Drought Adaptation of the Fine Root System and Hydraulic Architecture of *Larix sibirica* at its Southern Distribution Limit

---

Dissertation

zur Erlangung des Doktorgrades

der Mathematisch-Naturwissenschaftlichen Fakultäten

der Georg-August-Universität zu Göttingen

---

im Promotionsprogramm Biologische Dibersität und Ökologie

der Georg-August University School of Science (GAUSS)

vorgelegt von

Tselmeg Chenlemuge

aus China

Göttingen, October, 2014

Thesis Committee

Prof. Dr. Markus Hauck

Plant Ecology and Ecosystem Research, Albrecht von Haller Institute of Plant Sciences, University of Göttingen

Prof. Dr. Christoph Leuschner

Plant Ecology and Ecosystem Research, Albrecht von Haller Institute of Plant Sciences, University of Göttingen

PD Dr. Dirk Gansert

Plant Ecology and Ecosystem Research, Albrecht von Haller Institute of Plant Sciences, University of Göttingen

Members of the Examination Board

Reviewer: Prof. Dr. Markus Hauck

Plant Ecology and Ecosystem Research, Albrecht von Haller Institute of Plant Sciences, University of Göttingen

Second Reviewer: Prof. Dr. Christoph Leuschner

Plant Ecology and Ecosystem Research, Albrecht von Haller Institute of Plant Sciences, University of Göttingen

Further members of the Examination Board:

Prof. Dr. Erwin Bergmeier

Department Vegetation & Phytodiversity Analysis, Albrecht-von-Haller-Institute for Plant Sciences, Faculty of Biology and Psychology, University of Göttingen

Prof. Dr. Dirk Hölscher

Tropical Silviculture and Forest Ecology, Faculty of Forest Sciences and Forest Ecology, University of Göttingen

Prof. Dr. Hermann Behling

Department of Palynology and Climate Dynamics, Albrecht-von-Haller Institute for Plant Sciences, University of Göttingen

PD Dr. Dirk Gansert

Plant Ecology and Ecosystem Research, Albrecht von Haller Institute of Plant Sciences, University of Göttingen

Tag der mündlichen Prüfung: 21st October, 2014

Summary

Taiga-steppe ecotone is a natural grassland habitat with isolated forest islands and low precipitation (*c.* 100-250 mm yr^{-1}), and is an important part of the boreal biome. The southernmost distribution limit of Siberian taiga occurs in the mountainous areas of Northern and Western Mongolia. In these areas, larch (*Larix sibirica*) forest patches are normally restricted to the upper part of humid north-facing slopes, whereas steppe covers south-facing slopes and most valley bottoms. Temperatures have been rising faster here than the the global average for decades, but precipitation has not increased concomitantly. Induced by the increasing aridity, a decades-long decline in the growth and regeneration of the larch forests, and differentiation in the growth performance of *L. sibirica* between within-stand microhabitats (forest edge vs. forest interior) was evidenced by earlier work. However, the physiological mechanisms underlying these ecological responses to drought stress and climate warming are not fully understood.

As a contribution to answer these questions, bio- and necromass and morphological properties of fine roots, xylem hydraulic conductivity and wood anatomical properties along the flow pass (root, stem, and branch) together with tree productivity in monospecific *L. sibirica* stands were studied in this thesis. The study was conducted in two dry sites (the Altai and the Khangai Mountains) in the Mongolian forest-steppe ecotone and a moist site in Central Europe (the Ore Mts. in Germany). The dry sites contain natural *L. sibirica* stands while the moist site is a *L. sibirica* plantation outside its natural range. Field work was carried out during three continuous growing seasons (July/August 2010, 2011 and 2012) which started with two dry years (2010–2011) and a subsequent wet year (2012). Variations in fine root mass and morphological properties between the dry and moist years and between the dry and moist site were examined. Spatial distribution of fine roots was also investigated in the Mongolian Altai. The hydraulic architecture of *L. sibirica* between the dry and moist sites was compared in relation to macroclimate (precipitation, temperature) and tree productivity. We also studied how branch and coarse root hydraulic architecture and xylem conductivity, fine root biomass and necromass, and fine root morphology of *L. sibirica* respond to different microhabitat conditions in terms of water availability.

Fluctuations in fine root biomass (FRB) between years and among study areas revealed high plasticity in fine root system of *L. sibirica* to different precipitation regimes. In general, increasing FRB was associated with increasing precipitation. Comparatively deep fine root distribution was found in the larch stand in the Altai Mt., which might be an adaptation to top soil drying. However, no obvious plastic change in fine root morphology was observed. Mean annual precipitation was directly related to wood anatomical and hydraulic traits across the three sites, and a higher sapwood area-specific hydraulic conductivity in both roots and branches is correlated with higher productivity in terms of annual radial stem increment. We found a significant reduction of branch hydraulic conductivity in the putatively more drought-affected forest interior in the driest Mongolian Altai site, while no branch xylem modification occurred in the moister Khangai Mountain site. Hydraulic conductivity was several times larger in roots than in branches, but root hydraulics was not influenced by stand density or mean annual precipitation. Very low fine root biomass : necromass ratios at all sites, and in the forest interior in particular, suggest that *L. sibirica* maintains a relatively high root conductivity by producing large conduits, which results in high root mortality due to embolism during drought.

In summary, our results suggest that *L. sibirica* is adapted to the semi-arid climate at its southernmost distribution limit by considerable plasticity of the branch hydraulic system and a small but apparently dynamic fine root system.

List of abbreviations

a.s.l.	Above sea level	L:D	Live to dead fine-root mass ratio
A_{cross}	Cross-sectional area	LAI	Leaf area index
A_{L}	Leaf area	LSD	Least significant difference
ANOVA	Analysis of variances	MAP	Mean annual precipitation
A_{S}	Sapwood area	MAT	Mean annual temperature
AvgDiam	Average root diameter	MGSP	Mean growing season precipitation
A_{xylem}	Xylem cross-sectional area	MGST	Mean growing season temperature
BAI	Basal area increment	Mt.	Mountain
c.	Circa	Mts.	Mountains
$CaCO_3$	Calcium carbonate	MycorCol	Mycorrhizal colonization rate
CV	Coefficient of variation	NTRM	Non-tree roots mass
d	Tracheid diameters	P	Precipitation
d_{h}	Hydraulic mean diameter	SOC	Soil organic carbon
DBH	Diameter at breast height	SRA	Specific root surface area
DM	Dry mass	SRL	Specific root length
FE	Forest edge	SRTA	Specific root tip abundance
FI	Forest interior	T	Temperature
FRB	Fine root biomass	*TD*	Tracheid density
FRN	Fine root necromass	TisDens	Root tissue density
GL	Gleichläufigkeit	TRW	Tree-ring width
GLM	General linear models	TSAP	Time Series Analysis and Presentation
IPCC	Intergovernmental panel on climate change	vs.	Versus
J_{V}	Flow rate	X	Segment length
KCl	Potassium chloride	ΔP	Pressure gradient
K_{h}	Hydraulic conductivity for a given segment length	η	Viscosity
K_{L}	Leaf-area specific hydraulic conductivity	ρ	Density
K_{p}	Potential sapwood area-specific hydraulic conductivity		
K_{S}	Sapwood area-specific hydraulic conductivity		

Table of contents

List of figures

List of tables

Chapter 1

General Introduction

1.1 Siberian boreal and Inner Asian forests under climate change

Forests cover more than 4.1 billion hectares of the earth's land area and store 80% of the aboveground and 40% of the belowground terrestrial carbon (Dixon et al., 1994; Valentini et al., 2000). As boreal forests cover around 15% of the global land surface area (11.6 million km^2) and contain soil carbon equivalent to 50% of the carbon that occurs in the atmosphere (Bonan and Pollard, 1992; Gower et al., 2001). The Siberian boreal forest, the largest continuous forest on earth contains roughly half of the world's growing stock volume of coniferous species and is thus expected to affect the global carbon balance significantly (Shuman et al., 2011).

Much of the Siberian taiga consists of deciduous larch forests (*Larix* spp.) growing on continuous permafrost in Central and Northeastern Siberia where larch is dominant, and on the discontinuous or non-permafrost regions of Western or Southern Mountainous Siberia where larch co-occurs with other tree species (Sugimoto et al., 2002; Kajimoto et al., 2010). Larch trees cover about 42% of Russian forested area and constitute about a half of the total carbon pool of the Siberian taiga forests (Kajimoto et al., 2010).

It is generally accepted that mean global temperatures are increasing and that particularly largetemperature increases are currently found in the northern hemisphere upper latitudes in the boreal and arctic vegetation belts (IPCC, 2013). The Siberian forestsare said to be one of the regions most affected by climate warming (Soja et al., 2007; Shuman et al., 2011). Increasing drought, shrinking permafrost, insect outbreaks and increased wildfire disturbance were frequently observed throughout entire Siberia and adjacent forests in Kazakhstan and Mongolia (Sugimoto et al., 2002; Kajimoto et al., 2003; Sharkhuu, 2003; Ishikawa et al., 2005; Sharkhuu et al., 2007; Soja et al., 2007; Dulamsuren and Hauck, 2008; Dulamsuren et al., 2010a, 2010b, 2010c, 2013; Zhao et al., 2010). Climate-vegetation models have predicted an upward and a poleward shift of vegetation zones (IPCC, 2001; Soja et al., 2007; Benito-Garzón et al., 2014), conversion of larch forests to evergreen conifer forests (Sudachkova et al., 2002; Lloyd et al., 2011) and decreasing regional surface albedo (Shuman et al., 2011). Both remote sensing and dendrochronological studies show evidence supporting these predictions (Tchebakova et al., 1994, 1995; Kobak et al., 1996; Kharuk et al., 2009, 2010a, 2010b; Allen et al., 2010; Liu et al., 2013).

1.2 Drought impacts on the Southern Siberian and Inner Asian boreal forest

Productivity of forest ecosystems is largely constrained by water availability. Drought stress occurs whenever soil water drops below a threshold inducing restrictions to growth and transpiration. Reduced water availability threatens the integrity of the liquid phase along the soil-plant-atmosphere continuum. Decreased water and CO_2 fluxes could limit tree growth and individual tree survival may become problematic under extreme soil water depletion. Increases in the frequency, duration, and/or severity of drought and heat stress associated with climate change have already altered the composition, structure, and ranges of forests in many regions (Bréda et al., 2006; Allen et al., 2010).

At the southern fringe of the Siberian boreal forest (i.e., the interface between Siberian taiga and temperate grassland), an increase in temperature above global average and no accompanying precipitation have been lasting for decades (Batima et al., 2005; Soja et al., 2007; Dulamsuren et al., 2010b). Dendrochronological studies have provided increasing evidence that the coniferous forests of the southern boreal zone in Northern Mongolia and north-eastern Kazakhstan and also in Central mountainous China are affected by lasting growth reductions and regeneration attributed to aridity increase in these regions (Dulamsuren et al., 2010b, 2011, 2013, 2014; Liu et al., 2013). Consequently, a declineof forest and an expansion of the transitional lowland forest-steppe biome was predicted in Southern Siberia (Tchebakova et al., 1995). Increasing human activities put additional pressure on the forest in the forest-steppe ecotone (Fernandez-Gimenez, 1999; Dulamsuren et al., 2009; Khishigjargal et al., 2013; Lkhagvadorj et al., 2013).

Future climate scenarios suggest that the temperature will continue increasing by an least2K until 2100 in the boreal region (IPCC, 2007; Soja et al., 2007). This warming is expected to enhance the frequency and the severity of drought events (Bréda et al., 2006), which give reason to a growing concern that climate change induced disturbances, together with increasing anthropogenic interfere may fundamentally alter the composition, structure, and productivity of forests in Southern Siberian region.

1.3 Drought impacts on tree fine root

Fine roots (<2 mm in diameter) play a crucial role in the global carbon cycle, because they contribute with up to 40% of the total ecosystem production (Vogt et al., 1986) and 75% of mature forests net primary production (Jackson et al., 1997; Gill and Jackson, 2000). In a state of constant flux, with death and replacement taking place simultaneously, fine roots contribute substantially to the organic matter content of soil together with litterfall (Persson, 1983; Nadelhoffer and Raich, 1992). Fine roots are also the primary pathway for water and nutrient uptake (Strand et al., 2008) and are the most sensitive plant part in response to soil water deficit. Both the spatial extension and density of the plant fine root system and the morphology and physiological activity of absorbing root tips control the efficiency of soil water and nutrient absorption (Bréda et al., 2006; Ostonen et al., 2011).

Published work showed that deficit in soil moisture may reduce soil nutrient transport via mass flow and diffusion from soil surface to the roots, resulting in decreased nutrient availability at the root surface and reduced root growth (North and Nobel, 1997). Fine root biomass was found to be reduced with increasing drought in several tree species, including *Fagus sylvatica*, *Picea abies*, and *Pinus sylvestris* of temperate forests (Dreyer et al., 2001; Leuschner et al., 2001; Meier and Leuschner, 2008). In controlled garden experiments, reduced irrigation treatment could reduce fine root growth of oak saplings (Fort et al., 1997). Yuan and Chen (2010) reported that fine root biomass and production in boreal forests increased with the amount of annual precipitation, although fine root turnover seemed to be unaffected. In temperate forests, the fine root biomass-precipitation relationship showed a slight non-linear increase with precipitation in coniferous forests, but not in broad-leaved stands (Leuschner and Hertel, 2003). Whereas Joslin et al. (2000) found responses of roots to irrigation treatments have been mixed and at any rate were difficult to extend to long-term change in precipitation at the ecosystem scale. Finér et al. (2011a, b) found no significant relationship between precipitation and fine root biomass, production and turnover at a global scale. Fine root turnover across different ecosystems was not correlated with precipitation when the effects of temperature were taken into consideration (Gill and Jackson, 2000; Norby and Jackson, 2000). Thus, the relationships between fine root biomass, productivity and turnover and precipitation or water availability are not completely clear.

The potential for water uptake of fine roots is more likely to be related to the surface area than to the biomass of the fine roots (Coomes and Grubb, 2000). Water and nutrient uptake per unit root mass will be higher at a larger specific root area if area-related uptake rates remain unchanged (Tyree et al., 1998). Thus, the carbon and nutrient costs of water and nutrient uptake may be lower at smaller root diameters. Mycorrhizal colonization can enhance root longevity via diverse mechanisms, including enhanced tolerance of drying soil and enhanced defense against root pathogens (Eissenstat et al., 2000). Uptake rates of nutrients and water may also depend on the frequency of mycorrhizal root tips per root mass, the type of mycorrhizal association, and the total length of fungal hyphae (Leuschner et al., 2004).

Study of the fine root system to drought under different climate conditions is important in order toassess the consequences of climate warming, given the large proportion of fine root production on total net primary production in forests. However, such studies are especially scarce from the Siberian boreal region (Kajimoto et al., 2003). Data on biomass stocks and productivity in boreal forests dominated by the *Larix* species in Siberia or Inner Asia are relatively rare (Shvidenko et al., 2001; Kajimoto et al., 2010). This is especially the case for root biomass and primary production, since most previous studies were conducted on aboveground parts (e.g., Schulze et al., 1995; Kirdyanov et al., 2008).

1.4 Drought impact on tree hydraulic architecture

Productivity of forest ecosystems is constrained by water availability because photosynthesis and transpiration are coupled, as plants absorb carbon dioxide from the atmosphere through stomata and transpire water at the same time. Transpired water moves from the soil through the plant and finally to the atmosphere along a continuum of gradually decreasing water potentials. According to the "tension-cohesion" theory (Dixon, 1914) and its "Ohm's analogy" formalism (van den Honert, 1948), the actual water flux through any water conducting segment of the organ (petiole, leaf, stem and root) depends on the gradient of water potential within the segment and the hydraulic conductance (K_h) per unit length, i.e., the conductivity of the segment (K_L), which can be expressed either as a function of the leaf area (A_L) connected to the segment ($K_L = K_h/A_L$) and is then defined as the leaf specific conductivity or as a function of the transverse sapwood area (A_S) of the segment ($K_S = K_h/A_S$). K_L is an estimation of hydraulic "sufficiency" of a segment that is its ability to supply the leaves distally to that segment with sufficient water while K_S refers to the intrinsic "efficiency" of branches and roots to conduct water (Bréda et al., 2006).

Water transport through the xylem conduits is considered to be meta-stable because water column breaks when tension becomes excessive, a phenomenon referred to as cavitation (McElrone, 2013). Drought may induce cavitation as plants become drier tension in the water column increases. To prevent cavitation leaf stomata can be closed resulting in lower stomatal conductance (g_s) and photosynthesis (A). This reduces transpiration and also carbon gain. Thus thetree's productivity is constrained as the result of stomatal regulation (Ryan et al., 1997; Ryan and Yoder, 1997; Tyree, 2003).

Hydraulic conductivity should increase linearly with sapwood cross-sectional area, conduit density within sapwood and the fourth power of the radius of the conduits size as the Hagen-Poiseuille law stated, which means large vessels can transport a higher amount of water (Zimmermann, 1983; Tyree et al., 1994). The relationship between hydraulic conductivity and conduit anatomical features has been confirmed by many empirical studies (Tyree et al., 1991; Sperry et al., 1994; Ladjal et al., 2005; Gonçalves et al., 2007; Sterck et al., 2008). However, large vessels are more prone to dysfunctions because plants having large, efficient conduits are threatened, at the same time, by increasing vulnerability to cavitation (Sperry et al., 1994; Tyree et al., 1994; Zimmermann et al., 2004; Sperry et al., 2008; Sonsin et al., 2012). In most plants, the diameter of xylem conduits (vessels and tracheids) and the related hydraulic conductance in the xylem decrease from roots to the terminal branches while the vulnerability to cavitation increases in transverse direction (Tyree et al., 1993; Hacke and Sauter, 1996; Tyree and Zimmermann, 2002; Gonçalves et al., 2007).

Published studies on hydraulic conductivity and wood anatomy in relation to tree productivity in the *Larix* forests of Southern Siberia and adjacent Kazakhstan and Mongolia are extremely scarce. Mechanisms for adaptation of the hydraulic architecture of *Larix sibirica* to increasing drought stress at the tree's southern drought limit is largely unknown.

1.5 Study objectives and hypotheses

This study was conducted 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. The study regions covered gradients of annual mean precipitation of roughly 700 mm and of annual mean temperature of more than 10 K. The objectives of this study were to examine:

(1) To what extent differ drought-affected boreal *L. sibirica* forests from planted *L. sibirica* outside its natural range under much milder and more humid climatic conditions than in the Mongolian forest-steppe in the amount of fine-root biomass, root necromass and root morphological properties (Chapter 2)?

(2) How does macroclimate affect the relationships between hydraulic conductivity and wood anatomical properties in roots, stems and branches and the tree's productivity in *L. sibirica* forests (Chapter 3)?

(3) How does the microhabitat (forest edge vs. forest interior) within *L. sibirica* stands in Inner Asia affect fine root distribution, demography and morphology, as well as tree hydraulic conductivity and wood anatomical properties in relation to tree productivity of larch (Chapter 4)?

In Chapter 2, three hypotheses were tested: (i) Both fine-root bio- and necromass of *Larix sibirica* forests in the dry sites in the Mongolian forest-steppe region are lower than the moister site in the Ore Mountains, Germany. (ii) In the Mongolian *Larix sibirica* forests, fine-root biomass is lower while fine-root necromass is higher in the dry year

(2010-11) than in the moist year (2012). (iii) Fine root morphological characteristics should differ between dry and moist sites and also between dry and moist years.

In Chapter 3, three hypotheses were tested: (i) mean annual precipitation is directly related to wood anatomical and hydraulic traits across the three sites in Mongolia and Germany (ii) a higher sapwood area-specific hydraulic conductivity in both roots and branches is correlated with higher productivity in terms of annual radial stem increment, and that (iii) the hydraulic conductivity and tracheid diameters in conifer roots and branches are positively correlated with precipitation.

In Chapter 4, the tested hypotheses were: (i) conduit size and related hydraulic conductivity are higher in branches and roots of trees at the forest edge than in the interior, (ii) the anatomy and functionality of roots are more plastic than of branches and roots thus show a higher responsiveness to the interior-edge gradient in stem density, and (iii) with increasing competition intensity from the edge to the interior, fine root biomass decreases per tree individual and also per stand area reflecting the deterioration of soil water availability.

1.6 Study design

1.6.1 Study areas

The study included two Siberian larch (*Larix sibirica* Lebed.) forests in western Mongolia (Mongolian Altai, western Khangai Mountains) located at the southern fringe of the Eurosiberian boreal forest belt in the transition zone to the steppe (Fig. 1.1) as well as a mature *L. sibirica* plantation stand in the Ore Mountains, south-eastern Germany. The study area in the Mongolian Altai was located south and southeast of Lake Dayan (48°14'39"-48°16'3" N, 88°50'17"-88°57'0" E; 2300-2375 m a.s.l.) in the Dayan administrative subunit ('bag') in the Altai Tavan Bogd National Park in the province ('aimag') of Bayan-Ulgii, 110 km SW of the city of Ulgii. The study area in the western Khangai Mountains (600 km east of Lake Dayan) was located in the valley of the river Shireegiin Gol (47°29'11"-47°30'37" N, 96°59'20"-97°13'59" E; 2100-2300 m a.s.l.), c. 30 km SSE of the city of Uliastai and 40 SW of Mt. Otgontenger in the province of Zavkhan. The *L. sibirica* plantation in Germany is located in the Ore Mountains at Giegengrün near Kirchberg (50°35'13" N, 12°31'37" E), 15 km SSE of the city of Zwickau at 465 m a.s.l. The climate of Mongolian study areas is semi-arid and highly continental, whereas the climate of the study area in Central Europe (Ore Mountains, Germany) is suboceanic, which made comparison of fine root distribution and plasticity of the hydraulic system of *L. sibirica* between drought-stressed environment ample-water environment possible (Table 1.1).

All the studied stands are monospecific larch forests. Both study areas in Mongolia are located in the forest-steppe ecotone in mountainous terrain where *L. sibirica* forests occur on north-facing slopes, whereas steppe covers south-facing slopes and most valley bottoms. Most larch woodlands are forest islands of variable size that were partly converted into pasture by the local herdsmen over time. The stand in the Ore Mountains was an even-aged plantation of c. 0.5 ha with about 100 trees with a canopy cover of 80–90 % (Table 1.2).

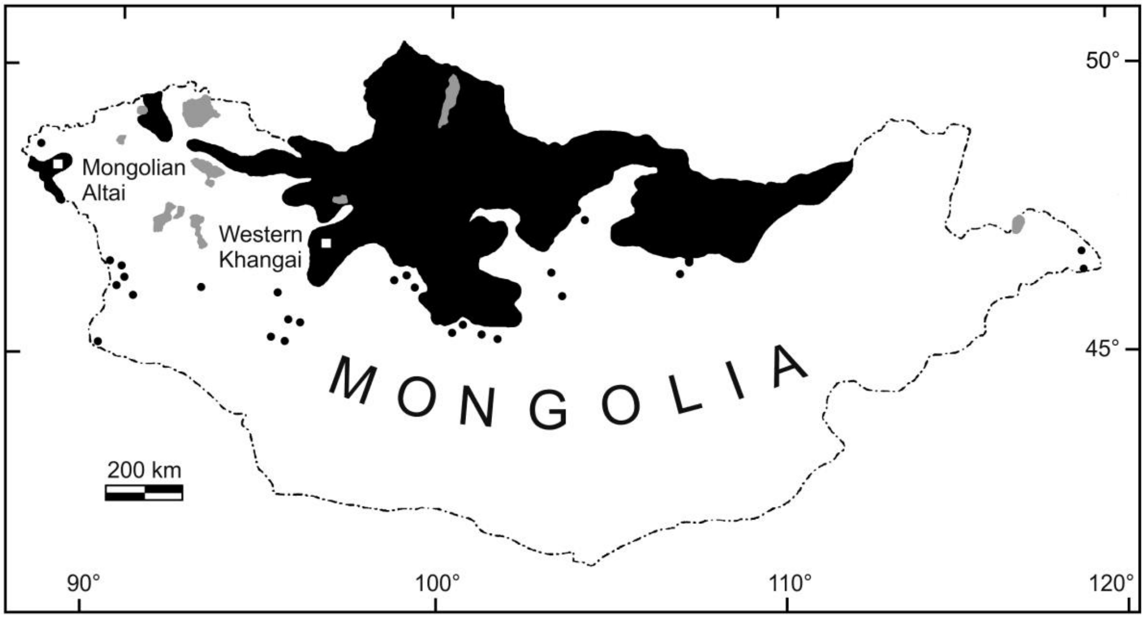

Fig. 1.1 Location of the two study areas in the Mongolian Altai and the western Khangai Mountains in Mongolia. The black areas are landscapes dominated by continuous boreal conifer forests or forest-steppe; black dots mark isolated conifer forests. Gray areas are lakes.

Table 1.1 Precipitation (P) and temperature (T) in the period from 1940 to 2010 in the Mongolian Altai, Khangai**[1]** and the Ore Mountains[2]. Given are annual mean and mean values for the growing season (May to September)

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

[1] Weather data was measured from weather station Altai-Yalalt, 40 km east of the studied forests, 2150 m a.s.l. in the Mongolian Altai and weather station Uliastai, 30 km NNW of the studied forests, 1760 m a.s.l. in the Khangai

[2] Weather data in the Ore Mts. was obtained from Klima-Atlas, 1958

Table 1.2 Stand characteristics (means ± SE) of the studied larch forest sites in the Mongolian Altai, Khangai and Ore Mountains.

	Altai	**Khangai**	**Ore Mts.**
Age of canopy trees (years)	155 ±11	137 ±15	118
Age of all trees (years)	85 ±7	109 ±18	
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
Average tree height (m)	7.0 ±1.3	9.9 ±0.5	
Mean stem diameter of canopy trees (cm)	32.2 ±3.6	22.4 ±1.4	54.0 ±2.3
Mean stem diameter, all trees (cm)	13.8 ±1.3	14.7 ±1.8	
Stand basal area of canopy trees (m^2ha^{-1})	38.6 ±3	15.5 ±2.7	
Total stand basal area (m^2ha^{-1})	47.8 ±3.8	28.9 ±3.7	
Canopy cover (%)	43.3 ±1.1	31.7 ±2.7	
Cover of herb and shrub layers (%)	76.7 ±2.1	75.0 ±2.6	

1.6.2 Sample plots

Field work was carried out during three subsequent growing seasons (July/August 2010, 2011 and 2012) which started with two dry years (2010–11) and continued with a subsequent moist year (2012) in both Mongolian sites (Table 1.3). Sampling was conducted in six stands each of the Mongolian Altai and the Khangai on 12 plots of 20 m × 20 m size. Six plots of hese plots were established in the forest interior, c. 50–100 m behind the forest line, and another six plots at the forest edge. The lower boundary of the forest edge plots was identical with the forest line. Same plot setting procedure in the Ore Mountains site was not possible due to limited size of the site.

Table 1.3 Precipitation and temperature characteristics in the Mongolian Altai in the period 2009-2012. Altai-Yalalt and Ulgii are located 40 and 110 km east of the study site and the station Dayan in close to the study site. The summers of 2010 and 2011 were drier and that of 2012 was wetter than the long-term average. The percent values give the amount of precipitation in 2012 compared to the mean of 2009-2011.

