Trees
DOI 10.1007/s00468-014-1131-x

ORIGINAL PAPER

Stem increment and hydraulic architecture of a boreal conifer (*Larix sibirica*) under contrasting macroclimates

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Received: 3 July 2014 / Revised: 16 October 2014 / Accepted: 6 November 2014

Abstract

Key message **Hydraulic conductivity and wood anatomical traits in *Larix sibirica* are correlated with macroclimate, and growing season precipitation in particular, along a precipitation gradient of 700 mm year^{-1}.**

Abstract Empirical (K_s) and theoretical (K_p) sapwood area-specific hydraulic conductivity, hydraulically weighted (d_h) and simple (d) tracheid diameters as well as tracheid density (TD) in roots, stems, and branches were studied in *Larix sibirica* trees, the dominant conifer at the southern, drought-affected range limit of the boreal forest in Inner Asia. We compared the hydraulic architecture of *L. sibirica* in two stands in Mongolia to larch trees grown in Central Europe under moist conditions and related hydraulics to macroclimate (precipitation, temperature) and productivity (basal area increment, BAI). K_s, K_p, d_h, and d correlated positively, and TD negatively with precipitation, temperature, and also BAI. Mean growing season precipitation (MGSP) seemed to affect the hydraulic traits more than temperature. A meta-analysis covering data of 14 conifer species from the northern hemisphere revealed a general relationship between MGSP and hydraulic traits. In contrast to expectation, K_p and d_h did not show a steady decline from roots through the stem to branches in *L. sibirica*, but were of similar size or larger in the stem. Our results suggest that considerable plasticity in the hydraulic architecture is an important element of the drought adaptation of *L. sibirica*. It combines with drought-induced fine root abscission (as reported from earlier work) which may help to protect larger roots and the stem from cavitation.

Keywords Hydraulic conductivity · Wood anatomy · Xylem anatomical plasticity · Precipitation · Drought adaptation

Introduction

Carbon assimilation and the water balance of plants are closely linked to each other because stomatal regulation needed to avoid excessive water loss and hydraulic failure during drought interferes with the uptake of carbon dioxide (Sala et al. 2012; Sevanto et al. 2014). As a consequence, trees in drought-prone semi-arid forests typically grow more slowly than trees in regions with ample water supply. Reduced growth activity under elevated drought exposure may result in modifications in the hydraulic architecture of the trees along the flow path from roots to distal branches. Not much is known about the relation between productivity and hydraulic architecture in the coniferous forests dominated by Siberian larch (*Larix sibirica* Ledeb.) at the southernmost fringe of the Eurosiberian forest in Inner Asia, although these forests receive only little and unreliable precipitation and are thus frequently affected by drought (Gunin et al. 1999). It has been shown that water shortage reduces the stem wood production of these forests (De Grandpré et al. 2011; Dulamsuren et al. 2013) and is thought to cause high fine root mortality (Chenlemuge

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Communicated by M. Zwieniecki.

Electronic supplementary material The online version of this article (doi:10.1007/s00468-014-1131-x) contains supplementary material, which is available to authorized users.

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et al. 2013). Recent climate warming has increased the limiting effect of summer drought on productivity (Dulamsuren et al. 2010, 2013) and has resulted in tree mortality in certain regions (Liu et al. 2013).

Large-diameter conduits ensure efficient sap flow in the xylem, increase plant water consumption, and are one prerequisite of high canopy carbon gain (Tyree and Zimmermann 2002), but they increase the risk of drought-induced embolism (Choat et al. 2005; Domec et al. 2008; Brown 2013). The anatomy of the xylem is thus a compromise between the opposing needs for efficient transport of water and the prevention of hydraulic failure. Therefore, low hydraulic conductivity is thought to be a critical factor for biomass production in forest trees, which may add to the effect of soil moisture shortage (Tyree 2003; Ryan et al. 2006). Trees showing low hydraulic conductivity along the flow path from roots to the distal branches can be expected to experience high within-tree water potential gradients, which may cause more frequent stomatal closure and thus reduced carbon gain and growth (Tyree 1997, 2003). Consistently, Dulamsuren et al. (2009) showed that minimum shoot water potential close to the point of zero turgor frequently occurred throughout the growing season in *L. sibirica* trees growing in the forest-steppe ecotone of Mongolia, indicating that water relations were often critical.

The existence of significant relationships between climate, wood anatomy, hydraulic conductivity, and productivity has repeatedly been demonstrated for the stem wood of trees, but less information is available about the relatedness of the hydraulic architecture of roots and branches, the distal woody organs of the flow path, to climate and also to the trees' productivity (Thibeault-Martel et al. 2008; Hajek et al. 2014). Hydraulic conductivity is determined by the structure and size of the conduits (Tyree and Ewers 1991) and by their conducting efficiency (Lovisolo and Schubert 1998). The specific conductivity of the xylem decreases along the flow path (Tyree and Zimmermann 2002), and the root system normally shows vessels of at least twice the size compared to branches. Due to the frequently observed relation between conduit size and vulnerability to cavitation (Hargrave et al. 1994; Tyree and Zimmermann 2002; Cai and Tyree 2010), it has repeatedly been demonstrated that roots are more vulnerable than branches (Martínez-Vilalta et al. 2002; Maherali et al. 2006; Domec et al. 2009). In addition to the observed within-tree differences in hydraulic architecture, the amount and distribution of rainfall strongly affects wood anatomical properties, since increasing precipitation commonly induces the formation of large-diameter conduits and thus lower conduit numbers per cross-sectional area (Carlquist 1977; Lens et al. 2004; De Micco et al. 2008). Dendrochronological analyses showed that trees adjust the shape of their conduits to the tree's specific drought exposure (Sass and Eckstein 1995; Eilmann et al. 2006), reflecting the effect of cell or tissue water status at the time of conduit differentiation (González and Eckstein, 2003). Antonova and Stasova (1997) determined a mean daily air temperature of 21 °C and precipitation of at least 14–15 mm during the period of conduit development as the climatic optima for radial cell expansion in *L. sibirica*.

We studied how the macroclimate in two study areas of the Mongolian forest-steppe at the southern distribution limit of *L. sibirica* and in a forest plantation outside the natural range of this tree species in Central Europe does affect the relationships between hydraulic conductivity in roots, stems, and branches and the tree's productivity. The study regions covered a range of annual mean precipitation of roughly 700 mm and of annual mean temperature of more than 10 K. Roots and branches were included in the analysis not only because their hydraulic traits are less frequently studied than stems, but primarily as they are exposed to the steepest gradients in water potential at the distal ends of the flow path. With our field and laboratory studies in *L. sibirica*, we tested the hypotheses that (a) mean annual precipitation is directly related to wood anatomical and hydraulic traits across the three sites, and that (b) a higher sapwood area-specific hydraulic conductivity in both roots and branches is correlated with higher productivity in terms of annual radial stem increment. To extend the validity of the findings from the *L. sibirica* study, we conducted a meta-analysis covering 13 other conifer species from the northern hemisphere and extracted data on hydraulic conductivity and conduit diameters in branches and roots. With this dataset, we tested the hypothesis that (c) the hydraulic conductivity and tracheid diameters in conifer roots and branches are positively correlated with precipitation.

