvatica* having the lowest root conductance and susceptibility to cavitation. All species showed a similar irradiance-related plasticity in LSC.

Keywords: *Acer*, *Betula*, cavitation, *Fagus*, *Fraxinus*, hydraulic architecture, hydraulic efficiency, leaf-specific hydraulic conductance, phenotypic plasticity, *Quercus*, shade tolerance, vulnerability, xylem.

Introduction

In forest regeneration, light availability below the canopy of adult trees is of primary importance for seedling establishment and growth (Kitajima 1994). The light requirement for survival and growth varies among species, some being able to

cope with low irradiances (shade tolerant), and others requiring high irradiances (shade intolerant; see Niinemets (2006) for a review). Moreover, shade induces large phenotypic (plastic) responses (Bloom et al. 1985, Coleman et al. 1994, Barigah et al. 2004) including reductions in growth, biomass allocation to roots, photosynthetic capacity and increases in specific leaf area (Givnish 1988, Messier et al. 1999, Walters 2005).

Potential evapotranspiration below closed canopies is usually smaller than in the open owing to low energy input and to smaller vapor pressure deficits. Production of vascular tissue in excess of that required for support and water transport wastes resources, whereas production of insufficient vascular tissue restricts growth (Sperry 1995). Whole-plant leaf-specific hydraulic conductance (LSC, i.e., hydraulic conductance scaled to total leaf area) is a measure of the capacity of a plant's vascular tissue to supply water to leaves and has been shown to undergo acclimatory changes in response to long-term changes in soil water availability and atmospheric CO₂ concentration (Mencuccini 2003).

Plastic responses of forest tree saplings to decreasing irradiance may include increasing biomass allocation to stem and leaf growth and decreasing biomass allocation to roots (Veneklaas and Poorter 1998). Consistent with this pattern of response, interspecific comparisons indicate that leaf-specific hydraulic conductance of roots is lower in shade-grown than in sun-grown neotropical trees (Tyree et al. 1998). However, such comparisons depended on observations in replacement gradients, with different species in the different irradiance regimes, so that the effect of irradiance on phenotype may have been confounded by species differences.

Studies of intra-crown hydraulic properties show that reduced irradiance in the lower crown is associated with a reduced hydraulic conductivity of branches and twigs (Schultz and Matthews 1993, Cochard et al. 1997, Lemoine et al. 2002a, 2002b, Sellin and Kupper 2005), and in a study with

silver birch (*Betula pendula* Roth.), Sellin (1993) showed that LSC of saplings was reduced by shade.

Irradiance affects sapling growth, and sapling size affects many plant functions including hydraulic architecture (Meinzer 2003, West et al. 1999) and biomass allocation. Thus effects of irradiance on hydraulic architecture may result either through an effect on plant size ("ontogenic" plasticity) or by a size-independent mechanism (McConnaughay and Coleman 1999).

A major constraint on hydraulic architecture is the need to support rapid transpiration while limiting the risk of cavitation in water conducting xylem elements (Engelbrecht et al. 2000). There is wide interspecific variation among tree species in vulnerability to cavitation (Tyree and Sperry 1989, Cruziat et al. 2002). In beech (*Fagus sylvatica* L.), vulnerability to cavitation is modulated by irradiance: shaded branches in the lower canopy being more vulnerable than well-lit branches in the upper canopy (Cochard et al. 1999). Similarly, shade-grown beech seedlings are more vulnerable to cavitation than sun-grown plants (Cochard et al. 1999), with the water potential inducing 50% loss of conductivity varying by almost 1 MPa among irradiance regimes. This is an example of true plasticity, as vulnerability to cavitation is a size-independent property of conducting tissues. Such plasticity imposes an additional constraint on hydraulic architecture that may be reflected in increased LSC of shade-grown plants to counteract increased vulnerability to cavitation.

Interspecific diversity of hydraulic architecture is large, with fast-growing pioneer species usually having a higher LSC than slow-growing late-successional species (Tyree et al. 1998, Engelbrecht et al. 2000, Kyllö et al. 2003). Such variation may help explain the functional basis of the different growth strategies that govern the distribution of species along irradiance gradients.

The present study aimed to determine whether the hydraulic architecture and xylem vulnerability to cavitation of temperate broad-leaved trees shows phenotypic plasticity in response to shade, and if so, whether the degree of plasticity depend on a species' successional status and shade tolerance.

Material and methods

Plant material and growth conditions

Saplings of sycamore maple (*Acer pseudoplatanus* L.), silver birch (*Betula pendula*), European beech (*Fagus sylvatica*), European ash (*Fraxinus excelsior* L.), sessile oak (*Quercus petraea* Matt. Liebl.) and pedunculate oak (*Q. robur* L.) were raised from seed and grown in 10-l containers under neutral shading nets (OLS screens, Ludvig Svensson, Kinna, Sweden) for 1 to 3 years at the INRA nursery, Champenoux (48°44' N, 6°14' E, elevation 237 m). The rooting substrate consisted of a 1:3 (v/v) mix of washed sand and of peat supplemented twice a year with 40 g per plant of slow release fertilizer (Nutricote100, N,P,K 13,13,13) plus trace elements. Around 90 plants per species were randomly allocated to three shade

treatments (4, 16 and 36% of full sunlight). In addition, a few plants were grown in full sun.

Plant biomass and leaf area determination

Roots were washed free of soil, and the lateral roots separated from the taproot. Total leaf area (*L*) was measured with a leaf area meter (Li-Cor model 3000-A equipped with a Li-Cor Belt Conveyor 3050-A, Li-Cor Instruments, Lincoln, NE). After leaf area had been measured, leaf, branch and root biomass was determined after drying at 70 °C. Immediately after determination of hydraulic conductance, roots were washed (see Table 1 for a detailed list of replicates per treatment).

Measuring hydraulic conductance

Hydraulic conductance of shoots and roots was measured during summer 2001, 2002 and 2003 between mid-September and mid-October, for current-year seedlings, and from July to mid-September for 2- and 3-year-old saplings. Table 1 presents the cumulative numbers of samples per species and treatment. As a result, the experiment had a full factorial design (6 species × 3 irradiances) with unbalanced sample numbers, and with a range of sizes among individuals in each treatment. Total leaf area was taken as a measure of plant size and the covariate in the statistical analyses.

Whole, decapitated root systems and excised shoots were perfused with distilled and de-gassed ultra-pure water filtered through a 0.1 µm filtration membrane (Calyx capsule, Osmotics, Westborough, MA) and delivered via a high pressure flow meter (HPFM; Tyree et al. 1995).

Shoots were infiltrated at a pressure of 0.3 MPa for at least 30 min until water dripped from the stomata. This ensured zero leaf water potential in the whole shoot, and dissolved air bubbles from potentially embolized xylem. Flow rates were recorded every 4 s until stable values were obtained (i.e., standard deviation < 5% in the course of a few minutes). Quasi-steady-state parameters were recorded and hydraulic resistances were computed. Xylem temperature was assumed to be close to air temperature. Laboratory temperature varied no more than 0.5–1.5 °C during any set of measurements and between 20 to 25 °C between one set of measurements and another. Temperatures in the nursery where root hydraulic resistance was measured ranged from 18 to 38 °C. All conductance values were standardized to a temperature of 20 °C. In some cases measurements of hydraulic resistance were erratic (Bo-

Table 1. Number of saplings measured for hydraulic conductance and biomass in the different irradiance treatments.

