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Research paper



Trade-offs between xylem hydraulic properties, wood anatomy and yield in *Populus*

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Trees face the dilemma that achieving high plant productivity is accompanied by a risk of drought-induced hydraulic failure due to a trade-off in the trees' vascular system between hydraulic efficiency and safety. By investigating the xylem anatomy of branches and coarse roots, and measuring branch axial hydraulic conductivity and vulnerability to cavitation in 4-year-old field-grown aspen plants of five demes (*Populus tremula* L. and *Populus tremuloides* Michx.) differing in growth rate, we tested the hypotheses that (i) demes differ in wood anatomical and hydraulic properties, (ii) hydraulic efficiency and safety are related to xylem anatomical traits, and (iii) aboveground productivity and hydraulic efficiency are negatively correlated to cavitation resistance. Significant deme differences existed in seven of the nine investigated branch-related anatomical and hydraulic traits but only in one of the four coarse-root-related anatomical traits; this likely is a consequence of high intra-plant variation in root morphology and the occurrence of a few 'high-conductivity roots'. Growth rate was positively related to branch hydraulic efficiency (xylem-specific conductivity) but not to cavitation resistance; this indicates that no marked trade-off exists between cavitation resistance and growth. Both branch hydraulic safety and hydraulic efficiency significantly depended on vessel size and were related to the genetic distance between the demes, while the xylem pressure causing 88% loss of hydraulic conductivity (P_{88} value) was more closely related to hydraulic efficiency than the commonly used P_{50} value. Deme-specific variation in the pit membrane structure may explain why vessel size was not directly linked to growth rate. We conclude that branch hydraulic efficiency is an important growth-influencing trait in aspen, while the assumed trade-off between productivity and hydraulic safety is weak.

Keywords: coarse root and branch xylem anatomy, genetic variability, high-conductivity roots, hydraulic conductivity, *P*₅₀, relative growth rate, vessel diameter, vulnerability to cavitation.

Introduction

While the global demand for wood products is steadily growing (FAO 2009), drought exposure is likely to increase with climate warming in many temperate and tropical forests (IPCC 2007). Thus, forest management faces the challenge of combining high timber yield with drought resistance of the trees in order to minimize the risk of failure. This may be even more relevant if the frequency of extreme climatic events increases in future (Schär et al. 2004). However, the production goal could be difficult to achieve due to a trade-off between hydraulic efficiency and hydraulic safety in the conducting system of trees. When plants produce larger vessel diameters in the xylem, hydraulic efficiency increases over-proportionally according to Hagen–Poiseuille's law (Tyree and Zimmermann 2002), but the risk of hydraulic failure due to embolism rises as well (Tyree et al. 1994, Awad et al. 2010). Since fast growth tends to be associated with elevated transpiration rates and higher hydraulic efficiency (Tyree 2003, Monclus et al. 2006), high forest productivity may only be achieved at the cost of increased cavitation vulnerability and thus higher drought sensitivity. How different tree species cope with this trade-off is not well studied. While much research has focused on intra-specific differences in productivity and in cavitation vulnerability (e.g., Martínez-Vilalta et al. 2009, Corcuera et al. 2011, Lamy et al. 2011, Wortemann et al. 2011), the relation between xylem anatomical traits, axial hydraulic conductivity and aboveground growth performance is not well understood. Several studies compared different tree species or hybrids (e.g., Wikberg and Ögren 2004, Cochard et al. 2007, Fichot et al. 2009, Delzon et al. 2010), while intra-specific differences in the hydraulics-growth relationship have only rarely been examined in field-grown trees (e.g., Rosner et al. 2008, Zhang and Cao 2009, Lamy et al. 2014). Although a growing number of studies have revealed a close relation between hydraulic efficiency and growth rate (e.g., Russo et al. 2010, Fan et al. 2012), these studies were all based on stem wood anatomical measurements and derived hydraulic traits, but they did not measure the actual hydraulic conductivity in the branch wood directly. Thus, the results will be partly biased by the effect of vessel tapering with increasing tree height (Anfodillo et al. 2013).

One way of increasing woody biomass production is the establishment of short-rotation tree plantations with highly productive woody plants such as poplar (Populus spp.) or willow (Salix spp.). It is well established that genotype plays a crucial role in determining the productivity of Populus species or hybrids in plantation forestry (Marron and Ceulemans 2006, Müller et al. 2012a, 2012b). Studies on the relatedness of vessel anatomy and drought resistance showed that the drought resistance of different poplar populations or genotypes also differs within a species (Sparks and Black 1999, Cochard et al. 2007, Awad et al. 2010). This suggests that intra-specific differences in hydraulic traits may be one factor influencing productivity, but information on within-species variation in wood hydraulic properties and their effect on plant growth is scarce. However, with the prospect of climate warming, a better understanding of the genetic control of anatomical and hydraulic properties and their relevance for productivity is a prerequisite for selecting productive and drought-tolerant plant material for short-rotation forestry.

The two aims of the present study were (i) to examine the genetic differentiation in wood anatomical and hydraulic properties of branches and coarse roots in five genetically distinct demes (groups of closely related individuals) of European and North American aspen (*Populus tremula* L. and *Populus tremuloides* Michx.), and (ii) to relate these results to the variation in aboveground productivity. The major study goal was to analyze the dependence of growth on xylem hydraulic efficiency and safety. We hypothesized that (i) demes differ in wood anatomical and hydraulic properties, (ii) hydraulic efficiency and vulnerability to cavitation are related to xylem anatomy and

(iii) hydraulic efficiency is a main determinant of aboveground productivity which trades off with xylem safety.

Materials and methods

Experimental site and plant material

The study was embedded in the framework of the research project 'POPDIV' at the University of Göttingen, which investigates the role of intra-specific diversity in aspen for productivity and selected ecosystem functions. A common garden experiment with different poplar (*Populus*) demes was established on the Relliehausen Experimental Farm near Silberborn (51°44′56″N, 09°32′28″E) in the Solling Mountains, ~60 km west of Göttingen (Lower Saxony, Germany). The study area is located at 485 m above sea level in the uplands of Central Germany with a sub-oceanic, cool-temperate climate (mean annual temperature of 6.6 °C; annual mean precipitation of 1110 mm). The soil is unfertilized relatively nutrient-poor haplic Cambisol on Triassic sandstone (Middle Bunter) of sandyloamy texture (Keuter et al. 2013). The site was previously used as cattle pasture.

Our investigations were carried out on four P. tremula demes and one P. tremuloides deme. The term 'deme' is used here for defining aspen progeny arrays; it follows the definition of Gilmour and Gregor (1939) and relates to an assemblage of taxonomically closely related individuals. The demes do not necessarily represent a specific taxonomic category of poplars (e.g., species, subspecies or varieties) or a specific origin of a species in the sense of a locally interbreeding population (Zhang 2012). Since all demes were grown in the same common garden, possible effects of environmental variability on the investigated traits were minimized. Both aspen species are closely related and are considered as sister species (Cervera et al. 2005, Pakull et al. 2009, Grant and Mitton 2010) or as conspecific subspecies (Eckenwalder 1996), depending on the criteria of relatedness used. The places of origin of the different demes cover gradients in mean annual temperature (8.5-10.7 °C) and annual precipitation (600–1112 mm; Table 1). Saplings of all demes were seed-grown and out-planted in 2008. The common garden trial consists of 120 plots, each containing 25 poplar plants arranged in a rectangular grid with a planting distance of 1.5 m. Blocks comprising six plots were surrounded by a single border tree row serving as a buffer zone to avoid edge effects. Thirteen of the plots (i.e., two or three per deme) were selected and 10-15 plant individuals per deme (i.e., typically five per plot) were sampled for branch and root segments, but for some measures not all samples could be processed. In total, we selected 62 representative sample trees (replicates), chosen randomly from the different plots in June and July 2012. A list of all the measured traits, their symbols and units are given in Table 2; the processed analyses are described below.