Materials and methods

Study design

The relation between annual radial stem increment and hydraulic traits was examined in *Larix sibirica* Ledeb. (Siberian larch) in two study areas at the southernmost edge of the distribution range of this tree species and of the Eurosiberian boreal forest in general. The study areas are located in the Mongolian Altai and the Khangai Mountains in the forest-steppe of western Mongolia. While the climate of these areas is semi-arid and highly continental, a third study area was selected in Central Europe in a larch plantation far west of the present natural range limit of *L. sibirica*. The natural distribution range comprises western Siberia, the southern part of central Siberia as well as the forest-steppe regions of Kazakhstan, Mongolia, and the Chinese Altai (Araki et al. 2008). The climate of the study area in Central Europe (Ore Mountains, Germany) is suboceanic and was chosen for examining the plasticity of the hydraulic system of *L. sibirica* when the species is exposed to ample water supply.

The study sites in the Mongolian Altai are located in the Dayan administrative subunit ('bag') of the Altai Tavan Bogd National Park in the province ('aimag') of Bayan-Ulgii, 110 km SW of the city of Ulgii south and southeast of Lake Dayan (48°14′–48°16′N, 88°50′–88°57′E; 2,300–2,375 m a.s.l.). The study area in the Khangai Mountains (600 km east of the study sites in the Mongolian Altai) is located c. 30 km SSE of the city of Uliastai and 40 SW of Mt. Otgontenger in the province of Zavkhan in the valley of the river Shireegiin Gol (47°29′–47°31′N, 96°59′–97°14′E; 2,100–2,300 m a.s.l.). In Germany, we studied a *L. sibirica* plantation in the vicinity of the village of Giegengrün near Kirchberg in the Ore Mountains, 15 km SSE of the city of Zwickau (50°35′N, 12°32′E; 465 m a.s.l).

Climate of the study areas

The climate of the Mongolian forest-steppe is a semi-arid, highly continental mountain climate with a subzero annual mean temperature, whereas that of the Ore Mountains is humid and suboceanic with much higher precipitation and temperature. Weather data from 1940 to 2010 were analyzed from the weather station Altai-Yalalt (48°17′N, 89°31′E, 2,150 m a.s.l.) 40 km east of the forests studied in the Mongolian Altai, and Uliastai (47°75′N, 96°85′E, 1,760 m a.s.l.), 30 km NNW of the forests studied in the Khangai Mountains. Climatic data (precipitation, temperature) for the Central European site located in the Ore Mountains were obtained from a 1 km × 1 km grid dataset of the German Meteorological Service (Deutscher Wetterdienst, Offenbach, Germany). Because data from the station Altai-Yalalt were only available since 1970, data reconstructed by Dulamsuren et al. (2014) were used for the interval from 1940 to 1969 (station Ulgii City 1,960 m a.s.l.).

Mean annual temperature was below −2 °C in the two study areas in Mongolia, but 7.7 °C in the Ore Mountains (Table 1). Mean annual precipitation was 120 mm in the Mongolian Altai, 215 mm in the Khangai Mountains, and 841 mm in the Ore Mountains. In Mongolia, precipitation has a strong peak in summer with 73 and 83 % received during the growing season (May–September) in the Altai and the Khangai Mountains, respectively. Trees in the Mongolian forest-steppe are not only supplied with water from current precipitation, but presumably also profit from water accumulated in permafrost and meltwater from alpine grasslands above the forest belt (Dulamsuren et al. 2014). Hence, the exact amount of water, which is available to the trees in Mongolian Altai, remains unclear, but is certainly higher than the 120 mm year^{-1} of precipitation recorded (Dulamsuren et al. 2014).

Sample plots

Sampling in the two Mongolian study areas included six monospecific *L. sibirica* stands per area. In each of the six forest stands per study region, we established a plot of 20 m × 20 m c. 50–100 m behind the forest line. Sample plot selection was facilitated by the rather regular landscape structure in the Mongolian forest-steppe with a mosaic of forests on north-facing slopes and grasslands on the drier south-facing slopes and in moist valleys. This landscape structure was used to select forest stands in near equidistance along one valley each in the Altai and the Khangai Mountains. The mean distance between neighboring plots was 2.2 ± 0.5 km in the Mongolian Altai and 3.8 ± 0.5 km in the Khangai, depending on the natural settings in the study regions. We excluded sites in moist depressions on the slopes which were not representative for the study area. We could not employ the same sampling design in the Ore Mountains, since here only a single stand of c. 0.5 ha with about 100 trees, which are regularly used for seed harvesting, was available.

Forests in the Mongolian forest-steppe typically have low canopy covers of ~20–50 % which is a consequence of water shortage. The studied stands in the Mongolian Altai and the Khangai Mountains had a mean canopy cover of 43 and 32 %, respectively (Table 2). In both Mongolian forest regions, a dense herb layer was present, which was occasionally grazed by livestock. The stand in the Ore Mountains was an even-aged plantation with a canopy cover of 80–90 %. The trees in this plantation were

Table 1 Precipitation (*P*) and temperature (*T*) in the period from 1940 to 2010 in the Mongolian Altai, Khangai, and the Ore Mountains. Given are the annual mean and mean values for the growing season (May–September)

	Altai		Khangai		Ore Mountains	
	Annual mean	May–September	Annual mean	May–September	Annual mean	May–September
P (mm)	120	87	215	179	841	427
T (°C)	−3.4	9.0	−2.4	11.9	7.7	14.6

Table 2 Stand characteristics (mean ± SE) of the studied larch forest sites in the Mongolian Altai, Khangai, and Ore Mountains

	Altai	Khangai	Ore Mountains
Mean age of canopy trees (years)	155	137	118
Age range (years)	45–435	29–396	Even-aged
Canopy tree height (m)	15.9 ± 0.9	16.8 ± 0.4	30.9 ± 0.8
Mean stem diameter of canopy trees (cm)	32.2 ± 3.6	22.4 ± 1.4	54.0 ± 2.3

somewhat younger (118 years) than the trees in the Altai (155 years) and Khangai (137 years) stands (Table 2). The prevailing soils in the Mongolian Altai and the Khangai are Leptosols stocking on siliceous rock, whereas Podzol over granite rock was characteristic of the Ore Mountains site.