Transmitted irradiance (as a fraction of incident)	4%	16%	36%
<i>Acer pseudoplatanus</i>	21	11	10
<i>Betula pendula</i>	8	11	9
<i>Fagus sylvatica</i>	8	12	16
<i>Fraxinus excelsior</i>	22	11	11
<i>Quercus petraea</i>	6	14	10
<i>Quercus robur</i>	12	21	12

geat-Triboulot et al. 2002) leading us to discard all measurements for that particular sapling.

The contributions of leaf blades, petioles and stems to overall shoot resistance were estimated according to Yang and Tyree (1994). The procedure is based on the simplifying assumption that each compartment contributes to whole-shoot resistance as a resistance in series with the others. Differences in whole-shoot resistance (R_S) recorded before and after removal of the leaf lamina, were ascribed to the lamina (R_{lam}). The same procedure was repeated with petioles (R_{pet}). Leaf resistance (R_L) was computed as $R_{lam} + R_{pet}$. All measurements were conducted in the laboratory under low irradiance. The resulting estimates of R_L , therefore, correspond to the lower range of values during a diurnal cycle (Tyree et al. 2005), but under high water availability, and therefore with no diurnal increase such as reported by Brodribb and Holbrook (2004).

Whole-root-system conductance (K_R) was measured on severed root systems kept in their substrate, with the stump connected to the HPFM. Air temperature was recorded and substrate temperature was assumed to be the same as air temperature. The pressure (P) applied to the stump was increased from 0 to 0.5 MPa at a constant rate of 3–7 kPa s⁻¹ and the flow rate (F) was recorded every 3 s. The hydraulic conductance (K_R) was calculated from the linear region of the relationship between F and P (Tyree et al. 1995).

Whole-plant hydraulic conductance (K_T) was calculated as $1/(R_R + R_S)$ (where R_R is root resistance). Whole-plant leaf-specific hydraulic conductance was computed as $LSC = K_T/L$ (with L = total leaf area per sapling). The contribution of root systems and leaves (lamina + petioles) to whole-plant resistance (R_T) was assessed from measured values of root system resistance (R_R/R_T) and from the computed resistance of leaves ($(R_{lam} + R_{pet})/R_T$).

Vulnerability to cavitation curves

Vulnerability curves were established on saplings during their second year of growth. Two sets of measurements were conducted either during 1999, before the main experiment, or during 2001. The same shading nets and growth conditions were imposed during the two experiments, except that the 1999 experiment comprised a set of saplings grown under full irradiance. The air-injection method was used with current-year twigs, as described by Sperry and Saliendra (1994). Branches were severed in the morning, enclosed in wet, black plastic bags and brought rapidly to the laboratory for hydraulic analysis. The branches were inserted in a single-ended 1.2-m-long pressure chamber, as described by Cochard et al. (1992), and pressurized with air for 30–45 min at: (1) 1.0, 1.5 or 2.0 MPa for birch and 2.0, 2.5 or 3.0 MPa for the other species during 1999; and (2) 1.0, 1.5, 2.0, 2.5, 3.0 and 3.5 MPa during 2001. When sap exudation through the protruding cut end ceased, branches were removed from the pressure chamber and enclosed for at least 1 h in a wet, black plastic bag to allow water potential equilibration among the different compartments and for pressure relaxation in the gas phase. Around six, 0.02-m stem segments were cut under water from lateral twigs and were fitted to water-filled tubing with one end connected to a

tank of de-gassed filtered (0.2 μm) water and the other end to an electronic balance. The flux of water through a stem section under low pressure (6 kPa; k_{ini}) was recorded. The stem segment was then perfused two to three times with water at 0.1 MPa for 15 min to displace air from embolised vessels and maximum hydraulic conductance (k_{max}) was determined.

Percent loss of conductivity (PLC) was calculated for each segment as:

$$PLC = 100 \left(\frac{1 - k_{ini}}{k_{max}} \right) \quad (1)$$

The PLC curves were constructed from mean values of PLC at each pressure assumed to represent xylem water potential (Ψ_x)

Statistical analysis

Data were evaluated by linear models with the statistical software package R 2.2.0 (R Development Core Team 2004). The impact of treatment and species on LSC (which was log transformed to stabilize variance) was evaluated by analysis of variance (ANOVA) followed by contrast analysis with the multcomp R package (Bretz et al. 2004). The effect of irradiance on tree-size independent K_T was evaluated by analysis of covariance (ANCOVA) with L as a covariate:

$$\ln K_T = a \ln L + \ln b \quad (2)$$

We first tested whether the slope a was common to all treatments and species. In the case of a positive outcome, a contrast analysis was conducted to test for an impact of irradiance (within species) and of species (within irradiance treatments) on the intercept $\ln b$. Significant differences in $\ln b$ were taken as an index for significant size-independent effects of irradiance on K_T . A similar procedure was used to analyze for the plasticity in root hydraulic conductance (K_R) with root biomass as the dimensional variable.

Loss of hydraulic conductivity versus Ψ_x curves were taken as an estimate of vulnerability to cavitation expressed as Ψ_{PLC50} , the xylem water potential inducing 50% loss of hydraulic conductivity. The Ψ_{PLC50} was estimated by fitting a sigmoid model (Pammenter and Van der Willigen 1998) to the PLC versus applied pressure data:

$$PLC = \frac{100}{1 + \exp[a(\Psi_x - \Psi_{PLC50})]}$$

Fitting was done with the statistical software R and a contrast analysis was performed with the multcomp package to compare the resulting values of Ψ_{PLC50} among treatments and species. Residual normality and homoscedasticity were graphically checked by means of residual versus predicted plots and normal quantile-quantile plots.

Results

Plant size, LSC and irradiance

Saplings biomass varied with irradiance (data not shown). Even under low irradiance, the most shade-tolerant species (*F. sylvatica*) produced less biomass than the other, more light-demanding, species (*A. pseudoplatanus*, *F. excelsior*, *Q. petraea* and *Q. robur*), whereas the pioneer species (*B. pendula*) had the largest biomass increment under all light regimes.

Under the highest irradiance, LSC ranged from 13.2 to $66 \cdot 10^{-6} \text{ kg MPa}^{-1} \text{ m}^{-2} \text{ s}^{-1}$ (Table 2). Irrespective of treatment, LSC of *B. pendula* was two to three times that of all other species. The other species had rather similar, intermediate LSC values (Table 2). In all species, there was a two- to threefold increase in LSC with increase in irradiance from 4 to 36% of full sunlight.

Vulnerability to cavitation

Vulnerability curves determined for four of the studied species are presented in Figure 1 together with values of Ψ_{PLC50} derived from these curves. Significant species-specific differences were detected, with *B. pendula* displaying the greatest vulnerability under all irradiance regimes, followed by *Q. robur*, *F. sylvatica* and *Q. petraea*. Irradiance had a significant effect on Ψ_{PLC50} in all four species. Vulnerability to cavitation increased with decreasing irradiance, with a 0.15–0.3 MPa difference between the highest and lowest irradiance.