Table 1. Origin and some characteristics of the five aspen demes investigated in the study with deme acronym, climate data at the place of origin (elevation, mean annual precipitation (MAP), mean annual temperature (MAT)), root collar diameter (RCD) and plant height at the beginning of the experiment (2009). Given are means \pm SE (T-test, P < 0.05).

Acronym	Species	Place of origin	Coordinates	Elevation (m)	Mean annual precipitation (mm)	Mean annual temperature (°C)	Climate characteristics	RCD ₂₀₀₉ (mm)	Height ₂₀₀₉ (cm)
AU	P. tremula	Austria, Vienna	48°16′N 16°19′E	390	600	9.9	Moderately cold winters, warm summers	3.69 ± 0.18a	31.71 ± 2.28a
СН	P. tremula	Switzerland, Birmensdorf	47°21'N 08°24'E	692	1101	8.5	Moderately cold winters, moderately warm summers	2.65 ± 0.29b	19.16 ± 2.29b
G2	P. tremula	Germany, Göttingen	51°32′N 09°56′E	315	645	8.7	Mild winters, moderately warm summers	3.98 ± 0.16a	40.40 ± 1.51c
G8	P. tremula	Germany, Göttingen	51°32′N 09°56′E	315	645	8.7	Mild winters, moderately warm summers	4.33 ± 0.10a	39.67 ± 2.44ac
US	P. tremuloides	USA: Mass., Boston/ Sandwich	42°14′N 71°23′W	80	1112	10.7	Relatively cold winters, warm summers	3.59 ± 0.16a	32.78 ± 2.06ac

Table 2. List of abbreviations used in the study.

Symbol	Unit	Definition
h	cm	Tree height
RCD	mm	Root collar diameter
AGB	g	Aboveground biomass
AGR	g year ^{_1}	Absolute AGB increment (in the period April 2011–April 2012)
RGR	g g ⁻¹ year ⁻¹	Relative growth rate
d	μm	Vessel diameter
$d_{\rm h}$	μm	Hydraulically weighted diameter
$d_{\rm wm}$	μm	Weighted mean diameter according to vessel size distribution
VD	n mm ⁻²	Vessel density
$A_{\rm cross}$	mm ²	Cross-sectional sapwood area in a segment
Avulam	mm ²	Xylem sapwood area in a segment
A _{lumen}	%	Relative vessel lumen area in a segment (cumulative vessel lumen in percent of sapwood area in a segment)
Ks	kg m ⁻¹ MPa ⁻¹ s ⁻¹	Empirical sapwood area-specific hydraulic conductivity
K _p	kg m ⁻¹ MPa ⁻¹ s ⁻¹	Potential sapwood area-specific hydraulic conductivity
P ₁₂	MPa	Xylem pressure causing 12% loss of hydraulic conductivity
P ₅₀	MPa	Xylem pressure causing 50% loss of hydraulic conductivity
P ₈₈	MPa	Xylem pressure causing 88% loss of hydraulic conductivity

The data on genetic differentiation among the demes, i.e., the analysis of simple sequence repeats (SSRs) and amplified fragment length polymorphism (AFLP) markers, were kindly provided by the Department of Forest Genetics and Forest Tree Breeding at the University of Göttingen (Zhang 2012).

Aboveground plant growth performance

As the experiment was part of a long-term study, tree harvest for obtaining biomass data to assess the aboveground growth performance of the tree individuals was not possible. Instead, aboveground biomass (AGB, in g) was estimated from root collar diameter (RCD, in mm) and tree height (*h*, in cm) as $AGB = 0.038 \times RCD^{1.270} \times h^{1.388}$ by applying the allometric equation established empirically by Heinrichs (2010) in a nearby young *P. tremula* stand on a forest clear-cut with similar site conditions. Aboveground productivity was calculated from two sequential measurements of *h* and RCD before the onset of bud flush in April 2010 and April 2011 as described above and was expressed as absolute growth rate (AGR, g year⁻¹) or relative growth rate (RGR, g g⁻¹ year⁻¹).

Branch and coarse root sampling

One 3- to 4-year-old branch segment (first-order twig on the main terminal shoot, mean age \pm SE: 3.6 \pm 0.1 years) of ~40-cm length was cut near the stem, defoliated and immediately put in water-filled plastic tubes for transport to the laboratory. Thereafter, all samples were placed in deionized water containing Micropur (Katadyn, Wallisellen, Switzerland) to prevent microbial activity and stored at 4 °C until further processing. From the same tree individuals, coarse root segments of similar length were excavated from the soil by tracing single root strands towards the stem to ensure they belonged to the respective tree. Immediately after cutting, coarse roots were cleaned from adherent soil and stored under the same conditions as the branch samples.

Xylem anatomy of branches and coarse roots

For each deme, 8–11 branch and 9–11 coarse root transverse sections were cut using a sliding microtome (G.S.L.1,

Schenkung Dapples, Zürich, Switzerland), yielding 49 branch and 54 root samples in total. Prior to cutting, the segments were stained with safranin (1% in 50% ethanol, Merck, Darmstadt, Germany) and samples were washed three times with 70% ethanol. The total transverse section of each sample was digitalized at ×100 magnification using a stereomicroscope equipped with an automatic stage (SteREOV20, Carl Zeiss Microlmaging GmbH, Jena, Germany; Software: AxioVision v4.8.2, Carl Zeiss Microlmaging GmbH). Image processing was done using the software Adobe Photoshop CS2 (Version 9.0, Adobe Systems Inc., San Jose, CA, USA) and ImageJ (v1.44p, http://rsb.info.nih.gov/ij) using the particle analysis function. For all subsequent calculations, the complete xylem cross-section without pith and bark was analyzed, yielding 4133-21,863 measured vessels per branch sample and 293-5421 measured vessels per root sample. Measured parameters included idealized vessel diameter (d, µm) as obtained from major (a) and minor (b) vessel radii according to White (1991) as $d = ((32 \times (a \times b)^3)/(a^2 \times b^2))^{1/4}$, vessel density (VD, n mm⁻²) and single and cumulative vessel lumen area (A_{lumen} , mm²). Relative vessel lumen area (A_{lumen} , %) was obtained by dividing cumulative vessel lumen area (Alumen, mm²) by the corresponding sapwood area (A_{xylem} , mm²). The diameter of individual vessels was used to calculate hydraulically weighted vessel diameter (d_h , μ m) according to Sperry and Saliendra (1994) as $d_{\rm h} = \Sigma d^4 / \Sigma d^5$. Additionally, weighted mean vessel diameter (d_{wm} , μ m) was calculated from the relative contribution of a vessel size class to total hydraulic conductivity as $d_{\rm wm} = \Sigma (\rm VSC \times R K_h)/100)$, where VSC (µm) is the given vessel size class (e.g. 15 µm for the vessel size class 10-20 µm) and RK_h (%) the percentage contribution to total conductivity of that class. Potential sapwood area-specific hydraulic conductivity ($K_{\rm p}$, kg m⁻¹ MPa⁻¹ s⁻¹) was calculated according to the Hagen–Poiseuille equation as $K_p = ((\pi \times \Sigma t^4)/8\eta) \times \rho)/A_{xylem}$, where η is the viscosity of water (1.002 \times 10⁻⁹ MPa s), ρ the density of water (998.2 kg m⁻³), both at 20 °C, and A_{xylem} (m²) the corresponding xylem area without pith and bark.