Selection of sample trees

In Mongolia, wood cores from all trees with a diameter at breast height (DBH; c. 1.3 m above the ground) >3 cm growing on the 20 m × 20 m plots were available from previous analyses of our group in the Altai (Dulamsuren et al. 2014) and the Khangai Mountains (Dulamsuren unpublished). Tree-ring data of a total of 397 *L. sibirica* trees from the Altai and from 306 trees of the Khangai were available (DBH > 3 cm). Since the planted *L. sibirica* trees in the Ore Mountains all were of the same age (118 years), whereas those from the old-growth forests in Mongolia had a heterogeneous age structure, we investigated only those Mongolian trees that had a similar DBH as the trees from the Ore Mountains. We thus had radial stem increment data from 17 trees from the Mongolian Altai, 10 trees from the Khangai Mountains, and 3 trees from the Ore Mountains available for the analysis that were similar in DBH (Table 3). The number of cores in the Ore Mountains was low because destructive sampling had to be restricted to the minimum in this stand. Nevertheless, the small sample size in the Ore Mountains is acceptable, since all trees had the same age and were similar in diameter and height in this plantation. The selection of trees with comparable size in the Mongolian stands was done in order to eliminate tree diameter effects on radial growth from the analysis. As the result of keeping the DBH constant, we had a gradient of increasing tree age from the Ore Mountains via the Khangai Mountains to the Mongolian Altai in our data. Such gradient was to be inevitable, since trees of the same age are to be expected to grow faster under the milder and moister climate of Central Europe than under the highly continental climate of Inner Asia. Since we expected that tree size exerts a greater influence of the trees' hydraulic traits than age, we accepted the variation in tree age to keep the DBH of our sample trees constant.

Tree-ring analysis

Wood cores from larch stems were collected in July 2010 (Altai), August 2011 (Khangai) and September 2012 (Ore Mountains). Wood cores were taken with an increment borer of an inner diameter of 5 mm (Haglöf, Långsele, Sweden) at breast height parallel to the contour lines of the mountain slopes to avoid compression wood. Annual tree-ring width (TRW) was measured with a precision of 10 µm on a movable object table (Lintab 6, Rinntech, Heidelberg, Germany), the movements of which are electronically transmitted to a computer system equipped with TSAP (Time Series Analysis and Presentation)-Win software (Rinntech). Tree-ring series were cross-dated, involving the calculation of coefficients of agreement ('Gleichläufigkeit', *GL*) values >60 % ($P \leq 0.05$) and t values >3, before mean TRW were computed. From TRW and the DBH data, we calculated the 11-year (2000–2010) mean of annual basal area increment per tree (BAI, in mm^2 year^{-1}).

Determination of empirical hydraulic conductivity

Empirical hydraulic conductivity was measured in roots and branches, which were collected from six trees per plot in the Altai and Khangai Mountains in August 2011 and from six trees in the Ore Mountains in September 2012.

Table 3 Diameter at breast height (DBH), tree-ring width (TRW), and stem basal area increment (BAI) averaged over the period from 2000 to 2010 and age of sample trees in stands of the Mongolian Altai ($N = 17$ trees), Khangai ($N = 10$) and Ore Mountains ($N = 3$). Mean ± SE (number of trees) are given

	Altai	Khangai	Ore Mts.
DBH (cm)	48.7 ± 1.5a	45.0 ± 1.9a	48.7 ± 4.9a
TRW (mm)	0.37 ± 0.04a	0.67 ± 0.12b	1.63 ± 0.08c
BAI (mm^2)	560 ± 64a	930 ± 164a	2495 ± 259b
Age (years)	235 (117–343)	180 (107–249)	118 (even-aged)

Significant differences among study areas are indicated by lowercase letters ($P \leq 0.05$, Tukey's test, $df_{\text{model,error}} = 2, 27$)

From each sample tree, 1–3 coarse root segments and 1–3 branch segments were collected, yielding a total of 71 root (mean diameter ± SE 7.8 ± 0.3 mm, mean length ± SE 110 ± 2 mm) and 73 branch samples (mean diameter ± SE 8.0 ± 0.2 mm, mean length ± SE 118 ± 2 mm). Branch samples were collected from the sun crown. Mean diameter and length of the segments were not significantly different between the three study areas ($P \leq 0.05$, Tukey's test). Sampled segments were cut and immediately sealed in polyethylene tubes filled with 0.1 M KCl and a sodium-silver chloride complex (Micropur, Katadyn Products, Kemptthal, Switzerland) was added to minimize microbial growth and air entry. Samples were stored at 4 °C after sampling, during transport and during storage in the laboratory where the analyses were carried out within 1 month after collection.

Immediately before analysis, each root and branch segment was recut under water with a razor blade and mounted in the xylem apparatus for hydraulic conductivity measurement, which was operated with XylWin 3.0 software (Bronkhorst, Montigny-les-Cormeilles, France). Deionized filtered (0.2 µm, Maxi Capsule, Pall, Port Washington, New York, USA) and degassed water containing 10 mM KCl and 1 mM $CaCO_3$ was used for conductivity measurements. Hydraulic conductivity was measured three times across a 6 kPa pressure gradient. After the first and second measurements, the segments were flushed at a pressure of 120 kPa to remove potential emboli and to determine maximal hydraulic conductivity for further calculations. The hydraulic conductivity for a given segment length (K_h, in kg m MPa^{-1} s^{-1}) was calculated as $K_h = J_v$ ($\Delta P/X$), where J_v is the flow rate through the segment (kg s^{-1}) and ΔP the pressure gradient along the segment of length X (MPa m^{-1}).

After K_h had been determined, segment length was measured and the cross-sectional area including bark and pith (A_{cross}, in m^2) was derived from diameter measurements at the proximal segment end. For estimating the xylem cross-sectional area (=sapwood area) without pith and bark (A_{xylem}, in m^2), a regression analysis between A_{cross} and A_{xylem} was carried out in twelve root and twelve branch segments per study region, yielding 72 analyzed samples in total. A light microscope (DM 5000B, Leica Microsystems, Wetzlar, Germany) equipped with a digital camera (DFC 300FX, Leica Microsystems) was used to obtain high-quality top-view images of the chosen segments, which were subsequently analyzed using ImageJ 1.42q software (Rasband, National Institute of Health, Bethesda, Maryland, USA). Studies on area-specific linear regressions were conducted between A_{cross} and A_{xylem} for each organ and the resulting regression equation (Table S1 in the Supplementary Information) was used for deriving A_{xylem} from A_{cross} for all samples. Subsequently, K_h was divided by the corresponding A_{xylem} value to calculate empirical sapwood area-specific hydraulic conductivity (K_s, kg m^{-1} MPa^{-1} s^{-1}).