Similar results were found during the 1999 experiments on five species (Table 3), with *Betula pendula* showing the greatest vulnerability to cavitation. There was a sharp increase in Ψ_{PLC50} with decreasing irradiance. The difference in Ψ_{PLC50} between 100 and 4% relative irradiance was 0.6–1.0 MPa.

Irradiance, plant size and LSC

Figure 2 shows the log-log relationships between K_T and L in the different species and treatments. A large overlap in L was obtained among treatments, which allows direct comparisons

Table 2. Results of the two-way ANOVA to evaluate the effects of species and irradiance on whole-plant leaf-specific hydraulic conductance (LSC, $10^{-6} \text{ kg MPa}^{-1} \text{ s}^{-1} \text{ m}^{-2}$) in saplings of six forest tree species grown under 4, 16 and 36% of full sunlight. Data are least square means of saplings harvested 5 to 30 months after germination (no interaction; adjusted $r^2 = 0.998$). Species differences are indicated by different lower-case letters, and treatment differences by different upper-case letters (contrast analysis, $p < 0.05$).

Relative irradiance	4% A	16% B	36% C
<i>Acer pseudoplatanus</i> ab	6.65	14.7	23.4
<i>Betula pendula</i> c	19.5	34.8	66.0
<i>Fagus sylvatica</i> a	8.22	8.94	13.2
<i>Fraxinus excelsior</i> b	10.1	15.1	21.0
<i>Quercus petraea</i> ab	7.57	12.5	21.4
<i>Quercus robur</i> ab	7.24	11.9	16.3

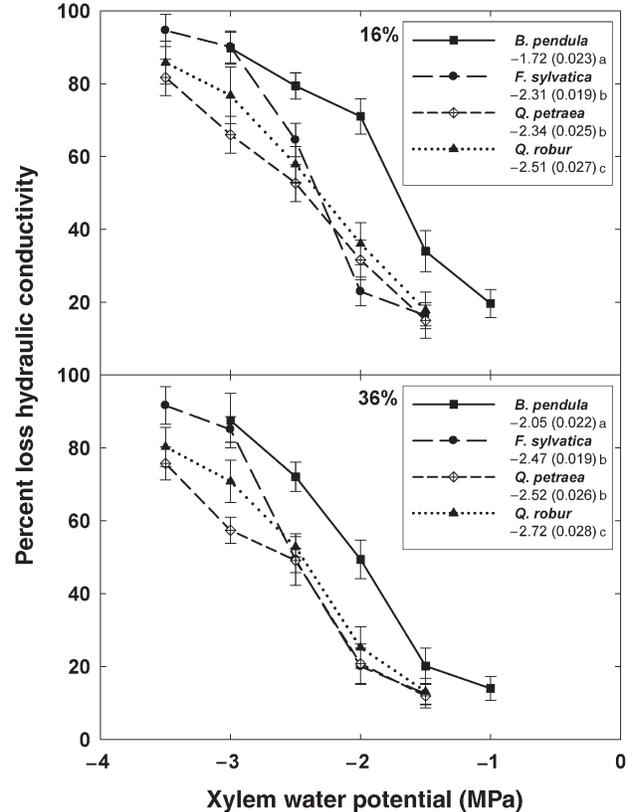


Figure 1. Vulnerability to cavitation (percent loss of conductivity) versus xylem water potential for current-year twigs of 2-year-old saplings of *B. pendula*, *F. sylvatica*, *Q. petraea* and *Q. robur* grown under 16 or 36% of full sunlight. Vertical bars are standard errors of the mean ($n = 10-15$). Water potential at 50% loss of conductivity is indicated for each species \times irradiance combination.

of the relationships between K_T and L . The outcome of the model, $\ln K_T = a \ln L + \ln b$, was highly significant, and both slopes and intercepts differed from zero in all species \times irradiance combinations. No interaction could be detected between any combination of the factors irradiance, species and the covariate leaf area (Table 4A). A reduced model with a common slope for all treatments and species (constant factor a , estimated to be 0.990 ± 0.039) produced the intercepts ($\ln b$) displayed in Table 4B. A contrast analysis revealed that within species the irradiance effect was significant and that the intercept $\ln b$ increased with irradiance. This unambiguously demonstrates a size-independent plasticity in K_T . Significant species effects were detected within the different treatments. At all irradiances, the highest values of $\ln b$ were detected in *B. pendula*, and the lowest in *F. sylvatica* and *Q. robur*.

Contribution of plant compartments to overall hydraulic resistance

The contribution of root resistance to R_T was highly variable and usually large (reaching values close to 85% in shade saplings of *Q. petraea*, Figure 3). The impact of irradiance was highly variable. Four species showed a visible decrease of

Table 3. Values of xylem water potential (MPa) inducing 50% loss of conductivity (Ψ_{PLC50}) in twigs of seedlings of five species grown in 4, 16, and 100% of full sunlight. Shown are means of 12 replicates with standard errors of the means. Different letters within a species indicate significant irradiance-related differences. Measurements were made during summer 1999.

Irradiance	4%	16%	36%	100%
<i>Betula pendula</i>	-1.49 (0.023) a	-1.68 (0.026) b	-2.30 (0.089) c	-2.13 (0.043) c
<i>Acer pseudoplatanus</i>	-1.83 (0.13) a	-2.47 (0.038) b	-2.55 (0.038) b	-2.85 (0.039) c
<i>Fagus sylvatica</i>	-2.09 (0.019) a	-2.32 (0.020) b	-2.45 (0.021) c	-2.94 (0.041) d
<i>Quercus robur</i>	-2.25 (0.038) a	-2.46 (0.037) b	-2.63 (0.041) c	-2.91 (0.043) d
<i>Quercus petraea</i>	-2.32 (0.042) a	-2.56 (0.035) b	-2.69 (0.041) c	-2.94 (0.031) d

R_R/R_T with increasing irradiance (*Q. robur*, *Q. petraea*, *B. pendula* and *F. excelsior*), and two did not (*A. pseudoplatanus* and *F. sylvatica*). The fractional resistance of leaves (R_L/R_T) was smaller than that of roots, but nevertheless quite high (10–50%), probably because of large resistances in the lamina. The observed changes were anti-parallel to those for R_R/R_T , with *B. pendula* having the highest values and the remaining four species showing irradiance-related increases. The contribution of stems and branches to whole-plant resistance remained small, frequently below 10% (not shown).

Irradiance, plant size and leaf area to root biomass ratio

Different irradiance regimes modify the relative allocation of biomass to roots, which could be the main cause for the observed plasticity in whole-plant hydraulic conductance independently of L . Figure 3C shows that leaf area to root biomass ratio decreased with increasing irradiance. The response varied with species. The general outcome of the covariance model $\ln \text{RootBiomass} = a \ln L + \ln b$ was a severe effect of leaf area modulated by irradiance (with significant interactions; Table 5). The statistical model was reduced to a model with a

common slope within each species, and different intercepts according to irradiance. Within each species, a significant L -independent plasticity was evidenced as the intercept $\ln b$ increased with irradiance, revealing an increased investment in root biomass at common L , except in *Q. petraea*. Species comparisons were difficult because of interactions between leaf area and species. Nevertheless, *F. sylvatica* displayed both the lowest slope and a low intercept, i.e., the smallest investment in root biomass, whereas *B. pendula* displayed the largest irradiance-related plasticity.