Hydraulic conductivity measurement

Hydraulic traits were measured in each 10–13 branch segments (replicates; mean diameter \pm SE: 7.01 \pm 0.27 mm) per deme according to Sperry et al. (1988) using a Xyl'em apparatus (Bronkhorst, Montigny-les-Cormeilles, France), yielding 57 samples in total. Coarse roots, however, showed an extremely high conductivity and exceeded by far the measureable range (20 g h⁻¹) of our Liqui-Flow meter inside the Xyl'em apparatus with ~300 g h⁻¹, and were excluded from all further analyses.

In the laboratory, all lateral branches, if present, were cut off and the scars sealed with quick-drying superglue (Loctite 431, Henkel, Düsseldorf, Germany) applicable to wet surfaces, and segments were subsequently shortened to a length of 294.9 ± 2.0 mm (mean \pm SE) under water. For the determination of maximal hydraulic conductivity (K_h , kg m MPa⁻¹ s⁻¹) at 6 kPa, demineralized filtered (0.22 μ m) and degassed water (10 mM KCl and 1 mM CaCO₃) was used, interrupted by three 10-min flushes at 120 kPa to ensure removal of all potential emboli. Subsequently, top-view images of the planed basipetal and distal ends of each branch segment were taken at high resolution with a stereomicroscope (SteREOV20), and images were analyzed with the software ImageJ (v1.44p, http://rsb. info.nih.gov/ij) for total cross-sectional (Across, mm²) and corresponding xylem area without pith and bark (A_{xylem} , mm²). Empirical sapwood area-specific hydraulic conductivity (K_s , kg m⁻¹ MPa⁻¹ s⁻¹) was calculated by dividing $K_{\rm h}$ by the corresponding basipetal maximal xylem area without pith and bark. For deciding which xylem area from the ~30-cm-long branch segments should be used to calculate K_s due to the sample tapering effect, regression models for the relation between A_{xvlem} and the corresponding total cross-sectional area (A_{cross} , mm²) were derived for each deme (Table A1 available as Supplementary Data at Tree Physiology Online) and applied to calculate the corresponding maximal, mean or minimal xylem area for each segment from eight diameter measurements. Subsequently, $K_{\rm h}$ was divided by these three measures and related to four wood anatomical and hydraulic traits on the sample level. According to this linear regression analysis, $K_{\rm h}^{\rm emp}$ divided by the maximal basipetal xylem area revealed stronger relations than when calculated with mean or minimum xylem area (Table A2 available as Supplementary Data at *Tree* Physiology Online).

Xylem resistance to cavitation and estimation of hydraulic safety margins

We used the Cavitron technique (Cochard et al. 2005) for measuring vulnerability to xylem cavitation on 4-12 branch samples (replicates) per deme, each taken from different tree individuals. The same samples previously flushed with the Xyl'em apparatus were mounted in a custom-built rotor chamber of the Cavitron, which uses a commercially available centrifuge as the basis (Sorvall RC-5C, Thermo Fisher Scientific, Waltham, MA, USA), and spun at defined velocities recorded with the software CaviSoft (version 2.1, University of Bordeaux, Bordeaux, France). Measurements started at a pressure of -0.37 MPa. The negative pressure was then increased stepwise until the percentage loss of conductivity (PLC) reached at least 90%. For each branch segment, a sigmoid function (Willigen and Pammenter 1998) was fitted to describe the relationship between PLC and xylem pressure (vulnerability curve, VC) using the expression $PLC = 100/(1 + \exp(s/25 \times (P_i - P_{50})))$, where P_{50} (MPa) is the xylem pressure causing 50% loss of hydraulic conductivity and s (% MPa⁻¹) is the slope of the curve at the inflexion point. The xylem pressures causing 12 and 88% loss of conductivity (P_{12} and P_{88}) were calculated as well following Domec and Gartner

(2001) and Choat et al. (2012). We further used available leaf water potential data from the trees of this experiment after Müller et al. (2012*a*, 2012*b*) to calculate deme-specific hydraulic safety margins, which are defined as the difference between the minimum leaf water potential measured in the field and the corresponding P_{50} value (Choat et al. 2012).

All coarse roots measured by the centrifuge technique revealed r-shaped VCs (Figure 4), i.e., these segments lose their conductance at modest pressure and must possess open vessels in segments of 28-cm length; this was confirmed for a subsample of 10 coarse roots by the air injection method (data not shown) and they thus were excluded from further analyses.

Statistical analysis

Statistical analyses were performed with the software R, version 2.13.2 (R Development Core Team 2011). Prior to analysis, the data were tested for normal distribution by the Shapiro– Wilk test and for homogeneity of variances by the Bartlett test. One-way analysis of variance (ANOVA) was used to analyze the influence of deme on the investigated traits. The general linear hypotheses procedure with Tukey's post hoc test was applied to detect significant differences in the analyzed trait means among the eight demes. Pearson's correlation analysis was used to test for inter-relationships between different branch and coarse root traits of the plants and for detecting relationships between above- and belowground traits based on data pooled across all demes; some data had to be logtransformed in order to achieve normal distribution. To test for the relatedness of morphological trait variation and genetic variation across the five demes, a Mantel test was performed (5000 permuted data sets) using the software PAST (Hammer et al. 2001). Several linear and non-linear regression analyses were carried out with the software Xact 8.03 (SciLab, Hamburg, Germany).

Results

Between-deme variation in branch and coarse root xylem anatomy and hydraulics

We found significant differences between the demes in four of the five branch anatomical traits (exception: A_{lumen} ; ANOVA) but in only one of the root anatomical traits (mean vessel diameter; Table 3). The demes from Austria (AU) and Germany (G2 and G8) were very similar in their branch anatomy; the Swiss deme

Table 3. Traits related to plant size and morphology, to biomass production in the period April 2010 to April 2011, and to wood anatomy and hydraulics of branch and coarse root samples of the five aspen demes (four *P. tremula* and one *P. tremuloides* [US] deme). Different letters indicate significant differences in the means between demes (P < 0.05, means ± SE). The number of investigated trees is given in parentheses. For abbreviations see Table 2.

