

Xylem plasticity allows rapid hydraulic adjustment to annual climatic variability

Marina Bryukhanova · Patrick Fonti

Received: 5 May 2012/Revised: 5 October 2012/Accepted: 31 October 2012/Published online: 22 November 2012
© Springer-Verlag Berlin Heidelberg 2012

Abstract Thanks to acclimation, trees overcome environmental changes and endure for centuries. The anatomy of water conducting cells is an important factor determining plant success. Forming cells are coupled with the environment and their properties are naturally archived in the wood. Its variability across tree rings can thus provide a retrospective of plant's hydraulic adjustments. In this work, we measured lumen and wall thickness of tracheids along tree-rings to explore how trees regulate their conducting system under variable plant-water conditions. Tracheids were measured along 51 dated rings of five mature *Larix decidua* and *Picea abies* trees from a low elevation site. Anatomical-based chronologies of annual growth performance, hydraulic conductance and safety, and construction costs were built. Similarities among chronologies and the relation to monthly climate data were analyzed. Most parameters displayed high annual plasticity which was partly coherent among trees and mostly associated with radial growth. In general, summer drought reduced growth and potential hydraulic conductivity of the forming ring, and increased hydraulic safety and construction costs. To evaluate the functional relevance of the annual acclimation,

the conductivity of the forming ring relative to the entire sapwood needs to be assessed.

Keywords Tree-ring anatomy · Tracheid-cell chronologies · Plant-water relations · *Larix decidua* · *Picea abies*

Introduction

To grow, trees must collect water from the root and transport it to the canopy, where photosynthesis occurs. However, because the hydraulic pathway is under strong negative pressures, the system is vulnerable to the formation of bubbles (cavitation or embolism) breaking water uplift (Hacke and Sperry 2001) and leading to serious consequences for survival and performance (McDowell et al. 2008). Thus, especially for trees growing in water-limited environment, it is essential to find an optimal hydraulic architecture that can guarantee both an efficient and safe water transport.

Over their lifespan, trees have a wide range of possibilities to adjust their hydraulic structure by increasing negative pressure. Among them, stomatal closure is an effective and immediate physiological response. However, this is not an ideal long-term solution because photosynthetic carbon uptake is significantly impeded. Long-term solutions are oriented to reduce evaporative demand, increase access to soil water, or increase conductive area, but whole-tree architectural changes are not adequate to rapidly respond to the inter-annual climatic variability.

The adjustment to climatic variability is usually controlled at xylem level by regulating conduits hydraulic properties (Tyree and Zimmermann 2002) as the size and number of conduits and their type of interconnections. For

Communicated by Y. Sano.

M. Bryukhanova
V.N. Sukachev Institute of Forest SB RAS, Akademgorodok 50,
bld. 28, Krasnoyarsk 660036, Russia
e-mail: mbryukhanova@mail.ru

P. Fonti (✉)
Landscape Dynamics, WSL Swiss Federal
Research Institute, Zürcherstr. 111, Birmensdorf,
8903 Zurich, Switzerland
e-mail: patrick.fonti@wsl.ch

example, within the same individual, larger conduits allow more efficient water flow but are simultaneously more prone to failure. The risk of failure can be reduced at the cost of efficiency, i.e., by reducing the proportion of hydraulically efficient conduits (Pittermann et al. 2006a, b); by reinforcing conduit wall (Chave et al. 2006; Martinez-Cabrera et al. 2009) or interconduit pits aperture (Choat et al. 2008; Hacke and Jansen 2009); by increasing redundancy through independent modular pathways (Schenk et al. 2008); and by refilling embolized conduits (Salleo et al. 2009).

Insights into xylem hydraulic adjustments to changing environmental conditions have primarily been obtained through structural and functional comparative studies between or within *taxa* on contrasting sites or along environmental gradients (e.g., Maherali et al. 2004; Beikircher and Mayr 2009; Barnard et al. 2011). Presently, the study of xylem hydraulic adjustments in response to changes occurring over a tree's lifetime has been minimally investigated (Meinzer 2011). Since growth represents the ability of the tree to actively perform these adjustments and since these modifications are, year after year, archived in the growing rings, the radial variation of wood structure along tree-rings might reflect the changing hydraulic and mechanical demands placed upon the trees. Therefore, the potential to use time series of hydraulic relevant properties of water conducting cells as an ecological proxy for plant-water relations providing a basis for better predictions of woody plant behaviour across environments exists (Holbrook and Zwieniecki 2005).

To date, cell anatomical analyses along tree-rings have explored the potential for obtaining high-resolution proxies through identification of the environmental factor and the period of the growing season that primarily influences year-to-year cell lumen variability. Analyses of inter-annual variability in the size of water conducting cells—vessels in deciduous trees and tracheids in conifers—have shown that conduits can carry sub-annual information reflecting changes in regional environmental conditions [see (Fonti et al. 2010) for a review]. Despite the close link between wood anatomy and water transport, wood anatomical variables have rarely been used to investigate xylem hydraulic adjustments to changes in water availability over the life of a tree. The study of these changes in relation to the climatic variability can likely provide valuable insight of tree hydraulic acclimation.

In this study, we developed new chronologies of xylem hydraulic relevant parameters, relative to growth performance, hydraulic efficiency, hydraulic safety, and costs of conduit construction, to retrospectively evaluate how trees have modified their wood structure to regulate the delicate balance between hydraulic efficiency and safety in response to varying climatic conditions. From these

observations, we hope to contribute a more detailed understanding of hydraulic adjustment strategies. In particular, we collected a new complete data set of tracheid anatomical measurements along series of tree-rings from two coniferous species (*Larix decidua* and *Picea abies*) grown in a dry environment. A tree-ring anatomical approach will be applied to evaluate the annual plasticity of competing hydraulic properties and the strength of the environmental response will be explored and discussed.

Materials and methods

Study site and wood sampling

The study site is located at 800 m a.s.l on a north facing slope above the village of Gampel (46°18'10"N, 7°44'30"W) within the inner-alpine Swiss Rhone valley (Canton Valais). The climate in the valley is continental with a mean annual temperature of 9.6 °C and an annual precipitation of 604 mm (data for the period 1958–2006 from MeteoSwiss weather station of Sion, 492 m a.s.l., 30 km east of the study site). The summer months are usually dry due to warm day temperatures (average 25–35 °C from June to September) and little precipitation (45 mm/months). The forest on the site is a mixture of *Larix decidua*, *Picea abies* and *Pinus sylvestris*, which are 120–180 years old and 20–25 m in height.

For the study, 15 mature and dominant trees of both *Larix* and *Picea* were selected. From each tree, we sampled two 5 mm diameter wood cores. Stem cores were taken close to each other at breast height and perpendicular to slope direction to avoid reaction wood. One core was used for tree-ring width measurement and dating, while the second one served for tracheid anatomical measurements.