Analysis of xylem anatomy

The anatomy of the root, stem, and branch xylem, together with the derived potential hydraulic conductivity, was studied in a subset of seven trees from the Mongolian Altai, five trees from the Khangai Mountains, and six trees from the Ore Mountains. Since the stand in the Ore Mountains is used for seed harvesting, we were allowed to extract only three trunk core samples for stem wood anatomical analyses. Wood samples were stored in 70 % ethanol prior to analysis. The samples were stained with safranin (1 in 50 % ethanol, Merck, Darmstadt, Germany) for 3 days followed by rinsing the samples with 70 % ethanol three times while shaking for 12 h. Subsequently, the samples were washed in distilled water and cut on the following day with a sliding microtome (Hn 40, Reichert-Jung, Nußloch, Germany) into semi-thin transverse sections (roots and branches: 10–20 µm; stem: 3–5 µm thick). Afterward, the complete sections were photographed at 100–120× magnification using the above-mentioned Leica camera system. Image analysis was done for the complete cross-sections of root and branch samples without pith and bark as well as for tree-ring sections produced in the period 2000–2010. Image analysis was conducted with Adobe Photoshop CS2 9.0 (Adobe Systems Incorporated, San Jose, California, USA) and ImageJ software using the particle analysis function. We estimated single and cumulative tracheid lumen areas, tracheid density (TD, in N mm^{-2}) and idealized tracheid diameters (d, in µm) from both major (a) and minor (b) tracheid radii using the equation given by White (1991) as $d = ((32(ab)^3)/(a^2 + b^2))^{1/4}$. Hydraulic mean diameter (d_h, in µm), which puts more weight on large than small conducting vessels (Sperry et al. 1994), was calculated from tracheid diameters (d) as $d_h = \sum d^5/\sum d^4$. According to the Hagen–Poiseuille equation, potential sapwood area-specific hydraulic conductivity (K_p, in kg m^{-1} MPa^{-1} s^{-1}) was calculated from the tracheid radii as $K_p = \pi\ (\sum r^4)\ \rho/(8\ \eta\ A_{xylem})$, where η is the viscosity and ρ is the density of water at 20 °C, while A_{xylem} is the corresponding cross-sectional area without pith and bark. We measured the diameters of c. 3,000–80,000 tracheids per root cross section and c. 39,000–156,000 tracheids per branch cross section. In the stem wood, we analyzed a range of 79–10,234 tracheids per tree ring or 2,691–69,989 tracheids per complete cross section. The high variability is due to interannual variation in increment.

Wood anatomical analyses, including the calculation of K_p, were carried out separately for earlywood and latewood in the stem, but for the entire cross section in roots and branches. This analysis was done in all stem samples ($N = 7$ in the Altai, $N = 5$ in the Khangai and $N = 3$ in the Ore Mountains) and in five root and five branch samples per study area. Earlywood and latewood were visually differentiated according to color and tracheid size.

Meta-analysis of precipitation effects on K_s and d_h

We compiled a data bank from literature values of K_s and d_h from roots and branches of boreal, temperate, and Mediterranean conifers from the northern hemisphere. The evaluated literature included studies by Joseph et al. (1998), Piñol and Sala (2000), Martínez-Vilalta and Piñol (2002), Mayr et al. (2003), Oliveras et al. (2003), Stout and Sala (2003), Domec et al. (2004), Mainiero and Kazda (2006), Martínez-Vilalta et al. (2009), and Charra-Vaskou et al. (2012). The Tables S2 and S3 in the Supplementary Information contain these variables for 51 stands together with climatic data. Since the comparability of K_s calculations in branch samples done with different methods is limited, we restricted the correlation analysis between K_s and precipitation to branch samples with $K_s < 1.5$ kg m^{-1} MPa^{-1} s^{-1}. We choose this threshold based on an earlier large meta-analysis by Maherali et al. (2004) on xylem hydraulic properties of woody plant species from a global dataset that showed a mean K_s value for all ($N = 87$) species of 1.35 ± 0.15 kg m^{-1} MPa^{-1} s^{-1} and a mean for all conifer species ($N = 24$) of 0.46 ± 0.05 kg m^{-1} MPa^{-1} s^{-1}.

Data processing and statistical analysis

Arithmetic means ± standard errors are given throughout the paper. Subsamples derived from the same tree individual were averaged before further calculation, since the data were not independent. Wood anatomical and hydraulic data from stem samples were first averaged for individual tree rings, then on the tree level, and afterward on the site level. Trees were treated as true replicates in each statistical test. Data were tested for normal distribution using the Shapiro–Wilk test and for homogeneity of variances using Levene's test. One-way analysis of variance (ANOVA) was combined with Tukey's post hoc test. Multifactorial analysis of unbalanced samples was done with general linear models (GLM) followed by the least significant difference (LSD) test. Multiple comparisons of means of non-normally distributed data were made with the Kruskal–Wallis test followed by pair-wise Mann–Whitney U tests if the Kruskal–Wallis test result was significant. Pearson coefficients were calculated in linear regression analysis. All statistical analyses were carried out with SAS 9.13 software (SAS Institute Inc., Cary, North Carolina, USA).

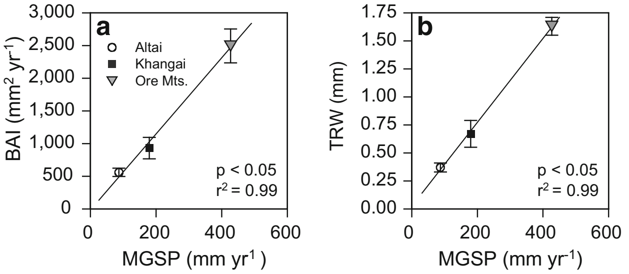


Fig. 1 Linear regression of **a** mean basal area increment (BAI; ± SE) and **b** mean tree ring width (TRW; ± SE) of *L. sibirica* in the Mongolian Altai, Khangai, and Ore Mountains versus mean growing season precipitation (MGSP)