Variable	Unit	AU	СН	G2	G8	US
Stand charac	teristics					
Height ₂₀₁₁	m	161.90±7.83a (10)	128.58±6.63b (12)	131.23 ± 9.63b (11)	142.64 ± 8.27ab (14)	193.83±8.89c (15)
RCD ₂₀₁₁	cm	16.99±1.04a (10)	13.47 ± 0.66b (12)	14.1 ± 0.50ab (11)	16.18±0.82ab (14)	22.83 ± 1.14c (15)
AGB ₂₀₁₁	g	92.16±13.41a (10)	48.34 ± 6.26b (12)	53.49 ± 8.76b (11)	73.4±10.94ab (14)	160.78 ± 12.21c (15)
Growth-relate	ed traits					
$AGR_{biomass}$	g year-1	54.79 ± 9.43a (11)	20.89 ± 4.66b (10)	22.13 ± 4.41b (10)	39.25 ± 7.63ab (11)	108.99 ± 12.54c (11)
$RGR_{biomass}$	g g ⁻¹ year ⁻¹	1.25±0.14a (11)	0.68±0.08b (10)	0.82 ± 0.15ab (10)	0.93±0.11ab (11)	2.49 ± 0.39c (11)
Branch-relate	ed traits					
Wood anat	omy					
d	μm	22.35±0.43a (8)	24.32 ± 0.53ab (11)	23.40±0.50ab (8)	22.21 ± 0.34a (9)	23.55±0.29b (9)
d_{h}	μm	28.6±0.65a (7)	31.36±0.75ab (11)	28.83±0.57a (6)	26.96±0.60a (9)	28.82±0.55b (11)
VD	n mm ⁻²	298.22±10.29a (7)	270.80 ± 10.12b (10)	286.87 ± 16.26ab (8)	281.80 ± 13.45ab (11)	297.37 ± 9.25a (10)
A_{lumen}	%	0.12±0.01a (8)	0.14±0.01a (11)	0.12±0.01a (8)	0.12±0.01a (11)	0.14 ± 0.01a (11)
Hydraulic	properties					
P ₁₂		-1.26±0.21a (10)	–1.03 ± 0.35ab (4)	–2.15±0.21b (11)	–1.97 ± 0.22ab (12)	–1.97 ± 0.22ab (6)
P ₅₀		–2.53±0.15ab (10)	-2.21 ± 0.19a (4)	-2.96±0.09b (11)	-2.97 ± 0.12b (12)	–2.62±0.12ab (6)
P ₈₈		–3.79±0.19ab (10)	-3.38±0.09ab (4)	−3.78±0.07ab (11)	-3.97 ± 0.09b (12)	-3.27±0.08a (6)
Ks	kg m ⁻¹ MPa ⁻¹ s ⁻¹	1.30±0.13ab (10)	1.12 ± 0.12ab (11)	0.94 ± 0.14b (10)	1.05±0.17b (12)	1.63±0.15a (14)
Safety margin	MPa	1.57 ± 0.15ac (10)	1.30±0.19a (4)	2.20±0.0.06b (10)	1.95±0.12bc (12)	1.86±0.12ab (6)
Root-related	traits					
Wood anat	omy					
d	μm	52.03 ± 0.74ab (7)	53.98 ± 1.43b (11)	51.46 ± 1.79b (11)	50.23 ± 1.19b (9)	56.97 ± 1.24a (11)
$d_{\rm h}$	μm	71.86±2.43a (8)	75.75 ± 2.21a (11)	74.07 ± 2.77a (11)	73.55 ± 2.76a (10)	77.78±2.38a (11)
VD	n mm ⁻²	98.82±3.66a (7)	104.94 ± 4.23a (11)	93.91 ± 1.16a (9)	98.67 ± 5.43a (10)	92.82±0.85a (9)
A_{lumen}	%	0.24 ± 0.01a (9)	0.27 ± 0.01a (11)	0.22±0.01a (11)	0.21 ± 0.02a (10)	0.26±0.01a (11)

(CH) differed more from these three Central European demes than did the *P. tremuloides* deme (US), despite its relatively large genetic distance to the *P. tremula* demes. In contrast, the coarse roots of *P. tremuloides* were more different in their anatomy from the European *P. tremula* demes (significant for vessel diameter). The comparison of branch and coarse root xylem in the same plants revealed a two times larger mean vessel diameter, a 2.4–2.7 times larger hydraulically weighted vessel diameter (d_h) and a twice as large relative vessel lumen area (A_{lumen}), but a three times lower VD in coarse root xylem than in branch xylem (Tables 3 and 5, Figures 1a, b and 4).

The branch sapwood area-specific hydraulic conductivity (K_s) significantly differed between demes (Table 3). Mean vessel diameter (d), hydraulically weighted vessel diameter $(d_{\rm h})$ and $A_{\rm lumen}$ were closely related to sapwood area-specific hydraulic conductivity, while no relation was found between VD and K_s (Table 4). In the coarse root xylem, similar relationships were observed between d, d_h and A_{lumen} . Demes with large d_h displayed lower VD in the coarse root xylem (Pearson's r = -0.31, P < 0.05, Table 4). According to the relative abundance of vessel size classes in the xylem and the resulting relative contribution of a diameter class to potential sapwood area-specific hydraulic conductivity derived from the Hagen-Poiseuille equation $(K_{\rm p})$, we grouped the coarse roots into four categories (Figure 1). Root categories 1-4 represent gradients in d, d_h, d_{\rm wm}, VD and $K_{\rm p}$ in the root xylem. Although root categories 2 and 3 did not differ in $d_{\rm h}$ and $K_{\rm p}$, the weighted mean vessel diameter (d_{wm}) as derived from vessel size distribution enabled a clear separation. Roots in category 4 with highest conductivity possessed by far the largest vessels with 40% of all vessels being >100 µm. For comparison, mean vessel diameter in the root xylem averaged only 72–78 μ m in the five demes (all demes pooled; Table 5).

Cavitation resistance expressed by the negative pressure causing 50% loss of conductivity (P_{50}) significantly differed between demes (Table 3). The P_{50} value of branch segments varied from -2.21 MPa in the most vulnerable deme (CH) to -2.96 and -2.97 MPa in the most resistant demes G2 and G8 (Table 3). Significant differences were also found for the mean P_{88} value (range: -3.38 to -3.97 MPa) and the mean P_{12} value of the branch xylem. Across all demes, the mean P_{50} scaled positively with vessel size (d and d_h , Pearson's r = 0.40 and 0.46, P < 0.05; Table 4, Figure 2a) but not with VD and A_{lumen} .



Figure 1. (a) Relative abundance of vessels in 10 diameter classes (white bars) and relative contribution of a vessel size class to total hydraulic conductivity (in percent; black bars) in the branch and root xylem of aspen plants. The coarse root samples (b–e) were grouped into four categories differing in the frequency distribution of vessel size classes and the vessel size class which contributed most to total hydraulic conductivity (K_h). Data are pooled across the five demes. Given are means ± SE of *n* replicates (see the upper right corner of the graph). The size class with the largest number of vessels and its relative contribution to K_h is also indicated.

	Height ₂₀₁₁	RCD ₂₀₁₁	AGR_{biom}	RGR_{biom}	d	$d_{\rm h}$	VD	A_{lumen}	Ks	P ₁₂	P ₅₀	P ₈₈
Height ₂₀₁₁		_	_	_	0.19	-0.01	-0.26	-0.04	_	_	_	_
RCD ₂₀₁₁	0.79***		_	_	0.21	-0.02	-0.26	-0.06	_	_	_	_
AGR	0.87***	0.91***		_	0.26	0.04	-0.26	0.02	_	_	_	_
RGR _{biom}	0.49***	0.57***	0.69***		0.33*	0.22	-0.17	0.23	_	_	_	_
d	-0.11	-0.08	-0.11	0.06		0.68***	-0.18	0.81***	-	-	-	_
d _h	-0.22	-0.21	-0.20	-0.09	0.85***		-0.31*	0.66***	_	_	_	_
VD	0.01	0.04	0.04	0.20	-0.07	0.02		0.31*	_	_	_	_
A _{lumen}	0.01	0.08	0.05	0.08	0.65***	0.66***	0.62***		_	_	_	_
Ks	0.29*	0.51***	0.46***	0.28*	0.44**	0.47**	0.04	0.47**		-	_	-
P ₁₂	-0.07	-0.16	-0.08	0.13	0.26	0.24	0.11	0.08	-0.02		-	-
P ₅₀	-0.09	-0.14	-0.06	0.23	0.40*	0.46*	0.05	0.17	0.28	0.88***		-
P ₈₈	-0.02	0.06	0.08	0.28	0.44*	0.48**	-0.12	0.30	0.61***	-0.03	0.44**	

Table 4. Pearson correlation coefficients for linear relationships among four growth-related traits and nine xylem anatomical and wood hydraulic traits of branch segments (below diagonal) and coarse root segments (above diagonal) in the five aspen demes (n = 25-63).