	Precipitation (mm)	**Mean temperature (°C)**
Altai-Yalalt:		
Annual mean 2009-2011	112±10	-2.3±0.4
May-September 2009-2011	90±7.1	9.8±0.6
May-September 2012	189 (210%)	9.9
Ulgii:		
Annual mean 2009-2011	90±6	1.0±0.3
May-September 2009-2011	76±8	13.6±0.2
May-September 2012	137 (179%)	14.2
Dayan:		
Annual mean 2009-2011	177±30	-4.9±0.3
May-September 2010-2011	149±22	8.4±0.1
May-September 2012	240 (162%)	8.7

1.6.3 Fine root sampling and analysis

In 2010, root samples were collected in the Mongolian Altai at six randomly chosen locations per plot from the 0-15 and 15-30 cm layers of the upper soil including the organic layer. In 2011, a stem-centered root sampling scheme was applied to examine the effect of stem distance on root mass. In both the Altai and Khangai sites, coring was conducted at each five sampling locations per plot at 1, 2 and 3 m distance to a larch stem in the top 20 cm of the organic layer and the upper mineral soil. In 2012, root sampling was conducted only at the Altai site with a focus on the vertical distribution of fine roots in the profile. Each one soil profile was dug in the six plots in forest interior and each one soil sample was taken from the organic layer (8.0 ± 1.6 cm) and the 0-10, 10-20, 20-40, 40-60 and 60-80 cm mineral soil layers. In the *L. sibirica* plantation in the Ore Mountains, Germany, nine trees were randomly chosen and soil cores were taken at 1, 2 and 3 m distance to the tree stems in the top 20 cm of the soil (organic layer plus upper mineral soil). In all cases, a soil borer (inner diameter 33 mm) was used to collect the root samples. The samples were stored at 4 °C until root extraction and analysis was carried out in the laboratory.

In the laboratory, the fine root samples were sorted into three groups, namely fine living roots (fine-root biomass, FRB) and fine dead roots (fine-root necromass, FRN) of Siberian larch as well as non-tree roots (NTRM; mostly herbaceous root mass) based on their color, elasticity, and the degree of cohesion of cortex, periderm and stele as inspected under the stereomicroscope (Persson, 1978; Hertel and Leuschner, 2002). Only fine roots (<2 mm diameter) were selected for analysis. Living rootlets (>1 cm in length) were randomly selected for analyzing root morphological characteristics using a WinRhizo (Régent Instruments Inc., Quebec, Canada) visual analysis system connected to a scanner. Root morphological parameters including tissue density, average root diameter, specific root surface area (SRA) and specific root length (SRL), mycorrhizal infection rate (%) and specific root tip abundance (SRTA) were analyzed.

1.6.4 Wood cores sampling and tree-ring analysis

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). Trunk core samples were collected only from 3 trees in the Ore Mountains, because destructive sampling had to be restricted to the minimum in this stand. Mongolian trees that had a similar DBH as the trees from the Ore Mountains were used in comparison, since the planted *L. sibirica* trees in the Ore Mountains all were of the same age, whereas those from the old-growth forests in Mongolia had a heterogeneous age structure. 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. 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.

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) and stem basal area increment (BAI) was measured to evaluate tree growth rate. 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 '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 BAI per tree.

1.6.5 Hydraulic conductivity measurement and xylem anatomy analysis

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. From each sample tree, 1–3 coarse root segments and 1–3 branch segments were collected. Samples were stored at 4 °C after sampling, during transport and during storage in the laboratory where the analyses were carried out within one month after collection.

Empirical hydraulic conductivity was measured for each root and branch segment using the Xyl’em apparatus, which was operated with XylWin 3.0 software (Bronkhorst, Montigny-les-Cormeilles, France). Sapwood area-specific hydraulic conductivity (K_s) was counted afterwards by dividing hydraulic conductivity with sapwood cross-sectional area. Wood-anatomical analyses were carried out separately for earlywood and latewood in the stem, and the entire cross-section in roots and branches. Earlywood and latewood was visually differentiated according to color and tracheid size. Wood anatomical parameters including tracheid density (*TD*), idealized tracheid diameters (*d*), hydraulic mean diameter (d_h), potential sapwood area-specific hydraulic conductivity (K_p) were analyzed.

References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manage 259, 660-684.

ávan den Honert, T., 1948. Water transport in plants as a catenary process. Discuss Faraday Soc 3, 146-153.

Batima, P., Natsagdorj, L., Gomboluudev, P., Erdenetsetseg, B., 2005. Observed climate change in Mongolia. AIACC Working Paper 13, 4-25.

Benito-Garzón, M., Leadley, P.W., Fernández-Manjarrés, J.F., 2014. Assessing global biome exposure to climate change through the Holocene–Anthropocene transition. Glob Ecol Biogeogr 23, 235-244.

Bonan, G.B., Pollard, D., and Thompson, S.L., 1992. Effects of boreal forest vegetation on global climate. Nature, 359, 716-718..

Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63, 625-644.

Coomes, D.A., Grubb, P.J., 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. Ecol Monogr 70, 171-207.

Dixon, H.H., 1914. Transpiration and the ascent of sap in plants. Macmillan and Company, limited.

Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexier, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185-190.

Dreyer, E., Le Roux, X., Montpied, P., Daudet, F.A., Masson, F., 2001. Temperature response of leaf photosynthetic capacity in seedlings from seven temperate tree species. Tree Physiol 21, 223-232.

Dulamsuren, C., Hauck, M., 2008. Spatial and seasonal variation of climate on steppe slopes of the northern Mongolian mountain taiga. Grassl Sci 54, 217-230.

Dulamsuren, C., Hauck, M., Bader, M., Oyungerel, S., Osokhjargal, D., Nyambayar, S., Leuschner, C., 2009. The different strategies of *Pinus sylvestris* and *Larix sibirica* to deal with summer drought in a northern Mongolian forest-steppe ecotone suggest a future superiority of pine in a warming climate. Can J For Res 39, 2520-2528.

Dulamsuren, C., Hauck, M., Khishigjargal, M., Leuschner, H.H., Leuschner, C., 2010a. Diverging climate trends in Mongolian taiga forests influence growth and regeneration of *Larix sibirica*. Oecologia 163, 1091-1102.

Dulamsuren, C., Hauck, M., Leuschner, C., 2010b. Recent drought stress leads to growth reductions in *Larix sibirica* in the western Khentey, Mongolia. Glob Change Biol. 16, 3024-3035.

Dulamsuren, C., Hauck, M., Leuschner, H.H., Leuschner, C., 2010c. Gypsy moth-induced growth decline of *Larix sibirica* in a forest-steppe ecotone. Dendrochronologia 28, 207-213.

Dulamsuren, C., Hauck, M., Leuschner, H.H., Leuschner, C., 2011. Climate response of tree-ring width in *Larix sibirica* growing in the drought-stressed forest-steppe ecotone of northern Mongolia. Ann For Sci 68, 275-282.

Dulamsuren, C., Khishigjargal, M., Leuschner, C., Hauck, M., 2014. Response of tree-ring width to climate warming and selective logging in larch forests of the Mongolian Altai. J Plant Ecol 7, 24-38.

Dulamsuren, C., Wommelsdorf, T., Zhao, F., Xue, Y., Zhumadilov, B., Leuschner, C., Hauck, M., 2013. Increased summer temperatures reduce the growth and regeneration of *Larix sibirica* in southern boreal forests of Eastern Kazakhstan. Ecosystems 16, 1-14.

Eissenstat, D.M., Wells, C.E., Yanai, R.D., Whitbeck, J.L., 2000. Building roots in a changing environment: implications for root longevity. New Phytol 147, 33-42.

Fernandez-Gimenez, M.E., 1999. Sustaining the steppes: A geographical history of pastoral land use in Mongolia. Geogr Rev 89, 315-342.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011a. Factors causing variation in fine root biomass in forest ecosystems. For Ecol Manage 261, 265-277.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011b. Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. For Ecol Manage 262, 2008-2023.

Fort, C., Fauveau, M.L., Muller, F., Label, P., Granier, A., Dreyer, E., 1997. Stomatal conductance, growth and root signaling in young oak seedlings subjected to partial soil drying. Tree Physiol 17, 281-289.

Gill, R.A., Jackson, R.B., 2000. Global patterns of root turnover for terrestrial ecosystems, New Phytologist. Cambridge University Press, pp. 13-31.

Gonçalves, B., Correia, C.M., Silva, A.P., Bacelar, E.A., Santos, A., Ferreira, H., Moutinho-Pereira, J.M., 2007. Variation in xylem structure and function in roots and stems of scion–rootstock combinations of sweet cherry tree (*Prunus avium* L.). Trees 21, 121-130.

Gower, S.T., Krankina, O., Olson, R.J., Apps, M., Linder, S., Wang, C., 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecol Appl 11, 1395-1411.

Hacke, U., Sauter, J.J., 1996. Drought-induced xylem dysfunction in petioles, branches, and roots of *Populus balsamifera* L. and *Alnus glutinosa* (L.) Gaertn Plant Physiol 111, 413-417.

Hertel, D., Leuschner, C., 2002. A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus–Quercus* mixed forest. Plant Soil 239, 237-251.

IPCC, 2001. Climate change 2001: the scientific basis. Contribution of Working Group II to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, USA.

IPCC, 2007. Climate change 2007: the physical scientific basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, USA.

Ishikawa, M., Sharkuu, N., Zhang, Y.S., Kadota, T., Ohata, T.T., 2005. Ground thermal and moisture conditions at the southern boundary of discontinuous permafrost, Mongolia. Permafrost Periglac 16, 209-216.

Jackson, R.B., Mooney, H.A., Schulze, E.D., 1997. A global budget for fine root biomass, surface area, and nutrient contents. PNAS 94, 7362-7366.

Joslin, J., Wolfe, M., Hanson, P., 2000. Effects of altered water regimes on forest root systems. New Phytol 147, 117-129.

Kajimoto, T., Matsuura, Y., Osawa, A., Prokushkin, A.S., Sofronov, M.A., Abaimov, A.P., 2003. Root system development of *Larix gmelinii* trees affected by micro-scale conditions of permafrost soils in central Siberia. Plant Soil 255, 281-292.

Kajimoto, T., Osawa, A., Usoltsev, V.A., Abaimov, A.P., 2010. Biomass and productivity of Siberian larch forest ecosystems, in: Osawa, A., Zyryanova, O.A., Matsuura, Y., Kajimoto, T., Wein, R.W. (Eds.). Springer Netherlands, pp. 99-122.

Kharuk, V.I., Im, S.T., Dvinskaya, M.L., Ranson, K.J., 2010a. Climate-induced mountain tree-line evolution in southern Siberia. Scand J For Res 25, 446-454.

Kharuk, V.I., Ranson, K.J., Im, S.T., Dvinskaya, M.L., 2009. Response of *Pinus sibirica* and *Larix sibirica* to climate change in southern Siberian alpine forest–tundra ecotone. Scand J For Res 24, 130-139.

Kharuk, V.I., Ranson, K.J., Im, S.T., Vdovin, A.S., 2010b. Spatial distribution and temporal dynamics of high-elevation forest stands in southern Siberia. Glob Ecol Biogeogr 19, 822-830.

Khishigjargal, M., Dulamsuren, C., Lkhagvadorj, D., Leuschner, C., Hauck, M., 2013. Contrasting responses of seedling and sapling densities to livestock density in the Mongolian forest-steppe. Plant Ecol 214, 1391-1403.

Kirdyanov, A.V., Treydte, K.S., Nikolaev, A., Helle, G., Schleser, G.H., 2008. Climate signals in tree-ring width, density and δ13 C from larches in Eastern Siberia (Russia). Chem Geol 252, 31-41.

Kobak, K.I., Turchinovich, I.Y., Kondrasheva, N.Y., Schulze, E.D., Schulze, W., Koch, H., Vygodskaya, N.N., 1996. Vulnerability and adaptation of the larch forest in eastern Siberia to climate change. Water Air Soil Pollnt 92, 119-127.

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.

Leuschner, C., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O., Runge, M., 2001. Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. For Ecol Manage 149, 33-46.

Leuschner, C., Hertel, D., 2003. Fine root biomass of temperate forests in relation to soil acidity and fertility, climate, age and species. Prog Bot, 405-438.

Leuschner, C., Hertel, D., Schmid, I., Koch, O., Muhs, A., Hölscher, D., 2004. Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. Plant Soil 258, 43-56.

Liu, H., Park Williams, A., Allen, C.D., Guo, D., Wu, X., Anenkhonov, O.A., Liang, E., Sandanov, D.V., Yin, Y., Qi, Z., Badmaeva, N.K., 2013. Rapid warming accelerates tree growth decline in semi-arid forests of Inner Asia. Glob Change Biol 19, 2500-2510.

Lkhagvadorj, D., Hauck, M., Dulamsuren, C., Tsogtbaatar, J., 2013. Pastoral nomadism in the forest-steppe of the Mongolian Altai under a changing economy and a warming climate. J Arid Environ 88, 82-89.

Lloyd, A.H., Bunn, A.G., Berner, L., 2011. A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. Glob Change Biol 17, 1935-1945.

McElrone, A.J., Choat, B., Gambetta, G. A. & Brodersen, C. R. , 2013. Water uptake and transport in vascular plants. Nature Educ Knowl 4(5):6.

Meier, I.C., Leuschner, C., 2008. Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. Glob Change Biol 14, 2081-2095.

Nadelhoffer, K.J., Raich, J.W., 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73, 1139-1147.

Norby, R.J., Jackson, R.B., 2000. Root dynamics and global change: seeking an ecosystem perspective. New Phytol 147, 3-12.

North, G.B., Nobel, P.S., 1997. Root-soil contact for the desert succulent Agave deserti in wet and drying soil. New Phytol 135, 21-29.

Ostonen, I., Helmisaari, H.S., Borken, W., Tedersoo, L., Kukumagi, M., Bahram, M., Lindroos, A.J., Nojd, P., Uri, V., Merila, P., Asi, E., Lohmus, K., 2011. Fine root foraging strategies in Norway spruce forests across a European climate gradient. Glob Change Biol 17, 3620-3632.

Persson, H., 1978. Root dynamics in a young Scots pine stand in Central Sweden. Oikos 30, 508-519.

Persson, H., 1983. The distribution and productivity of fine roots in boreal forests. Plant Soil 71, 87-101.

Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process, in: Begon, M., Fitter, A.H. (Eds.), Advances in ecological research. Academic Press, pp. 213-262.

Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth. Bioscience 47, 235-242.

Schulze, E.D., Schulze, W., Kelliher, F.M., Vygodskaya, N.N., Ziegler, W., Kobak, K.I., Koch, H., Arneth, A., Kusnetsova, W.A., Sogatchev, A., Issajev, A., Bauer, G., Hollinger, D.Y., 1995. Aboveground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian *Larix* stands in Eastern Siberia. Can J Forest Res 25, 943-960.

Sharkhuu, A., Sharkhuu, N., Etzelmuller, B., Heggem, E.S.F., Nelson, F.E., Shiklomanov, N.I., Goulden, C.E., Brown, J., 2007. Permafrost monitoring in the Hovsgol mountain region, Mongolia. J Geophys Res-Earth 112, F02S06.

Sharkhuu, N., 2003. Recent changes in the permafrost of Mongolia. Proc 8th Int Conf Perm 2, 1029-1034.

Shuman, J.K., Shugart, H.H., O'Halloran, T.L., 2011. Sensitivity of Siberian larch forests to climate change. Glob Change Biol 17, 2370-2384.

Shvidenko, A.Z., Nilsson, S., Stolbovoi, V.S., Rozhkov, V.A., Gluck, M., 2001. Aggregated estimation of basic parameters of biological production and the carbon budget of Russian terrestrial ecosystems: 2. Net primary production. Russ J Ecol 32, 71-77.

Soja, A.J., Tchebakova, N.M., French, N.H., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E., Chapin III, F.S., Stackhouse Jr, P.W., 2007. Climate-induced boreal forest change: predictions versus current observations. Glob Planet Change 56, 274-296.

Sonsin, J.O., Gasson, P.E., Barros, C.F., Marcati, C.R., 2012. A comparison of the wood anatomy of 11 species from two cerrado habitats (cerrado *s.s.* and adjacent gallery forest). Bot J Linn Soc 170, 257-276.

Sperry, J.S., Meinzer, F.C., McCulloh, K.A., 2008. Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. Plant Cell Environ 31(5), 632-645.

Sperry, J.S., Nichols, K.L., Sullivan, J.E., Eastlack, S.E., 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology 75(6), 1736-1752.

Sterck, F.J., Zweifel, R., Sass-Klaassen, U., Chowdhury, Q., 2008. Persisting soil drought reduces leaf specific conductivity in Scots pine (*Pinus sylvestris*) and pubescent oak (*Quercus pubescens*). Tree Physiol 28, 529-536.

Strand, A.E., Pritchard, S.G., McCormack, M.L., Davis, M.A., Oren, R., 2008. Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319, 456-458.

Sudachkova, N.E., Milyutina, I.L., Semenova, G.P., 2002. Influence of water deficit on contents of carbohydrates and nitrogenous compounds in *Pinus sylvestris* L. and *Larix sibirica* Ledeb. tissues. Eurasian J For Res -Hokkaido University 4, 1-11.

Sugimoto, A., Yanagisawa, N., Naito, D., Fujita, N., Maximov, T.C., 2002. Importance of permafrost as a source of water for plants in east Siberian taiga. Ecol Res 17, 493-503.

Tchebakova N.M., Monserud R.A., Leemans R. and Nazimova D.I. 1995. Possible vegetation shifts in Siberia under climate change. In: Pernetta J.C., Leemans R., Elder D. and Humphrey S. (eds) Impacts of Climate Change on Ecosystems and Species: Terrestrial Ecosystems. IUCN, Gland, Switzerland, pp. 67–82.

Tchebakova, N.M., Monserud, R.A., Nazimova, D.I., 1994. A Siberian vegetation model-based on climatic parameters. Can J For Res 24, 1597-1607.

Tyree, M., 2003. Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. Trees 17, 95-100.

Tyree, M., Cochard, H., Cruiziat, P., Sinclair, B., Ameglio, T., 1993. Drought - induced leaf shedding in walnut: evidence for vulnerability segmentation. Plant, Cell Environ 16, 879-882.

Tyree, M.T., Davis, S.D., Cochard, H., 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? . IAWA 15, 335-360.

Tyree, M.T., Snyderman, D.A., Wilmot, T.R., Machado, J.L., 1991. Water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*) : data, models, and a comparison with two temperate species (*Acer saccharum* and *Thuja occidentalis*). Plant Physiol 96, 1105-1113.

Tyree, M.T., Velez, V., Dalling, J., 1998. Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to differing light regimes. Oecologia 114, 293-298.

Tyree, M.T., Zimmermann, M.H., 2002. Xylem structure and the ascent of sap. Springer Verlag.

Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861-865.

Vogt, K.A., Grier, C.C., Vogt, D.J., 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests, in: MacFadyen, A., Ford, E.D. (Eds.), Advances in Ecological Research. Academic Press, pp. 303-377.

Yuan, Z.Y., Chen, H., 2010. Fine Root Biomass, Production, Turnover Rates, and Nutrient Contents in Boreal Forest Ecosystems in Relation to Species, Climate, Fertility, and Stand Age: Literature Review and Meta-Analyses. Crit Rev Plant Sci 29, 204-221.

Zhao, L., Wu, Q.B., Marchenko, S.S., Sharkhuu, N., 2010. Thermal state of permafrost and active layer in Central Asia during the international polar year. Permafrost Periglac 21, 198-207.

Zimmermann, M.H., 1983. Xylem structure and the ascent of sap. Springer-Verlag.

Zimmermann, U., Schneider, H., Wegner, L.H., Haase, A., 2004. Water ascent in tall trees: does evolution of land plants rely on a highly metastable state? New Phytol 162, 575-615.

Chapter 2

Extremely Low Fine-Root Biomass in *Larix sibirica* Forests at the Southern Drought Limit of the Boreal Forest[1]

Tselmeg Chenlemuge, Dietrich Hertel , Choimaa Dulamsuren, Mookhor Khishigjargal,
Christoph Leuschner, Markus Hauck

---

[1] Published in: Flora 2013, 208:488-496
DOI: 10.1016/j.flora.2013.08.002

2.1 Abstract

Mongolia’s *Larix sibirica* forests at the southern fringe of the Eurosiberian boreal forest belt are exposed not only to very low winter temperatures, but also to frequent summer droughts. It is not completely known how Siberian larch adapts to these stressors. We examined whether (i) these forests differ in their fine-root bio- and necromass from more humid boreal forests further in the North, and (ii) inter-annual fluctuations in fine-root biomass are related to tree vitality. In two exceptionally dry summers, we found only 4-5 g DM m^{-2} of fine-root biomass (FRB; 0-20 cm), which is far less than typical FRB figures from boreal forests (c. 200-400 g m^{-2}) and the lowest forest FRB reported worldwide; in a moist summer, FRB was 20 fold higher. In contrast to FRB, both necromass (FRN) and non-tree root mass (NTRM) were high in all three years. From the large FRB increase in the moist summer and the generally high root necromass, we conclude that drought-induced fine-root dieback was the likely cause of the very small amount of live root mass in the dry summers. Larch fine roots seem to be more drought-sensitive than shoots, since marked needle loss did not occur.

Keywords

Drought, forest-steppe ecotone, root dieback, root necromass, vertical fine-root distribution

2.2 Introduction

The forests of northern and western Mongolia represent the southernmost extension of the Eurosiberian boreal forest belt. At its interface with the steppe, the southernmost fringe of the Siberian taiga receives only relatively low precipitation amounts (c. 100-250 mm yr^{-1}) and the woodland consists of a forest-steppe ecotone with increasingly isolated forest islands. The most important tree species in these presumably drought-affected forests is the deciduous conifer *Larix sibirica* Lebed. Recent climatic change has increased the aridity in many regions of Central Asia owing to a pronounced temperature increase during the last decades that was accompanied by decreasing summer precipitation in many, but not all, regions (Gießе and Moßig, 2004; Li et al., 2009). In Mongolia, annual temperature has increased by 1.7 K in the last 60 years (Batima et al., 2005) which is above the global average of warming. Reports on precipitation change are more variable. Several regions in the forest-steppe ecotone experienced significant precipitation decreases in the last 50 years or so while others showed no change in precipitation (Dagvadorj et al., 2009, Dulamsuren et al., 2010a). Consequently, the tree response to climate change is variable in the region. Dendrochronological studies in various *L. sibirica* forests of northern Mongolia and eastern Kazakhstan have shown lasting growth reductions in the past decades which have been attributed to increasing aridity in those regions (Dulamsuren et al., 2010b, 2013a), while other forest remained vital (D'Arrigo et al., 2000; Dulamsuren et al., 2013b).

Here we present the results of a study on the biomass and morphology of the fine-root system of two *L. sibirica* forest complexes in western Mongolia, which receive less than 250 mm of annual precipitation on average and that may be exposed to increasing aridity as a consequence of warmer summers. To compare the results from continental Mongolia with an oceanic area, root samples were also taken from a 118-year old plantation of Siberian larch far west of its natural distribution range in Germany. Fine roots (roots <2 mm in diameter) represent only a few percent of the total biomass of a tree, but may consume as much as estimated 30-50 percent of annual carbon gain because turnover is often rapid (Janssens et al., 2002; Matamala et al., 2003; Ruess et al., 1996). Fine roots have been found to respond sensitively to drought in certain conifers (e.g. Santantonio and Hermann, 1985; Nisbet and Mullins, 1986; Valdés et al., 2006), but it is not known whether drought-induced fine-root dieback is a relevant mechanism causing the death of adult trees in the southern boreal zone. In the southern Eurosiberian boreal zone at the drought limit of tree growth, fine-root studies are lacking, so far. The key objective of our study was to examine whether drought-affected boreal forests differ in the amount of fine-root biomass and root necromass as well an in different root morphological properties from more humid boreal forests further in the North and from planted *L. sibirica* outside its natural range under much milder and more humid climatic conditions than in the Mongolian forest-steppe. The study was conducted during three field campaigns in 2010-2012 in two remote *L. sibirica* forests of the Mongolian forest-steppe in the Mongolian Altai and Khangai Mountains and was supplemented by field work in a *L. sibirica* plantation in the Ore Mountains, Germany. Our analyses included fine-root biomass and necromass inventories in two relatively dry and one moist summer and an examination of the vertical and horizontal variability of root mass in the stands.

2.3 Material and methods

2.3.1 Study areas

The study included two Siberian larch (*Larix sibirica* Lebed.) forests in western Mongolia (Mongolian Altai, western Khangai Mountains) located at the southern fringe of the Eurosiberian boreal forest belt in the transition zone to the steppe (Fig. 1.2) as well as a mature *L. sibirica* plantation stand in the Ore Mountains, south-eastern Germany. The study area in the Mongolian Altai was located south and southeast of Lake Dayan (48°14'39"-48°16'3" N, 88°50'17"-88°57'0" E; 2300-2375 m a.s.l.) in the Dayan administrative subunit ('bag') in the Altai Tavan Bogd National Park in the province ('aimag') of Bayan-Ulgii, 110 km SW of the city of Ulgii. The study area in the western Khangai Mountains (600 km east of Lake Dayan) was located in the valley of the river Shireegiin Gol (47°29'11"-47°30'37" N, 96°59'20"-97°13'59" E; 2100-2300 m a.s.l.), c. 30 km SSE of the city of Uliastai and 40 SW of Mt. Otgontenger in the province of Zavkhan.

Both study areas in Mongolia are located in the forest-steppe ecotone in mountainous terrain where *L. sibirica* forests occur on north-facing slopes, whereas steppe covers south-facing slopes and the most valley bottoms. Most larch woodlands are forest islands of variable size that were partly converted into pasture by the local herdsmen over time. Siberian larch is the dominant tree species in the Mongolian forests that reach a rather low canopy cover of typically 20-50 %. The studied forests were monospecific larch forests; in the whole of Mongolia, Siberian larch covers 80 % of the forested area (Tsogtbaatar, 2004). The forest floor is covered by a relatively species-rich layer of low shrubs and an herb layer that reaches cover values of 50 to 100 %. The prevailing soils are Leptosols, which lie over siliceous rock. The forests are subject to varying intensities of livestock grazing (Lkhagvadorj et al., 2013a, b).

The climate of the Mongolian forest-steppe is semiarid and highly continental with a subzero annual mean temperature and an annual precipitation between 100 and 400 mm. Mean temperatures in the study areas were -3.4 °C (year; January: -21.2 °C; July: 12.9 °C) in the Mongolian Altai (weather station Altai-Yalalt, 40 km east of the studied forests, 2150 m a.s.l.; since 1940) and -2.4 °C (year; January: -23.5 °C; July: 15.8 °) in the Khangai (weather station Uliastai, 30 km NNW of the studied forests, 1760 m a.s.l.; since 1937). Precipitation was 120 mm yr^{-1} at the weather station Altai-Jalalt and 213 mm yr^{-1} in Uliastai; both values are somewhat underestimating the precipitation in the studied forests.

The *L. sibirica* plantation in Germany is located in the Ore Mountains at Giegengrün near Kirchberg (50°35'13" N, 12°31'37" E), 15 km SSE of the city of Zwickau at 465 m a.s.l. The mean annual temperature at Giegengrün is estimated to be 7-8 °C and precipitation to amount 720-800 mm yr^{-1} (Klima-Atlas, 1958). The canopy cover was c. 80-90 %.