Tree-ring width and tracheid anatomical measurements

Ring widths (TRW) were measured along the whole core using the LINTAB and TSAP system (Rinntech, Germany) with dating verified using COFECHA. Tracheids were measured on a selection of 5 cores per species for all the rings formed between 1960 and 2010 (51 rings). This selection considered the cores having the highest correlation with the TRW master chronology. All anatomical measurements have been performed using the image analysis software Image-Pro Plus (Media Cybernetic, Inc., Silver Spring, MD, USA). Images of thin ring cross sections (RGB, 24 bit colour) were captured using a digital video camera (ColorView III, Soft Imaging System, Germany) connected to a transmitted light microscope (Olympus BX41, Japan) with a 100 × magnification (image resolution: 2.93 pixel/μm; tangential and radial field of view:

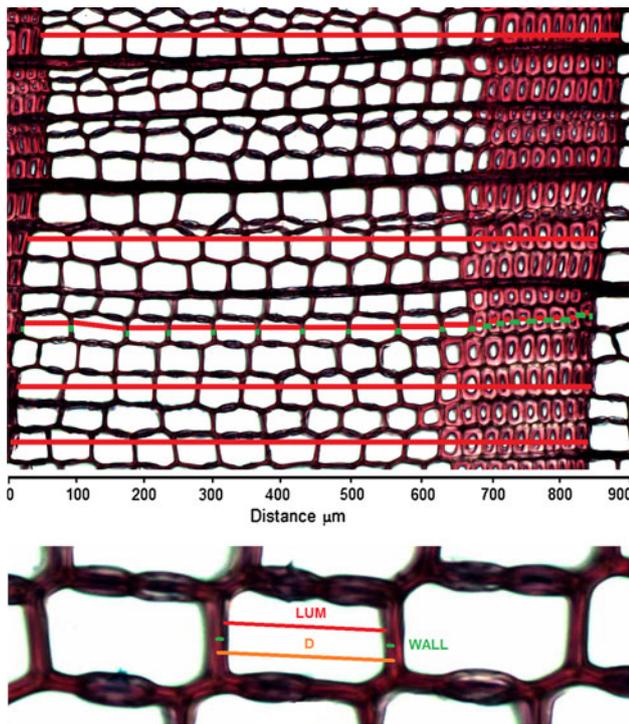


Fig. 1 Example of a captured image of *Larix decidua* and relative cell anatomical measurements. Red lines indicate the radial files measured. On the lower image a magnification to explain how the tracheid lumen (LUM), wall thickness (WALL), and diameter (D) have been measured

0.66 × 0.87 mm) (Fig. 1). Images from the same annual ring were stitched together using the program PTgui (New House Internet Services B.V., The Netherlands). Thin sections (aprox. 20 μm thick) were prepared with a sliding

microtome (Reichert, Germany), stained with safranin and astrablue, and fixed with Canada balsam.

Tracheids were measured cell by cell along five tracheid radial files of each ring. Within each cell, we measured the radial lumen width (LUM), the cell wall thickness (WALL, calculated as the sum of half the double cell wall thickness common to the adjacent cells), and the diameter ($D = LUM + WALL$). To consider only tracheids cut close to the middle of their longitudinal length, we selected tracheid files showing the largest tangential cells. Cells were then assigned to earlywood or latewood according to the LUM/WALL-ratio (Fig. 2). We applied two criteria to distinguish earlywood to latewood tracheids. First, using a threshold value defined as the minimum distribution frequency of the LUM/WALL-ratio of all measured tracheids (i.e., 2.21 for larch and 2.5 for spruce). Along the radial file, all cells located before two consecutive latewood cells were considered earlywood cells. Second, to evaluate the influence on the final results of the EW-LW definition, more conservative criteria excluding the cells in the transition zone (i.e., LUM/WALL-ratio between 1.5–3.0 for larch and 1.5–2.5 for spruce) were also applied.

Chronology building and climate–growth relationships

The tracheid measurements performed for each annual ring supplied the basis for the calculation of 30 tree-ring anatomical chronologies assembled in 4 functional groups, i.e., indicative of growth performance, hydraulic conductivity, hydraulic safety and mechanical support, and cost of conduit construction (Table 1). Parameters include cellular metrics commonly used in plant hydraulic studies as well

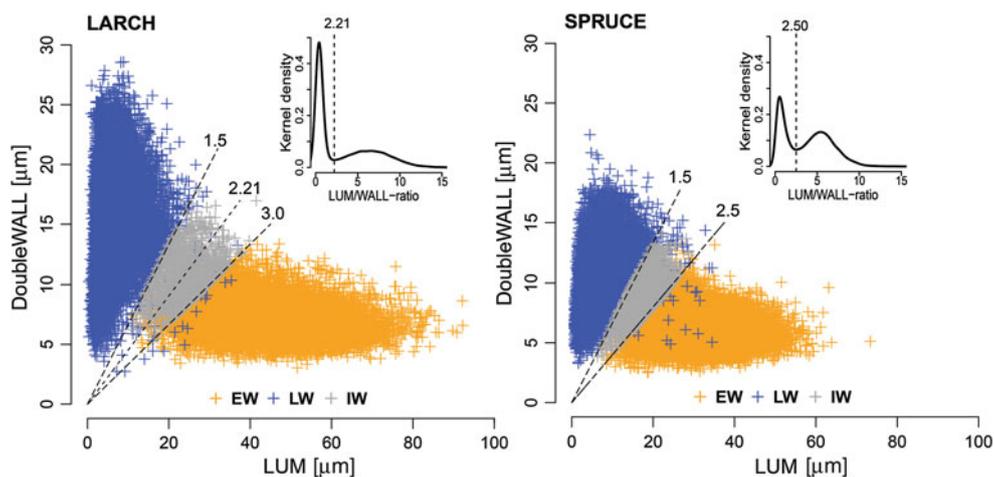


Fig. 2 Distinction between earlywood and latewood tracheids. The threshold value has been defined as the value corresponding to the kernel density minima on the distribution of the LUM/WALL-ratio (see indent plot). The distinction of earlywood (orange circle) and latewood tracheids (blue circle) according to the value of the

threshold ratio (dotted line) is shown in the LUM versus WALL plot. The more conservative assignment of earlywood to latewood exclude the cells of the transition zones (IW, grey circle), i.e., the cells in the area between the LUM/WALL-ratio lines (1.5 and 3.0 for larch and 1.5 and 2.5 for spruce)

as in new self-developed parameters, which consider the performance of tracheids with different sizes (i.e., the size distribution of tracheids). The parameters were calculated by averaging the measurements of the five radial files for each annual ring and each tree. Subsequently, to only focus on the high-frequency signal, long-term trends have been removed from the individual time series by fitting a cubic smoothing spline function with 32-year stiffness and 50 % cut-off. The ratio between the measured values and the fit spline was used as the high-frequency variability (Cook and Kairiukstis 1990). Finally, the chronologies were obtained by averaging the new obtained indexed time series. The quality of the signal was assessed by calculating the mean correlation between trees (Rbt). To evaluate the similarities between the 30 chronologies, we used a principal component analysis to ordinate all parameters along two principal components. The correlation matrix has been used to avoid differences in variance between the factors. The significance of the principal components was verified with the Scree plot method (Horn 1965), which compare the ordered eigenvalues of the observed data with the eigenvalues of matrices of rank equal to the observed data, but with uncorrelated variables. If the eigenvalue of the principal component of the observed data is higher than the random matrix, the principal component is considered interpretable. Climate–growth relationships were established by computing Pearson’s correlations between the detrended tree-ring anatomical chronologies and the equally 32-year spline detrended monthly average temperature, total monthly precipitation and soil water deficit. The soil water deficit was obtained using the AET-calculator, a program for calculating the annual climatic water balance using the modified Thornthwaite method considering a field capacity of 100 mm and the declining availability function G (Schenk et al. 2008). Climatic data were obtained from the MeteoSwiss weather station of Sion (1960–2010).