Significant correlations are marked by *P < 0.05, **P < 0.01, ***P < 0.001 and are in bold. AGR_{biom}, RGR_{biom} and K_s were log-transformed prior to analysis. For abbreviations see Table 2.

Table 5. Differences in five wood anatomical traits and derived theoretical sapwood area-specific hydraulic conductivity for branches and four different coarse root categories in the pooled sample of all five demes. The four root categories were distinguished according to relative vessel size distribution and the percentage contribution of a specific vessel size class to hydraulic conductivity (see Figure 2).

Organ	n	d (μm)	d _h (μm)	d _{wm} (μm)	VD (n mm ⁻²)	$K_{\rm p}~{\rm (kg~m^{-1}~MPa^{-1}~s^{-1})}$	A _{xylem} ^{mean} (mm ²)
Branch	42	23.39 ± 0.23	29.35 ± 0.37	29.35	289.55 ± 5.76	2.88 ± 0.14	23.37 ± 1.22
Root Cat. 1	10	50.64 ± 2.16	71.91 ± 2.12	63.78	96.45 ± 6.51	28.73 ± 3.26	19.18 ± 3.80
Root Cat. 2	25	52.86 ± 1.08	76.02 ± 1.54	73.43	98.13 ± 2.01	36.58 ± 2.58	19.02 ± 1.87
Root Cat. 3	12	53.21 ± 1.64	74.63 ± 2.40	80.84	96.97 ± 4.20	35.79 ± 4.15	14.41 ± 3.30
Root Cat. 4	5	56.43 ± 5.27	78.92 ± 9.38	89.94	100.61 ± 13.28	45.46 ± 14.05	13.44 ± 3.65

n, number of replicates. Values are means \pm SE; for abbreviations see Table 2.

Moreover, the mean P_{50} was not related to the hydraulic conductivity of the demes. However, the mean P_{88} value scaled positively with $K_{\rm s}$ (Pearson's r = 0.61, P < 0.001), indicating that hydraulic conductivity is closely related to the xylem pressure at the 'point of no return', i.e., the limiting pressure before the xylem becomes totally non-conductive (Table 4). The hydraulic safety margin, i.e., the difference between mid-day leaf water potential ($\Psi_{\rm min}$) and the corresponding P_{50} value, was dependent on genotype as well. The $\Psi_{\rm min} - P_{50}$ difference was largest in the German G2 deme and smallest in the Swiss (CH) deme, and it generally increased with decreasing P_{50} (Figure 2b).

Influence of genetic variation on xylem anatomy and hydraulic properties

The results of the Mantel test revealed a close relation between the phylogenetic distances among the demes according to the AFLP markers, and the variation in A_{lumen} and the P_{88} value of the branch xylem. The SSR markers supported this relation and additionally showed a genetic influence on K_s in the branch sample. When all the anatomical and hydraulic traits were pooled in the Mantel test analysis, significant relations to the genetic variation did not appear (Table 6).

Aboveground growth performance and its relatedness to xylem anatomy and hydraulic properties

The five demes differed by factors of four to five in their aboveground productivity in the period April 2010 to April 2011 (measured either as AGR or as RGR; 21.0–109.0 g year⁻¹ for AGR and 0.68–2.49 g g⁻¹ year⁻¹ for RGR, P < 0.001; Table 3).

Among the nine investigated xylem anatomical and hydraulic traits of the branches, only K_s was related to growth rate (AGR and RGR) and also to plant height and RCD. This relation held for the pooled data (Table 4) and also when the RGR means of the demes were plotted against K_s (Figure 3). This was not the case for vessel size (*d* and d_h). Thus, demes with higher growth rates were characterized by higher measured hydraulic conductivities in the branches, while fast growth was not reflected in specific xylem anatomical properties.

Discussion

Intra-specific differences in xylem architecture and hydraulic conductivity in the aspen demes

We found only moderate-to-low genetic variation in branch xylem anatomical traits among the five aspen demes; only a minority



Figure 2. Relationship between hydraulically weighted vessel diameter $(d_{\rm h})$ in the branch xylem and (a) cavitation vulnerability (P_{50}) or (b) cavitation safety margin (i.e., the difference between minimum water potential observed in the field $[\Psi_{\rm min}]$ and P_{50}) in the sample of five demes (*P. tremula*: AU, CH, G2, G8; *P. tremuloides*: US). $\Psi_{\rm min}$ after Müller et al. (2012*a*, 2012*b*).

of intra-specific differences (between the *P. tremula* demes) and also inter-specific differences (between *P. tremula* and *P. tremuloides*) were significant. Fichot et al. (2009) compared the stem xylem anatomy of different *Populus deltoides* × *Populus nigra* hybrids and found relatively large variation, which they explained by the heterogeneity of the plant material, consisting of unrelated inter-specific crossings. Our data seem to support the concept of a close relationship between the two Eurasian and North American aspen species as it appears from genetic and morphological investigations (Eckenwalder 1996).

In contrast to the branches, we observed a high heterogeneity in root-related anatomical and derived hydraulic traits, which enabled a classification of four distinct root categories. We found a strong indication for the existence of several 'highconductivity roots' in these aspen demes, as were described in other temperate broad-leaved tree genera by Rewald et al. (2011) and Köcher et al. (2012). We initially assumed that the four root anatomical categories were mainly an expression of different root diameters, i.e., reflected differences in root age. However, several of the thinnest roots with presumably young age were included in root category 4 which included the 'highconductivity roots'. This finding is highly relevant for studies on root functioning, because it shows that roots in a given diameter class can differ largely in their potential sapwood areaspecific hydraulic conductivity and presumably also in their vulnerability to drought-induced embolism due to the commonly observed relation between vessel size and cavitation resistance (e.g., Awad et al. 2010, Cai and Tyree 2010); simple inference from root diameter on function is thus not possible. Further, aspen branches and roots of similar diameter are largely different in their anatomical properties with no indication of the existence of 'high-conductivity branches'. This large plasticity in root anatomy and functioning is thought to reflect a functional divergence within the root system of trees (McElrone et al. 2004). Surface-directed fine roots may primarily be responsible for nutrient absorption, while deep-reaching roots could mainly serve as water-absorbing and -conducting organs.

The branch sapwood area-specific hydraulic conductivity (K_s) , on the other hand, differed more between the demes than the measured anatomical traits, even though the observed variation in hydraulic efficiency should relate to anatomical differences. However, despite a close relation of K_s to vessel size, the 60% larger K_s in the *P. tremuloides* deme (US) than in the G2 deme is hardly explained by differences in vessel size. This suggests that intra-specific differences in hydraulic conductivity must be at least partly dependent on other conduit properties such as pit membrane structure.