2.3.2 Sample plots

Field work was carried out during three subsequent growing seasons (July/August 2010, 2011 and 2012). Sampling was conducted in six stands each of the Mongolian Altai and the Khangai on plots of 20 m × 20 m size, which were located at 50-100 m within the forest interior. Sample plot selection was a non-random procedure, but was little subjective because of the regular landscape structure of the Mongolian forest-steppe with patches of larch forests on most north-facing mountain slopes. The studied larch stands on north-facing slopes were selected in near equidistance along one valley each in the Altai and the Khangai. 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. Sample plot selection was not biased by preselecting plots after local differences in vegetation, forest stand structure or land-use pressure, but moist depressions on the mountain slopes, which were not representative of the bulk of the total area and were likely to deviate from most other areas in terms of biomass production were deliberately excluded at the expense of equidistance between plots. Principal stand characteristics of the studied forests in the Altai and the Khangai are compiled in Table 1.2.

2.3.3 Root sampling and analysis

In 2010, root samples were collected in the six 20 m × 20 m plots in the Mongolian Altai at at six randomly chosen locations per plot. A soil borer (inner diameter 33 mm) was used to collect the samples from the 0-15 and 15-30 cm layers of the upper soil including the organic layer. In 2011, samples were taken from both the Altai and Khangai sites resulting in 12 plots in total. In 2011, a stem-centered root sampling scheme was applied to examine the effect of stem distance on root mass. In every plot, coring was conducted at each five sampling locations per plot at 1, 2 and 3 m distance to a larch stem in the top 20 cm of the organic layer and the upper mineral soil. In 2012, root sampling was conducted at reduced intensity only at the Altai site with a focus on the vertical distribution of fine roots in the profile. Each one soil profile was dug in the six plots and each one soil sample was taken from the organic layer (8.0 ± 1.6 cm) and the 0-10, 10-20, 20-40, 40-60 and 60-80 cm mineral soil layers. In the *L. sibirica* plantation in the Ore Mountains, Germany, nine trees were randomly chosen and soil cores were taken at 1, 2 and 3 m distance to the tree stems in the top 20 cm of the soil (organic layer plus upper mineral soil). The samples were stored at 4 °C until root extraction and analysis was carried out in the laboratory.

In the laboratory, the samples were cleaned with tap water from soil residues using a sieve with a mesh size of 0.625 mm. Only fine roots (<2 mm diameter) were selected for analysis. Larger (>1 cm long) fine-root fractions were sorted into 3 groups, namely fine living roots (fine-root biomass, FRB) and fine dead roots (fine-root necromass, FRN) of Siberian larch as well as non-tree roots (NTRM; mostly herbaceous root mass) based on their color, elasticity, and the degree of cohesion of cortex, periderm and stele as inspected under the stereomicroscope (Hertel and Leuschner, 2002; Persson, 1978). Dead *L. sibirica* roots are dark black and mostly fractured, whereas living roots have a bright black, sometimes reddish tinge and are morphologically intact. The cortex and periderm of dead roots are not cohesive and are easily stripped; the stele is dark yellowish or even brown. In living roots, the cortex and periderm are coherent and are not easily peeled off from the stele, which has a bright white color. We separated the roots in distilled water and dead roots mostly float in the water in contrast to living roots. If squeezed, dead roots, but not living roots, often release air bubbles. In the studied material, visual differences between living and dead roots were so apparent that it is unlikely that a considerable number of living roots was misidentified as dead roots. Smaller root fractions (<1 cm in length) were evenly spread on a large sheet of filter paper (730 cm^2) with 36 squares marked on it. Six of the squares were randomly selected and analyzed under the stereomicroscope for even the smallest dead fine-root fragments. The total mass of small dead rootlets was extrapolated by regression analysis from the ratio of small rootlets to large dead roots (>10 mm in length) recorded in the same subsample (Hertel and Schöling, 2011; van Praag et al., 1988). Sorted samples were dried at 70 °C for 48 h and weighed.

Up to 10 living rootlets per soil sample, if available, were randomly selected for analyzing root morphological characteristics using a WinRhizo (Régent Instruments Inc., Quebec, Canada) visual analysis system connected to a scanner. The dry biomass of the scanned living rootlets was measured afterwards. Tissue density, average root diameter, specific root surface area (SRA) and specific root length (SRL) were determined in the <2 mm fraction. Mycorrhizal infection rate (%) and specific root tip abundance (SRTA, tips per fine-root biomass) were determined by counting all living tips and all tips with mycorrhizal infection under the stereomicroscope in the same rootlet.

2.3.4 Root mass data base for boreal forests

For comparing our results with literature data, we compiled a data base on fine-root biomass inventories in boreal (and temperate) coniferous forests. Only data from coring studies yielding fine-root biomass totals for the stand for at least the upper 20 cm of the mineral soil and the organic layer were included. With few exceptions, the data refer to the <2 mm diameter class. If repeated sampling and several locations were sampled, averages were calculated from the given data. In manipulation studies, only the data from the control plots were included.

2.3.5 Data processing and statistical analysis

Considering the differences in sampling depths and locations, fine-root mass data from different study years and areas were standardized to be representative for upper 0-20 cm soil layers. Specifically, for the fine-root mass data from the Altai of 2010, one third of root mass from the lower 15-30 cm soil layers were added up to the upper 0-15 cm soil layers to represent the root mass in upper 20 cm soil depth. For the fine-root mass data from the Altai and the Khangai of 2011 and the Ore Mountains of 2012, fine-root mass values from three positions (1, 2 and 3 m to the stems) were averaged to stand for the location means. In 2012, the organic layer was sampled separately from the mineral soil layers. To extrapolate the fine-root mass on the top 20 cm soil layer, a proportional part of the fine-root mass from the lower mineral soil layer was added to that from the organic layer. In detail, the proportion was calculated using the equation y = (20 cm - organic layer depth)/mineral soil layer depth.

Arithmetic means ± standard errors are given throughout the paper. Data were tested for normality with the Shapiro-Wilk test. Analysis of variances (ANOVA) with subsequent post-hoc tests (Tukey's test) were calculated to test for the significance of differences between samples. Pearson coefficients were calculated in linear regression analysis. All statistical analyses were carried out with SPSS 16.0.0 software (SPSS Inc., Chicago, Illinois, USA). All calculations were conducted with the site means that base on the means over 6 plots per site (which themselves base on 5-6 samples per plot) with the different plots considered as true replicates in the analysis.

2.4 Results

2.4.1 Fine-root inventory

The fine-root inventories in 2010 (Altai) and 2011 (Altai and Khangai) in the upper soil (0-20 cm) of the larch forests yielded very low tree fine-root biomass values (FRB; site means of 3.5-5.2 g DM m^{-2}; Fig. 2.2a). Fine-root density was not related to the stand basal area (Fig. 2.1). In the 2010 data from the Altai, none of the plot means (based on each six coring locations) exceeded 15.3 g m^{-2}; plot minima were as low as 1.7 g m^{-2}. The coring campaign in wet July 2012 in the Altai (for climate data see Table 1.3) gave more than 20 times higher FRB means for the 0-20 cm layer (143 g m^{-2}). The low tree FRB contrasts with a 50-200 fold larger root biomass of the dwarf shrub and herb layer (NTRM) in the Altai and Khangai plots in 2010 and 2011 (site means of 272 to 609 g m^{-2}; no separation between live and dead roots in this fraction; Fig. 2.2c). In the wet summer of 2012, the NTRM was also higher (714 g m^{-2}) than in the dry summers. Tree fine-root necromass (FRN) was very high in the 0-20 cm layer at both sites in all three years with site means of 946 to 1396 g DM m^{-2}; Fig. 2.2b). The planted *L. sibirica* stand in the Ore Mountains (southeastern Germany), which was investigated for comparison, showed a much higher FRB (300 g m^{-2}; 0-20 cm) than the Mongolian stands in both wet and dry years. Furthermore, FRN was much lower in Germany than in the Mongolian forest-steppe (Fig. 2.2a, b). For larch fine-root mass, we obtained mean biomass : necromass ratios of 0.04 (mean over study year 2010–2012) in the Altai, of 0.004 (study year 2011) in the Khangai, and of 0.77 (study year 2012) in the Ore Mountains.

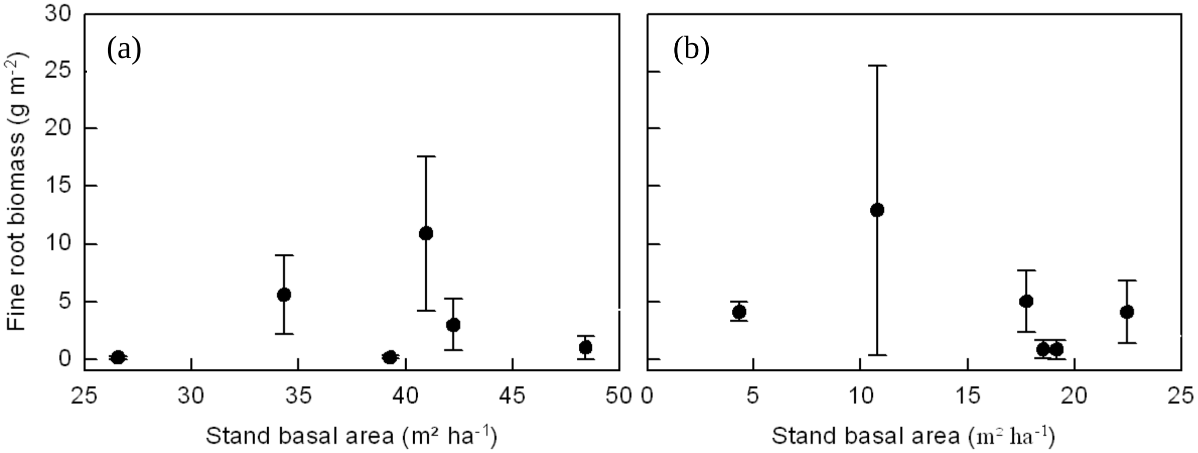

Fig. 2.1 Fine-root biomass of *L. sibirica* (0-20 cm layer) in relation to stand basal area in the each six study plots in the (a) Altai and (b) Khangai Mountains in July/August 2011. Given are the means and standard errors of 5 fine-root samples per stand.

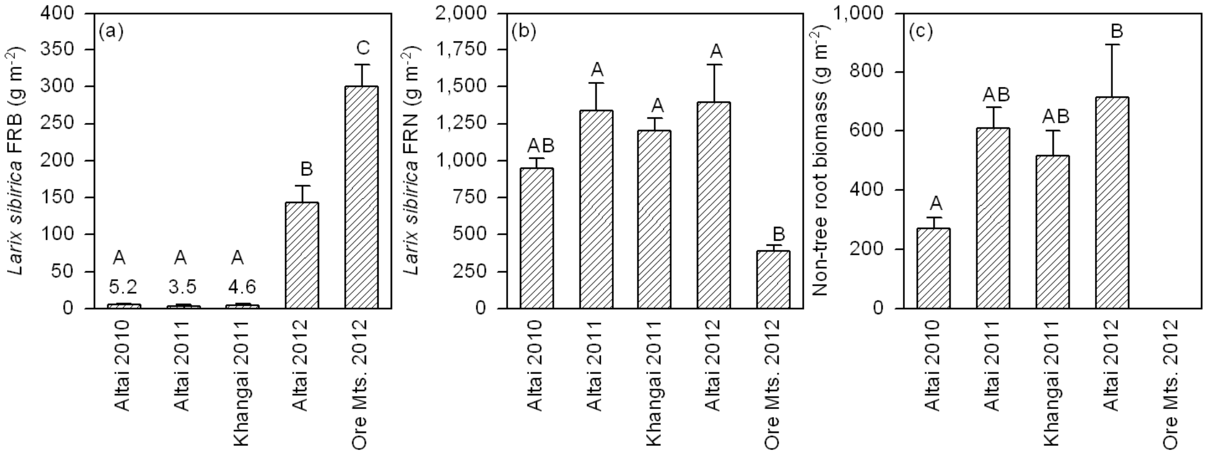

Fig. 2.2 Fine-root biomass, FRB (a) and fine-root necromass, FRN (b) of *Larix sibirica*, and non-tree root mass (c) in the studied larch stands in Mongolia in the years 2010-2012. In addition, data from a *L. sibirica* plantation in the Ore Mountains, Germany are presented (in all cases means and standard errors for the 0-20 cm layer). Note different scale of y-axis in the three figures. In figure (a), the absolute numbers of the first three columns are included. Within a figure, means with a common letter do not differ significantly (Tukey's test, P≤0.05).

2.4.2 Fine-root distribution patterns and fine-root morphology

In the 2010 study in the Altai, no significant difference in FRB was found between the 0-15 and 15-30 cm layers. However, the upper layer contained significantly more NTRM and also FRN than the 15-30 cm layer (ANOVA, $P \leq 0.05$; results not shown). In the 2012 study to 80 cm depth in the Altai, neither FRB nor FRN differed significantly (ANOVA, *P*>0.05) between the six examined soil layers (Fig. 2.3a). At the most, a slight tendency for a root mass decrease with increasing soil depth could be recognized. In contrast, the organic layer and the 0-10 cm mineral soil layer contained significantly higher concentrations of non-tree root mass than the lower profile. The FRB and NTRM reached mean densities (mass per soil volume) of 1.05 and 4.96 g L^{-1} in the Oh layer and of 0.54 and 1.75 mg L^{-1} in the 0-10 cm layer (Fig. 2.3b).

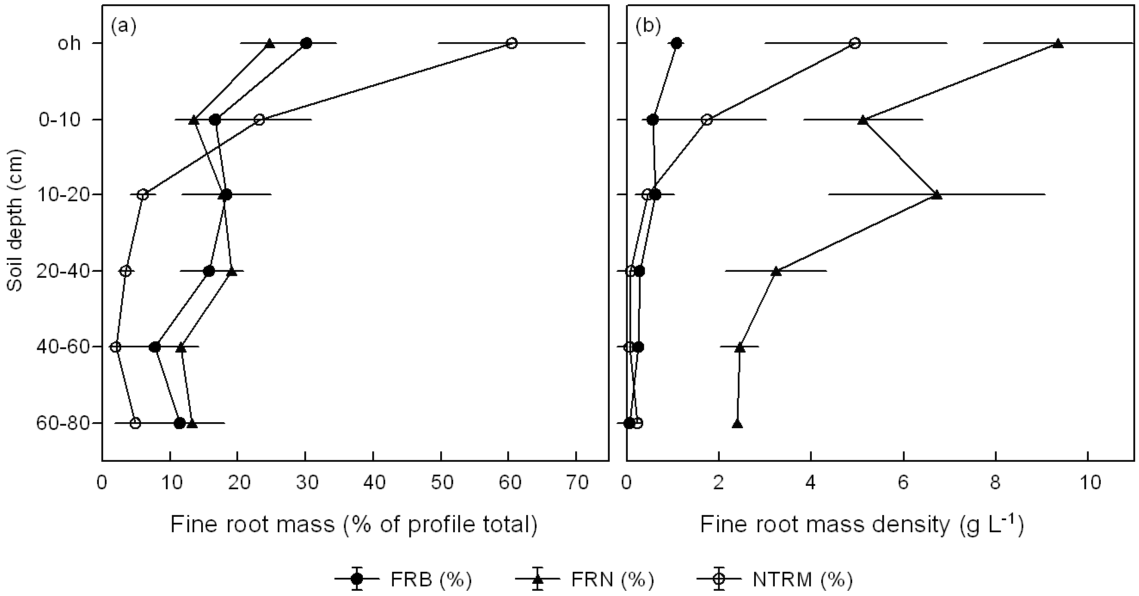

Fig. 2.3 Vertical distribution of *L. sibirica* fine-root biomass (FRB) and necromass (FRN) and non-tree root biomass (NTRM) in the profile to 80 cm depth at the Altai site in 2012: (a) relative root mass abundance in percent of the profile total; (b) root mass density (mass per soil volume). Given are means and standard errors from one deep soil profile from the six different plots.

The study of horizontal fine-root distribution in the Altai and Khangai stands in 2011 revealed no significant differences in FRB, FRN and NTRM between the stem distances of 1, 2 or 3 m (Table 2.1). The FRB in the 0-20 cm layer in the Altai and Khangai stands was neither dependant on the stand basal area nor stem diameter or canopy cover (Table 2.2). However, FRB showed a significant positive relation to FRN in the Altai in 2012.

Table 2.1 Fine-root biomass (FRB), fine roor necromass (FRN) and non-tree fine-root mass (NTRM) at 1 to 3 m distance from a tree stem in the Altai and Khangai in 2011 from 36 replicate sample points (in g DM m^{-2} for the 0-20 cm soil depth). Differences between the individual distances are not significant (Repeated-measures ANOVA, $P \leq 0.05$).

	Region	**Distance from sample tree**		
		1 m	2 m	3 m
FRB	Altai	5.08 ±3.90	2.25 ±1.05	3.07 ±1.33
	Khangai	0.51 ±0.35	3.35 ±1.45	10.05 ±5.05
FRN	Altai	1178 ±124	1368 ±227	1467 ±240
	Khangai	1081 ±68	1201 ±130	1326 ±64
NTRM	Altai	637 ±88	622 ±78	568 ±56
	Khangai	546 ±106	513 ±60	489 ±92

Table 2.2 Results of a regression analysis analyzing the dependence of larch fine-root biomass on stand structural variables or fine-root necromass in the three different study years.

Descriptor	**R^2**	**P**	**Slope direction**
Stand basal area:			
Altai 2011	0.30	0.13	+
Khangai 2011	0.00	0.47	-
Altai 2012	0.10	0.27	-
Stem diameter of canopy trees:			
Altai 2011	0.07	0.31	+
Khangai 2011	0.08	0.29	+
Altai 2012	0.30	0.13	-
Canopy cover:			
Altai 2011	0.29	0.14	+
Khangai 2011	0.43	0.08	+
Altai 2012	0.28	0.14	-
Tree fine-root necromass:			
Altai 2011	0.00	0.49	-
Khangai 2011	0.02	0.39	-
Altai 2012	0.52	0.05	+

Despite some variation across the sites and sampling years, we found no significant differences in fine-root morphological traits between the dry years 2010 and 2011 and the moister year 2012 (Altai) or the mesic Ore Mts. site (2012) (Table 2.3). An exception was the ectomycorrhizal colonization rate that ranged between 80 and 100 % in the 2011 and

2012 samples at all sites, but was significantly lower (59 %) in the Altai plots in 2010. In this year, the larch fine roots of the Altai sites showed also an insignificant trend for higher root tissue density than in the other two years (0.67 vs. 0.36-0.40 g cm^{-3}).

Table 2.3 Mycorrhizal colonization rate (MycorCol), root tissue density (TisDens), average root diameter (AvgDiam), specific root surface area (SRA), specific root length (SRL) and specific root tip abundance (SRTA) of living tree fine roots in *L. sibirica* stands of the Altai, Khangai and Ore Mountains in the respective study years. Given are means and standard errors[1]

	Altai 2010	**Altai 2011**	**Altai 2012**	**Khangai 2011**	**Ore Mts. 2012**
MycorCol (%)	59 ±3 a	95 ±5 b	80 ±7 a	89 ±11 ab	100 ±0 b
TisDens (g cm^{-3})	0.67 ±0.20 a	0.36 ±0.03 a	0.40 ±0.02 a	0.36 ±0.02 a	0.35 ±0.01 a
AvgDiam (mm)	0.67 ±0.05 a	0.59 ±0.06 a	0.62 ±0.03 a	0.53 ±0.03 a	0.59 ±0.02 a
SRTA (n mg^{-1})	1.98 ±1.13 a	3.73 ±1.46 a	1.61 ±0.34 a	3.11 ±0.94 a	3.84 ±0.55 a
SRA (cm^2 g^{-1})	225 ±55 a	245 ±35 a	181 ±10 a	288 ±18 a	247 ±15 a
SRL (cm g^{-1})	1576 ±573 a	1532 ±369 a	1079 ±82 a	1886 ±227 a	1573 ±126 a

[1] Within a row, means followed by the same letter do not differ significantly (Tukey's test, $P \leq 0.05$).

2.5 Discussion

With less than 10 g DM m^{-2}, our fine-root biomass (FRB) stand totals are far smaller than FRB values reported from other boreal forests (Tables 2.4 and 2.5). Based on literature surveys, Vogt et al. (1996) give a FRB range for boreal evergreen coniferous forests of 60-165 g m^{-2}, Jackson et al. (1996) of 290 g m^{-2} for boreal forests in general, and Yuan and Chen (201) of 292 g m^{-2} for boreal coniferous forests. On the species level, a FRB range of 89-575 g m^{-2} has been reported for Norway spruce stands and of 130-357 g m^{-2} for boreal pine stands (Table 2.4). Data for larch forests are relatively scarce varying between 73 and 690 g m^{-2} (Sakai et al., 2007; Son and Hwang, 2003). An old-growth *L. gmelinii* stand in Central Siberia had a FRB of (roots <3 mm) of 370 g m^{-2} (Kajimoto et al., 1999). Coniferous forests of the temperate zone may have higher FRB than boreal forests (Bauhus and Messier, 1999; Finér et al., 2011). The lowest FRB value reported in the literature for a conifer stand was 10.4 g m^{-2}, but it originates from a 12-year old Douglas fir stand (Vogt et al., 1987). A nearby 150-year old forest of the same species was characterized by a much higher FRB of 112 g m^{-2}, indicating a strong stand age effect on FRB (Børja et al., 2008; Pearson et al., 1987; Vogt et al., 1983). In a *Pinus* *oaxacana* forest in Mexico, the FRB in the uppermost 20 cm of the soil was found to be as low as 18.1 g m^{-2} in a drought year, but recovered to 59.4 g m^{-2} in a subsequent wet year (Valdés et al., 2006).

Table 2.4 Published reports on fine-root biomass (FRB) and fine-root necromass (FRN) and live to dead fine-root ratio (L:D ratio) of coniferous species in the boreal and temperate zones.

Species	**Stand** age (yr)	**Soil** depth (cm)	**Root** diameter (mm)	**FRB** (g m^{-2})	**FRN** (g m^{-2})	**L:D**	**Source**
Larix sibirica							This study
Altai, dry year	155	201	<2	4	946	0.003	
Altai, wet year	155	201	<2	143	1396	0.1	
Altai, wet year	155	Oh[2]	<2	96	919	0.08	
Altai, wet year	155	0-80[2]	<2	223	2798	0.12	
Khangai, dry year	137	201	<2	5	1202	0.004	
Ore Mountains	118	201	<2	301	392	0.77	
Larix gmelinii	17	30	<2	87-178	33-88	0.99-5.39	Cheng et al., 2006
L. gmelinii	260	20	<3	370	-	-	Kajimoto et al., 1999
L. leptolepis	40	20	<2	73	23	3.17	Son and Hwang, 2003
L. kaempferi, Betula platyphylla	39	30	<2	300	-	-	Sakai *et al.*, 2007
Pinus contorta	13	30	<2	75	-	-	Litton et al., 2003
P. sylvestris	17	40	<2	220	500	0.44	Makkonen and Helmisaari, 2001
P. sylvestris	37	40	<2	357	1044	0.34	Makkonen and Helmisaari, 2001
P. sylvestris	102	40	<2	259	1895	0.14	Makkonen and Helmisaari, 2001
P. sylvestris	130	30	<2	207	-	-	Ahlström et al., 1988
Picea abies	28	201	<1	234	594	0.39	Persson et al., 1995
P. abies	28	201	<2	495	46	14.5	Majdi and Persson, 1995
P. abies	45	40	<2	559	33	29.6	Eldhuset et al., 2006
P. abies	120	201	<2	136	-	-	Børja et al., 2008
Pseudotsuga menziesii	12	151	<2	10	-	-	Vogt et al., 1987
P. menziesii	98	30	<2	78	-	-	McDowell et al., 2001
P. menziesii	150	151	<2	317	-	-	Vogt et al., 1987

[1] Specified sampling depth plus organic layer

[2] Data are not directly comparable with the other data in the table due to different soil depths

A FRB <10 g m^{-2} may have not been sufficient to meet the water and nutrient demand of the investigated larch stands in the summers of 2010 and 2011, even if a rather small needle mass and needle surface area index (leaf area index, LAI) are assumed for these stands (c. 150-250 g DM m^{-2} and a projected LAI of c. 2-3). The small size of the fine-root system becomes even more obvious when FRB is expressed per tree individual. We obtained very small amounts of 22.6 ± 7.3 g (2010) and 15.8 ± 8.1 g FRB (2011) per tree for the Altai plots and of 22.9 ± 6.5 g (2011) for the Khangai plots. Clearly, coring to a mineral soil depth of 30 cm may not be adequate for obtaining a reliable estimate of the FRB profile total. Indeed, in our examination of deeper soil horizons in the 2012 measuring campaign in the Altai, we found an only a slight decrease of FRB toward greater soil depth, indicating that the true FRB total may indeed have been higher than the 4-5 g m^{-2} recorded in 2010 and 2011 at the Altai and Khangai sites.

In 2010 and 2011, we did not collect root samples from deeper soil layers, because we believed that majority of FRB should be distributed in shallower soil layers as demonstrated in many other studies. In a meta-analysis of boreal forests, Yuan and Chen (2010) found that half of the FRB was allocated in the uppermost 10 cm of soil (including the organic layer), as was 90 % in the top 30 cm. Many case studies compound this result. For example, 83-85 % of the total FRB was concentrated at 0-15 cm depth in a 39-year old *L. kaempferi* plantation (Sakai et al., 2007). In a boreal peat soil in northeastern Ontario, Bhatti et al. (1998) found 80% of the fine-root mass of *Picea mariana* in moss plus the uppermost 10 cm of the peat. In a *Picea* abies forest of Norway, 73-76 % of the FRB was allocated in the organic layer and the uppermost 20 cm of the mineral soil (Børja et al., 2008). Kajimoto et al. (2007) found that fine roots were mostly distributed in <5-10 cm in a *L. gmelinii* stand of central Siberia providing no exact value. To our knowledge, relevant values for *L. sibirica* were never reported, so far. To confirm that no considerable proportion of living roots existed in deeper soil layers, we collected soil samples from deeper soil layers up to 80 cm in 2012, and unexpectedly found comparatively large proportion of living roots in the deeper soil, since only 47 % of FRB was found in the organic and the 0-10 cm mineral soil layers. However, even if we assume that 50 % of FRB was distributed in the deeper soil layers, in other words, we would have underestimated FRB in 2010 and 2011 by 50 %, the fine root biomass for the whole soil profile up to 80 cm would not have exceeded 8-10 g m^{-2} in the dry years 2010 and 2011. Though this estimate would double the original value, the FRB is still astonishingly low. There is no reason to believe that more fine roots than assumed in this error estimation were formed at high soil depth, because than we should have found increasing fine-root necromass (FRN) with increasing soil depth in 2012 given the slow decomposition, which has to be assumed at the low soil temperatures at the bottom of our soil profiles. Own measurements at the Altai site showed a soil temperature of 3 ℃ in 80 cm depth well above a possible permafrost horizon in July 2012. Therefore, the fact that we found a 20 times larger FRB in the 0-20 cm layer in the wet summer of 2012 than in the drier summer of 2010 and 2011, is evidence that the living root biomass was indeed greatly reduced in the first two study years in these larch forests. In 2010 and 2011, the Altai site received only 90 and 76 mm of rain in summer (May-September).