Results

Tree-ring width and cross-dating

The 15 selected trees per species show a slight decreasing growth trend, except for a growth release following a thinning around 1950 (Fig. 3). TRW is similar between species, and is on average 0.913 mm for larch and 0.805 mm for spruce (Table 2). The common signal (Rbt) calculated as the correlation among the 32-year spline detrended time series over the period covered by at least five trees is 0.56 for larch and 0.42 for spruce. The correlation between the full detrended chronologies of the two species is 0.60. Considering the last 51 years (i.e., the years

used for the anatomical measurements), there is no evidence of major events affecting the growth trend. The TRW of the 5 trees selected for the anatomical measurements are representative of the stand, and the correlation between these chronologies over the common period from 1960 to 2010 is 0.92 for larch and 0.88 for spruce.

Tracheid characteristics

Considering the five trees per species, a total of 62,893 tracheids, 31,888 for larch and 31,005 for spruce were measured (Table 2). This corresponds to a total of approximately 130 cells per ring (26 per radial file). On average, an annual ring includes 11 earlywood and 15 latewood cells in larch and 15 earlywood and 11 latewood cells in spruce. Overall, larch cells are larger and with thicker cell walls than spruce cells. Mean earlywood D is 52.75 and 38.24 μm , and latewood D is 22.65 and 19.75 μm for larch and spruce, respectively. Larch earlywood tracheids have 38 % larger lumina and 20 % thicker cell walls than spruce. These values are +14 and +45 % for latewood tracheid lumina and wall thickness, respectively. However, LUM and WALL vary from year-to-year. The observations of LUM and WALL distributions between the rings (Fig. 4) show that their frequency per size class can strongly vary for both earlywood and latewood in each species. Variation in the amount of tracheids per size class, especially for the LUM classes at the upper limit of the distribution, play a major role for water transport and safety. For example, the mean lumen width of earlywood tracheids (MTLUM.E) ranges from 41.7 to 51.4 (23 %) and from 28.13 to 34.55 (23 %) for larch and spruce, respectively. A similar range of variations have been observed for other cell size parameters in MTWALL.E (23 % for larch and 28 % for spruce), LUMrange.E (94 and 61 %) and WALLrange.E (49 and 31 %), which characteristics eventually determine the hydraulic properties of the annual ring (Table 3). This variability influences the annual variability of the other derived hydraulic characteristics. Other than a small decrease over time of latewood tracheid wall thickness, no long-term trends were detectable.

Common and climatic signal

The year-to-year variability observed in the tracheid size (LUM and WALL) is also reflected in the characteristics of the derived chronologies of the four functional groups. The strength of the common signal between the five trees indicates that for some of the parameters there is no common response between the trees (Table 3). The common signal quantified as the correlation between the trees (Rbt) ranges between 0.50 and slightly negative values for

Table 1 Description of anatomical parameters

Code	Description	Unit	Formula	Level
Anatomical cell parameters				
LUM	Radial lumen diameter	μm	–	Cell
WALL	Radial double wall thickness	μm	–	Cell
D	Radial diameter	μm	$D = \text{LUM} + \text{WALL}$	Cell
Derived tree-ring parameters				
Growth performance				
TRW	Tree-ring width	mm	ΣD	Row
EWW	Earlywood width	mm	ΣD_E	Row
LWW	Latewood width	mm	ΣD_E	Row
NT.E	Number of ET	–	–	Row
NT.L	Number of LT	–	–	Row
Hydraulic efficiency				
MTD.E	Diameter of ET	μm	Mean (D_E)	Row
MTLUM.E	Lumen diameter of ET	μm	Mean (LUM_E)	Row
MaxLUM.E	Lumen diameter of the largest ET	μm	Max (LUM_E)	Ring
LUM90.E	Lumen diameter of the 90th percentiles of ET	μm	$Q_{90}(\text{LUM}_E)$	Ring
Cond.E	Hydraulic conductivity of ET	μm^4	Sum (LUM_E^4)	Row
Cond5.E	Hydraulic conductivity of the 5 largest ET	μm^4	Sum (LUM_{E1-E5}^4)	Ring
HD.E (d_h)	Hydraulic conduit diameter of ET	μm	Sum (LUM_E^2)/sum (LUM_E^4)	Row
Hydraulic safety and mechanical support				
MTD.L	Diameter of LT	μm	Mean (D_L)	Row
MTLUM.L	Lumen diameter of LT	μm	Mean (LUM_L)	Row
MTWALL.E	Wall thickness of ET	μm	Mean (WALL_E)	Row
MaxWALL.E	Wall of the thickest ET	μm	Max (WALL_E)	Ring
MaxWALL.L	Wall of the thickest LT	μm	Max (WALL_L)	Ring
WALL90.E	Wall thickness of the 90th percentile of ET	μm	$Q_{90}(\text{WALL}_E)$	Ring
WALL90.L	Wall thickness of the 90th percentile of LT	μm	$Q_{90}(\text{WALL}_L)$	Ring
MTWALL.L	Wall thickness of LT	μm	Mean(WALL_L)	Row
CWA.E	Cell wall area of ET	μm^2	Mean ($\text{WALL}_E \times (T_E + D_E - \text{WALL}_E)$) <small>$T = \text{tracheid tangential thickness} = 30\mu\text{m}$</small>	Row
CWA.L	Cell wall area of LT	μm^2	Mean ($\text{WALL}_L \times (T_L + D_L - \text{WALL}_L)$) <small>$T = \text{tracheid tangential thickness} = 30\mu\text{m}$</small>	Row
TtoB	Cell wall reinforcement as “thickness to span ration” (t/b) _h ² (Hacke et al. 2001)	–	Mean ($2 \times \text{WALL}/\text{LUM}$) _($D_h \pm 10 \mu\text{m}$) ² <small>$D_h = \text{hydraulic conduit diameter}$</small>	Ring
PerLW	Percentage of latewood width	%	LTW/TRW	Row
LUMrange.E	Range between 10th and 90th percentiles of ET lumen diameter	μm	$Q_{90}(\text{LUM}_E) - q_{10}(\text{LUM}_E)$	Ring
WALLrange.E	Range between 10th and 90th percentiles of ET wall thickness	μm	$Q_{90}(\text{WALL}_E) - q_{10}(\text{WALL}_E)$	Ring
L50	Tracheid lumen by 50 % loss of conductivity	μm	LUM_E by 50 % Cond_E	Ring
Construction costs				
Ratio5.E	Ratio LUM/WALL of the five largest ET	–	Mean ($\text{LUM}_{E1-E5}/\text{LUM}_{E1-E5}$)	Ring
Carb.E	Cell wall area per hydraulic conductivity of ET	μm^{-2}	Sum ($\text{CWA}_E/\text{Cond}_E$)	Row
RatioEWLW	Ratio between ET and LT radial diameter	–	Mean (D_E)/mean (D_L)	Row