Compared with other temperate tree species or shrubs, poplars are particularly vulnerable to xylem cavitation, which seems to relate to the species' dependence on ample water supply (Tyree and Ewers 1991, Blake et al. 1996, Rood et al. 2003). By contrast, P. tremula and P. tremuloides were found to range among the less vulnerable taxa of the genus due to their adaptation to non-riparian, partly drought-affected habitats (Lieffers et al. 2001, Rood et al. 2007, Anderegg et al. 2012). Our results support the view that P. tremula has a far higher cavitation resistance than most other taxa of the genus. The P_{50} value differed substantially between the most resistant (G2 and G8) and the least resistant (CH) demes. The hydraulic safety margin was dependent on genotype and generally increased with decreasing P_{50} . When the hydraulic safety margin is considered as a key measure of drought tolerance (Choat et al. 2012, Delzon and Cochard 2014, Klein et al. 2014), the Swiss deme with its large branch and root vessels must be considered as the most vulnerable genotype. Surprisingly, the deme means of P_{88} , but not of P_{50} , were significantly related to the genetic constitution according to the AFLP and SSR markers, highlighting the importance of the P_{88} value in angiosperms for predicting the 'point of no return' (Barigah et al. 2013, Urli et al. 2013). The weak genetic differentiation with respect to P₅₀ found between different populations of Fagus sylvatica (Wortemann et al. 2011)

First matrix	Second matrix	Branch sample		Coarse root sample		
		Mantel's <i>r</i>	Probability P	Mantel's r	Probability P	
AGR _{biomass}	AFLPs	0.953	0.163	_	_	
RGR _{biomass}	AFLPs	0.970	0.139	-	_	
d _h	AFLPs	-0.434	0.956	0.707	0.037	
VD	AFLPs	-0.147	0.639	0.013	0.315	
A _{lumen}	AFLPs	0.292	0.027	-0.018	0.511	
Ks	AFLPs	0.330	0.341	0.532	0.146	
P ₁₂	AFLPs	-0.296	0.822	_	_	
P ₅₀	AFLPs	-0.321	0.957	_	_	
P ₈₈	AFLPs	0.343	0.031	-	-	
All anatomical traits	AFLPs	-0.156	0.656	0.208	0.313	
All hydraulic traits	AFLPs	-0.282	0.813	0.541	0.139	
All traits	AFLPs	-0.156	0.656	0.543	0.127	
AGR	SSRs	-0.848	0.879	_	_	
RGR	SSRs	-0.875	0.908	_	_	
d _h	SSRs	-0.356	0.748	0.700	0.049	
VD	SSRs	-0.237	0.820	-0.077	0.460	
A _{lumen}	SSRs	0.491	0.034	0.315	0.079	
P ₁₂	SSRs	-0.357	0.873	_	_	
P ₅₀	SSRs	-0.152	0.635	_	_	
P ₈₈	SSRs	0.554	0.022	-	-	
All anatomical traits	SSRs	-0.241	0.824	0.128	0.349	
All hydraulic traits	SSRs	-0.043	0.391	0.364	0.175	
All traits	SSRs	-0.242	0.7864	0.367	0.169	

Table 6. Results of a Mantel test conducted to analyze the relationship between trait variance (first matrix) and genetic variance according to AFLP or SSR markers (second matrix) in the sample of five demes.

Significantly correlating traits are in bold (P < 0.05). For abbreviations see Table 2.

and Pinus pinaster (Lamy et al. 2011) supports this observation. Thus, the limiting pressure before the xylem becomes totally non-conductive is an indication of the genotypic influence on drought adaptation, in which selection for a more negative P_{88} in trees exposed to water shortage may be a key trait. The branch xylem of the four P. tremula demes and the P. tremuloides deme was fully embolized (P_{88} value) at -3.5 MPa or below (up to -4.0 MPa), which, however, is still much higher than the thresholds reported for the majority of temperate tree species (P_{88} : -4 to -10 MPa; Hacke et al. 2000, Cochard et al. 2008, Urli et al. 2013). In contrast, most of the so far investigated Populus species or poplar hybrids face a fully embolized xylem (P_{88}) when the pressure approaches approximately -1.50 to -2.75 MPa (Cochard et al. 1996, 2007, Harvey and Driessche 1997, Hukin et al. 2005, Fichot et al. 2010). Certain populations or hybrids of P. trichocarpa are reported to be even more vulnerable. However, the genetically most distant demes in our study (US vs G8) were not the most different in terms of cavitation resistance. Thus, the identification of drought-tolerant genotypes for plantation forestry may require empirical testing of hydraulic properties.

Trade-off between growth performance, branch hydraulic conductivity and cavitation resistance

We obtained evidence that a high branch hydraulic conductivity is an important factor causing differences in growth rate

between the five poplar demes. In our study, growth rate (AGR and RGR) scaled positively with branch sapwood area-specific hydraulic conductivity (K_s), which in turn was determined by vessel size (d and $d_{\rm h}$) and the lumen-to-sapwood area ratio (A_{lumen}) . This confirms our assumption that K_{s} represents a suitable measure for comparing the productivity of different aspen demes and suggests that the maintenance of a high leaf area in mid-summer (Müller et al. 2012a, 2012b) depends critically on a minimum conductivity of the axes. The capacity for water transport hence represents another growth-determining factor besides the most widely used proxies for a high growth rate, e.g., a high specific leaf area (Poorter and Garnier 1999), a high leaf mass per plant mass (Poorter and Remkes 1990, Walters et al. 1993), high foliar nitrogen contents and low leaf longevity (Wright and Westoby 2000). However, phenological traits may also determine productivity as was shown by Müller et al. (2012a, 2012b) for the aspen demes investigated in this study. In our plants, neither vessel size nor vulnerability to cavitation directly influenced the growth rate of the five demes, even though $K_{\rm s}$ as well as P_{50} and P_{88} were closely related to vessel size. This indicates that efficient water supply in moist periods seems to be more important than the risk of losing conductivity in drought periods. It should be noted, however, that the intra-specific differences in vessel size between the demes were only small in our sample. Inter-specific contrasts



Figure 3. Sapwood area-specific hydraulic conductivity (K_s , kg m⁻¹ MPa⁻¹ s⁻¹) in relation to (a) absolute or (b) relative growth rate (AGR, g year⁻¹; RGR, g g⁻¹ year⁻¹, logarithmic scale). Data points are pooled samples across each deme (*P. tremula:* AU, CH, G2, G8; *P. tremuloides*: US).

may well show a significant relation between vessel dimensions and growth.

It has been suggested that xylem vulnerability to cavitation increases with increasing growth rate due to conflicting carbon allocation either to the construction of thicker cell walls with less pit-pairs or to the building of foliar and axial tissues destined to increase canopy carbon gain and growth rate (Wikberg and Ögren 2004). However, empirical data from different species or genotypes do not unequivocally support this trade-off. Even though Cochard et al. (2007) report a close relation between xylem vulnerability and productivity in different poplar and willow clones, Fichot et al. (2010) found that cavitation-resistant genotypes of poplar grew faster than the more vulnerable genotypes. This matches with our finding of the lack of a relationship between P_{50} in branches and growth rate across the demes. Drought-induced xylem cavitation as a symptom of distress (Delzon and Cochard 2014) might thus be more closely related to plant survival than to growth (Barigah et al. 2013, Urli et al. 2013).

Our data suggest that the anatomy of the branch xylem does affect growth mainly through axial conductivity and thus via the supply of water, while cavitation vulnerability seems to influence growth only indirectly through a constraining effect of P_{88} on hydraulic conductivity. Thus, faster-growing demes with higher $K_{\rm s}$ experienced earlier full blockage of conduits (higher P_{88} value) than demes with lower $K_{\rm s}$ and slower growth, while the P_{50} value was meaningless. Interestingly, the P_{88} value, and not the P_{50} value, was dependent on genotype. In the five aspen demes, a trade-off existed between hydraulic efficiency and related growth rate on the one hand, and safety from full conduit blocking on the other.