Despite the striking differences in FRB between the dry years 2010 and 2011 (Altai and Khangai sites) and the moister year 2012 (Altai) or the mesic German larch site, respectively, fine root morphological properties were obviously not affected in a significant way. This is surprising since the potential for water uptake of fine roots is more likely to be related to the surface area than to the biomass of fine roots (Coomes and Grubb, 2000). Moreover, fine root morphology is tightly linked to root turnover and lifespan (Eissenstat and Yanai, 1997; Eissenstat et al. 2000). Thinner fine roots with larger surface area and greater length per unit carbon invested may help trees to optimise the cost-benefit ratio of fine root construction (Eissenstat and Yanai 1997; Eissenstat *et al.* 2000; Pregitzer *et al.* 2002; Ostonen *et al.* 2007) and could represent a strategy of trees to cope with strong water limitation (Eissenstat 1992; West *et al.* 2004). However, empirical evidence for such a mechanism from mature tree stands has seldom found. While Meier and Leuschner (2008) reported an increase in specific fine root area (SRA) and a decrease in mean fine root diameter with decreasing rainfall along a precipitation transect, Leuschner et al. (2004), Hertel et al. (2008), and Hertel et al. (2013) did not find any significant change in fine root morphological properties comparing tree stands with contrasting soil water regimes. We conclude therefore, that modifications in root morphological properties might represent a less frequent response of trees to dry soil moisture conditions compared to changes in the fine root abundance (biomass) in the soil.

In all three years, we found an exceptionally high FRN (and most of it concentrated on the uppermost soil; Fig. 2.2) in both the Altai and Khangai plots, which was considerably higher than FRN values reported from boreal and temperate coniferous forests in the literature (Finér et al., 2007b; Jackson et al., 1997; Table 2.5). These findings suggest that drought must have led to increased fine-root mortality in the summers of 2010 and 2011, greatly reducing the standing stock of living root mass in the upper soil while increasing root necromass. Even though we cannot exclude that the likely fine-root dieback occurred only in the upper soil while more vital fine roots may have remained in deeper soil layers, the exceptionally small biomass : necromass ratio (less than 1 : 200) can only be interpreted as an indication that dying fine roots led to substantial belowground biomass losses in these larch stands as a consequence of the two exceptionally dry summers. At the same time, a considerable amount of root-borne carbon was transferred to the soil organic carbon pool.

Table 2.5 Compilation of reviews on averages (ranges) of fine-root biomass (FRB) and fine-root necromass (FRN) recorded in boreal and temperate coniferous forests.

	FRB (g m^{-2})	**FRN (g m^{-2})**	**Source**
Larix sibirica	4-301	392-1396	This study
Boreal coniferous forest	60-165	-	Vogt et al., 1996
Larix leptolepis/gmelinii	73-590	23-88	Kajimoto et al., 1999; Son and Hwang, 2003; Cheng et al., 2006
Cold-temperate coniferous forest	97-912	-	Vogt et al., 1996
***Pinus sylvestris*, boreal forest**	229	72	Finér et al., 2007
Boreal forest	230	600	Jackson et al., 1997
Pinus	252	-	Yuan and Chen, 2010
Picea	278	-	Yuan and Chen, 2010
Boreal forest	281	-	Finér et al., 2011
Abies	283	-	Yuan and Chen, 2010
Boreal forest	290	-	Jackson et al., 1996
Boreal coniferous forest	292	-	Yuan and Chen, 2010
Temperate coniferous forest	324	-	Finér et al., 2011
***Picea abies*, boreal forest**	330	221	Finér et al., 2007
Temperate coniferous forest	407	306	Leuschner and Hertel, 2003
Temperate coniferous forest	440	-	Jackson et al., 1996
Coniferous forest	500	-	Fogel, 1983
Boreal forest	528	-	Yuan and Chen, 2010
Temperate coniferous forest	820	500	Jackson et al., 1997

A striking result is that the non-tree fine-root mass (NTFB) greatly exceeded the living fine-root mass of larch in all three years at both sites. Even though we were not able to distinguish between live and dead root mass in the non-tree fraction, it is likely that the larch roots are facing pronounced competition by the roots of the dense shrub and herb layers in these stands where canopy closure was rather low (means of 32 and 43 %). We assume that extended periods of topsoil drying in the summers of 2010 and 2011 in combination with intense root competition must have caused the fine-root dieback in the two years.

What were the consequences of the apparent fine-root dieback in dry summers for the vitality and growth of the larch trees? We did not observe clear signs of vitality reduction in the stands in the years 2010-2012. Neither increased needle shedding nor a reduction in stem diameter growth could be observed (tree-ring analyses in >1800 trees by Dulamsuren et al., 2013b). However, large drains in the carbohydrate reserves, as they should have occurred with the apparent rebuilding of FRB from 2011 to 2012, may well reduce stem growth rate after a lag phase of one or two years; such responses were not detectable in the wood cores extracted in 2010 for dendrochronological analysis. The absence of drought-induced needle shedding in the summers of 2010 and 2011 indicates that the fine roots apparently are more sensitive to reduced rainfall than the needles in *L. sibirica*.

With annual precipitation varying between 50 and 250 mm (1940-2010), it is unlikely that the subsoil of the Altai site is storing larger amounts of rainfall water in average and dry years. However, it is known that permafrost islands are locally present in the region at altitudes of 2000-2500 m a.s.l., where the mean annual temperature was -3.4 ℃ between 1940 and 2011 (weather station Altai-Yalalt). It would thus be possible that deep-reaching roots are absorbing melt water near the surface of the soil ice, while the topsoil is desiccating in summer dry spells and much of the FRB is shed. A few sinker roots could well supply the bulk of water needed to maintain a more or less favorable shoot water status. While it is known from other tree species that a relatively small number of roots can be sufficient to meet the tree’s water demand (Vogt et al., 1987), the hypothesis of possibly melt-water fed larch forests at the southern dry limit of the Eurosiberian taiga raises some questions. First, no systematic mapping of the extent of the permafrost islands in the two study regions does yet exist. Second, the melt water must have temperatures of only 1-3 ℃ (given the soil temperature of 3 ℃ in 80 cm depth well above a possible permafrost horizon in the Mongolian Altai in July 2012), which would challenge current perceptions about a hampered root water uptake rate at temperatures <5 ℃ (Wan et al., 1999). Additional studies on deep-reaching roots and the possible role of permafrost as a water source are needed in this region in order to better understand the role of drought for the vitality of these southernmost boreal forests in Central Asia. Further, more detailed studies must show whether the observed large inter-annual FRB fluctuation is a typical phenomenon in the larch forests at the forest-steppe ecotone and whether high fine-root mortality is one of the causes of the marked stem diameter growth decline that was observed in other regions of the northern Mongolian and eastern Kazakh boreal forests (Dulamsuren et al., 2010b, 2013a).

References

Ahlström, K., Persson, H., Börjesson, I., 1988. Fertilization in a mature *Scots* pine (*Pinus sylvestris* L.) stand-effects on fine roots. Plant Soil 106, 179-190.

Batima, P., Natsagdorj, L., Gomboluudev, P., Erdenetsetseg, B., 2005. Observed climate change in Mongolia. AIACC Working Paper 13, 4-25.

Bauhus, J., Messier, C., 1999. Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada. Can J For Res 29, 260-273.

Bhatti, J.S., Foster, N.W., Hazlett, P.W., 1998. Fine root biomass and nutrient content in a black spruce peat soil with and without alder. Can J Soil Sci 78, 163-169.

Børja, I., De Wit, H.A., Steffenrem, A., Majdi, H., 2008. Stand age and fine root biomass, distribution and morphology in a Norway spruce chronosequence in southeast Norway. Tree Physiol 28, 773-784.

Cheng, Y., Han, Y., Wang, Q., Wang, Z., 2006. Seasonal dynamics of fine root biomass, root length density, specific root length, and soil resource availability in a *Larix gmelinii* plantation. Front Biol China 1, 310-317.

Coomes, D.A., Grubb, P.J., 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. Ecol Monogr 70, 171-207.

D'Arrigo, R., Jacoby, G., Pederson, N., Frank, D., Buckley, B., Nachin, B., Mijiddorj, R., Dugarjav, C., 2000. Mongolian tree-rings, temperature sensitivity and reconstructions of Northern Hemisphere temperature. Holocene 10, 669-672.

Dagvadorj, D., Khuldorj, B., Aldover, R., 2009. Mongolia assessment report on climate change 2009. Ministry of Nature, Environment and Tourism, Mongolia, Ulaanbaatar.

Dulamsuren, C., Hauck, M., Khishigjargal, M., Leuschner, H., Leuschner, C., 2010a. Diverging climate trends in Mongolian taiga forests influence growth and regeneration of *Larix sibirica*. Oecologia 163, 1091-1102.

Dulamsuren, C., Hauck, M., Leuschner, C., 2010b. Recent drought stress leads to growth reductions in *Larix sibirica* in the western Khentey, Mongolia. Glob Change Biol 16, 3024-3035.

Dulamsuren, Ch., Wommelsdorf, T., Zhao, F., Xue, Y., Zhumadilov, B.Z., Leuschner, C., Hauck, M., 2013a. Increased summer temperatures reduce the growth and regeneration of *Larix sibirica* in southern boreal forests of eastern Kazakhstan. Ecosystems 16(8), 1536-1549.

Dulamsuren, Ch., Khishigjargal, M., Hauck, M., Leuschner, C., 2103b. Response of tree-ring width to climate warming and selective logging in larch forests of the Mongolian Altai. J Plant Ecol 7(1), 24-38.

Eissenstat, D.M., 1992. Costs and benefits of constructing roots of small diameter. J Plant Nutr 15, 763-782.

Eissenstat, D.M., Yanai, R.D., 1997. The ecology of root life span. Adv Ecol Res 27, 1-62.

Eissenstat, D.M., Wells, C.E., Yanai, R.D., Whitbeck, J.L., 2000. Building roots in changing environment: implications for root longevity. New Phytol 147, 33-42.

Eldhuset, T.D., Lange, H., de Wit, H.A., 2006. Fine root biomass, necromass and chemistry during seven years of elevated aluminium concentrations in the soil solution of a middle-aged *Picea abies* stand. Sci Total Environ 369, 344-356.

Finér, L., Helmisaari, H.S., Lõhmus, K., Majdi, H., Brunner, I., Børja, I., Eldhuset, T., Godbold, D., Grebenc, T., Konôpka, B., Kraigher, H., Möttönen, M.R., Ohashi, M., Oleksyn, J., Ostonen, I., Uri, V., Vanguelova, E., 2007. Variation in fine root biomass of three European tree species: Beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.), and Scots pine (*Pinus sylvestris* L.). Plant Biosyst 141, 394-405.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011. Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. For Ecol Manage 262, 2008-2023.

Fogel, R., 1983. Root turnover and productivity of coniferous forests. Plant Soil 71, 75-85.

Giese, E., Moßig, I., 2004. Klimawandel in Zentralasien. Schriftenreihe des Zentrums für Internationale Entwicklung und Umweltforschung 1-70.

Hertel, D., Leuschner, C., 2002. A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus-Quercus* mixed forest. Plant Soil 239, 237-251.

Hertel, D., Therburg, A., Villalba, R., 2008. Above- and below-ground response of *Nothofagus pumilio* to growth conditions of the transition from the steppe-forest boundary to the alpine treeline in S Patagonia (Argentina). Plant Ecol Divers 1, 21-33.

Hertel, D., Schöling, D., 2011. Below-ground response of Norway spruce to climate conditions at Mt. Brocken (Germany) - A re-assessment of Central Europe's northernmost treeline. Flora 206, 127-135.

Hertel, D., Strecker, T., Müller-Haubold, H., Leuschner, C., 2013. Fine root biomass and dynamics in beech forests across a precipitation gradient – is optimal resource partitioning theory applicable to water-limited mature trees? J Ecol, 101(5), 1183–1200.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108, 389-411.

Jackson, R.B., Mooney, H.A., Schulze, E.-D., 1997. A global budget for fine root biomass, surface area, and nutrient?contents. PNAS 94, 7362-7366.

Janssens, I.A., Sampson, D.A., Curiel-Yuste, J., Carrara, A., Ceulemans, R., 2002. The carbon cost of fine root turnover in a Scots pine forest. For Ecol Manage 168, 231-240.

Kajimoto, T., Matsuura, Y., Sofronov, M.A., Volokitina, A.V., Mori, S., Osawa, A., Abaimov, A.P., 1999. Above- and belowground biomass and net primary productivity of a Larix gmelinii stand near Tura, central Siberia. Tree Physiol 19, 815-822.

Kajimoto, T., Osawa, A., Matsuura, Y., Abaimov, A.P., Zyryanova, O.A., Kondo, K., Tokuchi, N., Hirobe, M., 2007. Individual-based measurement and analysis of root system development: case studies for *Larix gmelinii* trees growing on the permafrost region in Siberia. J For Res 12, 103-112.

Klima-Atlas, 1958. Klima-Atlas für das Gebiet der DDR. Erste Ergänzung. Berlin: Meteorologischer und hydrologischer Dienst der DDR.

Leuschner, C., Hertel, D., 2003. Fine root biomass of temperate forests in relation to soil acidity and fertility, climate, age and species. Prog Bot 64, 405-438.

Leuschner, C., Hertel, D., Schmid, I., Koch, O., Muhs, A., Hölscher, D., 2004. Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. Plant Soil 258, 43-56.

Li, J., Cook, E., D'arrigo, R., Chen, F., Gou, X., 2009. Moisture variability across China and Mongolia: 1951-2005. Clim Dyn 32, 1173-1186.

Litton, C.M., Ryan, M.G., Tinker, D.B., Knight, D.H., 2003. Belowground and aboveground biomass in young postfire lodgepole pine forests of contrasting tree density. Can J For Res 33, 351-363.

Lkhagvadorj, D., Hauck, M., Dulamsuren, C., Tsogtbaatar, J., 2013a. Pastoral nomadism in the forest-steppe of the Mongolian Altai under a changing economy and a warming climate. J Arid Environ 88, 82-89.

Lkhagvadorj, D., Hauck, M., Dulamsuren, C., Tsogtbaatar, J., 2013b. Twenty years after decollectivization: mobile livestock husbandry and its ecological impact in the Mongolian forest-steppe. Hum Ecol 41(5), 725-735.

Majdi, H., Persson, H., 1995. Effects of ammonium sulphate application on the chemistry of bulk soil, rhizosphere, fine roots and fine-root distribution in a *Picea abies* (L.) Karst. stand. Plant Soil 168, 151-160.

Makkonen, K., Helmisaari, H.-S., 2001. Fine root biomass and production in Scots pine stands in relation to stand age. Tree Physiol 21, 193-198.

Matamala, R., González-Meler, M.A., Jastrow, J.D., Norby, R.J., Schlesinger, W.H., 2003. Impacts of fine root turnover on forest NPP and soil C sequestration potential. Science 302, 1385-1387.

McDowell, N.G., Balster, N.J., Marshall, J.D., 2001. Belowground carbon allocation of Rocky Mountain Douglas-fir. Can J For Res 31, 1425-1436.

Meier, I.C., Leuschner, C., 2008. The belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. Glob Change Biol 14, 2081-2095.

Nisbet, T.R., Mullins, C.E., 1986. A comparison of live and dead root weights in stands of Sitka spruce in contrasting soil water regimes. Can J For Res 16, 394-397.

Ostonen, I., Lõhmus, K., Helmisaari, H.S., Truu, J., Meel, S., 2007. Fine root morphological adaptations in Scots pine, Norway spruce and silver birch along a latitudinal gradient in boreal forests. Tree Physiol 27, 1627-1634.

Pearson, J.A., Knight, D.H., Fahey, T.J., 1987. Biomass and nutrient accumulation during stand development in Wyoming Lodgepole pine forests. Ecology 68, 1966-1973.

Persson, H., 1978. Root dynamics in a young Scots pine stand in central Sweden. Oikos 30, 508-519.

Persson, H., Fircks, Y., Majdi, H., Nilsson, L.O., 1995. Root distribution in a Norway spruce (*Picea abies* (L.) Karst.) stand subjected to drought and ammonium-sulphate application. Plant Soil 168, 161-165.

Ruess, R., Van Cleve, K., Yarie, J., Viereck, L., 1996. Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Can J For Res 26, 1326-1336.

Pregitzer, K.S., DeForest, J.L., Burton, A.J., Allen, M.F., Ruess, R.W., Hendrick, R.L., 2002. Fine root architecture of nine North American trees. Ecol Monogr 72, 293-309.

Sakai, Y., Takahashi, M., Tanaka, N., 2007. Root biomass and distribution of a *Picea-Abies* stand and a *Larix-Betula* stand in pumiceous Entisols in Japan. J For Res 12, 120-125.

Santantonio, D., Hermann, R.K., 1985. Standing crop, production, and turnover of fine roots on dry, moderate, and wet sites of mature Douglas fir in Western Oregon. Ann Sci For 42, 113-142.

Son, Y., Hwang, J.H., 2003. Fine root biomass, production and turnover in a fertilized *Larix leptolepis* plantation in central Korea. Ecol Res 18, 339-346.

Tsogtbaatar, J., 2004. Deforestation and reforestation needs in Mongolia. For Ecol Manage 201, 57-63.

Valdés, M., Asbjornsen, H., Gómez-Cárdenas, M., Juárez, M., Vogt, K., 2006. Drought effects on fine-root and ectomycorrhizal-root biomass in managed *Pinus oaxacana* Mirov stands in Oaxaca, Mexico. Mycorrhiza 16, 117-124.

van Praag, H., Sougnez-Remy, S., Weissen, F., Carletti, G., 1988. Root turnover in a beech and a spruce stand of the Belgian Ardennes. Plant Soil 105, 87-103.

Vogt, K.A., Moore, E.E., Vogt, D.J., Redlin, M.J., Edmonds, R.L., 1983. Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas-fir stands of different ages and site productivities. Can JFor Res 13, 429-437.

Vogt, K.A., Vogt, D.J., Moore, E.E., Fatuga, B.A., Redlin, M.R., Edmonds, R.L., 1987. Conifer and Angiosperm Fine-Root Biomass in Relation to Stand Age and Site Productivity in Douglas-Fir Forests. J Ecol 75, 857-870.

Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O'Hara, J., Asbjornsen, H., 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187, 159-219.

Walter, H., Breckle, S.W., 1994. Ökologie der Erde. Band 3: Spezielle Ökologie der Gemässigten und Arktischen Zonen Euro-Nordasiens: Zonobiom VI-IX. 2nd Edn. Fischer, Stuttgart.

Wan, X., Landhäusser, S.M., Zwiazek, J.J., Lieffers, V.J., 1999. Root water flow and growth of aspen (*Populus tremuloides*) at low root temperatures. Tree Physiol 19, 879-884.

West, J.B., Espeleta, J.F., Donovan, L.A., 2004. Fine root production and turnover across a complex edaphic gradient of a *Pinus palustris–Aristida stricta* savanna ecosystem. For Ecol Manage 189, 397-406.

Yuan, Z.Y., Chen, H.Y.H., 2010. Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. Crit Rev Plant Sci 29, 204-221.

Chapter 3

Stem Increment and Hydraulic Architecture of a Boreal Conifer (*Larix sibirica*) under Contrasting Macroclimates[2]

Tselmeg Chenlemuge, Bernhard Schuldt, Choimaa Dulamsuren, Dietrich Hertel, Christoph Leuschner, Markus Hauck

---

[2] In press: Trees - Structure and Function

3.1 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 yr^{-1}.

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 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

3.2 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, though 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 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 large-diameter conduits and thus lower conduit numbers per cross-section 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 (i) mean annual precipitation is directly related to wood anatomical and hydraulic traits across the three sites, and that (ii) 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 data set, we tested the hypothesis that (iii) the hydraulic conductivity and tracheid diameters in conifer roots and branches are positively correlated with precipitation.

3.3 Material and methods

3.3.1 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; 2300–2375 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; 2100–2300 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).

3.3.2 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 1940–2010 were analyzed from the weather station Altai-Yalalt (48°17' N, 89°31' E, 2150 m a.s.l.) 40 km east of the forests studied in the Mongolian Altai, and Uliastai (47°75' N, 96°85' E, 1760 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 data set 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 1940–1969 (station Ulgii City: 1960 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 1.1). 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 melt water 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 yr^{-1} of precipitation recorded (Dulamsuren et al. 2014).

3.3.3 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 1.2). 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 somewhat younger (118 years) than the trees in the Altai (155 years) and Khangai (137 years) stands (Table 1.2). 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.

3.3.4 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 > 3cm). 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 3.1). 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.

Table 3.1 Diameter at breast height (DBH), tree-ring width (TRW) and stem basal area increment (BAI) averaged over the period from 2000-2010 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. Significant differences among study areas are indicated by lowercase letters ($P \leq 0.05$, Tukey's test, $df_{model,\ error} = 2, 27$)

	Altai		**Khangai**		**Ore Mts.**	
DBH (cm)	48.7 ± 1.5	a	45.0 ± 1.9	a	48.7 ± 4.9	a
TRW (mm)	0.37 ± 0.04	a	0.67 ± 0.12	b	1.63 ± 0.08	c
BAI (mm2)	560 ± 64	a	930 ± 164	a	2495 ± 259	b
Age (years)	235 (117–343)		180 (107–249)		118 (even-aged)	

3.3.5 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 yr^{-1}).

3.3.6 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. 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). Branches 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 one month after collection.

Immediately before analysis, each root and branch segment was recut under water with a razor blade and mounted in the Xyl'em 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). Study area-specific linear regressions were conducted between A_{cross} and A_{xylem} for each organ and the resulting regression equation (Table A1 in the Annex) 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}).

3.3.7 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 7 trees from the Mongolian Altai, 5 trees from the Khangai Mountains and 6 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 three 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). Afterwards, 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 $d = ((32(ab)^3) / (a^2 + b^2))^{¼}$. 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 $d_\mathrm{h} = \sum d^5 / \sum d^4$. 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, whilst 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 stemwood, 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 was visually differentiated according to color and tracheid size.

3.3.8 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 A2 and A3 in the Annex 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 data set 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}.

3.3.9 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 afterwards 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).

3.4 Results

3.4.1 Stem radial increment

L. 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 3.1) and age (Table 1.2) 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 3.1), which received even less precipitation than the Khangai Mountains (Table 1.1). 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 3.1). The trend for lower stem increment in the Mongolian Altai than the Khangai Mountains was significant for TRW, but not BAI (Table 3.1).

Across the three sites, TRW and BAI were closely positively correlated with mean annual precipitation (MAP), mean growing season precipitation (MGSP; Fig. 3.1a, 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 ($P = 0.12$).

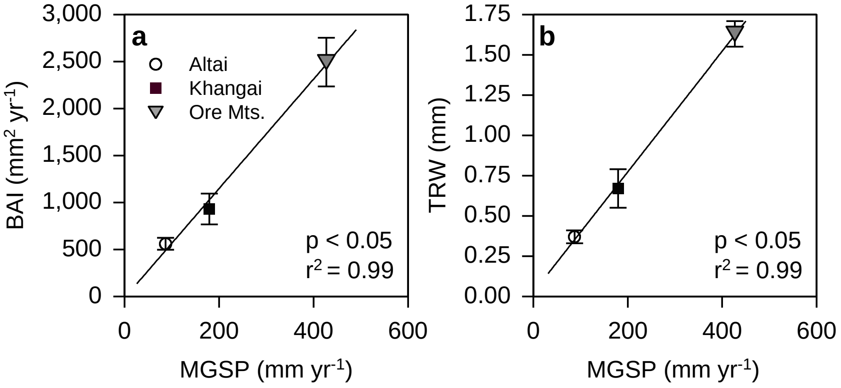

Fig. 3.1 Linear regression of (a) mean basal area increment (BAI; ± SE) and (b) mean tree ring width (TRW; ± SE) of *L. sibirica* in the Mongolian Altai, Khangai and Ore Mountains versus mean growing season precipitation (MGSP)

3.4.2 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. 3.2). Empirical sapwood area-specific hydraulic conductivity (K_s), which cannot be determined in the stem, was higher in the Ore Mountains than in the two sites in Mongolia in both roots and branches (Fig. 3.2a, 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. 3.2c–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. 3.2f–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. 3.3).Consistent with the pattern found for d, tracheid density (*TD*) in roots exhibited a minimum in the Ore Mountains, whereas differences between the study areas were lacking for stems and branches (Fig. 3.2m, 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 (Fig. A1 in the Annex). 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. 3.2). 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 A4 in the Annex).