Results

Stem radial increment

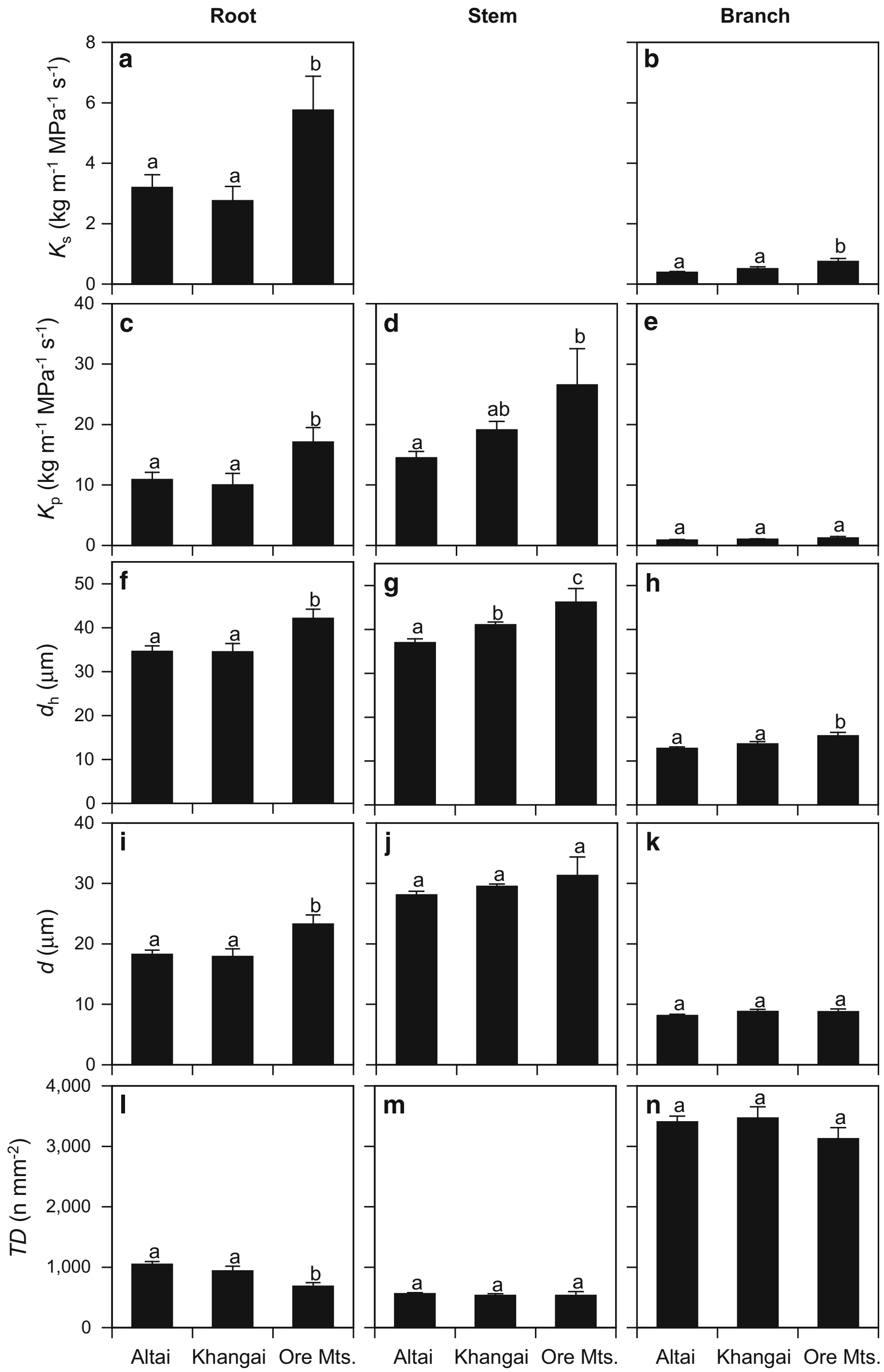
Larix sibirica trees growing outside their natural range in the sub-oceanic Central European Ore Mountains grew faster than under the highly continental semi-arid climate in the Mongolian forest-steppe where the species is native. This was also true, when only dominant and subdominant trees of similar diameter at breast height (DBH) (Table 3) and age (Table 1) were compared to exclude the age-dependent decline of tree-ring width (TRW). Mean TRW in the years 2000–2010 was 2.4-fold higher in the Ore Mountains than in the Khangai Mountains and 4.4-fold higher than in Mongolian Altai (Table 3), which received even less precipitation than the Khangai Mountains (Table 2). Mean basal area increment (BAI) in the Ore Mountains exceeded that in the Khangai Mountains by 2.7 times and that in the Mongolian Altai by 4.5 times (Table 3). The trend for lower stem increment in the Mongolian Altai than the Khangai Mountains was significant for TRW, but not BAI (Table 3).

Across the three sites, TRW and BAI were closely positively correlated with mean annual precipitation (MAP), mean growing season precipitation (MGSP; Fig. 1a, b), and mean annual temperature (MAT) showing high correlation coefficients ($r \geq 0.99$, $P \leq 0.05$). Mean growing season temperature (MGST) was not correlated with TRW ($P = 0.10$) or BAI ($P = 0.12$).

Site-dependent variation of hydraulic conductivity and xylem anatomical properties

Our analyses of hydraulic and wood anatomical properties of three different plant parts (roots, stem, branches) exhibited marked differences between the Central European and the Inner Asian sites (Fig. 2). Empirical sapwood area-specific hydraulic conductivity (K_s), which cannot be determined in the stem, was higher in the Ore Mountains

Fig. 2 Hydraulic and wood anatomical traits in roots (**a**, **c**, **f**, **i**, **l**), stems (**d**, **g**, **j**, **m**), and branches (**b**, **e**, **h**, **k**, **n**) of *L. sibirica* in the Mongolian Altai, Khangai, and the Ore Mountains. **a**, **b** empirical (K_s) and **c**–**e** theoretical (K_p) sapwood area-specific hydraulic conductivity, **f**–**h** hydraulically weighted diameter (d_h), **i**–**k** tracheid diameter (d), and **l**–**n** TD. Means (±SE) sharing the *same letter* within a subplot do not differ significantly ($P \leq 0.05$, LSD test)



than in the two sites in Mongolia in both roots and branches (Fig. 2a, b). Theoretical sapwood area-specific hydraulic conductivity (K_p) was higher in the Ore Mountains than in Mongolia in roots and the stem, but not in branches (Fig. 2c–e). Tracheid mean diameter was greater in the Ore Mountain than the Mongolian sites in roots, the stem, and branches if hydraulically weighted (d_h), but only in roots when not weighted (d) (Fig. 2f–k). Tracheid d_h in the Ore Mountains exceeded that in Mongolia by 13 % (stems and branches from the Khangai) or even by 22–25 % (roots from the Altai and Khangai, branches and stems from the Altai). In accordance with these data, large-diameter tracheids contributed more to K_h in the Ore Mountains than in the Mongolian Altai and the Khangai Mountains in roots, the stem, and to a lesser but significant degree in branches (Fig. 3).