Irradiance, leaf area and shoot and root hydraulic conductance

To check whether the observed plasticity in relative biomass allocation to roots was the only cause of the L -independent plasticity in K_T , we conducted a covariance analysis for shoot conductance (K_S) with L as covariate (model $\ln K_S = a \ln L + \ln b$). Large L and species effects and a small, but significant, irradiance effect were detected (Table 6A). The model was reduced to the main effects (i.e., a unique slope 0.867 ± 0.041 , and different intercepts), and allowed a ranking of treatments

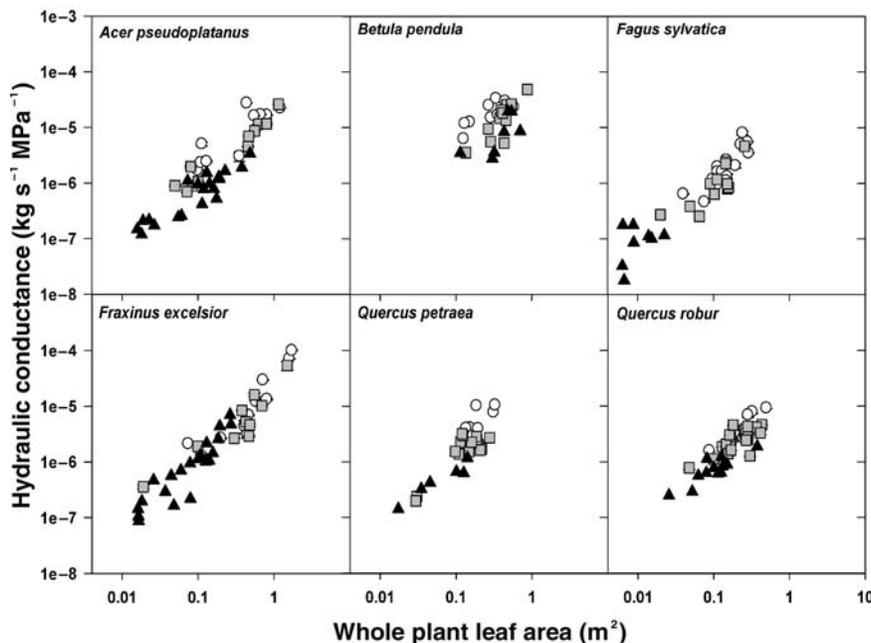


Figure 2. Relationships between total leaf area (L) and whole-plant hydraulic conductance (K_T) in saplings from six forest tree species grown under 4 (▲), 16 (■) and 36% (○) of full sunlight. Log-log scale. Each value represents a single sapling.

Table 4. Results of the two-way ANCOVA to evaluate the effects of species and irradiance and their interactions on log-transformed whole-plant hydraulic conductance ($\ln K_T$) with total leaf area ($\ln L$) as a covariate in saplings of six forest tree species grown under 4, 16 and 36% of full sun-light. (A) Main effects. (B) Computed values of the intercepts with only main effects and a common slope for the linear relationships. Contrast analysis revealed species (within treatments) and irradiance (within species) effects.

(A) Effect	df	F value	Pr(F)
<i>L</i>	1	274.7	< 0.0001
Species	5	5.25	0.0002
Irradiance	2	6.60	0.0017
<i>L</i> × Species	5	1.23	0.296
<i>L</i> × Irradiance	2	1.24	0.293
Species × Irradiance	10	1.13	0.341
<i>L</i> × Species × Irradiance	10	0.83	0.599

(B) Species	Species effect	SE	Irradiance	Irradiance effect	SE
<i>Acer pseudoplatanus</i>	-11.31 ab	0.099	4%	-0.480 a	0.057
<i>Betula pendula</i>	-10.24 c	0.103	15%	0.024 b	0.047
<i>Fagus sylvatica</i>	-11.60 a	0.136	34%	0.455 c	0.052
<i>Fraxinus excelsior</i>	-11.12 b	0.096			
<i>Quercus petraea</i>	-11.30 ab	0.124			
<i>Quercus robur</i>	-11.41 a	0.102			

and species (Table 6B). There was a considerable *L*-independent effect of irradiance on K_S . *Betula pendula* always had the largest intercept, whereas the intercepts of the other species were similar.

The same analysis was performed for K_R . All species, except *F. sylvatica* and *F. excelsior* showed an *L*-independent irradiance-related plasticity, with the highest values in all treatments for *B. pendula* (data not shown).

Root hydraulic conductance scaled to root biomass

A two-way ANOVA revealed that irradiance had no detectable effect on the root hydraulic conductance scaled to root biomass, although significant species-specific effects were evident, with *B. pendula* having by far the largest K_R values (Table 7). A covariance analysis of $\ln K_R$ with $\ln \text{RootBiomass}$ as covariate restricted to the main effects (i.e., common slope close to 1 in all species × irradiance combinations) revealed species-specific differences, but no detectable irradiance effect except in *Q. petraea* (Table 8). The species ranking showed that *B. pendula* had the largest intercept followed by *A. pseudoplatanus* and *F. excelsior*, followed by *Q. petraea*, *Q. robur* and *F. sylvatica*. Fine roots fraction in the whole-root system showed highly significant effects of species and irradiance. Except for *Q. petraea*, the fine root fraction increased with irradiance and was higher in *B. pendula* than in the other species (Table 7).

Discussion

Irradiance and hydraulic efficiency of forest tree saplings

Irradiance is well known to modulate growth of saplings in forest regeneration. Large differences in size are induced and usually result in large differences in functional properties such

as biomass allocation to different organs or hydraulic architecture. However, little attention has been given to the detection of what is frequently called “real” plasticity as opposed to size-related “ontogenetic” plasticity (McConaughay and Coleman 1999).

Vulnerability to cavitation in current-year twigs is an intrinsically size-independent property of xylem and is not expected to be affected by ontogenetic processes, at least in the short term. Our results consistently showed that this functional trait is strongly influenced by irradiance. In all tested species, vulnerability to cavitation scaled negatively with irradiance, with a gradual shift in Ψ_{PLC50} of about 0.6–1.0 MPa between extreme irradiances. This confirms earlier results obtained with *F. sylvatica* (Cochard et al. 1999) and shows that plasticity in vulnerability can be observed in species with quite distinct wood structures (diffuse-porous as in *B. pendula*, *F. sylvatica* and *A. pseudoplatanus*, and ring-porous as in *Q. robur* and *Q. petraea*). Shade-grown phenotypes are usually more vulnerable than sun-grown phenotypes. A larger survey including measurements on saplings grown under shade in forests would be useful to confirm the generality of this response. The plasticity in vulnerability to cavitation reported here is, to our knowledge, greater than previously reported, irrespective of the environmental constraint used.