Level indicates the organisation level the parameter refers to: *Cell* relative to each single measured tracheid, *Row* relative to each radial file and then averaged per the files in the ring, *Ring* for all cells in the ring, independently from which radial file the cells belong to, *ET* Earlywood tracheids, *LT* Latewood tracheids

some parameters describing the hydraulic safety. In general, Rbt is higher for larch than for spruce and for the parameters of growth performance and conductivity than

for other hydraulic parameters. The methods to discriminate between earlywood and latewood tracheids did not affect the signal, and the results are shown only for the

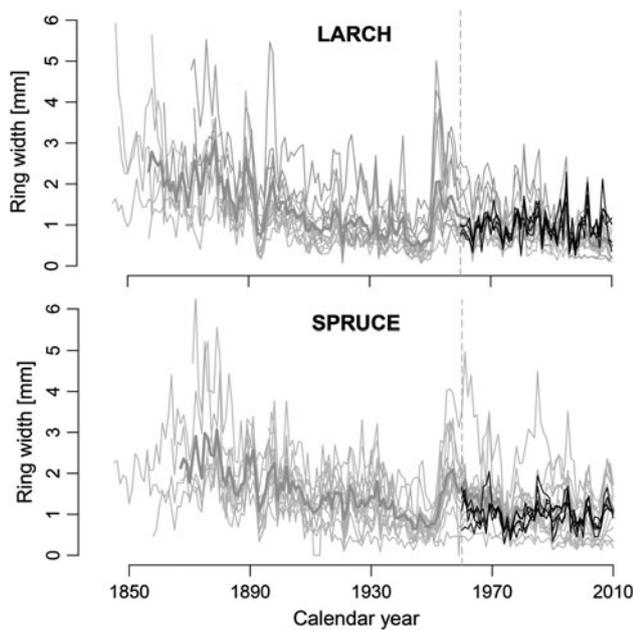


Fig. 3 Ring-width time series of sampled trees (*thin grey lines*) with average chronology (*grey thick line*, sample size >4). The annual rings used for wood anatomical measurements are indicated with *thin black lines* (period 1960–2010)

threshold method (Fig. 2). Detrending does not substantially improve the signal strength, indicating the absence of a common long-term trend in the chronologies.

The ordination of all parameters along two principal components was used to explore the relative similarities between the chronologies (Fig. 5). The results indicate that the first two principal components can explain 78 and 74 % of the variance for larch and spruce. The high proportion of variance explained indicated that there is not much

difference in the content of information between TRW and most of the other parameters, except for Carb.E which is a bit more dissociated. Correlations performed between TRW and all the others parameters quantify how close the parameters are related to TRW (Table 3).

The climate-growth relationships performed for a representative parameter of each functional group (TRW, Cond.E, MTWALL.E and Carb.E) indicate that, generally, there is no dominant and clear pattern of response to both temperature and precipitation (correlations are mostly not significant to $p < 0.05$). However, the signal appears slightly more distinct in regard to the summer soil water index (Fig. 6). Although not significant in most of the cases, TRW and Cond.E respond similarly and negatively to the summer soil water index, indicating the response in larch is more related to the previous year's growth than for the current growing season. Similar but weaker relationships to water availability are found for CARB.E (positive relationship over the current summer for both species) and for MTWALL.E (positive relationship over the current spring in larch).

Discussion

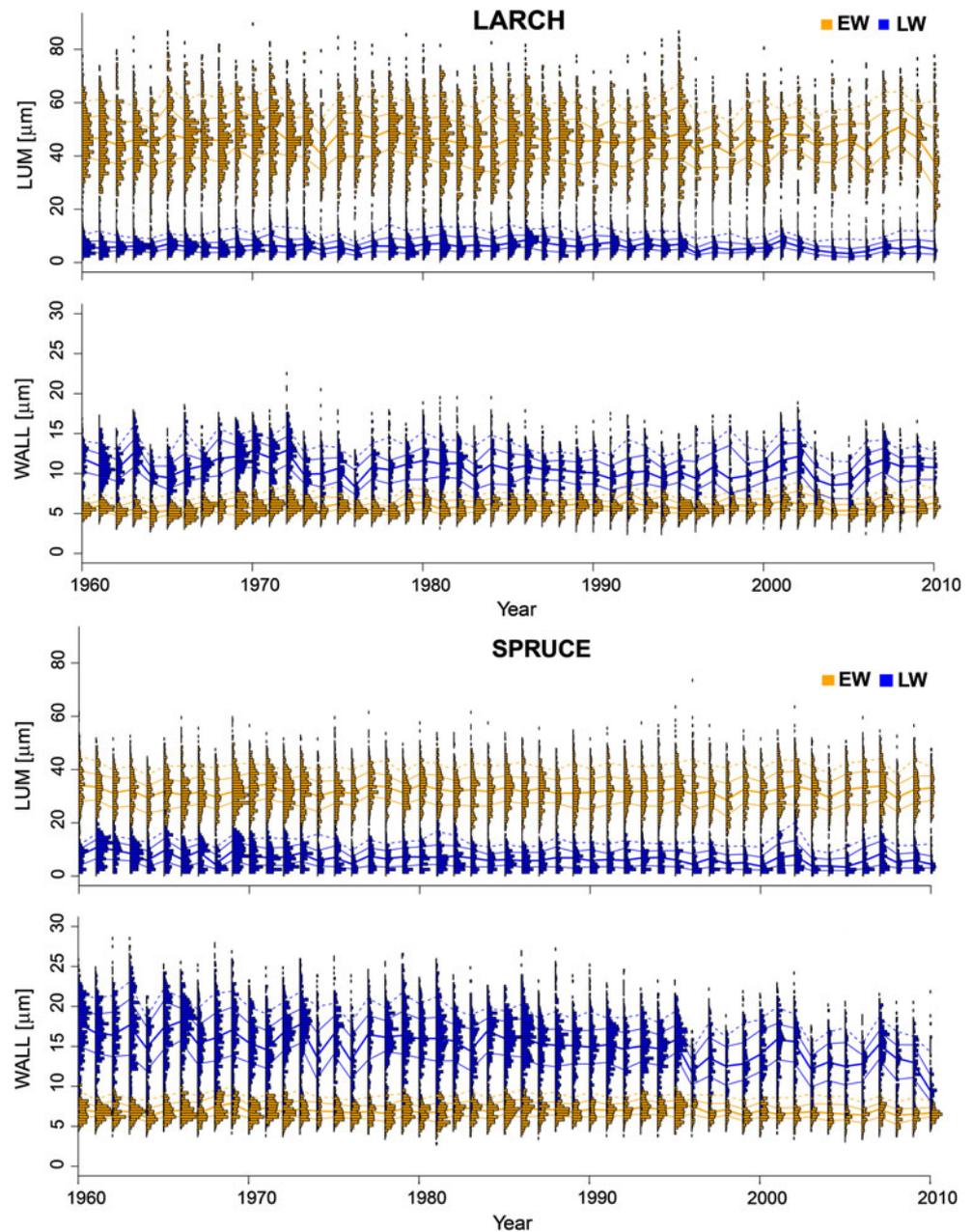
In this study, by analyzing the variability contained in the xylem structure of dominant and adult trees, our focus has been on changes induced by water availability conditions across years. Our description of tracheid anatomical features along 50 tree-rings clearly demonstrates that the majority of the derived hydraulic relevant parameters are (i) highly plastic (i.e., changes from year to year), (ii)