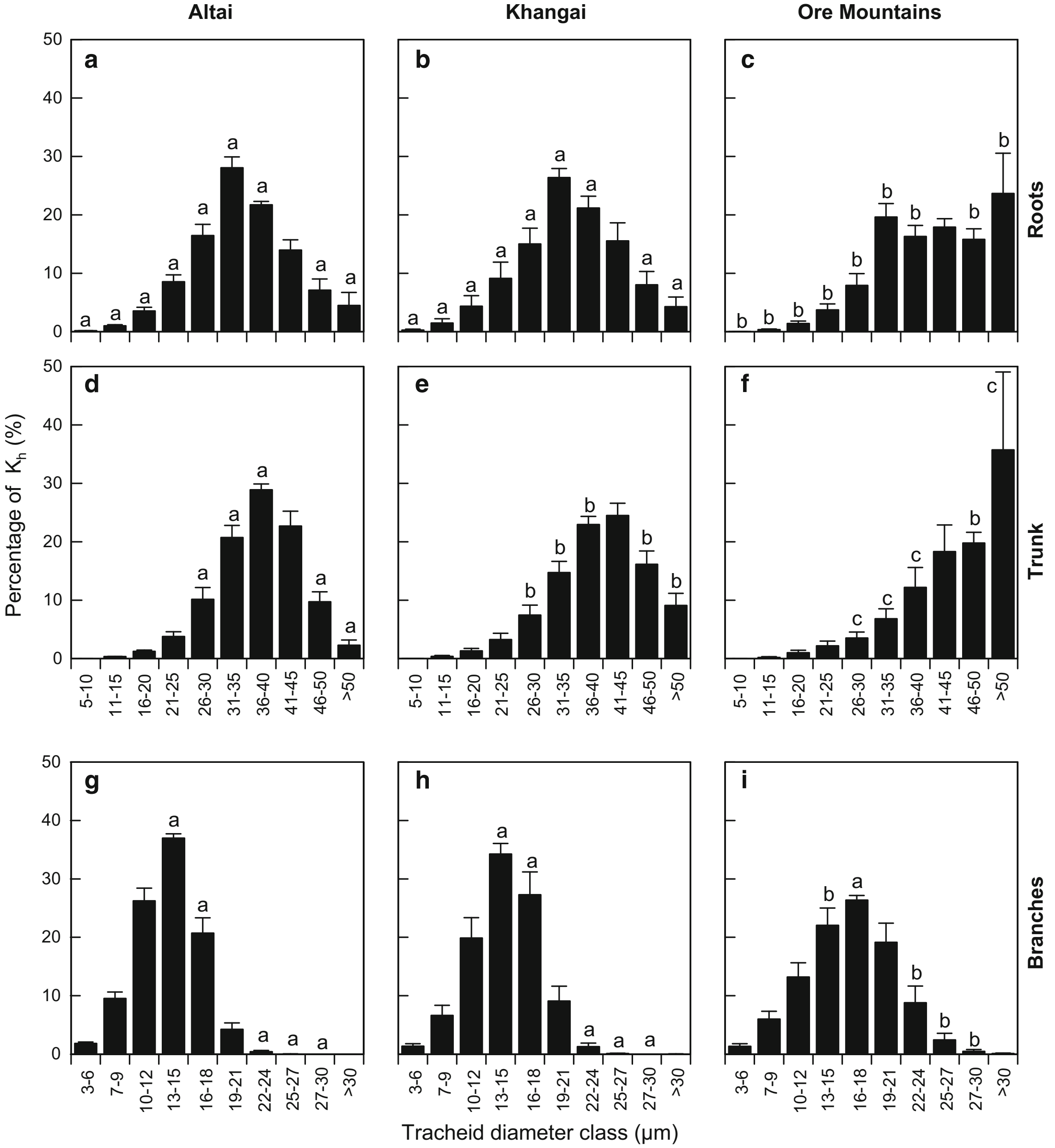


Fig. 3 Relative contribution of tracheids of different diameter classes to theoretical hydraulic conductivity (K_h) in **a**–**c** roots, **d**–**f** stems, and **g**–**i** branches of *L. sibirica* from **a**, **d**, **g** the Mongolian Altai, **b**, **e**, **h** the Khangai Mountains, and **c**, **f**, **i** the Ore Mountains. Within a plant organ (roots, stem, branches) means (±SE) of the same tracheid diameter class sharing the *same letter* do not differ significantly ($P \leq 0.05$, Kruskal–Wallis test followed by paired Mann–Whitney *U* tests; *absence of letters* indicates data with negative Kruskal–Wallis test result)

Consistent with the pattern found for d, TD in roots exhibited a minimum in the Ore Mountains, whereas differences between the study areas were lacking for stems and branches (Fig. 2m, n). The negative relationship between d and TD increased in tightness from branches through the stem to roots as evidenced by increasing coefficients of correlation (Figure S1 in the Supplementary Information). Hydraulic conductivity (K_s, K_p) and tracheid diameter (d, d_h) were generally much smaller and TD was much higher in branches than in roots and stems (Fig. 2). K_p and d, but not d_h, were also significantly smaller in roots than in stems ($P \leq 0.05$, LSD test).

Irrespective of the study area, the trees relied much more on earlywood than latewood for the formation of highly conductive large-diameter conduits. This is shown by significantly higher K_p, d_h, and d values for stem earlywood than latewood from all sites (Table S4 in the Supplementary Information).

Table 4 Linear correlation of hydraulic parameters (K_s, K_p, d_h, d, TD) in the xylem of roots, stems, and branches with mean growing season precipitation (MGSP), mean annual precipitation (MAP), mean growing season temperature (MGST), and mean annual temperature (MAT) in the three study areas in Mongolia (Mongolian Altai, Khangai) and Central Europe (Ore Mountains)

Organ	MGSP	MAP	MGST	MAT
K_s				
Roots	–	0.97(*)	–	0.98(*)
Branches	1.00*	0.98(*)	$0.98^{(*)}$	0.97(*)
K_p				
Roots	–	0.97(*)	–	0.98(*)
Stem	0.99*	0.96(*)	0.99*	0.95(*)
Branches	–	–	$0.96^{(*)}$	–
d_h				
Roots	0.96(*)	0.99*	–	1.00*
Stem	0.98(*)	–	1.00*	–
Branches	1.00*	0.97(*)	0.98(*)	0.96(*)
d				
Roots	–	0.98(*)	–	0.99*
Stem	0.98(*)	–	1.00*	–
Branches	–	–	–	–
TD				
Roots	−1.00*	−0.99(*)	−0.97(*)	−0.98(*)
Stem	–	–	–	–
Branches	–	−0.96(*)	–	−0.97(*)

Pearson correlation coefficients, * $P \leq 0.05$, (*) $P \leq 0.10$. Ks is only available for the total xylem cross section of roots and branches

Correlation of hydraulic properties with macroclimate and productivity

Notwithstanding the limited explanatory power of linear regression analysis based on only three study regions, positive correlations were found for both hydraulic conductivity (K_s, K_p) and tracheid diameters (d_h, d) with precipitation and temperature (Table 4). K_s and d_h increased with MGSP in branches. In the stem, positive correlation was found for K_p with MGSP and MGST as well as for d_h and d with MGST. Separate analysis for stem earlywood and latewood revealed significant correlation of K_p, d_h, d, and TD with precipitation and temperature variables in both stemwood fractions (Table S5 in Supplementary Information). In roots, d_h and d increased with MAT, whereas TD decreased with MGSP (Table 4).

BAI showed trends for increase with K_p, d_h, and d both in roots, stems, and branches, but most of these correlations were only marginally significant ($P \leq 0.10$; data not shown). Significant correlation at $P \leq 0.05$ was only found for BAI with branch K_s (positive) and root TD (negative). Furthermore, BAI increased with K_p and d in stem latewood ($P \leq 0.05$).

Meta-analysis of the relationship between precipitation and hydraulic properties in conifers

Comparison of our results for K_s and d_h from *L. sibirica* with other larch species and species of other conifer genera from Eurasia and North America showed that K_s values in both roots and branches were low compared to most other reported values (Table S6 in the Supplementary Information). In roots, the K_s mean of 2.8 kg m^{-1} MPa^{-1} s^{-1} in the Khangai Mountains and 3.2 kg m^{-1} MPa^{-1} s^{-1} in the Mongolian Altai were clearly below the range of 4.0–17.0 kg m^{-1} MPa^{-1} s^{-1} reported from Mediterranean Europe and temperate western North America. The higher K_s of 5.8 kg m^{-1} MPa^{-1} s^{-1} measured in *L. sibirica* roots from the Ore Mountains is in the range determined for *Pinus ponderosa* and *Pseudotsuga menziesii* in western North America.