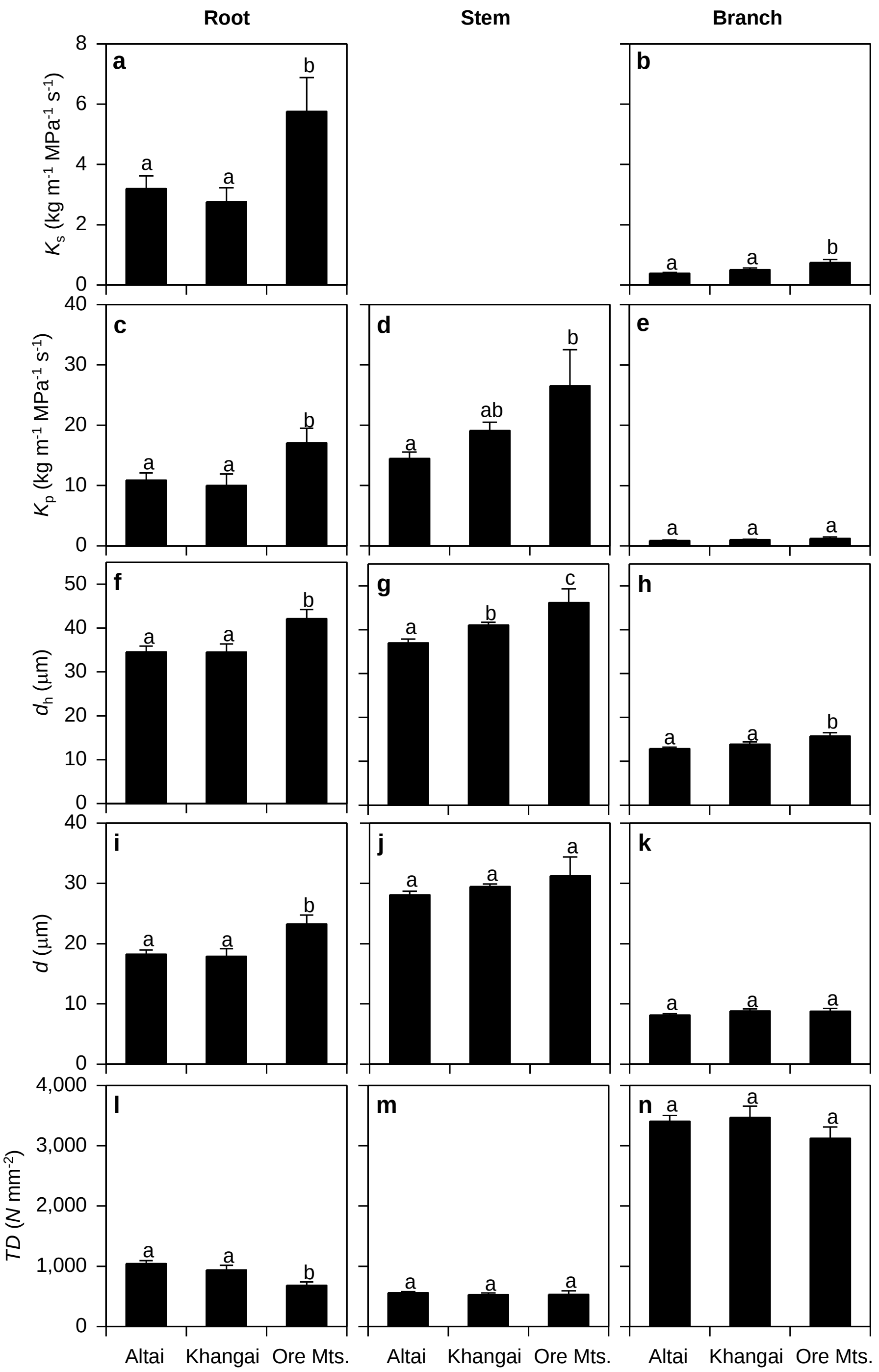

Fig. 3.2 Hydraulic and wood-anatomical traits in roots (a, c, f, i, l), stems (d, g, j, m), and branches (b, e, h, k, n) of *L. sibirica* in the Mongolian Altai, Khangai and the Ore Mountains. (a, b) emperical (K_s) and (c–e) theoretical (K_p) sapwood-area specific hydraulic conductivity, (f–h) hydraulically weighted diameter (d_h), (i–k) tracheid diameter (d) and (l–n) tracheid density (TD). Means (± SE) sharing the same letter within a subplot do not differ significantly ($P \leq 0.05$, LSD test)

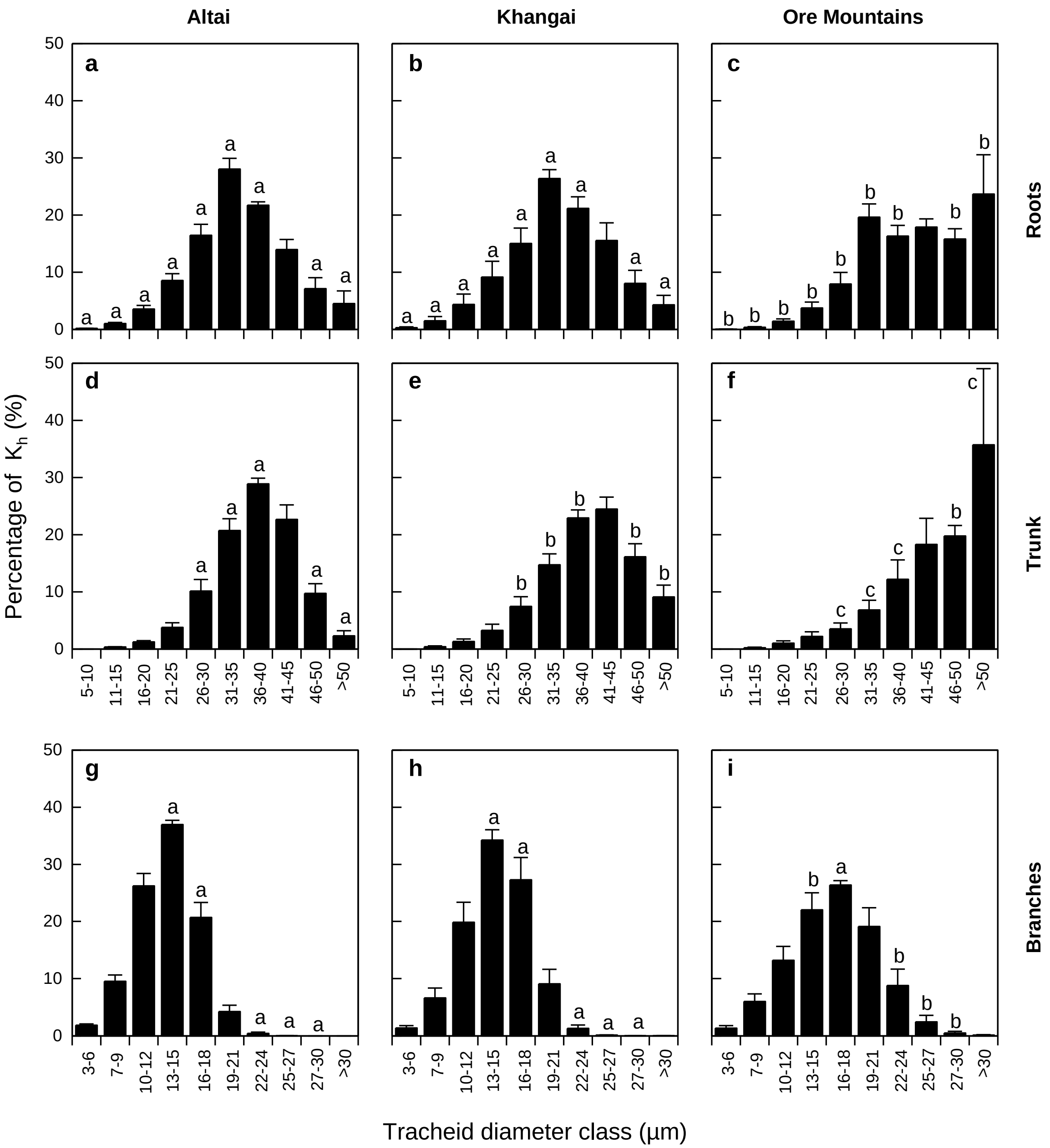

Fig. 3.3 Relative contribution of tracheids of different diameter classes to theoretical hydraulic conductivity (K_h) in (a–c) roots, (d–f) stems and (g–i) branches of *L. sibirica* from (a, d, g) the Mongolian Altai, (b, e, h) the Khangai Mountains and (c, f, i) the Ore Mountains. Within a plant organ (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)

3.4.3 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 3.2). 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 A5 in Annex). In roots, d_h and d increased with MAT, whereas TD decreased with MGSP (Table 3.2).

Table 3.2 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). Pearson correlation coefficients, * $P \leq 0.05$, (*)$P \leq 0.10$. K_s is only available for the total xylem cross-section of roots and branches

	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(*)

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 ($P \leq 0.05$).

3.4.4 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 A6 in the Annex). 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*, *Pinus ponderosa* and *Pinus sylvestris* (Table A6). 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 A6; 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 3.3). For *L. sibirica*, the correlation of K_s with MAP was only marginally significant (Table 3.2). For roots, there was no correlation with K_s in the data set from all species. For *Pinus 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 3.3).

Table 3.3 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*	0.97	0.09	3	**0.99**	**<0.05**	**3**	**0.99**	**<0.05**	**3**
Pinus ponderosa**	**0.99**	**<0.05**	**3**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
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**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Larix sibirica*	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**

* This study. For other sources see references in Tables A2 and A3 in the Annex. Significant ($P \leqslant 0.05$) correlations are printed in bold.

** n.a., no data available

3.5 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 *Larix 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, though in a less consistent manner. These correlations match with 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 steeep precipitation gradient of c. 700 mm yr^{-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 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. 3.2) and the relative contribution of tracheids of different diameter classes to hydraulic conductivity (Fig. 3.3), 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, Mart ńez-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 increase 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 towards 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 stemwood 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 moister 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.

3.6 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.

References

Antonova GF, Stasova VV (1997) Effects of environmental factors on wood formation in larch (*Larix sibirica* Ldb.) stems. Trees 11:462-468.

Araki NH, Khatab IA, Hemamali KK, Inomata N, Wang X-R, Szmidt AE (2008) Phylogeography of *Larix sukaczewii* Dyl. and *Larix sibirica* L. inferred from nucleotide variation of nuclear genes. Tree Genet Genom 4:611-623.

Battulga P, Tsogtbaatar J, Dulamsuren C, Hauck M (2013) Equations for estimating the above-ground biomass of *Larix sibirica* in the forest-steppe of Mongolia. J For Res 24:431-437.

Brodribb TJ, Feild TS (2000) Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. Plant Cell Environ 23:1381-1388.

Brown HR (2013) The theory of the rise of sap in trees: some historical and conceptual remarks. Phys Persp 15:320-358.

Bryukhanova M, Fonti P (2013) Xylem plasticity allows rapid hydraulic adjustment to annual climatic variability. Trees 27:485-496.

Bucci S, Goldstein G, Meinzer F, Scholz F, Franco A, Bustamante M (2004) Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. Tree Physiol 24:891-899.

Cai J, Tyree MT (2010) The impact of vessel size on vulnerability curves: data and models for within-species variability in saplings of aspen, *Populus tremuloides* Michx. Plant Cell Environ 33:1059-1069.

Carlquist S (1977) Ecological factors in wood evolution: a floristic approach. Am J Bot 64:887-896.

Charra-Vaskou K, Charrier G, Wortemann R, Beikircher B, Cochard H, Ameglio T, Mayr S (2012) Drought and frost resistance of trees: a comparison of four species at different sites and altitudes. Ann For Sci 69:325-333.

Chenlemuge T, Hertel D, Dulamsuren C, Khishigjargal M, Leuschner C, Hauck M (2013) Extremely low fine root biomass in *Larix sibirica* forests at the southern drought limit of the boreal forest. Flora 208:488-496.

Choat B, Ball MC, Luly JG, Holtum JA (2005) Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. Trees 19:305-311.

Choat B, Sack L, Holbrook NM (2007) Diversity of hydraulic traits in nine *Cordia* species growing in tropical forests with contrasting precipitation. New Phytol 175:686-698.

Corcuera L, Camarero JJ, Gil-Pelegrín E (2004) Effects of a severe drought on *Quercus ilex* radial growth and xylem anatomy. Trees 18:83-92.

Creese C, Benscoter AM, Maherali H (2011) Xylem function and climate adaptation in *Pinus*. Am J Bot 98:1437-1445.

D'Arrigo R, Jacoby G, Pederson N, Frank D, Buckley B, Nachin B, Mijiddorj R, Dugarjav C (2000) Mongolian tree-rings, temperature sensitivity and reconstructions of Northern Hemisphere temperature. Holocene 10:669-672.

De Grandpré L, Tardif JC, Hessl A, Pederson N, Conciatori F, Green TR, Oyunsanaa B, Baatarbileg N (2011) Seasonal shift in the climate responses of *Pinus sibirica*, *Pinus sylvestris*, and *Larix sibirica* trees from semi-arid, north-central Mongolia. Can J For Res 41:1242-1255.

De Micco V, Aronne G, Baas P (2008) Wood anatomy and hydraulic architecture of stems and twigs of some Mediterranean trees and shrubs along a mesic-xeric gradient. Trees 22:643-655.

Domec J-C, Gartner BL (2002) How do water transport and water storage differ in coniferous earlywood and latewood. J Exp Bot 53:2369-2379.

Domec J-C, Warren J, Meinzer F, Brooks J, Coulombe R (2004) Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. Oecologia 141:7-16.

Domec J-C, Lachenbruch B, Meinzer FC, Woodruff DR, Warren JM, McCulloh KA (2008) Maximum height in a conifer is associated with conflicting requirements for xylem design. Proc Natl Acad Sci USA 105:12069-12074.

Domec J-C, Warren JM, Meinzer FC, Lachenbruch B (2009) Safety factors for xylem failure by implosion and air-seeding within roots, trunks and branches of young and old conifer trees. IAWA J 30:100-120.

Dulamsuren Ch, Hauck M, Bader M, Osokhjargal D, Oyungerel S, Nyambayar S, Runge M, Leuschner C (2009) Water relations and photosynthetic performance in *Larix sibirica* growing in the forest-steppe ecotone of northern Mongolia. Tree Physiol 29:99-110.

Dulamsuren Ch, Hauck M, Leuschner C (2010) Recent drought stress leads to growth reductions in *Larix sibirica* in the western Khentey, Mongolia. Global Change Biol 16:3024-3035.

Dulamsuren Ch, Wommelsdorf T, Zhao F, Xue Y, Zhumadilov B, Leuschner C, Hauck M (2013) Increased summer temperatures reduce the growth and regeneration of *Larix sibirica* in southern boreal forests of Eastern Kazakhstan. Ecosystems 16:1-14.

Dulamsuren Ch, Khishigjargal M, Leuschner C, Hauck M (2014) Response of tree-ring width to climate warming and selective logging in larch forests of the Mongolian Altai. J Plant Ecol 7:24-38.

Edwards WRN, Jarvis PG (1982) Relationship between water content, potential and permeability in stems of conifers. Plant Cell Environ 5:271-277.

Eilmann B, Weber P, Rigling A, Eckstein D (2006) Growth reactions of *Pinus sylvestris* L. and *Quercus pubescens* Willd. to drought years at a xeric site in Valais, Switzerland. Dendrochronologia 23:121-132.

Fonti P, von Arx G, García-González I, Eilmann B, Sass-Klaassen U, Gärtner H, Eckstein D (2010) Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. New Phytol 185:42-53.

Fonti P, Bryukhanova MV, Myglan VS, Kirdyanov AV, Naumova OV, Vaganov EA (2013) Temperature-induced responses of xylem structure of *Larix sibirica* (Pinaceae) from the Russian Altay. Am J Bot 100:1332-1343.

Gonzalez-Benecke CA, Martin TA, Peter GF (2010) Hydraulic architecture and tracheid allometry in mature *Pinus palustris* and *Pinus elliottii* trees. Tree Physiol 30:361-375.

González IG, Eckstein D (2003) Climatic signal of earlywood vessels of oak on a maritime site. Tree Physiol 23:497-504.

Gunin PD, Vostokova EA, Dorofeyuk NI, Tarasov PE, Black CC (1999) Vegetation Dynamics of Mongolia. Kluwer, Dordrecht.

Hacke U, Sauter JJ (1996) Drought-induced xylem dysfunction in petioles, branches, and roots of *Populus balsamifera* L. and *Alnus glutinosa* (L.) Gaertn. Plant Physiol 111:413-417.

Hajek P, Leuschner C, Hertel D, Delzon S, Schuldt B (2014) Trade-offs between xylem hydraulic properties, wood anatomy and yield in *Populus*. Tree Physiol, 34(7), 744-756.

Hargrave K, Kolb K, Ewers F, Davis S (1994) Conduit diameter and drought-induced embolism in *Salvia mellifera* Greene (Labiatae). New Phytol 126:695-705.

Joseph G, Kelsey RG, Thies WG (1998) Hydraulic conductivity in roots of ponderosa pine infected with black-stain (*Leptographium wageneri*) or annosus (*Heterobasidion annosum*) root disease. Tree Physiol 18:333-339.

Leuschner, Ch., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O. & Runge, M. 2001. Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. For Ecol Manage 149: 33-46.

Lens F, Luteyn JL, Smets E, Jansen S (2004) Ecological trends in the wood anatomy of Vaccinioideae (Ericaceae s.l.). Flora 199:309-319.

Lintunen A, Kalliokoski T (2010) The effect of tree architecture on conduit diameter and frequency from small distal roots to branch tips in *Betula pendula*, *Picea abies* and *Pinus sylvestris*. Tree Physiol 30:1433-1447.

Liu H, Park Williams A, Allen CD, Guo D, Wu X, Anenkhonov OA, Liang E, Sandanov DV, Yin Y, Qi Z (2013) Rapid warming accelerates tree growth decline in semi-arid forests of Inner Asia. Glob Change Biol 19:2500-2510.

Lovisolo C, Schubert A (1998) Effects of water stress on vessel size and xylem hydraulic conductivity in *Vitis vinifera* L. J Exp Bot 49:693-700.

Maherali H, DeLucia EH (2000) Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. Tree Physiol 20:859-867.

Maherali H, DeLucia EH (2001) Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. Oecologia 129:481-491.

Maherali H, Pockman WT, Jackson RB (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 85:2184-2199.

Maherali H, Moura CF, Caldeira MC, Willson CJ, Jackson RB (2006) Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. Plant Cell Environ 29:571-583.

Mainiero R, Kazda M (2006) Depth-related fine root dynamics of *Fagus sylvatica* during exceptional drought. For Ecol Manage 237:135-142.

Martínez-Vilalta J, Piñol J (2002) Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. For Ecol Manage 161:247-256.

Martínez-Vilalta J, Prat E, Oliveras I, Piñol J (2002) Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. Oecologia 133:19-29.

Martínez-Vilalta J, Sala A, Piñol J (2004) The hydraulic architecture of Pinaceae – a review. Plant Ecol 171:3-13.

Martínez-Vilalta J, Cochard H, Mencuccini M, Sterck F, Herrero A, Korhonen J, Llorens P, Nikinmaa E, Nolè A, Poyatos R (2009) Hydraulic adjustment of Scots pine across Europe. New Phytol 184:353-364.

Matyssek R, Schulze E (1988) Carbon uptake and respiration in above-ground parts of a *Larix decidua* × *leptolepis* tree. Trees 2:233-241.

Melcher PJ, Michele Holbrook N, Burns MJ, Zwieniecki MA, Cobb AR, Brodribb TJ, Choat B, Sack L (2012) Measurements of stem xylem hydraulic conductivity in the laboratory and field. Methods Ecol Evol 3:685-694.

Mayr S, Schwienbacher F, Bauer H (2003) Winter at the alpine timberline. Why does embolism occur in Norway spruce but not in stone pine? Plant Physiol 131:780-792.

Mencuccini M, Grace J (1995) Climate influences the leaf area/sapwood area ratio in Scots pine. Tree Physiol 15:1-10.

Nardini A, Salleo S (2000) Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? Trees 15:14-24.

Nygren P, Pallardy SG (2008) Applying a universal scaling model to vascular allometry in a single-stemmed, monopodially branching deciduous tree (Attim's model). Tree Physiol 28:1-10.

Oliveras I, Martínez-Vilalta J, Jimenez-Ortiz T, Lledó MJ, Escarré A, Piñol J (2003) Hydraulic properties of *Pinus halepensis, Pinus pinea* and *Tetraclinis articulata* in a dune ecosystem of Eastern Spain. Plant Ecol 169:131-141.

Piñol J, Sala A (2000) Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA. Funct Ecol 14:538-545.

Rood SB, Patiño S, Coombs K, Tyree MT (2000) Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. Trees 14:248-257.

Ryan MG, Phillips N, Bond BJ (2006) The hydraulic limitation hypothesis revisited. Plant Cell Environ 29:367-381.

Sala A, Woodruff DR, Meinzer FC (2012) Carbon dynamics in trees: feast or famine? Tree Physiol 32:764-775.

Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. Oecologia 140:543-550.

Sass U, Eckstein D (1995) The variability of vessel size in beech (*Fagus sylvatica* L.) and its ecophysiological interpretation. Trees 9:247-252.

Schuldt B, Leuschner C, Brock N, Horna V (2013) Changes in wood density, wood anatomy and hydraulic properties of the xylem along the root-to-shoot flow path in tropical rainforest trees. Tree Physiol 33:161-174.

Schulze E-D, Schulze W, Koch H, Arneth A, Bauer G, Kelliher F, Hollinger D, Vygodskaya N, Kusnetsova W, Sogatchev A (1995) Aboveground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian *Larix* stands in eastern Siberia. Can J For Res 25:943-960.

Sevanto S, McDowell NG, Dickman LT, Pangle R, Pockman WT (2014) How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. Plant Cell Environ 37:153-161.

Sperry JS, Ikeda T (1997) Xylem cavitation in roots and stems of Douglas-fir and white fir. Tree Physiol 17:275-280.

Sperry JS, Nichols KL, Sullivan JE, Eastlack SE (1994) Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology 75:1736-1752.

Sterck FJ, Martínez-Vilalta J, Mencuccini M,, Cochard H, Gerrits P, Zweifel R, Herrero A, Korhonen JFJ, Llorens P, Nikinmaa E, Nolè A, Poyatos R, Ripullone F, Sass-Klaassen U (2012) Understanding trait interactions and their impacts on growth in Scots pine branches across Europe. Funct Ecol 26:541-549.

Stout DL, Sala A (2003) Xylem vulnerability to cavitation in *Pseudotsuga menziesii* and *Pinus ponderosa* from contrasting habitats. Tree Physiol 23:43-50.

Thibeault-Martel M, Krause C, Morin H, Rossi S (2008) Cambial activity and intra-annual xylem formation in roots and stems of *Abies balsamea* and *Picea mariana*. Ann Bot 102:667-674.

Tyree M (2003) Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. Trees 17:95-100.

Tyree MT (1997) The cohesion-tension theory of sap ascent: current controversies. J Exp Bot 48:1753-1765.

Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. New Phytol 119:345-360.

Tyree MT, Zimmermann MH (2002) Xylem Structure and The Ascent of Sap. 2nd ed. Springer, Berlin.

White F (1991) Viscous Fluid Flow. MacGraw, New York.

Chapter 4

Hydraulic Properties and Fine Root Mass of *Larix sibirica* along Forest Edge-Interior Gradients[3]

Tselmeg Chenlemuge, Choimaa Dulamsuren, Dietrich Hertel, Bernhard Schuldt, Christoph Leuschner, Markus Hauck

---

[3] Acta Oecologica, under review

4.1 Abstract

At its southernmost distribution limit in Inner Asia, the boreal forest disintegrates into forest fragments on moist sites (e.g. north-facing slopes), which are embedded in grasslands. This landscape mosaic is characterized by a much higher forest edge-to-interior ratio than in closed boreal forests. Earlier work in the forest-steppe ecotone of Mongolia has shown that *Larix sibirica* trees at forest edges grow faster than in the forest interior, as the more xeric environment at the edge promotes self-thinning and edges are preferentially targeted by selective logging and livestock grazing. Lowered stand density reduces competition for water in these semi-arid forests, where productivity is usually limited by summer drought. We studied how branch and coarse root hydraulic architecture and xylem conductivity, fine root biomass and necromass, and fine root morphology of *L. sibirica* respond to sites differing in water availability. Studying forest edge-interior gradients in two regions of western Mongolia, we found a significant reduction of branch theoretical (K_p) and empirical conductivity (K_s) in the putatively more drought-affected forest interior in the Mongolian Altai (mean precipitation: 120 mm yr^{-1}), while no branch xylem modification occurred in the moister Khangai Mountains (215 mm yr^{-1}). K_p and K_s were several times larger in roots than in branches, but root hydraulics were not influenced by stand density or mean annual precipitation. Very low fine root biomass : necromass ratios at all sites, and in the forest interior in particular, suggest that *L. sibirica* seeks to maintain a relatively high root conductivity by producing large conduits, which results in high root mortality due to embolism during drought. Our results suggest that *L. sibirica* is adapted to the semi-arid climate at its southernmost distribution limit by considerable plasticity of the branch hydraulic system and a small but apparently dynamic fine root system.

Keywords

Hydraulic architecture, xylem anatomy, tree-ring width, fine root mass, stem density, coarse roots

4.2 Introduction

The Inner Asian forest-steppe represents the southernmost fringe of the Eurosiberian boreal forest (Walter and Breckle, 1994) where it occurs at its drought limit (Gunin et al., 1999). Water shortage restricts the forests to locations with best water supply in the forest-steppe landscape, which are mainly found on north-facing slopes and in moist valleys. The unsuitability of the drier microsites (especially south-facing slopes) for tree growth has created a highly patchy landscape with islands of forests of variable size being separated by steppe. Humans have additionally modified the spatial pattern of forests and grasslands by millennia-long land use with activities such as pastoral livestock-keeping, selective logging, and unintentional spread of escaped campfires (Fernandez-Gimenez, 1999; Tsogtbaatar, 2004; Lkhagvadorj et al., 2013).

The high degree of natural and man-made forest fragmentation has resulted in a much greater length of forest edges in this ecotone than found elsewhere in the boreal forest, except for the forest-tundra ecotone at the northern distribution limit of the boreal forest. Thus, forest edge populations are very important in this ecotone and this situation raises the question how trees are responding to the specific growing conditions at the forest edge compared to the forest interior. Even though the forest line to the steppe is typically more sun-exposed, warmer and thus drier than the forest interior, annual radial stem increment in *Larix sibirica* from Mongolia and eastern Kazakhstan has been found to be greater in trees from the forest edge than in the interior (Dulamsuren et al. 2010, 2013, 2014). In the drought-prone environment of Inner Asian forest-steppes, higher stem increment at the more xeric forest edge might be unexpected at first glance, but is readily explainable by lower stand densities at the forest edges. Lower stand densities are the result of both more intense self-thinning due to elevated mortality in the drier edge climate (Vygodskaya et al., 2002) and more intense anthropo-zoogenic forest disturbance at the edge than in the interior (Sankey et al., 2006; Khishigjargal et al., 2014). Reduced stand density reduces possible drought effects on tree growth, as shown by comparative shoot water potential measurements at the forest edge and in the interior of *L. sibirica* forests (Dulamsuren et al., 2010). Dendrochronological data demonstrate that radial growth is limited by summer drought at many locations in the Inner Asian forest-steppe, caused by the combination of high summer temperatures and low summer rainfall (De Grandpré et al., 2011; Liu et al., 2013). Drought-related growth limitation is likely to increase in future with climate warming (D'Arrigo et al., 2008; Dulamsuren et al., 2013; Liu et al., 2013).

Carbon assimilation and wood production in drought-exposed trees depend on the hydraulic system in the flow path from the root to the canopy because it determines leaf water status (Choat et al., 2012). A high hydraulic conductivity in roots, stems and branches is a prerequisite for maintaining high stomatal conductance and thus high carbon assimilation rates (Sterck et al., 2012). However, large-diameter xylem conduits, which are the anatomical fundament of high hydraulic conductivity, are more prone to drought-induced embolism than smaller conduits (Maherali et al., 2006, Brodribb and Cochard, 2009; Domec et al., 2010). Hydraulic failure is a key cause of reduced productivity and even tree mortality in water-limited environments and its importance will increase with climate warming (Adams et al., 2009; McDowell, 2011; Anderegg et al., 2012). Studying the hydraulic architecture of *L. sibirica* along a macroclimatic gradient covering a range in annual precipitation of 700 mm, Chenlemuge et al. (2014) found that low precipitation especially in the early growing season was associated with low tracheid diameter and hydraulic conductance in the stem, branch and coarse root xylem.

Adaptive responses of trees to drought exposure have been studied mostly with a focus on stem, branches and foliage. Less is known about drought-induced modification in roots and root systems, which must be particularly flexible in their response. The root system may respond to reduced water availability by investing carbon in the production of additional roots to explore additional soil volume for water uptake. This was observed in certain tree species (Parker and Van Lear, 1996; Leuschner et al., 2001), whereas other species apparently are not capable of an expansive response, as they show lowered fine root biomass with reduced precipitation (Makkonen and Helmisaari, 1998; Joslin et al., 2000; Konôpka et al., 2005; Meier and Leuschner, 2008).