Table 2 Summary statistics (mean, minimum–maximum) of ring width and tracheid anatomical parameters (LUM, WALL and D) grouped for earlywood and latewood

	Ring width (mm)	Number of cells	LUM (μm)	WALL (μm)	D (μm)
Larch					
Earlywood	0.583	11.06	45.55	7.20	52.75
	0.099–1.446	2–31	10.59–92.24	3.04–16.95	16.89–100.79
Latewood	0.330	14.57	7.30	15.35	22.65
	0.009–1.314	1–50	0.34–49.10	2.74–28.58	5.96–55.76
All ring	0.913	25.63	23.80	11.83	35.64
	0.123–2.356	4–69	0.34–92.23	2.74–28.58	5.96–100.79
Spruce					
Earlywood	0.595	15.57	32.26	5.97	38.24
	0.049–2.109	2–55	7.49–73.38	2.51–13.31	11.78–78.51
Latewood	0.210	10.64	9.20	10.55	19.75
	0.015–1.788	2–73	0.68–35.05	3.28–22.35	4.90–47.19
All ring	0.805	26.21	22.89	7.83	30.73
	0.121–2.997	7–92	0.68–73.38	2.51–22.35	4.90–78.50

Earlywood and latewood has been discriminated according to the “threshold method” (Fig. 2)

Fig. 4 LUM and WALL distribution per annual ring differentiating between earlywood (*orange*) and latewood (*blue*) tracheid. The relative number of conduits is given for 1 μm classes. *Thick lines* indicate the mean, the *dotted line* in the 10 and 90 percentile respectively



partially coherent between trees, and (iii) strongly correlated to the radial growth. In general, drought induces increasing hydraulic safety with increasing construction costs and reduces the hydraulic efficiency and growth.

Plastic responses are mainly annually

Although it is difficult to detect long-term trends on such relatively short time series, the large majority of the variability observed was primarily related to changes occurring at the year-to-year level. Results clearly show substantial changes in the annual distributions and means of tracheid lumen (LUM) and cell wall (WALL) (Fig. 4). The absence

of a long-term trend might be explained by relatively stable tree height and crown size. First, the trees considered were already mature and around 100 years old in 1960 (i.e., the year of the youngest tree ring of the chronologies, Fig. 3), and thus, the hydraulic parameters were likely not affected by changes in tracheid size due to conduit tapering related to increasing tree height (Anfodillo et al. 2006). Second, although the absence of management over the last 60 years (last thinning in 1950) might have reduced crown sizes and evaporative demand due to an increased competition for space, the ring width pattern over the last 50 years appears almost free of long-term trends (Fig. 3). This hypothesis is supported by the absence of a long-term trend in the

Table 3 Summary statistics and common signal of anatomical and hydraulic chronologies

	Unit	LARCH						SPRUCE					
		Min	Mean	Max	Rbt raw	Rbt ratio	r to TRW	Min	Mean	Max	Rbt raw	Rbt ratio	r to TRW
Growth performance													
TRW	mm	0.328	0.915	1.510	0.50	0.47	1.00	0.409	0.807	1.584	0.23	0.33	1.00
EWV	mm	0.215	0.568	0.890	0.53	0.45	0.97	0.333	0.600	1.071	0.21	0.31	0.97
LWW	mm	0.072	0.318	0.615	0.41	0.44	0.92	0.054	0.166	0.472	0.15	0.16	0.83
NT.E	–	4.4	10.6	16.3	0.47	0.40	0.96	9.3	15.8	27.8	0.24	0.33	0.95
NT.L	–	4.5	14.2	25.1	0.42	0.45	0.94	4.1	9.0	22.1	0.16	0.19	0.83
Hydraulic conductance													
MTD.E	µm	48.03	54.09	57.91	0.17	0.21	0.70	34.22	37.32	40.15	0.02	0.11	0.57
MTLUM.E	µm	41.70	47.10	51.40	0.18	0.20	0.67	28.13	31.45	34.55	0.03	0.09	0.53
MaxLUM.E	µm	49.09	60.48	67.94	0.39	0.33	0.74	35.58	42.01	46.56	0.12	0.24	0.70
LUM90.E	µm	50.98	58.6	64.36	0.23	0.24	0.66	34.21	39.49	43.34	0.06	0.15	0.55
Cond.E	µm ⁴	1.6E + 07	6.8E + 07	1.3E + 08	0.54	0.45	0.93	1.0E + 07	2.3E + 07	4.1E + 07	0.12	0.23	0.89
Cond5.E	µm ⁴	3.6E + 07	8.7E + 07	1.4E + 08	0.31	0.24	0.72	1.2E + 07	2.0E + 07	3.4E + 07	0.11	0.20	0.63
HD.E	µm	45.15	52.75	57.71	0.31	0.30	0.71	30.94	35.71	38.95	0.09	0.19	0.55
Hydraulic safety													
MTD.L	µm	15.38	21.07	24.12	0.44	0.37	0.83	12.52	16.65	20.25	0.18	0.18	0.72
MTLUM.L	µm	4.41	6.56	8.09	0.28	0.25	0.72	4.49	6.52	9.73	0.18	0.18	0.58
MTWALLE	µm	6.31	6.99	7.73	0.00	0.06	0.38	5.08	5.87	6.76	0.07	0.15	0.42
MaxWALLE	µm	7.82	9.02	10.07	0.15	0.16	0.64	6.49	7.59	8.92	0.12	0.20	0.63
MaxWALL.L	µm	11.91	18.20	22.20	0.46	0.31	0.80	9.16	11.96	15.21	0.16	0.19	0.66
WALL90.E	µm	7.51	8.47	9.42	−0.01	−0.04	0.27	6.03	7.04	8.06	0.10	0.17	0.53
WALL90.L	µm	12.68	17.95	21.36	0.42	0.28	0.78	9.50	12.14	15.16	0.16	0.19	0.64
MTWALL.L	µm	10.40	14.51	17.25	0.42	0.30	0.79	8.03	10.12	12.49	0.14	0.17	0.63
CWA.E	µm ²	454.4	535.2	611.8	0.05	0.11	0.64	298	359.8	418.1	0.07	0.17	0.53
CWA.L	µm ²	366.4	533.8	630.1	0.44	0.35	0.82	279.5	373.5	471.1	0.15	0.17	0.69
TtoB	–	0.050	0.074	0.104	0.17	0.20	−0.34	0.087	0.124	0.208	0.16	0.19	−0.15
PerLW	%	0.141	0.321	0.413	0.34	0.34	0.52	0.100	0.191	0.286	0.07	0.06	0.34
LUMrange.E	µm	16.61	23.32	32.25	0.31	0.24	0.42	12.52	16.32	20.15	0.22	0.26	0.34
WALLrange.E	µm	2.21	2.74	3.29	−0.04	−0.01	0.03	1.35	2.20	2.99	0.06	0.10	0.56
L50	µm	46.44	54.77	61.83	0.27	0.27	0.55	32.02	36.78	40.16	0.08	0.08	0.48
Construction costs													
Ratio5.E	–	7.70	9.78	11.39	0.21	0.21	0.50	6.04	8.17	10.33	0.15	0.15	0.11
Carb.E	–	7.3E−05	1.1E−04	2.2E−04	0.29	0.28	−0.66	2.2E−04	3.6E−04	7.0E−04	0.10	0.15	−0.45
RatioEWLW	µm ^{−2}	2.30	2.63	3.25	0.35	0.24	−0.71	1.87	2.33	2.98	0.26	0.22	−0.51