The less variable K_s in branches of *L. sibirica* from our study (0.39, 0.51, and 0.75 kg m^{-1} MPa^{-1} s^{-1} in the Altai, Khangai, and Ore Mountains, respectively) was in the range of K_s values found in other studies on *Larix decidua*, *Picea abies*, *P. ponderosa*, and *Pinus sylvestris* (Table S6). Most branch K_s values in the evaluated literature, however, exceeded 1 kg m^{-1} MPa^{-1} s^{-1}. In contrast to K_s, d_h was in the same range in *L. sibirica* as in the other tree species compiled in Table S6; this applied to both roots and branches.

K_s in branches showed a close positive relation to mean annual precipitation (MAP) if data from different conifer species were merged (Table 5). For *L. sibirica*, the correlation of K_s with MAP was only marginally significant (Table 4). For roots, there was no correlation with K_s in the dataset from all species. For *P. ponderosa*, there was a positive correlation; the correlation for *L. sibirica* was marginally significant. Significant correlations of d_h with MAP were restricted to *Pinus* in branches and to *L. sibirica* in roots (Table 5).

Table 5 Meta-analysis based on a literature survey showing empirical sapwood area-specific hydraulic conductivity (K_s) and hydraulically weighted tracheid diameter (d_h) of different roots and branches in coniferous species from boreal, temperate, and Mediterranean climates in the northern hemisphere in relation to mean annual precipitation (MAP) and the relation between K_s and d_h (Pearson correlation coefficients)

	K_s vs. MAP			d_h vs. MAP			K_s vs. d_h		
	r	*P*	*N*	*r*	*P*	*N*	*r*	*P*	*N*
Roots									
All species	−0.20	0.30	9	0.55	0.17	5	**0.86**	**<0.05**	**5**
Larix sibirica[a]	0.97	0.09	3	**0.99**	**<0.05**	**3**	**0.99**	**<0.05**	**3**
Pinus ponderosa[b]	**0.99**	**<0.05**	**3**	na	na	na	na	na	na
Branches									
All species	**0.68**	**<0.001**	**22**	0.04	0.43	18	**0.83**	**<0.001**	**15**
Larix spec.	**0.83**	**<0.05**	**6**	0.97	0.08	3	**1.00**	**<0.01**	**3**
Larix decidua	**0.99**	**<0.05**	**3**	na	na	na	na	na	na
Larix sibirica[a]	0.98	0.07	3	0.97	0.08	3	**1.00**	**<0.01**	**3**
Pinus sylvestris	−0.04	0.45	12	**0.69**	**<0.01**	**12**	**0.69**	**<0.01**	**12**

Significant ($P \le 0.05$) correlations are in bold

[a] This study. For other sources see references in Tables S2 and S3 in the Supplementary Information

na No data available

Discussion

The contrasting macroclimates of Inner Asia (Mongolian Altai, Khangai Mountains) and Central Europe (Ore Mountains) showed clear covariation with tracheid diameters and densities as well as hydraulic conductivity in roots, stems, and branches of *L. sibirica*. The higher precipitation in Europe than in Inner Asia was correlated with higher K_p, d_h, and d and lower TD in roots and stemwood. In branches, only d_h and TD showed such match with precipitation. K_s, however, was significantly higher under the humid, suboceanic climate of the Ore Mountains than in the continental, semi-arid climate of the Mongolian Altai and the Khangai Mountains in both roots and branches. Consistent with earlier results from other tree species (Edwards and Jarvis 1982; Domec and Gartner 2002), early growing season climate seems to be most influential on the hydraulic architecture of *L. sibirica*, since K_p, d_h, and d were significantly higher in earlywood than in latewood, and tracheid diameters and conductivity are related to the climatic conditions during tree-ring formation (Fonti et al. 2010). Lower TD and higher d_h in the trees from the Ore Mountains than from Mongolia match with the observation that biomass equations established for planted *L. sibirica* in Iceland led to the underestimation of biomass of *L. sibirica* from Mongolia, which was attributed to higher wood density in semi-arid Mongolia than in oceanic Iceland (Battulga et al. 2013).

Positive correlation of hydraulic conductivity in branches (K_s) and also in stem earlywood (K_p) with MGSP, but not MGST or MAT, suggests that moisture availability during the early growing season is probably more effective in controlling hydraulic conductivity in *L. sibirica* than temperature. Correlation of hydraulic conductivity (and xylem anatomy as the structural basis for conductivity) with precipitation has earlier been reported from various tree species (Piñol and Sala 2000; Corcuera et al. 2004), including *L. decidua* (Bryukhanova and Fonti 2013). This suggests that relations found between precipitation and hydraulic traits in *L. sibirica* are causal. However, given the contrasting macroclimates of Inner Asia and Central Europe, our study sites in Mongolia and Germany differed not only in precipitation but also in temperature and other climate parameters as well as soil conditions. Indeed, hydraulic and wood anatomical traits correlated also with MGST and MAT, although in a less consistent manner. These correlations match with the findings of Fonti et al. (2013), who demonstrated that warm early growing seasons increased the diameter and absolute number of tracheids in stem earlywood of *L. sibirica* in the Russian Altai. Therefore, our findings support the first hypothesis that hydraulic and wood anatomical traits of *L. sibirica* are influenced by the steep precipitation gradient of c. 700 mm year^{-1}, but also suggest that temperature and perhaps other climatic factors, such as relative air humidity, which were not included in our study might have affected tracheid anatomy and thus hydraulic conductance. This suggests in agreement with the results on radial cell expansion by Antonova and Stasova (1997) that the hydraulic architecture of *L. sibirica* is not just a simple cause and effect relationship with soil water availability, but that other climatic parameters interfere with this relation. In the Mongolian Altai, tree-ring width in *L. sibirica* is primarily correlated with summer temperatures (D'Arrigo et al. 2000; Dulamsuren et al. 2014).