Whole-plant leaf-specific hydraulic conductance increased significantly with irradiance in all tested species. This confirms earlier observations of an increase in leaf-specific conductivity in branches from the bottom to the top of a canopy of beech and of birch (Lemoine et al. 2002a, Sellin and Kupper 2005), and in roots of shade-grown versus full sun-grown seedlings (Kyllo et al. 2003). Nevertheless, an ontogenetic (size-dependent) effect may be suspected even though LSC scales hydraulic conductance to leaf area. Increased sapling size results, in most cases, in increased leaf overlapping and

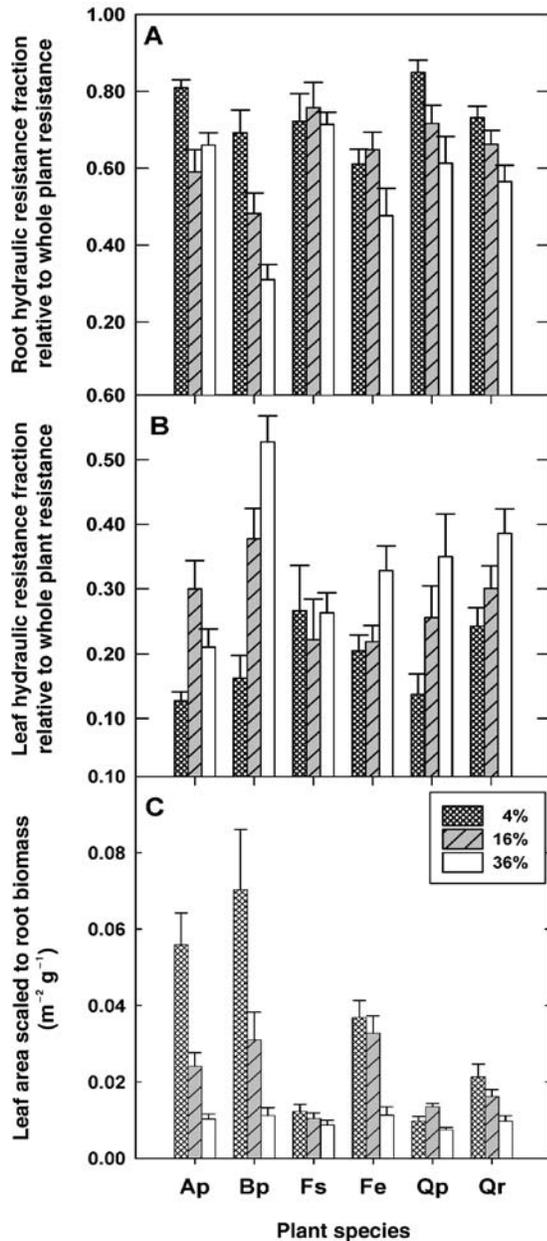


Figure 3. Mean values and standard errors (vertical bars) of the fraction of total hydraulic resistance (A) in roots (R_R/R_T) and (B) in leaves (R_L/R_T); and (C) the ratio of total leaf area to root biomass. Abbreviations: Ap = *Acer pseudoplatanus*; Bp = *Betula pendula*; Fs = *Fagus sylvatica*; Fe = *Fraxinus excelsior*; Qp = *Quercus petraea*; and Qr = *Quercus robur*.

reduced light capture per unit leaf area (Pearcy et al. 2005). As a consequence, whole-plant transpiration does not increase linearly with total leaf area, at least during the first stages of sapling development. In our experiment, the scaling and experimental procedures allowed comparison of saplings from different irradiance treatments, which were similar in size (though not in age). We used leaf area as a surrogate for sapling size because leaf area is directly linked to transpiration and is therefore probably the best estimate of size during the

early stages of tree ontogenesis. The linear relationships between total leaf area ($\ln L$) and whole-plant hydraulic conductance ($\ln K_T$) were highly significant in all species \times irradiance combinations and displayed a common slope. That the intercepts of the relationships were largely dependent on, and increased with, irradiance, unambiguously demonstrated true plasticity of K_T in addition to the size-induced plasticity.

Seasonal changes in hydraulic properties are unlikely to modify this conclusion. Xylem conductance may be slightly affected by irreversible embolism during summer (Cochard and Tyree 1990, Bréda et al. 1993), but (1) the saplings were grown under daily irrigation making severe embolism unlikely, and (2) our measurement procedure involving perfusion with water under high pressure, which likely redissolved native embolism in xylem vessels (Tyree et al. 1993). Leaf conductance, particularly in the extra-vascular pathway, is affected by leaf ontogeny mainly during leaf expansion (Aasamaa and Sober 2005) and leaf senescence (Brodribb and Holbrook 2003). Although our sampling excluded these two periods to avoid large artefacts; it could not exclude the impact of climate and smaller scale changes cannot be excluded, although they were minimized by the sampling procedure.

Temperature effects were corrected by taking into account the changes in kinematic viscosity of water, which is the principal cause of changes in LSC between 15 and 35 °C (Cochard et al. 2000). Additional effects related to the extravascular transfer of sap in root cortex and leaf lamina (Sack et al. 2004) were probably minimal in shoots due to the small temperature range experienced during our experiments, but may have been more important in a few measurements with roots. Correcting for such effects is impossible due to the lack of information on the relative contribution of extra-vascular resistance in our species and of information on temperature responses in these cases. However, we may safely assume the artefacts induced by differences in temperature were minimal.

The causes of the size-independent plasticity of whole-plant hydraulic conductance

One processes that might affect K_T independently of sapling size is the change in relative biomass allocation to roots resulting in a change in the leaf area to root biomass, with consequences for K_T at any given leaf area. Increased relative allocation to roots under high irradiance is well known and results partly from a true phenotypic plasticity (Givnish 1988). Such a change in relative biomass allocation was observed in all species, with an L -independent component and with larger relative allocation to roots in shade-acclimated saplings. Irradiance had no effect on root hydraulic conductance scaled to root biomass. The irradiance-induced changes in hydraulic conductance observed in the root systems of saplings were, therefore, largely mediated by changes in root biomass. This may not hold true for larger trees where root architecture is more likely to vary at constant biomass. Nevertheless, the visible shift in biomass allocation to roots was not the only cause for the irradiance-induced plasticity in LSC. A size-independent effect was also detected in severed shoots independently of

Table 5. Results of the two-way ANCOVA to evaluate the effects of species and irradiance and their interactions on log-transformed root biomass ($g; \ln\text{RootBiomass}$) with total leaf area ($m^2; \ln L$) as covariate. Saplings of six forest tree species grown under 4, 16 and 36% of full sunlight. (A) Effects of L , species, irradiance and interactions. (B) Results from a reduced model with a unique slope per species and the intercepts for each species \times irradiance combination. Contrast analysis among species on the slope revealed differences as indicated by different letters, and contrast analysis among treatments on the intercept, revealed differences as indicated by different symbols.

(A) Effect	df	<i>F</i> value	Pr(<i>F</i>)
<i>L</i>	1	174.3	< 0.0001
Species	5	1.77	0.121
Irradiance	2	4.00	0.0199
<i>L</i> \times Species	5	3.35	0.00637
<i>L</i> \times Irradiance	2	0.036	0.965
Species \times Irradiance	10	1.00	0.440
<i>L</i> \times Species \times Irradiance	10	1.08	0.381

(B) Species	Slope	SE	Int(4%)	Int(16%)	Int(36%)
<i>Acer pseudoplatanus</i>	1.11 b	0.0812	3.36 +	3.99 +	4.78 §
<i>Betula pendula</i>	0.917 ab	0.203	2.73 +	3.65 §	4.52 &
<i>Fagus sylvatica</i>	0.371 a	0.162	1.71 +	3.09 §	3.64 §
<i>Fraxinus excelsior</i>	1.17 b	0.083	3.95 +	4.13 +§	4.77 §
<i>Quercus petraea</i>	0.922 ab	0.166	4.44	4.17	4.80
<i>Quercus robur</i>	0.797 ab	0.152	3.50 +	3.91 +§	4.41 §

root biomass, and K_S decreased with irradiance in all species. There are many possible causes for such decreases of K_S at constant total leaf area. One is a change in sapwood to leaf area ratio due to decreased radial growth in shaded stems and twigs. Radial growth is well known to be reduced more severely under shade than is shoot elongation, resulting in thinner stems and twigs in shaded trees. Changes in sapwood-specific conductivity are also likely to occur as recorded in tree canopies

(Lemoine et al. 2002b), resulting in changed leaf-specific conductivity.