When relating cavitation resistance to xylem anatomy, only mean vessel diameter and hydraulically weighted diameter, but not VD or relative vessel lumen area, influenced P_{50} and P₈₈ values in our sample. This is in accordance with the growing evidence that variation in P_{50} , either between or within species, can be explained by differences in vessel size (e.g., Hacke et al. 2006, Maherali et al. 2006, Cai and Tyree 2010, Domec et al. 2010). A similar relatedness between P_{50} and vessel diameter with relatively little intra-specific variation was found in poplar hybrids (Awad et al. 2010). However, contrasting evidence is also available since several authors failed to detect a relation between vessel diameter and cavitation resistance in closely related genotypes or different hybrids of poplar (Cochard et al. 2007, Fichot et al. 2010). The mechanisms underlying the relationship between xylem anatomy and drought resistance of trees are currently intensively debated, yet with a somewhat different focus on wood density and fiber wall thickness (Hacke et al. 2006, Cochard et al. 2007), pit membrane structure (Choat et al. 2008, Jansen et al. 2009, Plavcova et al. 2013) and vessel grouping (Lens et al. 2011).

Conclusion

This study on the growth performance and hydraulic properties of branch segments in five aspen demes revealed considerable intra-specific differences in the ~20 investigated traits, which partly could be related to differences in the genetic constitution. We found a marked variation in vulnerability to cavitation of the branch xylem among the demes and a close dependence on vessel size. A key finding is that sapwood area-specific hydraulic conductivity in the branches was significantly related to aboveground productivity, while P₅₀ and other hydraulic traits were not. This suggests that axial conductivity and water transport to the leaves under conditions of ample moisture availability seem to be more important for growth than vulnerability to cavitation in dry periods. The branch xylem's vulnerability to cavitation was found to vary independently from sapwood area-specific hydraulic conductivity among the demes, suggesting that the trade-off between growth and xylem safety is not necessarily strong.



Figure 4. Exemplary cross-sectional images of branch (upper left) or coarse root segments (lower left) with sections displayed at higher magnification (upper right and lower right) of the aspen deme US (*P. tremuloides*). The graphs at the right give xylem VCs (PLC vs xylem pressure) for representative (a) branch segments (characteristic s-shaped curve) or (b) coarse root segments (r-shaped curve).

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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References

- Anderegg WRL, Berry JA, Smith DD, Sperry JS, Anderegg LDL, Field CB (2012) The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. Proc Natl Acad Sci USA 109:233–237.
- Anfodillo T, Petit G, Crivellaro A (2013) Axial conduit widening in woody species: a still neglected anatomical pattern. IAWA J 34:352– 364.
- Awad H, Barigah T, Badel E, Cochard H, Herbette S (2010) Poplar vulnerability to xylem cavitation acclimates to drier soil conditions. Physiol Plant 139:280–288.
- Barigah ST, Charrier O, Douris M, Bonhomme M, Herbette S, Ameglio T, Fichot R, Brignolas F, Cochard H (2013) Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. Ann Bot 112:1431–1437.
- Blake TJ, Sperry JS, Tschaplinski TJ, Wang SS (1996) Water relations. In: Stettler RF, Bradshaw HD, Heilman PE, Hinckley TM (eds) Biology of *Populus* and its implications for management and conservation. NRC Research Press, Ottawa, Canada, pp 401–422.
- Cai J, Tyree MT (2010) The impact of vessel size on vulnerability curves: data and models for within-species variability in saplings of aspen, *Populus tremuloides* Michx. Plant Cell Environ 33:1059–1069.
- Cervera MT, Storme V, Soto A, Ivens B, Montagu MV, Rajora OP, Boerjan W (2005) Intraspecific and interspecific genetic and phylogenetic

relationships in the genus *Populus* based on AFLP markers. Theor Appl Genet 111:1440–1456.

- Choat B, Cobb AR, Jansen S (2008) Structure and function of bordered pits: new discoveries and impacts on whole-plant hydraulic function. New Phytol 177:608–626.
- Choat B, Jansen S, Brodribb TJ et al. (2012) Global convergence in the vulnerability of forests to drought. Nature 491:752–755.
- Cochard H, Ridolfi M, Dreyer E (1996) Responses to water stress in an ABA-unresponsive hybrid poplar (*Populus koreana × trichocarpa* cv. *Peace*) II. Hydraulic properties and xylem embolism. New Phytol 134:455–461.
- Cochard H, Damour G, Bodet C, Tharwat I, Poirier M, Améglio T (2005) Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. Physiol Plant 124:410–418.
- Cochard H, Casella E, Mencuccini M (2007) Xylem vulnerability to cavitation varies among poplar and willow clones and correlates with yield. Tree Physiol 27:1761–1767.
- Cochard H, Barigah ST, Kleinhentz M, Eshel A (2008) Is xylem cavitation resistance a relevant criterion for screening drought resistance among *Prunus* species? J Plant Physiol 165:976–982.
- Corcuera L, Cochard H, Gil-Pelegrin E, Notivol E (2011) Phenotypic plasticity in mesic populations of *Pinus pinaster* improves resistance to xylem embolism (P50) under severe drought. Trees 25: 1033–1042.
- Delzon S, Cochard H (2014) Recent advances in tree hydraulics highlight the ecological significance of the hydraulic safety margin. New Phytol (doi:10.1111/nph.12798).
- Delzon S, Douthe C, Sala A, Cochard H (2010) Mechanism of waterstress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. Plant Cell Environ 33:2101–2111.
- Domec J-C, Gartner BI (2001) Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir. Trees 15:204–214.
- Domec JC, Schafer K, Oren R, Kim HS, McCarthy HR (2010) Variable conductivity and embolism in roots and branches of four contrasting tree species and their impacts on whole-plant hydraulic performance under future atmospheric CO₂ concentration. Tree Physiol 30:1001–1015.
- Eckenwalder JE (1996) Systematics and evolution of *Populus*. In: Stettler RF, Bradshaw HD, Heilman PE, Hinckley TM (eds) Biology of *Populus* and its implications for management and conservation. NRC Research Press, Ottawa, Canada, pp 7–32.
- Fan ZX, Zhang SB, Hao GY, Ferry Slik JW, Cao KF (2012) Hydraulic conductivity traits predict growth rates and adult stature of 40 Asian tropical tree species better than wood density. J Ecol 100:732–741.
 EAO (2009) State of the world's forgets EAO. Bend
- FAO (2009) State of the world's forests. FAO, Rome.
- Fichot R, Laurans F, Monclus R, Moreau A, Pilate G, Brignolas F (2009) Xylem anatomy correlates with gas exchange, water-use efficiency and growth performance under contrasting water regimes: evidence from *Populus deltoides* × *Populus nigra* hybrids. Tree Physiol 29:1537–1549.
- Fichot R, Barigah TS, Chamaillard S, Le Thiec D, Laurans F, Cochard H, Brignolas F (2010) Common trade-offs between xylem resistance to cavitation and other physiological traits do not hold among unrelated *Populus deltoides* × *Populus nigra* hybrids. Plant Cell Environ 33:1553–1568.
- Gilmour JSL, Gregor JW (1939) Demes: a suggested new terminology. Nature 144:333.
- Grant M, Mitton J (2010) Case study: the glorious, golden, and gigantic quaking aspen. Nat Educ Knowl 3(10):40.
- Hacke UG, Sperry JS, Pittermann J (2000) Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. Basic Appl Ecol 1:31–41.