Based on the comparison of means between study areas (Fig. 2) and the relative contribution of tracheids of different diameter classes to hydraulic conductivity (Fig. 3), it appears that root and stem hydraulic and wood anatomical parameters of *L. sibirica* were more responsive to macroclimate than branch traits. This is indicated by the lack of significant differences in branch K_p and d between the study regions. Nevertheless, K_s and d_h reached higher means in the samples from the Ore Mountains than from Mongolia in roots, stems, and branches as well. Several other studies found high responsiveness of the branch hydraulic traits to variation in precipitation (Mencuccini and Grace 1995; Maherali and DeLucia 2001, Martínez-Vilalta et al. 2009), but there are also reports about insensitivity (Choat et al. 2007; Creese et al. 2011) matching our results. Reducing the number of branches per tree, including active branch shedding during drought periods, is an alternative way to cope with drought stress, independent from reduction in conduit diameter during wood formation (Hacke and Sauter 1996; Rood et al. 2000). In *Pinus*, trees from dry regions have lower leaf-to-sapwood area ratios than trees from moist regions (Maherali and DeLucia 2000; Sterck et al. 2012). Moreover, Pinaceae with high risk of stem xylem cavitation apparently increases hydraulic safety by maintaining low leaf-to-wood area ratios (Martínez-Vilalta et al. 2004). Unfortunately, we have no data that could show whether branch shedding is a means of adaptation in *L. sibirica* in the Mongolian forest-steppe ecotone. *Larix* trees have been found to shed shade branches with low net carbon gain (Matyssek und Schulze 1988), but this response could also be an adaptation to fire, since a reduced downward extension of the crown reduces the risk of crown fires (Schulze et al. 1995).

Although root hydraulic and wood anatomical traits all differed significantly between Inner Asia and Europe, it is not very likely that a modified hydraulic architecture is a decisive element in the adaptation of *L. sibirica* to semi-arid climate in Mongolia because Chenlemuge et al. (2013) found very high fine root mortality in dry summer months in the studied stands. Apparently, the species forms fine roots with large-diameter conduits in moist periods with the disadvantage of high cavitation risk in subsequent drought periods for capturing the scarce water in rain periods as efficiently as possible. Drought-induced fine root mortality, or perhaps active shedding of fine roots at the onset of drought periods, could be a mechanism to prevent the spread of embolism into coarse roots, which are less easily replaced (Sperry and Ikeda 1997). Drought-induced fine root mortality has been repeatedly reported in trees (Sanantonio and Hermann 1985; Leuschner et al. 2001; Maniero and Kazda 2006).

A meta-analysis of K_s and d_h data from conifers from various regions of the northern hemisphere suggests that co-variation of hydraulic and wood anatomical traits with precipitation seems to be more common in branches than in roots. This seems to contrast with our observations in *L. sibirica.* This deciduous conifer, which extends its range further into semi-arid Inner Asia than any other boreal tree species, may have evolved a unique strategy to cope with pronounced summer drought. This assumption is supported by data on fine root biomass in Mongolian *L. sibirica* forests which was found to be far smaller than that in other conifer forests around the world (Chenlemuge et al. 2013). According to our results, K_s and K_p were an order of magnitude higher in roots than in branches in all study areas which meets the expectation (Nygren and Pallardy 2008; Gonzalez-Benecke et al. 2010; Lintunen and Kalliokoski 2010). However, it is interesting that K_p, d_h, and d were not higher in roots than in the stem suggesting that the hydraulic architecture of *L. sibirica* differs from that of many other species, which show steady tapering of conduit diameter along the flow path toward the distal branches (Tyree and Zimmermann 2002). Similarity of K_p, d_h, and d in coarse roots and stem, as observed in *L. sibirica*, has also been found in some tropical tree species (Schuldt et al. 2013).

The higher hydraulic conductivity in the European *L. sibirica* stand coincided with higher stem basal area increment (BAI) as compared to the Mongolian stands. Even though the correlations between K_s, K_p, d_h, and d with BAI were only partly significant at $P \leq 0.05$ (for the remaining relations, P was ≤ 0.1), our findings suggest a direct effect of the hydraulic architecture of roots and branches on the productivity of *L. sibirica*. Earlier studies could demonstrate a relation between the hydraulics of small terminal branches and the physiology of leaves (Brodribb and Feild 2000; Nardini and Salleo 2000; Bucci et al. 2004; Santiago et al. 2004), but the possible dependence of stem radial growth on root hydraulic or anatomical traits has rarely been studied so far. One reason is that root hydraulics in general has attracted only minor attention. Another point is that the specific conductivity of the xylem decreases along the flow path (Tyree and Zimmermann 2002), and small canopy branches thus should control flow through the trunk to a large extent (Melcher et al. 2012).

In addition to the different hydraulic and wood anatomical traits between Inner Asia and Europe following the gradient in macroclimate, we also observed significantly higher K_p, d_h, and d in the stem wood of trees from the Khangai Mountains than the Mongolian Altai, matching with the lower precipitation in the latter than the former region. Nevertheless, we did not find significant differences in K_s, K_p, d_h, and d in root and branch wood between the two Mongolian study areas in our data. This lack might be attributable to the higher significance of permafrost, which is assumed for the water supply of *L. sibirica* in the Mongolian Altai than in the Khangai as explained in the study site description. The hydraulic architecture of the stem apparently responds more sensitively even to small differences in soil moisture availability, since damage by hydraulic failure would have here more severe effects than in roots and branches.

Comparing the two Mongolian stands revealed that the hydraulically weighted tracheid diameter of the stem xylem, but not of the branch and root xylem, was larger in the somewhat moist Khangai Mountains than in the Altai. We speculate that the hydraulic architecture of the stem responds more sensitively to the rainfall difference between the two regions (179 vs. 87 mm of rain in May–September) than that in roots and branches because the cost of replacing roots or branches is less.

Conclusions

With both our field data from *L. sibirica* and the results of the meta-analysis covering various northern hemisphere conifers, we could substantiate the assumption that the formation of large-diameter tracheids with high conductivity is triggered by higher precipitation, supporting our first and third hypotheses. The field data showed in general a positive relation between precipitation and hydraulic conductivity and tracheid diameter (especially d_h) in roots, stems and branches, i.e., along the whole flow path, even though the correlation was less tight in branches than in the other organs. Correlation analyses further suggest that the hydraulic architecture is influencing productivity and that elevated stem increment is related not only to higher hydraulic conductivity in the stem but also in roots and branches. However, our results also indicate a temperature effect on the hydraulic architecture of *L. sibirica*. The water relations of this species close to the drought limit of its occurrence seem to be influenced by fine root abscission and perhaps also by branch shedding. Studies in a larger number of stands have to show whether these patterns are of more general validity across the southern boreal forest biome.

Author contribution statement All authors designed the study and wrote the paper. TC, CD and MH performed field work. TC and BS conducted laboratory work. TC, CD, MH and BS analyzed data. DH performed the meta-analysis.

Acknowledgments The study was supported by a grant from the Volkswagen Foundation to M. Hauck, Ch. Dulamsuren and Ch. Leuschner for the project ‘Forest regeneration and biodiversity at the forest-steppe border of the Altai and Khangai Mountains under contrasting developments of livestock numbers in Kazakhstan and Mongolia’. Tselmeg Chenlemuge was funded by a scholarship of the China Scholarship Council (CSC). We thank the Altai Tavan Bogd National Park (Ulgii) for permissions to carry out the field work and are very grateful that Hildegard Neeser allowed us to sample her trees at the Giegengrün plantation in the Ore Mountains (http://www.sibirische-laerche-pflanzensamen.de). We thank Claus Döring (University of Göttingen) for modeling the climate date for the Giegengrün site.

Conflict of interest The authors declare that they have no conflict of interest.

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