The largest hydraulic resistance within saplings is in fine roots and in leaves, mainly in the leaf lamina (Tyree et al. 1998). The resistance attributable to stems and twigs is generally minor (about 10–20% of the total). This was the case for the tested saplings (root resistance above 50% except in *B. pendula* under the highest irradiance regime; leaf resistance

Table 6. Results of the two-way ANCOVA to evaluate effects of species and irradiance and their interactions on log-transformed hydraulic conductance of the shoot ($\ln K_S$) with total leaf area ($\ln L$) as covariate. (A) Saplings of six forest tree species grown under 4, 16, and 36% of full sunlight. Nonsignificant interactions were iteratively removed from the model which resulted in a model restricted to the main effects with a common slope in all treatment \times species combinations (0.867 ± 0.0409). (B) *Y* intercepts are displayed together with the effects of irradiance on the intercepts. Contrast analysis among treatments within species and among species within treatments revealed in the differences indicated by different letters ($p < 0.05$).

(A) Effects	df	<i>F</i> value	Pr(<i>F</i>)
<i>L</i>	1	132.7	< 0.0001
Species	5	4.48	0.0007
Irradiance	2	3.35	0.0371
<i>L</i> \times Species	5	3.68	0.0033
<i>L</i> \times Irradiance	2	0.334	0.716
Species \times Irradiance	10	1.98	0.037
<i>L</i> \times Species \times Irradiance	10	1.52	0.134

(B) Species	Species effect	SE	Irradiance	Irradiance effect	SE
<i>Acer pseudoplatanus</i>	–10.17 ab	0.103	4%	–0.281 a	0.059
<i>Betula pendula</i>	–9.61 c	0.107	16%	0.034 b	0.049
<i>Fagus sylvatica</i>	–11.36 ab	0.142	36%	0.247 b	
<i>Fraxinus excelsior</i>	–10.37 ab	0.100			
<i>Quercus petraea</i>	–10.06 b	0.129			
<i>Quercus robur</i>	–10.46 a	0.106			

Table 7. Root hydraulic conductance scaled to root biomass ($K_R/\text{RootBiomass}$, $\text{g}_{\text{H}_2\text{O}} \text{s}^{-1} \text{MPa}^{-1} \text{kg}_{\text{DM}}^{-1}$) and the fraction of fine root biomass in the whole-root system for saplings of six forest tree species grown under 4, 16 and 36% of full sunlight. Data are least square means of saplings harvested 5 to 30 months after germination.

Relative irradiance	Root hydraulic conductance scaled to root biomass			Fine roots/total root biomass		
	4%	16%	36%	4%	16%	36%
<i>Acer pseudoplatanus</i>	0.451	0.615	0.419	0.31	0.45	0.49
<i>Betula pendula</i>	2.100	2.470	2.790	0.37	0.57	0.57
<i>Fagus sylvatica</i>	0.199	0.337	0.189	0.31	0.38	0.40
<i>Fraxinus excelsior</i>	0.552	0.587	0.586	0.29	0.38	0.40
<i>Quercus petraea</i>	0.090	0.264	0.347	0.42	0.32	0.29
<i>Quercus robur</i>	0.223	0.311	0.324	0.29	0.34	0.39
Species effect		$P < 0.0001$			$P < 0.0001$	
Irradiance effect		$P = 0.251$			$P < 0.0001$	

between 20–30% with occasional values up to 50% in *B. pendula*). We did not attempt to dissect leaf resistances into vascular and extra-vascular components, although recent studies have highlighted the importance of the latter, which may display significant diurnal changes paralleling the course of transpiration (Zwieniecki et al. 2002, Nardini and Salleo 2003). Our experiment did not take such variations into account, as the measurements were made under a standard low irradiance. The increased contribution of leaves to whole-plant resistance that we observed in all species under high irradiance (from 15 to 50% in the extreme case of *B. pendula*) is contrary to what is found at the individual leaf level, where resistance usually decreases under high irradiance (Sack et al. 2003). This apparent discrepancy can only be explained by the observed changes in biomass allocation to leaves relative to roots in particular. Decreased leaf area to total biomass ratio is common in saplings growing under high irradiances (Bloom et al. 1985, Coleman et al. 1994).

The ecological significance of phenotypic plasticity in hydraulic architecture

The observed plasticity shows that, under low irradiance, saplings (even of similar size) invest less in water-conducting tissues and roots, reflecting their low rates of transpiration. The

response of LSC in saplings corresponds to the observed reduction in leaf-specific conductivity recorded in shaded, lower-canopy branches (Schultz and Matthews 1993). Reduction in hydraulic efficiency in response to shade will be adaptive if (1) the transpiration load is smaller, as was the case in our shaded treatments and as usually is the case in forest understories; and (2) the risk of soil water depletion is lower under canopies, than in the open, which may not always be the case.

The reduced LSC of shade-grown saplings may result from shifts in carbon investments in different organs. This is apparent in the shifts of biomass allocation from roots to shoots, which reduces LSC at the whole-sapling scale, and potentially reduces production of xylem tissue. The changes in vulnerability to cavitation can similarly be viewed as a shift of carbon allocation. Maintaining a low vulnerability requires thicker vessel walls and dense wood (McCulloh and Sperry 2005). However, the simultaneous reduction of LSC and increase in vulnerability to cavitation in shade versus sun-grown saplings opposes the generally accepted idea of a trade-off between vulnerability to cavitation and hydraulic efficiency. As a result, such shade-acclimated saplings are at a high risk of massive embolism whenever exposed to higher irradiance than that prevailing during their initial growth.

Acclimation of trees to such a new irradiance regime may

Table 8. Results of the two-way ANCOVA to evaluate the effects of species and irradiance and their interactions on log-transformed root hydraulic conductance ($\ln K_R$) with root biomass as covariate. Saplings of six forest tree species grown under 4, 16 and 36% of full sunlight. The slope for the relationship was common (0.947 ± 0.048 , not significantly different from one). The Y intercepts ($= \ln b$, where b is the scaling factor) and standard errors are displayed; $P > |t|$ was below 0.0001. Probabilities of a contrast analysis (species within treatment and treatment within species) are indicated. Species ranking was: *B. pendula* > *A. pseudoplatanus*, *F. excelsior* > *Q. petraea*, *Q. robur* and *F. sylvatica*.