Modification in the tree’s hydraulic system is another possible adaptive response to drought. Increasing the hydraulic efficiency of the xylem by forming large-diameter conduits to increase water uptake in periods of rainfall at the risk of cavitation in drought periods, is less risky in roots than in branches or the stem, because embolism can be reversed more easily than in the stem or branches by generating low osmotic root pressures (Sperry et al., 1994; Nardini and Pitt, 1999; Ewers et al., 2001) or actively by osmotically-driven embolism repair with the release of low-molecular sugars (Zwieniecki and Holbrook, 1998; Brodersen and McElrone, 2013). Furthermore, if suffering drought-induced dieback, individual fine roots are much more easily replaced than the stem or branches. The inventory of fine root mass in *L. sibirica* forests during wet and dry years in the forest-steppe of the Mongolian Altai suggested that fine root biomass was strongly reduced in dry summers when high amounts of necromass were recorded (Chenlemuge et al., 2013). This result led us to speculate that small-diameter roots of *L. sibirica* may lack specific adaptation to drought periods, and that the species tolerates high drought-induced losses of fine root biomass, rather than producing roots with contrasting conduit sizes as a plastic response to variation in moisture availability.

Starting from the observation that higher radial stem growth in trees at the forest edge compared to the interior seems to be a characteristic feature of forests in the Inner Asian forest-steppe ecotone pointing at reduced competition for water, we ask whether (1) fine root biomass and (2) xylem anatomy and hydraulic architecture are also modified along the forest interior-edge gradient. We expected that higher stem wood production at the edge should be associated with higher hydraulic efficiency at the branch and root levels and elevated fine root biomass per tree. We selected two regions in western Mongolia with the characteristic patchy larch forest mosaic in the forest-steppe ecotone, which differed in annual precipitation (120 vs. 215 mm yr^{-1}), and measured wood anatomical and hydraulic properties in the branches and roots and determined the live and dead fine root mass at the edge and in the interior of monospecific *L. sibirica* stands with 6-fold replication at the plot level. We tested the hypotheses that (1) conduit size and related hydraulic conductivity are higher in branches and roots of trees at the forest edge than in the interior, (2) the anatomy and functionality of roots are more plastic than of branches and roots thus show a higher responsiveness to the interior-edge gradient in stem density, and (3) with increasing competition intensity from the edge to the interior, fine root biomass decreases per tree individual and also per stand area reflecting the deterioration of soil water availability.

4.2 Material and methods

4.2.1 Study area

The study was conducted in two Siberian larch (*Larix sibirica* Lebed.) forests in the Mongolian Altai and the western Khangai Mountains, Mongolia (Fig. 1). The study area in the Mongolian Altai was located in the Dayan administrative subunit ('bag') in the Altai Tavan Bogd National Park in the province ('aimag') of Bayan-Ulgii, 110 km SW of the city of Ulgii. The area is located south and southeast of Lake Dayan (48°14'39"-48°16'3" N, 88°50'17"-88°57'0" E; 2300-2375 m a.s.l.). The study area in the western Khangai Mountains (600 km east of Lake Dayan) was 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; 2100-2300 m a.s.l.).

The *L. sibirica* forests in the Altai and Khangai Mountains represent the southern fringe of the Eurosiberian forest belt. Both study areas were located in the transition zone between light taiga forest to steppe in mountainous terrain where *L. sibirica* forests occur on north-facing slopes, whereas steppe covers south-facing slopes and most valley bottoms. Most larch woodlands were forest islands of variable size that were partly converted into pasture by the local herdsmen over time. Siberian larch is the dominant tree species in the Mongolian forests that reach a rather low canopy cover of typically 20-50 %. The studied forests were monospecific larch forests; in the whole of Mongolia, Siberian larch covers 80 % of the forested area (Tsogtbaatar, 2004). The forest floor was covered by a relatively species-rich layer of low shrubs and a herb layer that reaches cover values of 50-100 %. The prevailing soils are Leptosols which formed from siliceous rock.

The climate of the Mongolian forest-steppe is semiarid and highly continental with a subzero annual mean temperature and an annual precipitation between 100 and 400 mm. Mean temperatures in the study areas were -3.4 °C (year; January: -21.2 °C; July: 12.9 °C) in the Mongolian Altai (weather station Altai-Yalalt, 40 km east of the studied forests, 2150 m a.s.l.; since 1940) and -2.4 ℃ (year; January: -23.5 ℃; July: 15.8 ℃) in the Khangai (weather station Uliastai, 30 km NNW of the studied forests, 1760 m a.s.l.; since 1940). Precipitation was 120 mm yr^{-1} at the weather station Altai-Yalalt and 215 mm yr^{-1} in Uliastai; both values are somewhat underestimating the precipitation in the studied forests.

4.2.2 Sample plots

Six forest stands on the north-facing mountain slopes were chosen in each study region. Twelve plots of 20 m × 20 m were established in each study region, six plots in the forest interior, c. 50-100 m from the forest line, and six plots at the forest edge. The lower boundary of the forest edge plots was identical with the forest line. Sample plot selection was a non-random, but systematic procedure because of the regular landscape structure of the Mongolian forest-steppe with patches of larch forests on most north-facing mountain slopes. The studied larch stands on north-facing slopes were selected in near equidistance along one valley each in the Altai and the Khangai. 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 two study regions. Sample plot selection was not biased by preselecting plots after local differences in vegetation, forest stand structure or land-use pressure. However, moist depressions on the mountain slopes, which were not representative of the bulk of the total area and were likely to deviate from most other areas in terms of biomass production, were deliberately excluded at the expense of equidistance between plots. The distance of 50-100 m between edge and interior plots was sufficient to study differences in the water supply, since the fine root abundance declines linearly or even exponentially with increasing distance from the tree and in most cases only a negligible amount of fine roots occurs at a distance beyond 10-15 m from the tree.

4.2.3 Survey of stand characteristics and tree-ring analysis

Stand characteristics were surveyed and wood cores from larch stems were collected in July 2010 (Altai) and August 2011 (Khangai). Canopy cover and cover of herb and shrub layers were estimated in percent. Within each plot, trees with diameter at breast height (DBH) > 3 cm were numbered and DBH, tree height, demographic status and canopy rank of these tree individuals were recorded. Wood-cores were collected at breast height (about 1.3 m above the ground) of all numbered trees using an increment borer of 5 mm inner diameter. The borer was driven into the wood parallel to the contour lines of the mountain slope 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). Detailed information on the results of tree-ring analyses has been published in (Dulamsuren et al., 2014) and will be compiled in a separate publication for the Khangai data. Stand basal area (m^2 ha^{-1}) and 10-year (2000-2010) mean annual basal area increment (BAI, in mm^2 yr^{-1}) were calculated from all trees with a DBH > 3 cm.

In both study regions, canopy cover was significantly higher in the forest interior plots than in the forest edge plots (*t*-test, $P < 0.05$). The stand's cumulative basal area and stem density exhibited trends for higher values in the interior than at the edges; however, these differences were only statistically significant in the Khangai Mountains (*t*-test, $P \leqslant 0.05$). Neither tree age, tree height, DBH nor cover of the ground vegetation showed significant differences between forest interior and edge (*t*-test, $P > 0.05$) (Table 4.1).

Table 4.1 Stand characteristics in plots at the forest edge (FE) and in the forest interior (FI) in the Mongolian Altai and Khangai Mountains.[a]

	Altai			**Khangai**		
	FE	FI		FE	FI	
Age of canopy trees (yr)	111±35	158±26		153±23	123±22	
Age (all trees) (yr)	71±3	86±7		134±25	109±18	
Canopy tree height (m)	14.0±2.3	15.4±2.2		11.9±0.6	3.4±0.6	
Tree height (all trees) (m)	8.7±0.7	8.2±0.5		9.9±1.0	11.1±0.7	
Stem diameter of canopy trees (cm)	31.8±9.4	34.1±7.5		24.5±2.9	17.3±2.3	
Stem diameter (all trees) (cm)	4.0±1.5	11.6±0.7		18.2±3.2	4.3±1.6	
Stand basal area of canopy trees (m^2 ha^{-1})	11.8±3.9	8.9±2.5		7.6±2.5	6.0±1.6	
Total stand basal area (m^2 ha^{-1})	38.7±4.9	47.8±3.8		14.5±1.8	9.4±3.7	*
Canopy cover (%)	38±2	43±1	*	16±2	33±5	*
Cover of herb and shrub layers (%)	78±1	77±2		78±2	74±3	
Stand density (adult trees) (trees ha^{-1})	1592±191	2067±282		767±317	1604±327	
Stand density (adult and juvenile trees) (trees ha^{-1})	3679±458	14100±5230		808±340	1933±334	*

[a] Means ± SE, $N = 6$. Significant differences between forest edge and interior within the same study region are indicated by asterisks (paired-samples *t*-test; $P \leqslant 0.05$)

4.2.4 Fine root sampling and morphological analysis

In August 2011, root samples were collected in each plot in the Mongolian Altai and Khangai regions at five randomly chosen locations per plot using a soil borer (inner diameter 33 mm). Samples were taken from the top 20 cm of the organic layer and the upper mineral soil at each of the five sampling locations per 20 m × 20 m plot. The samples were stored at 4 ℃ until root extraction in the laboratory.

In the laboratory, the samples were cleaned with tap water from soil residues using a sieve with a mesh size of 0.625 mm. Only fine roots (< 2 mm diameter) were selected for analysis. Larger (> 10 mm long) fine root fractions were sorted into 3 groups, namely living fine roots (for calculating fine root biomass) and dead fine roots (fine root necromass) of Siberian larch as well as understory roots (mostly herbaceous root mass) based on their color, elasticity, and the degree of cohesion of cortex, periderm and stele as inspected under the stereomicroscope (Persson, 1978; Hertel and Leuschner, 2002). Live and dead roots were not distinguished for the understory fine roots, because roots from herbaceous plants are not lignified and therefore more rapidly decompose after death. As a consequence, the collected understory fine root mass predominantly consists of living roots. Smaller root fractions (< 10 mm length) were evenly spread on a large sheet of filter paper (730 cm^2) with 36 squares marked on it. Six of the squares were randomly selected and analyzed under the stereomicroscope for even the smallest dead fine root fragments. The total mass of small dead rootlets was extrapolated by regression analysis from the ratio of small rootlets to large dead roots (> 10 mm in length) recorded in the same subsample (Praag et al., 1988; Hertel and Schöling, 2011). Sorted samples were dried at 70 °C for 48 h and weighed.

Up to 10 living rootlets per soil sample, if available, were randomly selected for analyzing root morphological characteristics using a WinRhizo (Regent Instruments Inc., Sainte-Foy, Quebec, Canada) visual analysis system connected to a scanner. The dry biomass of the scanned living rootlets was measured afterwards. Tissue density, average root diameter, specific root surface area (SRA) and specific root length (SRL) were determined in the < 2 mm fraction. Mycorrhizal infection rate (%) and specific root tip abundance (SRTA, tips per fine root biomass) were determined by counting all living tips and all tips with mycorrhizal infection under the stereomicroscope in the same rootlet.

4.2.5 Coarse root and branch sampling for hydraulic conductivity measurement

In August 2011, six trees were randomly chosen in each plot for coarse root and branch segment collection. One to three root (mean diameter ± SE: 7.8 ± 0.3 mm; mean length ± SE: 109.8 ± 1.9 mm) and branch (mean diameter ± SE: 8.0 ± 0.2 mm; mean length ± SE: 117.6 ± 1.6 mm) 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 until shipping to Germany within one month.

In the laboratory, the root and branch segments were recut under water with a razor blade and mounted in a Xyl'em 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 degased 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, and 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 determined 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, the 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. In order to estimate 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 one root and one branch segment per plot (i.e. each 24 root and branch samples in total). A light microscope (DM5000B, 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). Linear regressions of A_{xylem} on A_{cross} were conducted in every study region for each organ and the resulting regression equation (see Table A1 in Annex) was used to derive A_{xylem} for all samples from A_{cross}. 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}).

4.2.6 Xylem anatomy analysis

Samples chosen for A_{xylem} measurements were stored in 70% ethanol for subsequent xylem anatomical analysis. Prior to cutting, the samples were dyed with safranin (1% in 50% ethanol, Merck, Darmstadt, Germany) for three days and rinsed with 70% ethanol on a shaker three times for 12 h. Subsequently, the samples were washed with distilled water and cut on the following day with a sliding microtome (Hn 40, Reichert-Jung, Nußloch, Germany) into semi-thin transverse sections (10–20 µm), which were completely photographed at ×100 magnification with the above mentioned camera system. Complete cross-sections without pith and bark were analyzed with Adobe

Photoshop CS2 9.0 (Adobe Systems Incorporated, San Jose, California, USA) and ImageJ software using the particle analysis function to estimate single and cumulative tracheid lumen area (in m^2), tracheid density (*TD*, in n mm^{-2}) and idealized tracheid diameters (*d*, in µm) from 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*, in µm) 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, whilst A_{xylem} is the corresponding cross-sectional area without pith and bark (see Ch. 2.5). For each cross section, we measured the diameters of c. 3,000-80,000 tracheids in the root samples and of c. 39,000-156,000 tracheids in the branch samples.

4.2.7 Data processing and statistical analysis

Arithmetic means ± standard errors are given throughout the paper. Fine root biomass and necromass of *L. sibirica* and understory root mass were averaged among five samples taken from random locations within each plot, whereas fine root morphology parameters (tissue density, average root diameter, mycorrhizal infection rate, SRA, SRL, SRTA and tips per fine root biomass) were first averaged over replicate rootlets in a sample and then averaged over the random samples to generate plot-specific means. K_s, K_p, *TD*, *d*, and d_h data were first averaged over replicate root or branch segments of a tree and subsequently averaged over the six trees of a plot. Aboveground stand characteristics, plot-specific BAI, DBH and 10-yr-averaged tree-ring widths were derived by averaging over all trees measured in a plot. We treated the each six plots as true replicates in the statistical tests.

Data were tested for normality using the Shapiro-Wilk test and for homogeneity of variances using Levene's test. One-way analysis of variance (ANOVA) was conducted to compare between the study regions (Altai, Khangai) when homogeneity of variances of the data sets was confirmed; if not, the Mann-Whitney *U*-test was used. The paired-samples *t*-test was used to test for significantly different means of forest edge and interior. Pearson coefficients were calculated in linear regression analysis. All statistical analyses were carried out with SPSS 16.0.0 software (SPSS, Chicago, Illinois, USA).

4.3. Results

4.3.1 Radial stemwood increment

Tree-ring width (TRW) averaged over the years 2000 to 2010 was higher at the forest edge than in the interior in both study regions (Table 4.2). Mean basal area increment (BAI) tended to be higher in the trees at the edge than in the interior, but the difference was only significant in the Mongolian Altai, but not in the Khangai Mountains. There were no significant differences in TRW or BAI between the study regions (one-way ANOVA, $P \leqslant 0.05$).

Table 4.2 Tree-ring width (TRW, in mm) and stem basal area increment (BAI, in mm^2 yr^{-1}) averaged over 160-355 trees for the period 2000-2010 from the forest edge and averaged over 306-397 trees from the interior in the Mongolian Altai and Khangai Mountains.[a]

	Forest edge		**Forest interior**		***P***
	Mean ± SE	Trees	Mean ± SE	Trees	
Altai:					
TRW	0.74 ± 0.06	355	0.48 ± 0.07	397	*
BAI	305 ± 50	355	172 ± 33	397	*
Khangai:					
TRW	0.74 ± 0.12	160	0.50 ± 0.10	306	*
BAI	383 ± 91	160	228 ± 37	306	

[a] Significant differences between forest edge and interior within the same study region are indicated by asterisks (paired-samples *t*-test; $P \leqslant 0.05$; $N = 6$).

4.3.2 Fine root distribution and morphology

Fine root biomass of *L. sibirica* did not differ significantly between the forest edge and the interior in the two study regions (Table 4.3) when expressed per stand area, but was about four times larger per tree individual in the edge plots with lower stem density; this difference, however, was not significant (Khangai: $P = 0.06$; Altai: $P = 0.17$) due to high variation in the data from the forest edge. Stand-related, but not tree-related fine root necromass of *L. sibirica* was higher in the interior than at the edge ($P \leq 0.05$). One-way

ANOVA showed a higher stand area-related larch fine root necromass in the Mongolian Altai than at higher precipitation in the Khangai Mountains ($P \leqslant 0.01$). On a tree individual basis, there was an insignificant trend for higher fine root bio- and necromasses in the Khangai than in the Altai larch forests. Understory root mass did not show any significant differences between the two regions and the forest interior and edge (Table 4.3). For none of the investigated fine root morphological parameters (mycorrhizal colonization rate, root tissue density, average root diameter, specific root surface area, specific root length and specific root tip abundance), a significant difference between the regions or between forest edge and interior was found (Table 4.4).

Table 4.3 Fine root biomass (FRB) and necromass (FRN) of *L. sibirica* (given either per stand area or per tree) as well as understory root mass at the forest edge (FE) and in the forest interior (FI) of the Mongolian Altai and Khangai Mountains.[a]

	Altai			**Khangai**		
	FE	FI		FE	FI	
FRB (g m^{-2})	8.5 ± 4.5	3.5 ± 1.7		4.8 ± 1.4	4.6 ± 1.8	
FRN (g m^{-2})	829 ± 41	1338 ± 114	*	554 ± 45	1202 ± 56	*
Ratio FRB : FRN	0.010 ± 0.006	0.003 ± 0.002		0.009 ± 0.003	0.004 ± 0.001	
Understory root mass (g m^{-2})	643 ± 33	609 ± 41		510 ± 54	516 ± 48	
FRB (g tree^{-1})	61.2 ± 39.9	15.8 ± 8.1		101.5 ± 34.9	26.5 ± 7.0	
FRN (g tree^{-1})	5544 ± 662	6792 ± 959		11788 ± 2476	9357 ± 1908	

[a] Significant differences of means (± SE) between forest edge and interior within the same study region are indicated by asterisks (paired-samples *t*-test; $P \leqslant 0.05$; $N = 6$).

Table 4.4 Mycorrhizal colonization rate (MycorCol), root tissue density (TisDens), average root diameter in the <2 mm fraction (AvgDiam), specific root surface area (SRA), specific root length (SRL) and specific root tip abundance (SRTA) of living *L. sibirica* fine roots at the forest edge and in the forest interior of the Mongolian Altai and Khangai Mountains.[a]

	Altai		**Khangai**	
	Forest edge	Forest interior	Forest edge	Forest interior
MycorCol (%)	96.4 ± 2.7	95.0 ± 5.0	87.3 ± 6.4	89.4 ± 10.6
TisDens (g cm^{-3})	0.35 ± 0.02	0.36 ± 0.03	0.33 ± 0.01	0.36 ± 0.02
AvgDiam (mm)	0.79 ± 0.20	0.59 ± 0.06	0.49 ± 0.01	0.53 ± 0.03
SRTA (*N* mg^{-1})	2.18 ± 0.68	3.11 ± 1.34	4.19 ± 0.77	3.11 ± 0.94
SRA (cm^{2} g^{-1})	206 ± 31	245 ± 35	283 ± 7	288 ± 18

SRL (cm g^{-1})	1260 ± 241	1533 ± 369	2083 ± 155	1886 ± 227

[a] No significant differences were found between means (±SE) from edge and interior (paired-samples t-test; $P \leqslant 0.05$).

4.3.3 Hydraulic conductivity and anatomical traits of roots and branches

Both empirical (K_s) and theoretical (K_p) sapwood area-specific hydraulic conductivity of branches was significantly higher at the forest edge than in the forest interior of the Mongolian Altai (Table 4.5). This was not the case in the Khangai Mountains. Correspondingly, the hydraulically-weighted mean tracheid diameter (d_h) was higher and tracheid density (TD) was lower in branches from the forest edge than from the interior in the Mongolian Altai, but not in the Khangai Mountains. In contrast, the anatomical and hydraulic properties of coarse roots (mean diameter: 7.8 mm) did not differ between the two regions and between interior and edge. Here the means of tracheid diameter (d) and TD and hydraulic conductivity were remarkably similar across the different forest habitats and the study region had no effect (one-way ANOVA, $P \leq 0.05$; Table 4.5). Roots had generally higher d_h and d ($P \leqslant 0.01$), but lower TD values than branches ($P \leqslant 0.001$, paired samples t-test). Variation of hydraulic and wood-anatomical parameters across the plots tended to be higher in roots than branches, as indicated by a tendency for higher coefficients of variation in the former (Table 4.5).

Table 4.5 Empirical (K_s) and theoretical (K_p) sapwood area-specific hydraulic conductivity, hydraulically-weighted diameter (d_h), tracheid diameter (d) and tracheid density (TD) of coarse roots and branches from the forest edge and interior of the Mongolian Altai and Khangai Mountains.[a]

	Altai					**Khangai**			
	Forest edge	CV	Forest interior		CV	Forest edge	CV	Forest interior	CV
Roots:									
K_s (kg m^{-1} MPa^{-1} s^{-1})	3.23 ± 0.56	43	3.12 ± 0.35		27	2.47 ± 0.66	66	2.73 ± 0.77	69
K_p (kg m^{-1} MPa^{-1} s^{-1})	9.33 ± 0.41	11	10.9 ± 1.2		27	9.82 ± 1.5	37	10.0 ± 1.9	47
d_h (µm)	33.3 ± 0.8	6	34.6 ± 1.3		9	33.3 ± 1.6	12	34.5 ± 1.9	13
d (µm)	17.8 ± 0.6	8	18.3 ± 0.7		10	18.2 ± 0.9	13	17.9 ± 1.3	18
TD (N mm^{-2})	1029 ± 69	16	1047 ± 47		11	1000 ± 78	19	938 ± 79	21
Branches:									
K_s (kg m^{-1} MPa^{-1} s^{-1})	0.57 ± 0.05	23	0.39 ± 0.03	*	20	0.68 ± 0.13	48	0.57 ± 0.10	42

K_p (kg m^{-1} MPa^{-1} s^{-1})	1.32 ± 0.09	17	0.87 ± 0.08	*	24	1.11 ± 0.09	20	1.26 ± 0.19	36
d_h (µm)	14.1 ± 0.2	3	12.9 ± 0.3	*	6	13.6 ± 0.3	5	13.9 ± 0.5	10
d (µm)	8.8 ± 0.2	6	8.2 ± 0.2		7	8.2 ± 0.3	9	8.8 ± 0.4	10
TD (N mm^{-2})	3658 ± 113	8	3407 ± 94	*	7	3762 ± 243	16	3470 ± 184	13

[a] Significant differences of means (± SE) between forest edge and interior within the same study region are indicated by asterisks (paired-samples t-test; $P \leqslant 0.05$; $N = 6$); CV, coefficient of variation (in %).

4.4 Discussion

Trees in the Inner Asian forest-steppe at the southernmost distribution limit of the Eurosiberian boreal forest are frequently and increasingly exposed to drought stress (Liu et al., 2013). *Larix sibirica* is an anisohydric tree species, which can efficiently adjust the point of zero turgor of its cells to increasing atmospheric water vapour deficits and thus maintain high levels of transpiration and carbon assimilation even during periods of moderate drought (Dulamsuren et al., 2009a, b). Based on an analysis of climatically very different sites in Central Europe and Inner Asia, *L. sibirica* was found to reduce the risk of cavitation by reducing tracheid diameters under dry climate (Chenlemuge et al., 2014). While this result was obtained comparing stands strongly differing in precipitation, the present study addressed the potential contribution of hydraulic architecture and fine root mass for the adaptation of *L. sibirica* to fine-scale differences in the water supply within the semiarid forest-steppe ecotone of the southernmost Eurosiberian boreal forest.

Since the studied forests in western Mongolia exist at the drought limit of forest growth, they are very responsive to local variation in water availability caused by slope aspect, soil and stand factors. As previously shown for other regions of the Mongolian forest-steppe ecotone (Dulamsuren et al., 2010), reduced stem density at the forest edge, which is associated with reduced competition for water, had a positive effect on radial stem increment in both study regions and also affected shoot water potentials. Higher K_s, K_p and d_h in branches from the forest edge than the forest interior in the Mongolian Altai (Table 4.5) agree with these earlier findings and support our first hypothesis that higher radial stem increment is associated with the formation of wider xylem conduits and thus higher conductivity. Correlation between site water availability and hydraulic architecture (Eilmann et al., 2006; De Micco et al., 2008; Gleason et al., 2013) and between hydraulic architecture and productivity (Tyree, 2003; Russo et al., 2010; Fan et al., 2012) has repeatedly been demonstrated for woody plants in earlier studies.

In contrast to branches, coarse root hydraulics in the Altai forests did not show any difference in K_s, K_p and d_h between edge and interior (Table 4.5). This result conflicts with the first hypothesis. The low variation of coarse root xylem anatomy and hydraulic conductivity across the four larch forest sites suggests that *L. sibirica*, in contrast to other tree species from dry forests (Eilmann et al., 2009; Gonzalez-Benecke et al., 2010), responds to variation in water availability with relatively low hydraulic plasticity in the root system which contradicts our second hypothesis. A hydraulic mean tracheid diameter (d_h), that was consistently c. 2.5-fold larger in coarse roots than in branches (Table 4.5), indicates that *L. sibirica* forms root xylem conduits with elevated susceptibility to embolism during drought. Larger conduit sizes in roots compared to branches or stems, combined with narrower safety margins from hydraulic failure, have repeatedly been found in woody plants (Hacke et al., 2000; Mart ńez-Vilalta et al., 2002).

The enormous amounts of fine root necromass together with the very small live fine root mass (Table 4.3) suggest that *L. sibirica* might invest in the production of roots with relatively high conductivity to increase its water uptake capacity during the few rainfall events in summer at the cost of high fine root mortality. Although fine roots have lower conduits diameters resulting in lower hydraulic conductance than roots of higher root orders (Doussan et al., 1998; Valenzuela-Estrada et al., 2008), it is plausible to assume that the high tracheid diameters in the coarse roots of *L. sibirica* (Table 4.5) correspond to relatively high hydraulic conductivity in the individual fine roots. Alternatively, a high number of fine roots would have to be connected with each coarse root to fill their large-diameter conduits with water. Since the fine root biomass was low (Table 4.3), in fact lower than in any other previously studied forest ecosystem (Chenlemuge et al., 2013), it is not likely to assume that the second alternative is realized. High hydraulic conductivity in the fine roots of *L. sibirica* is also suggested by the generally high fine root turnover in larch species (Son and Hwang, 2003; Shi et al., 2008) compared to other tree species (Wells and Eissenstat, 2003) and the fact that short-lived fine roots tend to conduct water more efficiently than fine roots with long lifespan (Eissenstat et al., 2000; Bouma et al., 2001; Wells and Eissenstat, 2003).

Our assumption that *L. sibirica* forms highly conductive roots to use the precious water in the forest-steppe ecotone during wet phases implies that fine roots might be sacrificed in drought periods to protect the subsequent coarse root xylem from cavitation (Chenlemuge et al., 2014). This conclusion matches with the observation that *L. sibirica* maintains higher fine root biomass in moister years than in drier ones in the Mongolian forest-steppe (Chenlemuge et al., 2013). Higher stand area-related fine-root necromass in the forest interior than at the forest edge is also in line with these considerations and supports our third hypothesis, which predicts that increased soil moisture extraction in the dense forest interior acts negatively on fine root biomass by increasing fine root mortality. Clearly, other stressors such has cold winters can also cause high fine root mortality, but this factor should act similarly at the edge and interior. Moreover, throughout our sample plots, the ratio of live to dead fine root mass was much lower than observed elsewhere in boreal or temperate forests where summer drought is less severe (Majdi and Persson, 1995; Persson et al., 1995; Makkonen and Helmisaari, 2001; Son and Hwang, 2003; Cheng et al., 2006; Eldhuset et al., 2006). This suggests that summer drought is the factor leading to the massive fine root dieback. High fine root mortality may stimulate compensatory fine root growth (Keyer and Grier, 1981, Leuschner et al., 2001), which may be one cause of the generally low radial stem increment of the Mongolian larch forests in the forest-steppe (Dulamsuren et al., 2014; Khishigjargal et al., 2014). High fine-root mortality represents not only a significant sink for carbohydrates in the tree, but it might also lead to elevated carbon input into the soil which could influence SOC quality and its persistence in the soil (Gaudinski et al., 2001; Tierney and Fahey, 2002). In addition to the putatively high rates of fine root mortality, the cold and dry climate in the Mongolian forest-steppe resulting in slow decomposition probably also contributes to the high fine root necromass.