Rbt raw are average correlations between trees (Rbt) calculated for undetrended time series; Rbt ratio are calculated after 32-spline detrending with ratio-index of the time series; r to TRW indicate the correlations with Tree-ring width

undetrended chronologies of tracheids anatomical features (Fig. 4) and indicates a relatively stable crown size.

Responses between trees

Assuming that the observed year-to-year variability is mainly related to the climatic environment, we should expect that trees facing the same conditions will respond in a concerted way (Fritts 1976). Our observations of the common signal (Rbt, Table 3) contained in detrended individual anatomical series indicate the presence of a partial concurrent response within the population. Even if the common signal of the hydraulic parameters (i.e., $r_{bt} < 0.5$) is much lower than that required for climatic

reconstruction, these results are promising from the perspective of an improved understanding of the mechanism of response among species and environmental settings. In fact, Rbt values are still in the range of results obtained in other studies for anatomical chronologies of water conducting cells for both coniferous (Yasue et al. 2000; Panyushkina et al. 2003; Eilmann et al. 2009) and broad-leaved trees (García-González and Eckstein 2003; Fonti and García-González 2004, 2008). In addition, we should consider that the analyses have been performed only on a proportion of tracheids (five radial tracheids files per ring on five trees per species), which is minimal to fully represent the large intra- and inter-tree variation of wood anatomical properties (Zobel and van Buijtenen 1989). We

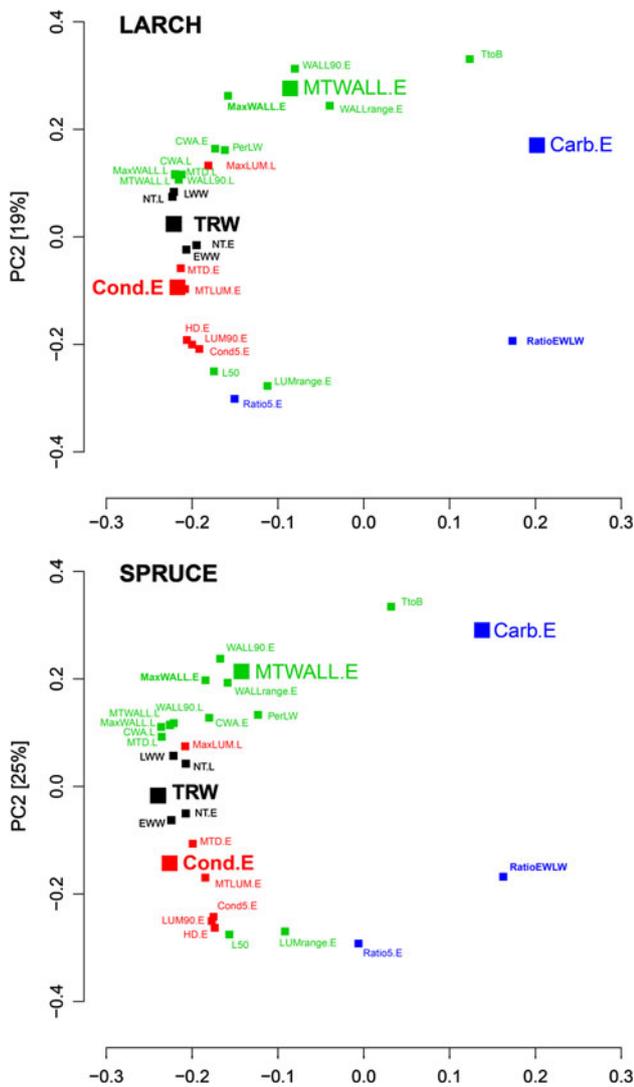


Fig. 5 Principal component analysis (PCA) of the correlation matrix of the 32 spline detrended chronologies of the anatomical parameters. The colours represent the four functional groups of anatomical and hydraulic parameters, i.e., parameters indicative of growth performance (*black*), hydraulic efficiency (*red*), hydraulic safety (*green*), and cost of conduit construction (*blue*). The parameters in *bold* have been selected for the climate–growth relationships (Fig. 6). The two principal components were significant for both the species

believe that increased tracheid sampling per annual ring (measured in the middle of their longitudinal length) combined with an adequate grouping of cells produced under the same weather conditions [sensu (García-González and Fonti 2006, 2008)] will help reduce noise and further improve extraction of the common signal. In contrast, there may be other factors involved in the response to climate, such as microtopographical conditions and tree status (competition level and architectural structure) which can affect the strength of the tracheid anatomical response of each single individual. To adjust to changing water availability, trees can regulate the sapwood area to reduce

hydraulic tension (Barnard et al. 2011), modify the crown or root morphology to regulate water demand and access (Meier and Leuschner 2008; Markesteijn and Poorter 2009; Klein et al. 2011), or increase water storage in the stem (Cermak et al. 2007; Meinzer et al. 2009; Martin et al. 2010). Differences between individuals at these levels may be responsible for a large part of the unexplained common signal.