Species/relative irradiance	4%	Error	16%	Error	36%	Error	$P > F$
<i>Acer pseudoplatanus</i>	-14.75	0.147	-14.25	0.229	-14.69	0.266	0.1178
<i>Betula pendula</i>	-13.10	0.262	-12.98	0.238	-12.76	0.270	0.5802
<i>Fagus sylvatica</i>	-15.92	0.231	-15.65	0.218	-15.60	0.215	0.5941
<i>Fraxinus excelsior</i>	-14.47	0.146	-14.35	0.236	-14.33	0.275	0.8547
<i>Quercus petraea</i>	-16.18	0.282	-15.13	0.205	-14.94	0.260	0.0010
<i>Quercus robur</i>	-15.39	0.205	-14.98	0.195	-14.95	0.250	0.1916
$P > F$	< 0.0001		< 0.0001		< 0.0001		

take several years (Collet et al. 2002). It usually implies growth of new roots, a shift in biomass allocation to roots and the production of new xylem to cope with the higher transpiration loads. A similar acclimation of hydraulic properties has been recorded in branches of *F. sylvatica* after exposure to increased irradiance following thinning (Lemoine et al. 2002b).

The observed plasticity of hydraulic architecture in saplings in response to irradiance (increased vulnerability to cavitation and size-independent decrease of LSC under shade) implies logically that shade saplings are less tolerant to drought than sun-exposed trees, although this remains open to debate (Sack 2004). Evidence on this point is scarce because of the difficulty in obtaining similar drought conditions under different irradiances. Sack's (2004) results show that relative growth rate is affected independently by shade and by moderate drought, but that seedlings died earlier during severe soil water depletion under the deepest shade. The finding is consistent with our results.

Interspecific differences in hydraulic architecture and acclimation to different irradiance regimes

The occurrence of species-specific differences in hydraulic architecture is well known. Differences in vulnerability to cavitation have been shown in a number of papers (review by Cruziat et al. 2002) and differences in LSC have frequently been shown in relationship to mean soil water availability. The question of the relationship between hydraulic properties and shade tolerance of species has been less frequently addressed. The fast-growing and pioneer *B. pendula* differed from all other species in having a much greater LSC for a given leaf area and the greatest root hydraulic efficiency (i.e., the ratio of hydraulic conductance to root biomass) among the studied species. This ability to efficiently explore a given soil volume and extract available water is possibly due to the highly ramified root system in this species (Curt and Prévosto 2003), as opposed to the presence of a large tap root as in oaks, for example. In addition, this species is more vulnerable to xylem cavitation. If we view low vulnerability to cavitation as a costly anatomical feature (McCulloh and Sperry 2005), a fast-growing species with a large LSC is likely to invest less into cavitation resistance. *Acer pseudoplatanus* and *F. excelsior* ranked intermediate in hydraulic efficiency and, in the case of *A. pseudoplatanus*, in vulnerability to cavitation, which is in line with the ability of these species to colonize forests gaps rapidly. Finally, the two oak species and the shade-tolerant beech displayed many common features, with a low vulnerability to cavitation and a low hydraulic efficiency. There is a consensus that species able to regenerate and grow in low light grow more slowly and have a lower LSC than either species requiring high light availability for regeneration or fast-growing pioneer species (Tyree et al. 1991, 1998). Leaf conductance is frequently lower in shade-tolerant species (Nardini et al. 2005, Sack et al. 2005). Vulnerability to cavitation relative to shade tolerance, however, has not previously been examined. Nevertheless, direct tests of drought tolerance in saplings revealed no trade-off between shade tolerance and drought tolerance among a large set of species (Sack 2004).

Conclusion

Our data illustrate the highly plastic response to shade of hydraulic properties in forest tree saplings. These plastic responses were partly size dependent (ontogenetic plasticity), size being strongly affected by irradiance, but nevertheless displayed a significant size-independent component (true plasticity). In particular, this was the case for LSC. True plasticity in LSC was partly due to increased allocation to root biomass (structural decrease in the ratio of root biomass to leaf area under shade), and partly, to possible changes in specific conductivity in shoot segments and leaves. The size-independent vulnerability to cavitation was greatly enhanced under shade in all species. These conclusions extend to all tested species irrespective of their degree of shade tolerance. Large interspecific differences were recorded, and the fast-growing and shade-intolerant *B. pendula* displayed a greater LSC and vulnerability to xylem cavitation than the other species.

Acknowledgments

This study was partly supported by the Programme "Forêts Hétérogènes" of GIP-ECOFOR and by the Council of Région Lorraine. We thank Alain Franc and Hervé Cochard for helpful discussions, Ioanna Desjeunes and Dédé M.A. Barigah for their assistance in measurements, and Jean-Marie Gioria and Jean-Philippe Lemaire for the maintenance of the experimental set up.

References

- Aasama, K. and A. Sober. 2005. Seasonal courses of maximal hydraulic conductances in shoots of six temperate deciduous species. *Funct. Plant Biol.* 32:1077–1087.
- Barigah, T.S., M. Béreau, P. Imbert and R. Huc. 2004. Effects of five light regimes on growth traits of seedlings of three ecological guilds tropical rain forest tree species. *In Ecology and Management of Neotropical Rain Forest. Lessons Drawn from Paracou, a Long-term Experimental Research Site in French Guiana.* Eds. G.J. Gourlet, S. Fleury and O. Laroussinie. Elsevier, Paris, pp 65–74.
- Bloom, A.J., S.F. Chapin and H.A. Money. 1985. Resource limitation in plants—an economic analogy. *Annu. Rev. Ecol. Systematics* 16:363–392.
- Bogeat-Triboulot, M.-B., R. Martin, D. Chatelet and H. Cochard 2002. Hydraulic conductance of root and shoot measured with the transient and dynamic modes of the high-pressure flowmeter. *Ann. For. Sci.* 59:389–396.
- Bréda, N., H. Cochard, E. Dreyer and A. Granier. 1993. Field comparison of transpiration, stomatal conductance and vulnerability to cavitation of *Quercus petraea* and *Quercus robur* under water stress. *Ann. For. Sci.* 50:571–582.
- Bretz, F., T. Hothorn and E. Al. 2004. Multcomp: multiple tests and simultaneous confidence intervals. R package. <http://r-project.org>.
- Brodribb, T.J. and N.M. Holbrook. 2003. Changes in leaf hydraulic conductance during leaf shedding in seasonally dry tropical forest. *New Phytol.* 158:295–303.
- Brodribb, T.J. and N.M. Holbrook. 2004. Diurnal depression of leaf hydraulic conductance in a tropical tree species. *Plant Cell Environ.* 27:820–827.
- Cochard, H. and M.T. Tyree. 1990. Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiol.* 6:393–407.