The absence of significant differences for K_s, K_p and d_h in the second study region (Khangai Mountains) suggests that other factors than assumed stand density-induced differences in the competition for water interfere with the hydraulic conductivity-growth relationship observed in the larch forests of the Mongolian Altai. Branch xylem anatomy and hydraulic conductivity had similar means at the forest edge and interior in this region with values being close to those from the edge plots in the Altai Mountains (Table 4.5). We explain the association of higher radial growth with higher K_s and K_p in the stands at the forest edge of the Altai, but not of the Khangai, with differences in precipitation between the two regions. At only slightly differing mean annual temperatures (-3.4 °C [Altai] vs. -2.4 °C [Khangai]), mean annual precipitation in the Altai is only 56 % of that in the Khangai (120 vs. 215 mm yr^{-1}). The very low annual precipitation in the Mongolian Altai, which is probably one of the driest boreal forest regions worldwide (Hogg, 1994; Walter and Breckle, 1994), may have forced the trees to decrease tracheid diameter and hydraulic conductivity in the forest interior with putatively stronger water limitation of growth for lowering the risk of cavitation.

4.5 Conclusions

L. sibirica trees in the drought-prone Mongolian forest-steppe at the southernmost fringe of the Eurosiberian boreal forest adapt to local variations in moisture availability due to different stem densities or to regional precipitation gradients by adjustment of branch hydraulic architecture and conductivity. The trees seem to respond to increased soil moisture availability with the formation of larger tracheid diameters, which is one prerequisite of higher productivity. Belowground, *L. sibirica* pursues a different strategy, as no effect of stand density and study region on root hydraulic architecture and empirical hydraulic conductivity was found. Rather, *L. sibirica* seems to produce roots with relatively high water conducting capacity but limited hydraulic safety as a flexible strategy to cope with rare and unpredictable rainfall events. The most likely explanation for minimizing the risk of cavitation in the perennial coarse roots despite their large-diameter tracheids is that fine root mortality is condoned to prevent the intrusion of air into the more costly coarse roots. Further studies on root water uptake using labelled water or miniature sap flow gauges on roots have to show how larch trees manage to supply sufficient water for growth with a very low standing fine root biomass.

References

Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. PNAS 106, 7063-7066.

Anderegg, W.R., Berry, J.A., Smith, D.D., Sperry, J.S., Anderegg, L.D., Field, C.B., 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. PNAS 109, 233-237.

Brodersen, C., McElrone, A., 2013. Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. Front Plant Sci 4,108.

Brodribb, T.J., Cochard, H., 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. Plant Physiol 149, 575-584.

Bouma, T.J., Yanai, R.D., Elkin, A.D., Hartmond, U., Flores-Alva, D.E., Eissenstat, D.M., 2001. Estimating age-dependent costs and benefits of roots with contrasting life span: comparing apples and oranges. New Phytol 150, 685-695.

Cheng, Y., Han, Y., Wang, Q., Wang, Z., 2006. Seasonal dynamics of fine root biomass, root length density, specific root length, and soil resource availability in a *Larix gmelinii* plantation. Front Biol China 1, 310-317.

Chenlemuge, T., Hertel, D., Dulamsuren, C., Khishigjargal, M., Leuschner, C., Hauck, M., 2013. Extremely low fine root biomass in *Larix sibirica* forests at the southern drought limit of the boreal forest. Flora 208, 488-496.

Chenlemuge, T., Schuldt, B., Dulamsuren, Ch., Hertel, D., Leuschner, C., Hauck, M., 2014. Stem increment and hydraulic architecture of a boreal conifer (*Larix sibirica*) under contrasting macroclimates. Trees, in press.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752-755.

D'Arrigo, R., Wilson, R., Liepert, B., Cherubini, P., 2008. On the 'divergence problem'in northern forests: a review of the tree-ring evidence and possible causes. Glob Planet Change 60, 289-305.

De Grandpré, L., Tardif, J.C., Hessl, A., Pederson, N., Conciatori, F., Green, T.R., Oyunsanaa, B., Baatarbileg, N., 2011. Seasonal shift in the climate responses of *Pinus sibirica*, *Pinus sylvestris*, and *Larix sibirica* trees from semi-arid, north-central Mongolia. Can J For Res 41, 1242-1255.

De Micco, V., Aronne, G., Baas, P., 2008. Wood anatomy and hydraulic architecture of stems and twigs of some Mediterranean trees and shrubs along a mesic-xeric gradient. Trees 22, 643-655.

Domec, J.-C., Schäfer, K., Oren, R., Kim, H.S., McCarthy, H.R., 2010. Variable conductivity and embolism in roots and branches of four contrasting tree species and their impacts on whole-plant hydraulic performance under future atmospheric CO_2 concentration. Tree Physiol 30, 1001-1015.

Doussan, C., Vercambre, G., Pagès, L., 1998. Modelling hydraulic architecture of root systems: an integrated approach to water absorption - distribution of axial and radial conductances in maize. Ann Bot 81, 225-232.

Dulamsuren, Ch., Hauck, M., Bader, M., Osokhjargal, D., Oyungerel, Sh., Nyambayar, S., Runge, M., Leuschner, C., 2009a. Water relations and photosynthetic performance in *Larix sibirica* growing in the forest-steppe ecotone of northern Mongolia. Tree Physiol 29, 99-110.

Dulamsuren, Ch., Hauck, M., Bader, M., Oyungerel, Sh., Osokhjargal, D., Nyambayar, S., Leuschner, C., 2009b. The different strategies of *Pinus sylvestris* and *Larix sibirica* to deal with summer drought in a northern Mongolian forest-steppe ecotone suggest a future superiority of pine in a warming climate. Can J For Res 39, 2520-2528.

Dulamsuren, Ch., Hauck, M., Leuschner, C., 2010. Recent drought stress leads to growth reductions in *Larix sibirica* in the western Khentey, Mongolia. Glob Change Biol 16, 3024-3035.

Dulamsuren, Ch., Wommelsdorf, T., Zhao, F., Xue, Y., Zhumadilov, B., Leuschner, C., Hauck, M., 2013. Increased summer temperatures reduce the growth and regeneration of *Larix sibirica* in southern boreal forests of eastern Kazakhstan. Ecosystems 16, 1536-1549.

Dulamsuren, Ch., Khishigjargal, M., Leuschner, C., Hauck, M., 2014. Response of tree-ring width to climate warming and selective logging in larch forests of the Mongolian Altai. J Plant Ecol 7, 24-38.

Eilmann, B., Weber, P., Rigling, A., Eckstein, D., 2006. Growth reactions of *Pinus sylvestris* L. and *Quercus pubescens* Willd. to drought years at a xeric site in Valais, Switzerland. Dendrochronologia 23, 121-132.

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.

Eissenstat, D.M., Wells, C.E., Yanai, R.D., Whitbeck, J.L., 2000. Building roots in a changing environment: implications for root longevity. New Phytol 147, 33-42.

Eldhuset, T.D., Lange, H., de Wit, H.A., 2006. Fine root biomass, necromass and chemistry during seven years of elevated aluminium concentrations in the soil solution of a middle-aged *Picea abies* stand. Sci Tot Environ 369, 344-356.

Ewers, F.W., Améglio, T., Cochard, H., Beaujard, F., Martignac, M., Vandame, M., Bodet, C., Cruiziat, P., 2001. Seasonal variation in xylem pressure of walnut trees: root and stem pressures. Tree Physiol 21, 1123-1132.

Fan, Z.X., Zhang, S.B., Hao, G.Y., Slik, J.W.F., Cao, K.F., 2012. Hydraulic conductivity traits predict growth rates and adult stature of 40 Asian tropical tree species better than wood density. J Ecol100, 732-741.

Fernandez-Gimenez, M.E., 1999. Sustaining the steppes: a geographical history of pastoral land use in Mongolia. Geogr Rev 89, 315-342.

Gaudinski, J., Trumbore, S., Davidson, E., Cook, A., Markewitz, D., Richter, D., 2001. The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. Oecologia 129, 420-429.

Gleason, S.M., Butler, D.W., Waryszak, P., 2013. Shifts in leaf and stem hydraulic traits across aridity gradients in Eastern Australia. Int J Plant Sci 174, 1292-1301.

Gonzalez-Benecke, C.A., Martin, T.A., Peter, G.F., 2010. Hydraulic architecture and tracheid allometry in mature *Pinus palustris* and *Pinus elliottii* trees. Tree Physiol 30, 361-375.

Gunin, P.D., Vostokova, E.A., Dorofeyuk, N.I., Tarasov, P.E., Black, C.C., 1999. Vegetation dynamics of Mongolia. Kluwer Academic Publishers.

Hacke, U.G., Sperry, J.S., Pittermann, J., 2000.Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. Basic Appl Ecol 1, 31-41.

Hertel, D., Leuschner, C., 2002. A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus*-*Quercus* mixed forest. Plant Soil 239, 237-251.

Hertel, D., Schöling, D., 2011. Below-ground response of Norway spruce to climate conditions at Mt. Brocken (Germany). A re-assessment of Central Europe's northernmost treeline. Flora 206, 127-135.

Hogg, E.H., 1994. Climate and the southern limit of the western Canadian boreal forest. Can J For Res 24, 1835-1845.

Hölscher, D., Hertel, D., Leuschner, C., Hottkowitz, M., 2002. Tree species diversity and soil patchiness in a temperate broad-leaved forest with limited rooting space. Flora 197, 118-125.

Joslin, J., Wolfe, M., Hanson, P., 2000. Effects of altered water regimes on forest root systems. New Phytol 147, 117-129.

Keyes, M.R., Grier, C.C., 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can J For Res 11, 599-605.

Khishigjargal, M., Dulamsuren, Ch., Leuschner, H.H., Leuschner, C., Hauck, M., 2014. Climate effects on inter-and intra-annual larch stemwood anomalies in the Mongolian forest-steppe. Acta Oecol 55, 113-121.

Konôpka, B., Yuste, J.C., Janssens, I.A., Ceulemans, R., 2005. Comparison of fine root dynamics in Scots pine and Pedunculate oak in sandy soil. Plant Soil 276, 33-45.

Leuschner, C., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O., Runge, M., 2001. Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. For Ecol Manage 149, 33-46.

Liu, H., Park Williams, A., Allen, C.D., Guo, D., Wu, X., Anenkhonov, O.A., Liang, E., Sandanov, D.V., Yin, Y., Qi, Z., Badmaeva, N.K., 2013. Rapid warming accelerates tree growth decline in semi-arid forests of Inner Asia. Glob Change Biol 19, 2500-2510.

Lkhagvadorj, D., Hauck, M., Dulamsuren, Ch ., Tsogtbaatar, J., 2013. Pastoral nomadism in the forest-steppe of the Mongolian Altai under a changing economy and a warming climate. J Arid Environ 88, 82-89.

Maherali, H., Moura, C.F., Caldeira, M.C., Willson, C.J., Jackson, R.B., 2006. Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. Plant Cell Environ 29, 571-583.

Majdi, H., Persson, H., 1995. Effects of ammonium sulphate application on the chemistry of bulk soil, rhizosphere, fine roots and fine-root distribution in a *Picea abies* (L.) karst. stand. Plant Soil 168-169, 151-160.

Makkonen, K., Helmisaari, H.-S., 1998. Seasonal and yearly variations of fine-root biomass and necromass in a Scots pine (*Pinus sylvestris* L.) stand. For Ecol Manage 102, 283-290.

Makkonen, K., Helmisaari, H.-S., 2001. Fine root biomass and production in Scots pine stands in relation to stand age. Tree Physiol 21, 193-198.

Martínez-Vilalta, J., Prat, E., Oliveras, I., Piñol, J. (2002) Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. Oecologia 133, 19-29.

McDowell, N.G., 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. Plant Physiol 155, 1051-1059.

Meier, I.C., Leuschner, C., 2008. Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. Glob Change Biol 14, 2081-2095.

Meinen, C., Leuschner, C., Ryan, N.T., Hertel, D., 2009. No evidence of spatial root system segregation and elevated fine root biomass in multi-species temperate broad-leaved forests. Trees 23, 941-950.

Nardini, A., Pitt, F., 1999. Drought resistance of *Quercus pubescens* as a function of root hydraulic conductance, xylem embolism and hydraulic architecture. New Phytol 143, 485-493.

Parker, M., Van Lear, D., 1996. Soil heterogeneity and root distribution of mature loblolly pine stands in piedmont soils. Soil Sci Soc Am J 60, 1920-1925.

Persson, H., 1978. Root dynamics in a young Scots pine stand in Central Sweden. Oikos 30, 508-519.

Persson, H., Fircks, Y., Majdi, H., Nilsson, L.O., 1995. Root distribution in a Norway spruce (*Picea abies* (L.) Karst.) stand subjected to drought and ammonium-sulphate application. Plant Soil 168-169, 161-165.

Praag, H.J., Sougnez-Remy, S., Weissen, F., Carletti, G., 1988. Root turnover in a beech and a spruce stand of the Belgian Ardennes. Plant Soil 105, 87-103.

Russo, S.E., Jenkins, K.L., Wiser, S.K., Uriarte, M., Duncan, R.P., Coomes, D.A., 2010. Interspecific relationships among growth, mortality and xylem traits of woody species from New Zealand. Funct Ecol 24, 253-262.

Sankey, T.T., Montagne, C., Graumlich, L., Lawrence, R., Nielsen, J., 2006. Lower forest-grassland ecotones and 20th century livestock herbivory effects in northern Mongolia. For Ecol Manage 233, 36-44.

Shi, J., Wang, Z., Yu, S., Quan, X., Sun, Y., Jia, S., Mei, L., 2008. Estimation of fine root production, mortality and turnover with Minirhizotron in *Larix gmelinii* and *Fraxinus mandshurica* plantations. Front Biol China 3, 496-506.

Son, Y., Hwang, J.H., 2003. Fine root biomass, production and turnover in a fertilized *Larix leptolepis* plantation in central Korea. Ecol Res 18, 339-346.

Sperry, J.S., Nichols, K.L., Sullivan, J.E., Eastlack, S.E., 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology, 1736-1752.

Sterck, F.J., Martínez-Vilalta, J., Mencuccini, M., Cochard, H., Gerrits, P., Zweifel, R., Herrero, A., Korhonen, J.F.J., Llorens, P., Nikinmaa, E., Nolè, A., Poyatos, R., Ripullone, F., Sass-Klaassen, U., 2012. Understanding trait interactions and their impacts on growth in Scots pine branches across Europe. Funct Ecol 26, 541-549.

Tierney, G.L., Fahey, T.J., 2002. Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. Can J For Res 32, 1692-1697.

Tsogtbaatar, J., 2004. Deforestation and reforestation needs in Mongolia. For Ecol Manage 201, 57-63.

Tyree, M., 2003. Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. Trees 17, 95-100.

Valenzuela-Estrada, L.R., Vera-Caraballo, V., Ruth, L.E., Eissenstat, D.M., 2008. Root anatomy, morphology, and longevity among root orders in *Vaccinium corymbosum* (Ericaceae). Am J Bot 95, 1506-1514.

Vygodskaya, N., Schulze, E.D., Tchebakova, N., Karpachevskii, L., Kozlov, D., Sidorov, K., Panfyorov, M., Abrazko, M., Shaposhnikov, E., Solnzeva, O., 2002. Climatic control of stand thinning in unmanaged spruce forests of the southern taiga in European Russia. Tellus B 54, 443-461.

Walter, H., Breckle, S.W., 1994. Spezielle Ökologie der gemässigten und arktischen Zonen Euro-Nordasiens: Zonobiom VI-IX. G. Fischer, Stuttgart.

Wells, C.E., Eissenstat, D.M., 2003. Beyond the roots of young seedlings: the influence of age and order on fine root physiology. J Plant Growth Regul 21, 324-334 White, F., 1991. Viscous fluid flow. 1991. MacGraw, New York.

Zwieniecki, M.A., Holbrook, N.M., 1998 Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.). Plant Cell Environ 21, 1173-1180.

Zwieniecki, M.A., Melcher, P.J., Holbrook, N.M., 2001. Hydraulic properties of individual xylem vessels of *Fraxinus americana*. J Exp Bot 52, 257-264.

Chapter 5

Synthesis

5.1 Adaptation of the fine root system of *Larix sibirica* to drought

We found striking differences in fine root biomass (FRB) between the dry years 2010 and 2011 (Altai and Khangai sites) and the moister year 2012 (Altai) or the mesic German larch site, respectively. In 2010 and 2011, FRB was less than 10 g DM m^{-2} (at 0-20 cm soil layer) in the Mongolian sites, which was far smaller than FRB values reported from other boreal forests. In the wet summer of 2012, FRB in the 0-20 cm layer was 20 times larger than in the drier summer of 2010 and 2011, which is evidence that the living root biomass was greatly reduced in the first two study years in these larch forests.

In all three years, fine-root necromass (FRN) (mostly concentrated in upper soil layer) was exceptionally high in both the Altai and Khangai plots, which was considerably higher than FRN values reported from boreal and temperate coniferous forests in the literature. An exceptionally small biomass : necromass ratio (less than 1 : 200) was found in the two dry summers of 2010 and 2011. These findings suggest that drought must have led to increased fine-root mortality in the summers of 2010 and 2011, greatly reducing the standing stock of living root mass in the upper soil while increasing root necromass. In addition, non-tree fine-root mass (NTFB) greatly exceeded the living fine-root mass of larch in all three years at both Mongolian sites. This is likely that the larch roots are facing pronounced competition by the roots of the dense shrub and herb layers in these stands.

Based on above findings, we assume that extended periods of topsoil drying in the summers of 2010 and 2011 in combination with intense root competition must have caused the fine-root dieback in the two years. Dying fine roots apparently led to substantial belowground biomass losses in these larch stands and a considerable amount of root-borne carbon was transferred to the soil organic carbon pool.

Despite the striking differences in FRB between the dry years and the moister year or between the dry sites and the mesic site, fine root morphological properties were not affected in a significant way. Except that the ectomycorrhizal colonization rate ranged between 80 and 100 % in the 2011 and 2012 samples at all sites, but was significantly lower (59 %) in the Altai plots in 2010. Lõhmus et al. (2006) proposed two different strategies by which trees may increase nutrients uptake in their root systems: (1) increasing either the biomass and length of fine roots to improve forage in nutrient-poor soils (extensive foraging strategy) or (2) increasing the nutrient uptake efficiency by improving symbiosis with ectomycorrhizal fungi or microorganisms in the rhizosphere (intensive foraging strategy). Both of those two strategies seemed to be adapted by *L. sibirica* growing in the Northern Mongolia at its southern drought limit. However, modifications in root morphological properties might represent a less frequent response of trees to dry soil moisture conditions compared to changes in the fine root abundance (biomass) in the soil in this study.

Clear signs of vitality reduction in the Mongolian stands in the years 2010-2012 was not observed. We found neither increased needle shedding nor a reduction in stem diameter growth (Dulamsuren et al., 2014). However, we cannot exclude the possibility that large drains in the carbohydrate reserves may reduce stem growth rate after a lag phase of one or two years. Further studies are needed to evaluate the consequence of high fine root mortality in dry years. The absence of drought-induced needle shedding in the summers of 2010 and 2011 indicates that the fine roots apparently are more sensitive to reduced rainfall than the needles in *L. sibirica*.

A unique vertical distribution pattern of fine root system was observed in larch stands in the driest Mongolian Altai site. In our examination of deeper soil horizons in the 2012 measuring campaign in the Altai, we found only a slight decrease of FRB toward greater soil depth, which was in contrary to former findings that found major amount of fine root biomass in the shallower soil layers and fine root biomass decrease exponentially with increasing soil depth (Bhatti et al., 1998; Børja et al., 2008; Sakai et al., 2007; Yuan and Chen, 2010). Receiving very low annual precipitation (between 50 and 250 mm during 1940-2010), it is unlikely that the subsoil of the Altai site is storing larger amounts of rainfall water in average and dry years. However, it is known that permafrost islands are locally present in the Altai region (Sharkhuu, 2003). It would thus be possible that deep-reaching roots are absorbing melt water from the permafrost active layer, while the topsoil is desiccating in summer dry spells and much of the FRB is shed. In a synthetic analysis based on 250 root studies, Jackson et al. (1996) found tundra, boreal forest, and temperate grasslands showed the shallowest rooting profiles, while deserts and temperate coniferous forests showed the deepest profiles. A few sinker roots could well supply the bulk of water needed to maintain a more or less favorable shoot water status, while it is known from other tree species that a relatively small number of roots can be sufficient to meet the tree’s water demand (Bréda et al., 1995; Vogt et al., 1987). However no systematic mapping of the extent of the permafrost islands in the two study regions in Mongolia does yet exist. Additional studies on deep-reaching roots and the possible role of permafrost as a water source are needed in this region in order to better understand the role of drought for the vitality of these southernmost boreal forests.

Combining all those findings, we conclude that the observed large inter-annual FRB fluctuation coordinated with precipitation amount and FRB distribution in deeper soil layer might be indications of adaptation strategy of *L. sibirica* to drought stress at its southern distribution limit. However, more detailed studies must show whether these adaptations are typical phenomenon in the larch forests at the forest-steppe ecotone.

5.2 Adaptation of the hydraulic architecture of *Larix sibirica* to drought

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 the hypotheses: (i) mean annual precipitation is directly related to wood anatomical and hydraulic traits across the three sites, and that (iii) the hydraulic conductivity and tracheid diameters in conifer roots and branches are positively correlated with precipitation. It has generally been demonstrated that conduits are on average larger in wet compared to dry habitats, both observed for gymnosperms and angiosperms as well as for tropical (Choat et al., 2007), temperate (Dettmann et al., 2013; Panek, 1996; Preston and Ackerly, 2003) and Mediterranean ecosystems (Dickison, 2000). 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. Our results also indicate a temperature effect on the hydraulic architecture of *L. sibirica*. However, moisture availability during the early growing season is probably more effective in controlling hydraulic conductivity in *L. sibirica* than temperature, because correlations between hydraulic conductivity and temperature were less tight.

Our study also showed that *L. sibirica* trees adapt to local variations in moisture availability due to different stem densities or to regional precipitation gradients by adjustment of branch hydraulic architecture and conductivity. We found that in the driest Altai site both hydraulic conductivity and tracheid diameter of branch was higher in the forest-edge where drought stress for individual tree was lower than the forest-interior habitat, although differences between two habitats was not significant in the Khangai site. The trees respond to increased soil moisture availability with the formation of larger tracheid diameters which is one prerequisite of higher productivity.

Belowground, *L. sibirica* pursues a different strategy, as no effect of stand density and study region on root hydraulic architecture and empirical hydraulic conductivity was found. Root hydraulic conductivity and tracheid size was not significantly differed between forest edge and forest interior in both of the Mongolian sites. This might be an indication of special adaptation of *L. sibirica* to extreme drought. In severe dry conditions as in Mongolia, having an efficient water absorption and transport root system is especially important to whole-plant functioning as forming wider conduits with high conductivity will enables the trees to capture the scarce water in rain periods as efficiently as possible. Trees growing in drier site has higher hydraulic conductivity in root than trees in moisture site was reported in other studies (Gonzalez-Benecke et al., 2010), which was said to be an adaptation of species to less water availability (Eilmann et al., 2009). Having wider and more conductive conduits in root might help mitigate the effect of severe drought stress in Mongolia, but will raise the risk of embolism at the same time, as conduit with wider diameter tends to be more vulnerable to drought induced embolism (Sperry and Ikeda, 1997). This trade-off seems to be solved by fine-root-shedding strategy in *L. sibirica*. It is likely that fine roots die at the start of drought stress, which might prevent coarse roots from cavitation. In support of this assumption, a high mortality of fine roots in dry years was observed in the Mongolian study areas as discussed in the former section. Higher fine root necromass in the more drought stressed forest interior seems also to support this assumption. *L. sibirica* seems to produce small-diameter roots with relatively high water conducting capacity but limited hydraulic safety as a flexible strategy to cope with rare and unpredictable rainfall events. Further studies on root water uptake using labeled water or miniature sap flow gauges on roots have to show how larch trees manage to supply sufficient water for growth with a very low standing fine root biomass.

Former studies have demonstrated correlation between hydraulics of the small terminal branches and physiology of leaves (Brodribb and Feild, 2000; Bucci et al., 2004; Nardini and Salleo, 2000; Santiago et al., 2004), but seldom had any study tested correlation between hydraulic or anatomical traits of root and tree productivity. 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 this study, 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.

5.3 Conclusion

Drought adaptation of fine root system and hydraulic architecture of *Larix sibirica* trees growing in the drought-prone Mongolian forest-steppe at the southernmost fringe of the Eurosiberian boreal forest was studied for the first time. The trees seem to respond to increasing drought stress with the formation of smaller tracheid diameters with lower hydraulic conductivity in branch and stem. Correlation analyses further suggest that the hydraulic architecture influences productivity and that elevated stem increment is related not only to higher hydraulic conductivity in the stem but also in roots and branches. Belowground, *L. sibirica* seems to produce roots with relatively high water conducting capacity but limited hydraulic safety as a flexible strategy to cope with rare and unpredictable rainfall events. In general, growing at its southern drought limit, *L. sibirica* has adopted drought-avoiding strategies that maximize resource capture during a limited growing season and then avoid stress with a deciduous leaf habit in the dry season. Further studies on root water uptake using labeled water or miniature sap flow gauges on roots have to show how larch trees manage to supply sufficient water for growth with a very low standing fine root biomass and whether the observed large inter-annual fine root biomass fluctuation is a typical phenomenon in the larch forests at the forest-steppe ecotone and whether high fine-root mortality is one of the causes of the marked stem diameter growth decline that was observed in other regions of the northern Mongolian and eastern Kazakh boreal forests.

References

Bhatti JS, Foster NW, Hazlett PW (1998) Fine root biomass and nutrient content in a black spruce peat soil with and without alder. Can J Soil Sci 78: 163-169.

Børja I, De Wit HA, Steffenrem A, Majdi H (2008) Stand age and fine root biomass, distribution and morphology in a Norway spruce chronosequence in southeast Norway. Tree Physiol 28: 773-784.

Bréda N, Granier A, Barataud F, Moyne C (1995) Soil water dynamics in an oak stand. Plant Soil 172: 17-27.

Brodribb TJ, Feild TS (2000) Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. Plant, Cell Environ 23: 1381-1388.

Bucci S, Goldstein G, Meinzer F, Scholz F, Franco A, Bustamante M (2004) Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. Tree Physiol 24: 891-899.