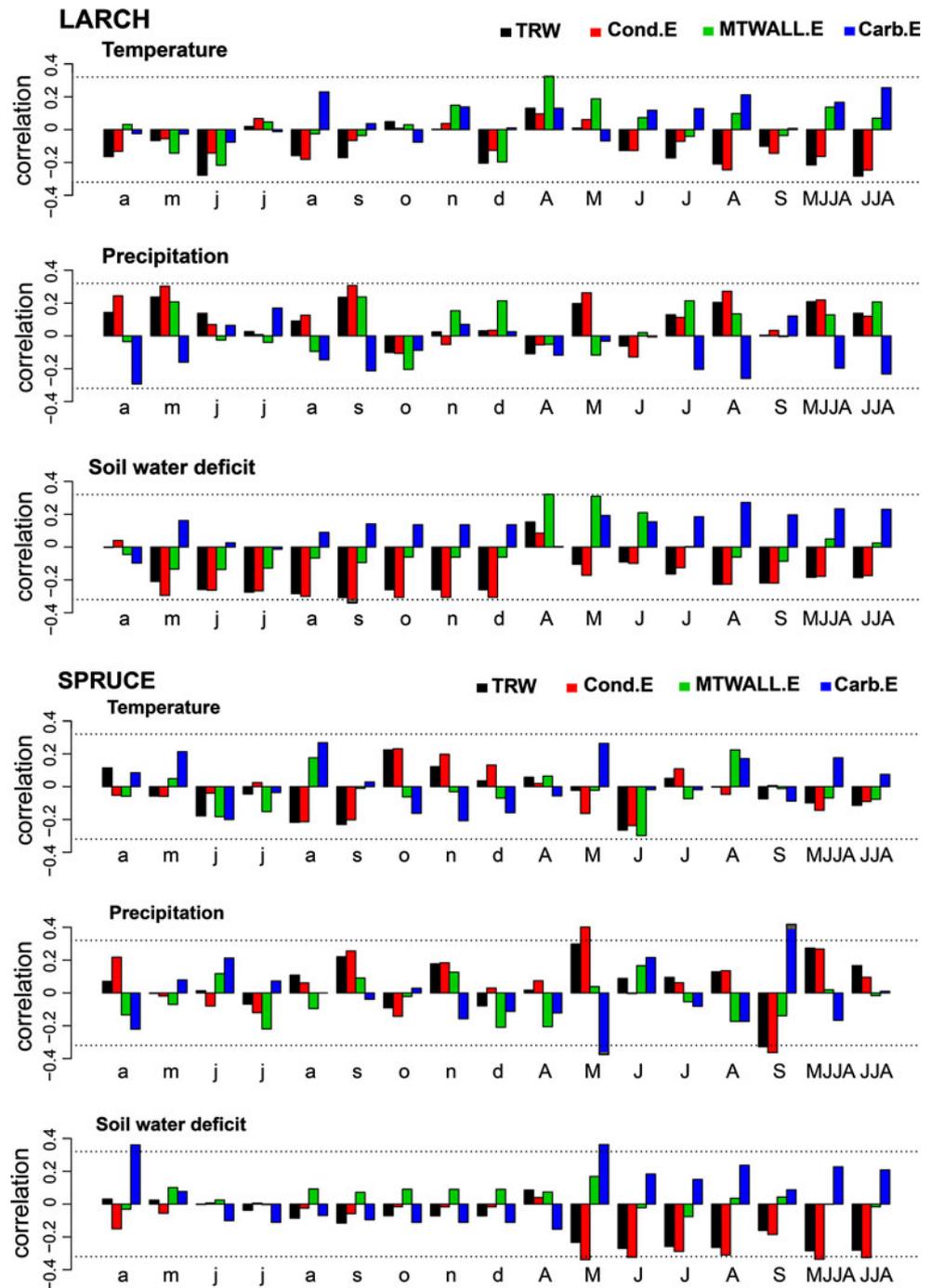
Common responses are related to drought

Results from the climate–growth relationships indicate that the common part of the signal found in the xylem hydraulic properties give indications for a response to limited summer water availability. Even if not always reaching a statistical significance ($p < 0.05$), the parameters related to the hydraulic conductivity and growth performance show a negative relation with plant-water status (negative to temperature and soil moisture and positive to precipitation, Fig. 6). These results are coherent with previous observations of cell anatomical characteristics for coniferous species (Weber et al. 2007; Eilmann et al. 2009; Markesteijn and Poorter 2009; Dobbertin et al. 2010; DeSoto et al. 2011) and for some hydraulic properties measured on newly formed xylem (Ladjal et al. 2005; Awad et al. 2010). Less prominent but still partially recognisable, especially for larch, are the positive responses to drought on hydraulic safety (MTWALL.E) and construction costs (Carb.E). Such analyses, although with weak correlations, indicate a direct influence of moisture conditions on the hydraulic characteristics of the forming xylem, and thus affecting future tree performance. In this study both the species analyzed, although with differing timing (with 1 year lag for larch) and magnitude (higher signal for larch than spruce) of the response likely due to differing metabolism (deciduous versus evergreen type) and sensitivity to drought, have shown the same type of anatomical adjustments.

Functional relevance of the adjustments

Anatomical adjustments in response to drought affected all four functional groups considered. When drought occurs, trees build a low number of smaller and thicker cells. These relatively small anatomical changes of the xylem structure have a substantial contribution to the annual hydraulic properties of the ring. Considering that the metrics of the conduits are relevant in determining hydraulic and mechanical properties as the conductivity and reinforcement against cavitations (Tyree and Zimmermann 2002), cell anatomical changes could have considerable influence in the plant-water relations and carbon assimilation over the coming years. Thus, although many parameters assigned to the same functional group encode similar

Fig. 6 Climate-growth relationships between four selected parameters (32 year spline detrended) and monthly climatic data of temperature, precipitation and soil water deficit for larch (*upper graph*) and spruce (*lower graph*). Months are abbreviated by their *initial letters, minuscule letters* for previous year, *capital letters* for current year and composite months. Climatic data were obtained from the MeteoSwiss weather station of Sion (1960–2010). *Horizontal dotted lines* indicate threshold for significant correlation at $p < 0.05$



information (Fig. 5), their functional significance can assume a different impact. Small increases in radial conduit diameter (MTD.E) results in large changes in conductivity due to the direct relationship between flow and radius to the fourth power. In our study for example, we observed that the ratio between the least and most conductive annual rings (Cond.E) in the same tree was on average 22-fold for larch and 23-fold for spruce. Respectively, changes in wall reinforcement (TtoB) were 77-fold and 82-fold. Other

tracheid anatomical characteristics not considered in this work, such as tracheid length (Makinen et al. 2008) and pit structure (Hacke and Jansen 2009; Schoonmaker et al. 2010) may have further contributed to regulate the hydraulic trade-off. Nevertheless, since sap transport usually occurs over several sapwood rings with declining conductivity toward the inner sapwood rings (Spicer and Gartner 2001), the relevance of the annual plasticity needs to be adjusted to its relative contribution to the whole

sapwood. More detailed knowledge on these characteristics will help improve interpretation of the relevance of such high annual plasticity on future tree growth.

Conclusions

Since environmental conditions change from year-to-year, we would also expect that the hydraulic architecture of trees is adjusted to fit different hydraulic requirements. The extraordinary plasticity of the cambium is an effective way to ensure rapid response to annual climate variation given in the available resources. Trees, by implementing changes in wood structure, adjust their hydraulic properties regulating the hydraulic trade-off. This study has quantified the range of annual xylem plasticity to climate variation by analyzing a whole suite of hydraulic parameters. Their relative importance for the regulation of plant-water relations depends upon the sapwood area. More research is required to assess the degree to which plants use older sapwood tissue throughout the season, and over the year to better quantify the functional significance of annual hydraulic adjustment of the xylem tissue on future performance. Furthermore, additional anatomical features such as pit structure or species growing in different environmental settings must be examined because it is evident that there is more than one evolutionary solution to the problems of water transport.

Acknowledgments This study was supported by Swiss National Foundation through an International short visit (Grant number: #131408) and through the cooperation on the project INTEGRAL (#121859). We would like to thank David Frank and Georg von Arx for their assistance and critical discussion of an earlier version of the manuscript, and Kathlene English and Gregory King for the English review.