- Hacke UG, Sperry JS, Wheeler JK, Castro L (2006) Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiol 26:689–701.
- Hammer, Harper DAT, Ryan PD (2001) PAST—palaeontological statistics software package for education and data analysis. Palaeontol Electron 4:1–9. http://www.uv.es/~pardomv/pe/2001_1/past/pastprog/past.pdf (1 February 2014, date last accessed).
- Harvey HP, van den Driessche R (1997) Nutrition, xylem cavitation and drought resistance in hybrid poplar. Tree Physiol 17:647–654.
- Heinrichs S (2010) Response of the understorey vegetation to selection cutting and clear cutting in the initial phase of Norway spruce conversion. Dissertation, University of Göttingen, Germany. http:// hdl.handle.net/11858/00–1735-0000-0006-B691-E.
- Hukin D, Cochard H, Dreyer E, Thiec DL, Bogeat-Triboulot MB (2005) Cavitation vulnerability in roots and shoots: does *Populus euphratica* Oliv., a poplar from arid areas of Central Asia, differ from other poplar species? J Exp Bot 56:2003–2010.
- IPCC (2007) Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Jansen S, Choat B, Pletsers A (2009) Morphological variation of intervessel pit membranes and implications to xylem function in angiosperms. Am J Bot 96:409–419.
- Keuter A, Hoeft I, Veldkamp E, Corre MD (2013) Nitrogen response efficiency of a managed and phytodiverse temperate grassland. Plant Soil 364:193–206.
- Klein T, Yakir D, Buchmann N, Grünzweig JM (2014) Towards an advanced assessment of the hydrological vulnerability of forests to climate change-induced drought. New Phytol 201:712–716.
- Köcher P, Horna V, Beckmeyer I, Leuschner C (2012) Hydraulic properties and embolism in small-diameter roots of five temperate broad-leaved tree species with contrasting drought tolerance. Ann For Sci 69:693–703.
- Lamy J-B, Bouffier L, Burlett R, Plomion C, Cochard H, Delzon S (2011) Uniform selection as a primary force reducing population genetic differentiation of cavitation resistance across a species range. PLoS ONE 6:e23476.
- Lamy J-B, Delzon S, Bouche PS, Alia R, Vendramin GG, Cochard H, Plomion C (2014) Limited genetic variability and phenotypic plasticity detected for cavitation resistance in a Mediterranean pine. New Phytol 201:874–886.
- Lens F, Sperry JS, Christman MA, Choat B, Rabaey D, Jansen S (2011) Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. New Phytol 190:709–723.
- Lieffers V, Landhäusser S, Hogg E (2001) Is the wide distribution of aspen a result of its stress tolerance? In: Shepperd WD, Binkley D, Bartos DL, Stohlgren TJ, Eskew LG (eds) Sustaining aspen in western landscapes: symposium proceedings. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Grand Junction, Colorado, pp 311–323.
- Maherali H, Moura CF, Caldeira MC, Willson CJ, Jackson RB (2006) Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. Plant Cell Environ 29:571–583.
- Marron N, Ceulemans R (2006) Genetic variation of leaf traits related to productivity in a *Populus deltoides* × *Populus nigra* family. Can J For Res 36:390–400.
- Martínez-Vilalta J, Cochard H, Mencuccini M et al. (2009) Hydraulic adjustment of Scots pine across Europe. New Phytol 184:353–364.
- McElrone AJ, Pockman WT, Martínez-Vilalta J, Jackson RB (2004) Variation in xylem structure and function in stems and roots of trees to 20 m depth. New Phytol 163:507–517.

- Monclus R, Dreyer E, Villar M et al. (2006) Impact of drought on productivity and water use efficiency in 29 genotypes of Populus deltoides × Populus nigra. New Phytol 169:765-777.
- Müller A, Horna V, Zhang C, Leuschner C (2012a) Different growth strategies determine the carbon gain and productivity of aspen collectives to be used in short-rotation plantations. Biomass Bioenerg 46:242-250.
- Müller A, Leuschner C, Horna V, Zhang C (2012b) Photosynthetic characteristics and growth performance of closely related aspen taxa: on the systematic relatedness of the Eurasian Populus tremula and the North American P. tremuloides. Flora 207:87-95.
- Pakull B, Groppe K, Meyer M, Markussen T, Fladung M (2009) Genetic linkage mapping in aspen (Populus tremula L. and Populus tremuloides Michx.). Tree Genet Genom 5:505-515.
- Plavcova L, Jansen S, Klepsch M, Hacke UG (2013) Nobody's perfect: can irregularities in pit structure influence vulnerability to cavitation? Front Plant Sci 4:453.
- Poorter H, Garnier E (1999) Ecological significance of inherent variation in relative growth rate and its components. In: Pugnaire FI, Valladares F (eds) Handbook of functional plant ecology. Marcel Dekker, New York, pp 81-120.
- Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia 83:553-559.
- R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rewald B, Leuschner C, Wiesman Z, Ephrath JE (2011) Influence of salinity on root hydraulic properties of three olive varieties. Plant Biosyst 145:12-22.
- Rood SB, Braatne JH, Hughes FMR (2003) Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. Tree Physiol 23:1113–1124.
- Rood SB, Goater LA, Mahoney JM, Pearce CM, Smith DG (2007) Floods, fire, and ice: disturbance ecology of riparian cottonwoods. Can J Bot 85:1019-1032.
- Rosner S, Klein A, Müller U, Karlsson B (2008) Tradeoffs between hydraulic and mechanical stress responses of mature Norway spruce trunk wood. Tree Physiol 28:1179–1188.
- Russo SE, Jenkins KL, Wiser SK, Uriarte M, Duncan RP, Coomes DA (2010) Interspecific relationships among growth, mortality and xylem traits of woody species from New Zealand. Funct Ecol 24:253-262.
- Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heat waves. Nature 427:332-336.

- Sparks JP, Black RA (1999) Regulation of water loss in populations of Populus trichocarpa: the role of stomatal control in preventing xylem cavitation. Tree Physiol 19:453-459.
- Sperry JS, Saliendra NZ (1994) Intra- and inter-plant variation in xylem cavitation in Betula occidentalis. Plant Cell Environ 17:1233-1241.
- Sperry JS, Donnelly JR, Tyree MT (1988) A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell Environ 11: 35 - 40
- Tyree MT (2003) Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. Trees 17:95-100.
- Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. New Phytol 119:345-360.
- Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap. Springer, Berlin, Heidelberg.
- Tyree MT, Kolb KJ, Rood SB, Patiño S (1994) Vulnerability to droughtinduced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? Tree Physiol 14:455-466.
- Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S (2013) Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. Tree Physiol 33:1-12.
- Van der Willigen C, Pammenter NW (1998) Relationship between growth and xylem hydraulic characteristics of clones of Eucalyptus spp. at contrasting sites. Tree Physiol 18:595-600.
- Walters MB, Kruger EL, Reich PB (1993) Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic considerations. Oecologia 96:219-231.
- White FM (1991) Viscous fluid flow. MacGraw, New York.
- Wikberg J, Ögren E (2004) Interrelationships between water use and growth traits in biomass-producing willows. Trees 18:70-76.
- Wortemann R, Herbette S, Barigah TS, Fumanal B, Alia R, Ducousso A, Gomory D, Roeckel-Drevet P, Cochard H (2011) Genotypic variability and phenotypic plasticity of cavitation resistance in Fagus sylvatica L. across Europe. Tree Physiol 31:1175-1182.
- Wright IJ, Westoby M (2000) Cross-species relationships between seedling relative growth rate, nitrogen productivity and root vs leaf function in 28 Australian woody species. Funct Ecol 14: 97-107.
- Zhang C (2012) Genetic analysis of aspen (Populus tremula L. and Populus tremuloides Michx.) in a diversity experiment. Dissertation, University of Göttingen, Germany.
- Zhang J-L, Cao KF (2009) Stem hydraulics mediates leaf water status, carbon gain, nutrient use efficiencies and plant growth rates across dipterocarp species. Funct Ecol 23:658-667.