- Cochard, H., P. Cruiziat and M.T. Tyree. 1992. Use of positive pressures to establish vulnerability curves: further support for air-seeding hypothesis and implications for pressure-volume analysis. *Plant Physiol.* 100:205–209.
- Cochard, H., D. Lemoine and E. Dreyer. 1999. The effects of acclimation to sunlight on the xylem vulnerability to embolism in *Fagus sylvatica* L. *Plant Cell Environ.* 22:101–108.
- Cochard, H., M. Peiffer, K. Le Gall and A. Granier. 1997. Development control of xylem hydraulic resistances and vulnerability to embolism in *Fraxinus excelsior* L.: impacts on water relations. *J. Exp. Bot.* 48:655–663.
- Cochard, H., R. Martin, P. Gross and M.B. Bogeat-Triboulot. 2000. Temperature effects on hydraulic conductance and water relations of *Quercus robur* L. *J. Exp. Bot.* 51:1255–1259.
- Coleman, J.S., K.D.M. McConnaughay and D.D. Ackerly. 1994. Interpreting phenotypic variation in plants. *Trends Ecol. Evol.* 9:187–191.
- Collet, C., O. Lanter and M. Pardos. 2002. Effects of canopy opening on the morphology and anatomy of naturally regenerated beech seedlings. *Trees* 16:291–298.
- Cruiziat, P., H. Cochard and T. Améglio. 2002. Hydraulic architecture of trees: main concepts and results. *Ann. For. Sci.* 59:723–752.
- Curt, T. and B. Prévosto. 2003. Rooting strategy of naturally regenerated beech in silver birch and Scots pine woodlands. *Plant Soil* 255:265–279.
- Engelbrecht, B.M.J., V. Velez and M.T. Tyree. 2000. Hydraulic conductance of two co-occurring neotropical understory shrubs with different habitat preferences. *Ann. For. Sci.* 57:201–208.
- Givnish, T.J. 1988. Adaptation to sun and shade: a whole plant perspective. *Aust. J. Plant Physiol.* 15:63–92.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.
- Kyllo, D.A., V. Velez and M.T. Tyree. 2003. Combined effects of arbuscular mycorrhizas and light on water uptake of neotropical understory shrubs, *Piper* and *Psychotria*. *New Phytol.* 160:443–454.
- Lemoine, D., H. Cochard and A. Granier. 2002a. Within crown variation in hydraulic architecture in beech (*Fagus sylvatica* L.): evidence for a stomatal control of xylem embolism. *Ann. For. Sci.* 59:19–27.
- Lemoine, D., S. Jacquemin and A. Granier. 2002b. Beech (*Fagus sylvatica* L.) branches show acclimation of xylem anatomy and hydraulic properties to increased light after thinning. *Ann. For. Sci.* 59:761–766.
- McConnaughay, K.D.M. and J.S. Coleman. 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* 80:2581–2593.
- McCulloh, K.A. and J.S. Sperry. 2005. Patterns in hydraulic architecture and their implications for transport efficiency. *Tree Physiol.* 25:257–267.
- Meinzer, F. 2003. Functional convergence in plant responses to the environment. *Oecologia* 134:1–11.
- Mencuccini, M. 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant Cell Environ.* 26:163–182.
- Messier, C., R. Doucet, J.-C. Ruel, Y. Claveau, C. Kelly and M.J. Lechowicz. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Can. J. For. Res.* 29:812–823.
- Niinemets, Ü. 2006. The controversy over traits conferring shade-tolerance in trees: ontogenetic changes revisited. *J. Ecol.* 94:464–470.
- Nardini, A. and S. Salleo. 2003. Effects of the experimental blockage of the major veins on hydraulics and gas exchange of *Prunus laurocerasus* L. leaves. *J. Exp. Bot.* 54:1213–1219.
- Nardini, A., E. Gortan and S. Salleo. 2005. Hydraulic efficiency of the leaf venation system in sun- and shade-adapted species. *Funct. Plant Biol.* 32:953–961.
- Pammenter, N.W. and C. Vander Willigen. 1998. A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiol.* 18:589–593.
- Pearcy, R.W., H. Muraoka and F. Valladares. 2005. Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. *New Phytol.* 166:791–800.
- R Development Core Team. 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://r-project.org>.
- Sack, L. 2004. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos* 107:110–127.
- Sack, L., P.D. Cowan, N. Jaikumar and N.M. Holbrook. 2003. The ‘hydrology’ of leaves: co-ordination of structure and function in temperate woody species. *Plant Cell Environ.* 26:1343–1356.
- Sack, L., C.M. Streeter and N.M. Holbrook. 2004. Hydraulic analysis of water flow through leaves of sugar maple and red oak. *Plant Physiol.* 134:1824–1833.
- Sack, L., M.T. Tyree and N.M. Holbrook. 2005. Leaf hydraulic architecture correlates with regeneration irradiance in tropical rain forest trees. *New Phytol.* 167:403–413.
- Schultz, H. and M. Matthews. 1993. Xylem development and hydraulic conductance in sun and shade shoots of grapevine (*Vitis vinifera* L.): evidence that low light uncouples water transport capacity from leaf area. *Planta* 190:393–406.
- Sellin, A. 1993. Resistance to water flow in xylem of *Picea abies* (L.) Karst. trees grown under contrasting light conditions. *Trees* 7:220–226.
- Sellin, A. and P. Küpper. 2005. Effects of light availability versus hydraulic constraints on stomatal responses within a crown of silver birch. *Oecologia* 142:388–397.
- Sperry, J.S. 1995. Limitations on stem water transport and their consequences. *In* *Plant Stems: Physiology and Functional Morphology*. Ed. B. Gartner. Academic Press, London, pp 105–124.
- Sperry, J.S. and N.Z. Saliendra. 1994. Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant Cell Environ.* 17:1233–1241.
- Tyree, M.T. and J.S. Sperry. 1989. Vulnerability of xylem to cavitation and embolism. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 40:19–38.
- Tyree, M.T., D.A. Snyderman, T.R. Wilmot and J.-L. Machado. 1991. Water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*). Data, models, and a comparison with two temperate species (*Acer saccharum* and *Thuja occidentalis*). *Plant Physiol.* 96:1105–1113.
- Tyree, M.T., B. Sinclair, P. Lu and A. Granier. 1993. Whole shoot hydraulic resistance in *Quercus* species measured with a new high-pressure flowmeter. *Ann. Sci. For.* 50:417–423.
- Tyree, M.T., S. Patino, J. Bennink and J. Alexander. 1995. Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field. *J. Exp. Bot.* 46:83–94.
- Tyree, M.T., V. Velez and J.W. Dalling. 1998. Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to differing light regimes. *Oecologia* 114:293–298.

- Tyree, M.T., A. Nardini, S. Salleo, L. Sack and B. El Omari. 2005. The dependence of leaf hydraulic conductance on irradiance during HPMF measurements: any role for stomatal response? *J. Exp. Bot.* 56:737–744.
- Veneklaas, E. and L. Poorter. 1998. Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. *In* *Inherent Variation in Plant Growth: Physiological Mechanisms and Ecological Consequences*. Eds. H. Lambers, H. Poorter and M. Van Vuuren. Backhuys publishers, Leiden, The Netherlands, pp 337–355.
- Walters, R.G. 2005. Towards an understanding of photosynthetic acclimation. *J. Exp. Bot.* 56:435–447.
- West, G.B., J.H. Brown and B.J. Enquist. 1999. A general model for the structure and allometry of plant vascular systems. *Nature* 400: 664–667.
- Yang, S. and M.T. Tyree. 1994. Hydraulic architecture of *Acer saccharum* and *A. rubrum* : comparison of branches to whole trees and the contribution of leaves to hydraulic resistance. *J. Exp. Bot.* 45: 179–186.
- Zwieniecki, M., P. Melcher, C. Boyce, L. Sack and N. Holbrook. 2002. Hydraulic architecture of leaf venation in *Laurus nobilis* L. *Plant Cell Environ.* 25:1445–1450.