References

- Anfodillo T, Carraro V, Carrer M, Fior C, Rossi S (2006) Convergent tapering of xylem conduits in different woody species. *New Phytol* 169:279–290
- 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
- Barnard DM, Meinzer FC, Lachenbruch B, McCulloh KA, Johnson DM, Woodruff DR (2011) Climate-related trends in sapwood biophysical properties in two conifers: avoidance of hydraulic dysfunction through coordinated adjustments in xylem efficiency, safety and capacitance. *Plant Cell Environ* 34:643–654
- Beikircher B, Mayr S (2009) Intraspecific differences in drought tolerance and acclimation in hydraulics of *Ligustrum vulgare* and *Viburnum lantana*. *Tree Physiol* 29:765–775
- Cermak J, Kucera J, Bauerle WL, Phillips N, Hinckley TM (2007) Tree water storage and its diurnal dynamics related to sap flow and changes in stem volume in old-growth Douglas-fir trees. *Tree Physiol* 27:181–198
- Chave J, Muller-Landau HC, Baker TR, Easdale TA, ter Steege H, Webb CO (2006) Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. *Ecol Appl* 16:2356–2367
- Choat B, Cobb AR, Jansen S (2008) Structure and function of bordered pits: new discoveries and impacts on whole-plant hydraulic function. *New Phytol* 177:608–625
- Cook ER, Kairiukstis LA (1990) Methods of dendrochronology applications in the environmental sciences. Kluwer, Dordrecht
- DeSoto L, De la Cruz M, Fonti P (2011) Intra-annual patterns of tracheid size in the Mediterranean tree *Juniperus thurifera* as an indicator of seasonal water stress. *Can J For Res* 41:1280–1294
- Dobbertin M, Eilmann B, Bleuler P, Giuggiola A, Pannatier EG, Landolt W, Schleppi P, Rigling A (2010) Effect of irrigation on needle morphology, shoot and stem growth in a drought-exposed *Pinus sylvestris* forest. *Tree Physiol* 30:346–360
- Eilmann B, Zweifel R, Buchmann N, Fonti P, Rigling A (2009) Drought-induced adaptation of the xylem in Scots pine and pubescent oak. *Tree Physiol* 29:1011–1020
- Fonti P, García-González I (2004) Suitability of chestnut earlywood vessel chronologies for ecological studies. *New Phytol* 163:77–86
- Fonti P, García-González I (2008) Earlywood vessel size of oak as a potential proxy for spring precipitation in mesic sites. *J Biogeogr* 35:2249–2257
- Fonti P, von Arx G, Garcia-Gonzalez I, Eilmann B, Sass-Klaassen U, Gartner H, Eckstein D (2010) Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. *New Phytol* 185:42–53
- Fritts HC (1976) Tree rings and climate. Academic Press, London
- García-González I, Eckstein D (2003) Climatic signal of earlywood vessels of oak on a maritime site. *Tree Physiol* 23:497–504
- García-González I, Fonti P (2006) Selecting earlywood vessels to maximize their environmental signal. *Tree Physiol* 26:1289–1296
- García-González I, Fonti P (2008) Ensuring a representative sample of earlywood vessels for dendroecological studies: an example from two ring-porous species. *Trees-Struct Funct* 22:237–244
- Hacke UG, Jansen S (2009) Embolism resistance of three boreal conifer species varies with pit structure. *New Phytol* 182:675–686
- Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. *Perspect Plant Ecol* 4:97–115
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461
- Holbrook NM, Zwieniecki MA (2005) Vascular transport in plants. Elsevier, Amsterdam
- Horn JL (1965) A rationale and test for the number of factors in factor analysis. *Psychometrika* 30:179–185
- Klein T, Cohen S, Yakir D (2011) Hydraulic adjustments underlying drought resistance of *Pinus halepensis*. *Tree Physiol* 31:637–648
- Ladjal M, Huc R, Ducrey M (2005) Drought effects on hydraulic conductivity and xylem vulnerability to embolism in diverse species and provenances of Mediterranean cedars. *Tree Physiol* 25:1109–1117
- Maherali H, Pockman WT, Jackson RB (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85:2184–2199
- Makinen H, Jyske T, Saranpää P (2008) Variation of tracheid length within annual rings of Scots pine and Norway spruce. *Holzforchung* 62:123–128
- Markestijn L, Poorter L (2009) Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *J Ecol* 97:311–325
- Martin JA, Esteban LG, de Palacios P, Fernandez FG (2010) Variation in wood anatomical traits of *Pinus sylvestris* L.

- between Spanish regions of provenance. *Trees-Struct Funct* 24:1017–1028
- Martinez-Cabrera HI, Jones CS, Espino S, Schenk HJ (2009) Wood anatomy and wood density in shrubs: responses to varying aridity along transcontinental transects. *Am J Bot* 96:1388–1398
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yezzer EA (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 178:719–739
- Meier IC, Leuschner C (2008) Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global Change Biol* 14:2081–2095
- Meinzer FC (2011) Size- and age-related changes in tree structure and function. Springer, Dordrecht
- Meinzer FC, Johnson DM, Lachenbruch B, McCulloh KA, Woodruff DR (2009) Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Funct Ecol* 23:922–930
- Panyushkina IP, Hughes MK, Vaganov EA, Munro MAR (2003) Summer temperature in northeastern Siberia since 1642 reconstructed from tracheid dimensions and cell numbers of *Larix cajanderi*. *Can J Forest Res* 33:1905–1914
- Pittermann J, Sperry JS, Hacke UG, Wheeler JK, Sikkema EH (2006a) Inter-tracheid pitting and the hydraulic efficiency of conifer wood: the role of tracheid allometry and cavitation protection. *Am J Bot* 93:1265–1273
- Pittermann J, Sperry JS, Wheeler JK, Hacke UG, Sikkema EH (2006b) Mechanical reinforcement of tracheids compromises the hydraulic efficiency of conifer xylem. *Plant Cell Environ* 29:1618–1628
- Salleo S, Trifilo P, Esposito S, Nardini A, Lo Gullo MA (2009) Starch-to-sugar conversion in wood parenchyma of field-growing *Laurus nobilis* plants: a component of the signal pathway for embolism repair? *Funct Plant Biol* 36:815–825
- Schenk HJ, Espino S, Goedhart CM, Nordenstahl M, Cabrera HIM, Jones CS (2008) Hydraulic integration and shrub growth form linked across continental aridity gradients. *Proc Natl Acad Sci USA* 105:11248–11253
- Schoonmaker AL, Hacke UG, Landhausser SM, Lieffers VJ, Tyree MT (2010) Hydraulic acclimation to shading in boreal conifers of varying shade tolerance. *Plant Cell Environ* 33:382–393
- Spicer R, Gartner BL (2001) The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. *Trees-Struct Funct* 15:222–229
- Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap, 2nd edn. Springer, Berlin
- Weber P, Bugmann H, Rigling A (2007) Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. *J Veg Sci* 18:777–792
- Yasue K, Funada R, Kobayashi O, Ohtani J (2000) The effects of tracheid dimensions on variations in maximum density of *Picea glehnii* and relationships to climatic factors. *Trees-Struct Funct* 14:223–229
- Zobel BJ, van Buijtenen JP (1989) Wood variation: its causes and control. Springer, Berlin