Choat B, Sack L, Holbrook NM (2007) Diversity of hydraulic traits in nine Cordia species growing in tropical forests with contrasting precipitation. New Phytol 175: 686-698.

Dettmann S, Pérez C, Thomas F (2013) Xylem anatomy and calculated hydraulic conductance of four Nothofagus species with contrasting distribution in South-Central Chile. Trees 27: 685-696.

Dickison WC (2000) Integrative plant anatomy. Access Online via Elsevier.

Dulamsuren C, Khishigjargal M, Leuschner C, Hauck M (2014) Response of tree-ring width to climate warming and selective logging in larch forests of the Mongolian Altai. J Plant Ecol 7: 24-38.

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.

Gonzalez-Benecke CA, Martin TA, Peter GF (2010) Hydraulic architecture and tracheid allometry in mature *Pinus palustris* and *Pinus elliottii* trees. Tree Physiol 30: 361-375.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108: 389-411.

Lõhmus K, Truu M, Truu J, Ostonen I, Kaar E, Vares A, Uri V, Alama S, Kanal A (2006) Functional diversity of culturable bacterial communities in the rhizosphere in relation to fine-root and soil parameters in alder stands on forest, abandoned agricultural, and oil-shale mining areas. Plant Soil 283: 1-10.

Melcher PJ, Michele Holbrook N, Burns MJ, Zwieniecki MA, Cobb AR, Brodribb TJ, Choat B, Sack L (2012) Measurements of stem xylem hydraulic conductivity in the laboratory and field. Methods Ecol Evol 3: 685-694.

Nardini A, Salleo S (2000) Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? Trees 15: 14-24.

Panek JA (1996) Correlations between stable carbon-isotope abundance and hydraulic conductivity in Douglas-fir across a climate gradient in Oregon, USA. Tree Physiol 16: 747-755.

Preston KA, Ackerly DD (2003) Hydraulic architecture and the evolution of shoot allometry in contrasting climates. Am J Bot 90: 1502-1512.

Sakai Y, Takahashi M, Tanaka N (2007) Root biomass and distribution of a *Picea–Abies* stand and a *Larix–Betula* stand in pumiceous Entisols in Japan. J For Res 12: 120-125.

Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. Oecologia 140: 543-550.

Sharkhuu N (2003) Recent changes in the permafrost of Mongolia. Proc 8th Int Conf Perm 2: 1029-1034.

Sperry JS, Ikeda T (1997) Xylem cavitation in roots and stems of Douglas-fir and white fir. Tree Physiol 17: 275-280.

Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap. Springer Verlag.

Vogt KA, Vogt DJ, Moore EE, Fatuga BA, Redlin MR, Edmonds RL (1987) Conifer and angiosperm fine-root biomass in relation to stand age and site productivity in Douglas-fir forests. J Ecol 75: 857-870.

Yuan ZY, Chen H (2010) Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. Crit Rev Plant Sci 29: 204-221.

Annex

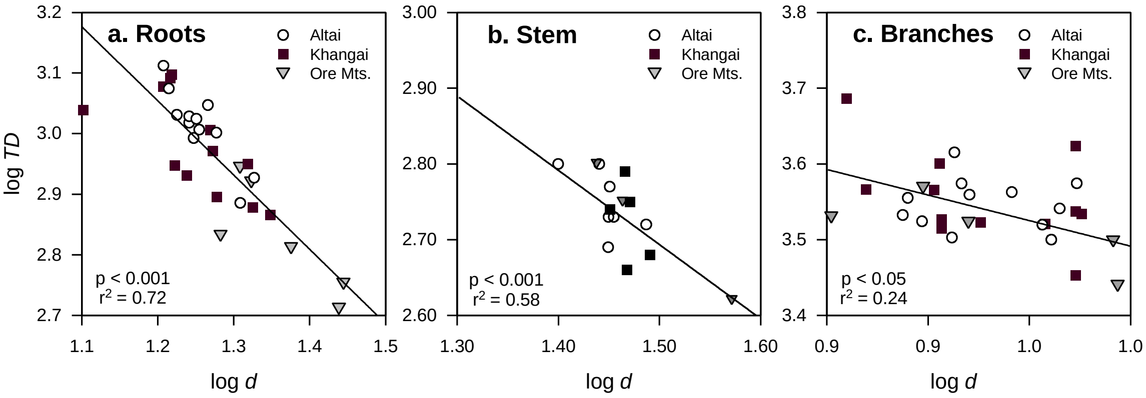

Fig. A1 Linear regression of logarithmized tracheid density (*TD*) versus logarithmized tracheid diameter (*d*) in roots, stems and branches of *L. sibirica* from the Mongolian Altai, Khangai and Ore Mountains

Table A1 Linear regression of xylem cross-sectional area (A_{xylem}) on the organ's cross-sectional area (A_{cross}) in branches and coarse roots in larch trees from the Mongolian Altai, Khangai and Ore Mountains. Given are the means ± SE) of A_{cross} and A_{xylem}, the relative A_{xylem} fraction, and the regressions parameters (intercept *a*, slope *b*, r^2 and *P*).

					$A_{\mathrm{xylem}} = a + b\,A_{\mathrm{cross}}$			
	N	A_{cross} (mm^2)	A_{xylem} (mm^2)	$A_{\mathrm{xylem}} / A_{\mathrm{cross}}$	*a*	*b*	r^2	*P*
Roots:								
Altai	12	44.8 ± 5.0	22.4 ± 2.5	50.1 ± 0.0	0.00	0.50	0.84	< 0.001
Khangai	12	58.4 ± 5.9	20.7 ± 1.8	37.3 ± 0.7	2.48	0.31	0.62	< 0.001
Ore Mts.	6	65.0 ± 9.6	23.7 ± 3.8	35.6 ± 0.5	-1.89	0.39	0.98	< 0.001
Branches:								
Altai	12	42.6 ± 2.3	18.2 ± 0.9	42.8 ± 0.1	0.59	0.41	0.91	< 0.001
Khangai	12	56.4 ± 4.1	22.3 ± 1.8	38.8 ± 0.3	-2.16	0.43	0.92	< 0.001
Ore Mts.	6	110 ± 8	60.1 ± 4.6	53.9 ± 0.7	-6.08	0.60	0.95	< 0.001

Table A2 Detailed information on tree age, tree height, tree diameter at breast height (DBH), elevation, mean annual precipitation (MAP), mean annual temperature (MAT), empirical sapwood-specific hydraulic conductivity (K_s, in kg m^{-1} s^{-1} MPa^{-1}) and hydraulically weighted tracheid diameter (d_h) and site coordinate compiled from literature used for meta-analysis (for further details of the data selection see material and methods section)

No.	Species	Age (yr)*	Height (m)	DBH (cm)	Elevation (m a.s.l.)	MAP (mm)	MAT (℃)	Organ	K_s	d_h (μm)
1	*Abies lasiocarpa*	mature	n.a.	15	2400	340	10.0	branch	3.22	n.a.
2	*Larix decidua*	mature	n.a.	n.a.	1300	1071	7.8	branch	1.42	n.a.
3	*Larix decidua*	mature	n.a.	n.a.	725	778	8.6	branch	2.63	n.a.
4	*Larix decidua*	mature	n.a.	n.a.	1850	822	1.0	branch	0.45	n.a.
5	*Larix decidua*	mature	n.a.	n.a.	850	911	10.3	branch	0.89	n.a.
6	*Larix occidentalis*	mature	n.a.	15	1750	340	10.0	branch	2.80	n.a.
7	*Larix sibirica*	137	17	22	2200	215	-2.4	branch	0.51	13.9
8	*Larix sibirica*	137	17	22	2200	215	-2.4	root	2.76	34.5
9	*Larix sibirica*	155	16	32	2340	120	-3.4	branch	0.39	12.9
10	*Larix sibirica*	155	16	32	2340	120	-3.4	root	3.20	34.6
11	*Larix sibirica*	118	31	54	465	841	7.7	branch	0.75	15.7
12	*Larix sibirica*	118	31	54	465	841	7.7	root	5.76	42.2
13	*Picea abies*	mature	n.a.	n.a.	1300	1071	7.8	branch	1.11	n.a.
14	*Picea abies*	mature	n.a.	n.a.	725	778	8.6	branch	2.00	n.a.
15	*Picea abies*	mature	n.a.	n.a.	1850	822	1.0	branch	0.27	n.a.
16	*Picea abies*	mature	n.a.	n.a.	850	911	10.3	branch	3.78	n.a.
17	*Picea abies*	mature	5	n.a.	1900	822	1.0	branch	2.36	11.4
18	*Pinus albicaulis*	mature	n.a.	15	2400	340	10.0	branch	2.08	n.a.
19	*Pinus contorta*	mature	n.a.	15	2000	340	10.0	branch	2.63	n.a.
20	*Pinus halepensis*	75	n.a.	n.a.	2	312	17.5	branch	1.52	11.3
21	*Pinus halepensis*	75	n.a.	n.a.	2	312	17.5	root	8.93	40.6
22	*Pinus nigra*	160	n.a.	n.a.	960	537	10.0	branch	4.07	n.a.
23	*Pinus pinaster*	40	n.a.	n.a.	960	537	10.0	branch	3.52	n.a.
24	*Pinus pinea*	75	n.a.	n.a.	2	312	17.5	branch	3.51	11.7
25	*Pinus pinea*	75	n.a.	n.a.	2	312	17.5	root	17.00	45.0
26	*Pinus ponderosa*	52	16	n.a.	915	525	7.7	root	4.20	n.a.
27	*Pinus ponderosa*	280	36	n.a.	915	525	7.7	root	4.90	n.a.
28	*Pinus ponderosa*	110	n.a.	n.a.	1690	635	n.a.	root	9.59	n.a.
29	*Pinus ponderosa*	mature	n.a.	n.a.	2100	510	14.8	branch	0.54	n.a.
30	*Pinus ponderosa*	mature	n.a.	n.a.	1500	235	18.7	branch	0.64	n.a.
31	*Pinus ponderosa*	mature	n.a.	15	1500	340	10.0	branch	2.58	n.a.
32	*Pinus ponderosa*	mature	n.a.	17	1120	340	n.a.	branch	2.77	n.a.
33	*Pinus ponderosa*	mature	n.a.	17	975	340	n.a.	branch	4.99	n.a.
34	*Pinus sylvestris*	90	7.7	32.9	2025	783	7.9	branch	0.32	11.6

35	*Pinus sylvestris*	25	13	17.6	957	685	10.7	branch	0.51	13.0
36	*Pinus sylvestris*	100	9.8	26.5	970	709	10.9	branch	0.35	12.0
37	*Pinus sylvestris*	45	11	15.2	1260	940	7.7	branch	0.50	12.1
38	*Pinus sylvestris*	35	11	12.2	940	931	7.3	branch	0.40	13.0
39	*Pinus sylvestris*	94	11	21.2	615	703	9.0	branch	0.58	13.1
40	*Pinus sylvestris*	125	4.0	16.3	975	738	9.0	branch	0.33	11.4
41	*Pinus sylvestris*	150	12	22.4	1270	694	7.5	branch	0.44	12.1
42	*Pinus sylvestris*	55	17	30	20	785	9.2	branch	0.40	12.5
43	*Pinus sylvestris*	50	20	25	20	785	9.2	branch	0.42	12.9
44	*Pinus sylvestris*	30	8.3	21.2	220	851	7.4	branch	0.45	12.9
45	*Pinus sylvestris*	45	14	13.4	181	585	2.8	branch	0.60	12.9
46	*Pinus sylvestris*	160	n.a.	n.a.	960	537	10.0	branch	4.03	n.a.
47	*Pinus sylvestris*	160	n.a.	n.a.	960	537	10.0	branch	4.97	n.a.
48	*Pseudotsuga menziesii*	450	60	n.a.	370	2500	8.7	root	4.00	n.a.
49	*Pseudotsuga menziesii*	mature	n.a.	15	1500	340	10.0	branch	1.99	n.a.
50	*Pseudotsuga menziesii*	mature	n.a.	17	1120	340	n.a.	branch	3.28	n.a.
51	*Pseudotsuga menziesii*	mature	n.a.	17	975	340	n.a.	branch	3.85	n.a.

* mature, mature trees but age not specified

Table A3 Locations and references of studies included in meta-analysis (confer Table A2)

No.	Coordinates	Location	Reference
1	46°55′ N, 114°5′ W	Buttler Creek valley, Montana, USA	Piñol and Sala (2000)
2	45°36′ N, 2°49′ E	Guéry, Auvergne, France, timberline	Charra-Vaskou et al. (2012)
3	45°46′ N, 3°5′ E	Royat, Auvergne, France	Charra-Vaskou et al. (2012)
4	47°11′ N, 11°19′ E	Birgitz Köpfl, Tyrol, Austria, timberline	Charra-Vaskou et al. (2012)
5	47°13′ N, 11°22′ E	Natters, Tyrol, Austria	Charra-Vaskou et al. (2012)
6	46°55′ N, 114°5′ W	Buttler Creek valley, Montana, USA	Piñol and Sala (2000)
7	47°30′ N, 97°8′ E	Western Khangai Mountains, Mongolia	This study
8	47°30′ N, 97°8′ E	Western Khangai Mountains, Mongolia	This study
9	48°15′ N, 88°54′ E	Altai Tavan Bogd National Park, Mongolia	This study
10	48°15′ N, 88°54′ E	Altai Tavan Bogd National Park, Mongolia	This study
11	50°35′ N, 12°32′ E	Ore Mountains, Germany	This study
12	50°35′ N, 12°32′ E	Ore Mountains, Germany	This study
13	45°36′ N, 2°49′ E	Guéry, Auvergne, France, timberline	Charra-Vaskou et al. (2012)
14	45°46′ N, 3°5′ E	Royat, Auvergne, France	Charra-Vaskou et al. (2012)
15	47°11′ N, 11°19′ E	Birgitz Köpfl, Tyrol, Austria, timberline	Charra-Vaskou et al. (2012)
16	47°13′ N, 11°22′ E	Natters, Tyrol, Austria	Charra-Vaskou et al. (2012)
17	47°11′ N, 11°19′ E	Birgitz Köpfl, Tyrol, Austria, timberline	Mayr et al. (2003)
18	46°55′ N, 114°5′ W	Buttler Creek valley, Montana, USA	Piñol and Sala (2000)
19	46°55′ N, 114°5′ W	Buttler Creek valley, Montana, USA	Piñol and Sala (2000)
20	38°10' N, 0°38' W	Guadama La Marina, Alicante, Spain	Oliveras et al. (2003)
21	38°10' N, 0°38' W	Guadama La Marina, Alicante, Spain	Oliveras et al. (2003)
22	41°13′ N, 0°55′ E	Castellfollit valley, Prades Mountains, Spain	Martínez-Vilalta and Piñol (2002)
23	41°13′ N, 0°55′ E	Castellfollit valley, Prades Mountains, Spain	Martínez-Vilalta and Piñol (2002)
24	38°10' N, 0°38' W	Guadama La Marina, Alicante, Spain	Oliveras et al. (2003)
25	38°10' N, 0°38' W	Guadama La Marina, Alicante, Spain	Oliveras et al. (2003)
26	44°30′ N, 121°37′ W	Metolius river, Oregon, USA	Domec et al. (2004)
27	44°30′ N, 121°37′ W	Metolius river, Oregon, USA	Domec et al. (2004)
28	43°52' N; 118°45' W	Malheur National Forest, Oregon, USA	Joseph et al. (1998)
29	38°41′/39°20' N, 119°44′ W	Sierra Nevada, USA (mountain forest)	Maherali and DeLucia (2000)
30	39°34′ N, 119°50′ W	Great Basin, Nevada, USA (forest-steppe)	Maherali and DeLucia (2000)
31	46°55′ N, 114°5′ W	Buttler Creek valley, Montana, USA	Piñol and Sala (2000)
32	47°00′ N, 114°28′ W	Petty Creek, Alberton, Montana, USA (slope)	Stout and Sala (2003)
33	47°00′ N, 114°28′ W	Petty Creek, Alberton, Montana, USA (river)	Stout and Sala (2003)
34	37°22′ N, 2°51′ W	Granada, Spain	Martínez-Vilalta et al. (2009)
35	40°36′ N, 15°48′ E	Potenza, Italy	Martínez-Vilalta et al. (2009)
36	41°20′ N, 1°1′ E	Prades, Spain	Martínez-Vilalta et al. (2009)
37	42°12′ N, 1°49′ E	Vallcebre, Spain	Martínez-Vilalta et al. (2009)
38	45°42′ N, 2°59′ E	Fonfreyde, France	Martínez-Vilalta et al. (2009)
39	46°18′ N, 7°37′ E	Pfyn, Switzerland	Martínez-Vilalta et al. (2009)

40	46°19′ N, 7°35′ E	Salgesch, Switzerland	Martínez-Vilalta et al. (2009)
41	46°19′ N, 7°43′ E	Jeizinen, Switzerland	Martínez-Vilalta et al. (2009)
42	52°10′ N, 5°44′ E	Kootwijk, Netherlands	Martínez-Vilalta et al. (2009)
43	52°18′ N, 5°43′ E	Leuvenumse, Netherlands	Martínez-Vilalta et al. (2009)
44	55°52′ N, 3°27′ W	Selm Muir, Scotland	Martínez-Vilalta et al. (2009)
45	61°51′ N, 24°18′ E	Hyytiala, Finland	Martínez-Vilalta et al. (2009)
46	41°13′ N, 0°55′ E	Tittlar valley, Prades Mountains, Spain	Martínez-Vilalta and Piñol (2002)
47	41°13′ N, 0°55′ E	Castellfollit valley, Prades Mountains, Spain	Martínez-Vilalta and Piñol (2002)
48	45°49′ N, 121°57′ W	Windriver Experimental Forest, Washington, USA	Domec et al. (2004)
49	46°55′ N, 114°5′ W	Buttler Creek, Montana, USA	Piñol and Sala (2000)
50	47°00′ N, 114°28′ W	Petty Creek, Alberton, Montana, USA (slope)	Stout and Sala (2003)
51	47°00′ N, 114°28′ W	Petty Creek, Alberton, Montana, USA (river)	Stout and Sala (2003)

Table A4 Theoretically calculated sapwood-area specific hydraulic conductivity (K_p, in kg m^{-1} MPa^{-1} s^{-1}), hydraulically weighted (d_h, in µm) and simple (d, in µm) mean tracheid diameters as well as tracheid density (TD, N mm^{-2}) in total xylem cross-sections (T), earlywood (E) and latewood (L) in stems of *L. sibirica* from the Mongolian Altai, Khangai and Ore Mountains*

		Altai		**Khangai**		**Ore Mts.**	
K_p	T	14.5 ± 1.1	a	19.12 ± 1.38	a	26.54 ± 5.99	ab
	E	17.2 ± 1.2	a	23.71 ± 1.68	a	34.74 ± 6.94	a
	L	1.01 ± 0.40	b	1.14 ± 0.27	b	4.72 ± 2.14	b
d_h	T	37.0 ± 0.9	a	41.0 ± 0.7	a	46.2 ± 3.1	a
	E	37.1 ± 0.9	a	41.3 ± 0.7	a	47.2 ± 3.2	a
	L	13.9 ± 3.2	b	18.2 ± 1.5	b	26.0 ± 3.8	b
d	T	28.1 ± 0.6	a	29.5 ± 0.4	a	31.3 ± 3.1	ab
	E	29.4 ± 0.6	a	32.7 ± 0.6	b	37.2 ± 3.1	a
	L	10.1 ± 2.1	b	13.3 ± 1.0	c	19.6 ± 2.4	b
TD	T	562 ± 20	a	532 ± 28	a	533 ± 63	a
	E	610 ± 26	a	544 ± 19	a	473 ± 50	a
	L	312 ± 75	b	475 ± 75	a	648 ± 100	a

*Lowercase letter following means (± SE) indicate differences between T, E, and L within the same parameter and study area ($P \leq 0.05$, LSD test). Number of sample trees: Altai, N=7; Khangai, N=5; Ore Mts., N=3

Table A5 Linear correlation of hydraulic parameters (K_s, K_p, d_h, d, TD) in stem earlywood and latewood 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). Correlation significant ($P \leq 0.05$): ● positive, ■ negative correlation; marginally significant ($P \leq 0.10$): ○ positive, □ negative correlation. K_s is only available for the total xylem cross-section of roots and branches

	Earlywood				**Latewood**			
	MGSP	MAP	MGST	MAT	MGSP	MAP	MGST	MAT
K_p	●	○	○	○	○	●		●
d_h	●	○	●		●	○	○	○
d		○	●		○	○	○	○
TD	□		■		○		●	

Table A6 Summary of empirical sapwood area-specific hydraulic conductivity (K_s) and hydraulically weighted tracheid diameter (d_h) in roots and branches of coniferous species from boreal, temperate and Mediterranean climate in the northern hemisphere together with elevation, mean annual precipitation (MAP) and mean annual temperature (MAT) of the sites (for more detailed information on study sites and individual measurements in different substudies see Tables A2 and A3)

Species	**Elevation (m a.s.l.)**	**MAP (mm yr^{-1})**	**MAT (°C)**	**K_s (kg m^{-1} s^{-1} MPa^{-1})**	**d_h (µm)**	**Number of data points**
Branches:						
Abies lasiocarpa	2400	340	10.0	3.22	n.a.	1
Larix decidua	725-1850	778-1071	1.0-10.3	0.45-1.42 (2.63)	n.a.	4
Larix occidentalis	1750	340	10.0	2.8	n.a.	1
Larix sibirica*	465-2340	120-841	–3.4-7.7	0.39-0.75	12.9-15.7	3
Picea abies	725-1900	778-1071	1.0-10.3	0.27-1.11 (3.78)	11.4	5
Pinus albicaulis	2400	340	10.0	2.08	n.a.	1
Pinus contorta	2000	340	10.0	2.63	n.a.	1
Pinus halepensis	2	312	17.5	1.52	11.3	1
Pinus nigra	160	537	10.0	4.07	n.a.	1
Pinus pinaster	160	537	10.0	3.52	n.a.	1
Pinus pinea	2	312	17.5	3.51	11.7	1
Pinus ponderosa	975-2100	235-510	10.0-18.7	0.54-0.64 (4.99)	n.a.	5
Pinus sylvestris	20-2025	537-940	2.8-10.9	0.32-0.60 (4.97)	11.4-13.1	14
Pseudotsuga menziesii	975-1500	340	10	1.99-3.85	n.a.	3
Roots:						
Larix sibirica*	465-2340	120-841	–3.4-7.7	2.76-5.76	34.5-42.2	3
Pinus halepensis	2	312	17.5	8.93	40.6	1
Pinus pinea	2	312	17.5	17.0	45.0	1
Pinus ponderosa	915-1690	525-635	7.7	4.20-9.59	n.a.	3
Pseudotsuga menziesii	370	2500	8.7	4.0	n.a.	1

* This study

Acknowledgments

First and foremost, I would like to thank my supervisor Prof. Markus Hauck for providing me an opportunity to join this research project and making this “PhD journey” possible for me, through which I have not only learned many research skills, broadened my horizon, but also enjoyed lots of “exotic” experiences outside of my home country which really opened my eyes.

Secondly, I would like to thank Dr. Dietrich Hertel, Dr. Bernhard Schuldt and Dr. Dulamsuren Choimaa for providing me enormous help and instructions during my work. The first-day round tour guided by Dietrich is still vivid in my mind. Bernhard’s pursuit of perfection spirit and super efficient work style has always been inspiring me. Duya’s very own laugh will be lingering in my ears for a long time.

Thanks to Prof. Christoph Leuschner for helping with revising my manuscripts. I appreciate his patience and very efficient work.

I thank Mechthild Stange for offering technical assistant on “root works” and offering me warm tea when I caught cold. Thanks to Dr. Heinz Coners for helping me solve all those complicated computer-related problems. Thanks to Astrid Rodriguez for her support with relevant paperwork. And thanks to PD Dr. Dirk Gansert for coordinating my PhD program.

I am grateful to Batdemberel Badamsambuu, Saskia and Ulrich Werder for their assists in lab and field works.

Thanks to all the colleagues from Plant Ecology department. Those who once shared office with me: Yaoqin, Fengjun, Sandra, and Martyna and who offered kind helps to me: Annca, Andreas, Bettina, Claudia, Carola, Daisy, Elmira, Fri, Fabi, Flo, Hilmar, Jorma, Nicole, Peter, Petra, Robin, Torben, Yasmin, … and all the others that had happy time together with me.

Special thanks to Khishigjargal Mookhor and her family for helping me settled down during my first days in Germany, which made my frustrating transaction period full of good memories!

I also thank those friends I made in Göttingen, with whom I have spent “volleyball time”, “travel time”, “dinner time”, “party time”, and so on…

Lots of thanks to Xu Chi and Dr. Laura Sutcliffe for proof reading my thesis! It is a very timely offer!

Finally, many thanks to my family for always supporting me and backing me up! Especially to my husband who has handled me at my worst and always been there for me! And my yet-to come daughter who has been very cooperative and thoughtful during my pregnancy.

I am grateful to China Scholarship Council (CSC) for offering me scholarship to fund my PhD study!

The study was supported by a grant from the Volkswagen Foundation to 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’. Thanks to the Altai Tavan Bogd National Park (Ulgii) for permissions to carry out the field work and Hildegard Neeser for allowing us to sample her trees at the Giegengrün plantation in the Ore Mountains and Claus Döring (University of Göttingen) for modeling the climate date for the Giegengrün site.

Curriculum vitae

Name:	Tselmeg Chenlemuge
Date of birth:	22/11/1984
Nationality:	China
Education:	
10/2010 onward	PhD at the Albrecht-von-Haller Institute for Plant Sciences at the University of Göttingen (Department of Ecology and Ecosystem Research).
09/2007-06/2010	M.S. Ecology, School of Life Sciences, Nanjing University, China.
09/2003-06/2007	B.S. Biology, School of Life Sciences, Nanjing University, China.
09/2000-06/2003	High school, Affiliated Middle School of Inner Mongolia Normal University, Inner Mongolia, China.
09/1996-06/2000	Middle school, National Middle School of Daerhanmaomingan United County, Inner Mongolia, China.
Conferences:	
Oral presentation	On the relation between productivity and hydraulic properties in Mongolian *Larix sibirica* forest-steppe ecotones. 43rd Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (gfö 2013), Potsdam, Germany. Extremely low fine root biomass in *Larix sibirica* forests at the southern drought limit of the boreal forest. 43rd Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (gfö 2013), Potsdam, Germany. Fine root mass and morphological traits in *Larix sibirica* forests at the forest-steppe treeline in Mongolia. Symposium "Biodiversity Research in Mongolia", Halle, Germany.
Poster	Extremely low fine root biomass in *Larix sibirica* forests at the southern drought limit of the boreal forest. 11th INTECOL Congress, Ecology: Into the next 100 years (INTECOL 2013), London, United Kingdom.
Language skills:	English (TOEFL IBT 100), Chinese, Mongolian

Eidesstattliche Erklärung

Hiermit versichere ich, die vorliegende Arbeit mit dem Titel “ Drought adaptation of the fine root system and hydraulic architecture of *Larix sibirica* at its southern distribution limit ”selbstständig und unter ausschließlicher Verwendung der angegebenen Literatur, Verweise und Hilfsmittel erstellt zu haben. Verwendete Quellen wurden als solche gekennzeichnet.