CrossMark

ORIGINAL ARTICLE

Age structure and trends in annual stem increment of *Larix sibirica* in two neighboring Mongolian forest–steppe regions differing in land use history

Elmira Khansaritoreh[1] · Mahammad Eldarov[1,2] · Kherlenchimeg Ganbaatar[3] ·
Davaadorj Saindovdon[4] · Christoph Leuschner[1] · Markus Hauck[1] ·
Choimaa Dulamsuren[1]

Abstract

Key message **Selective logging affects climate sensitivity of *Larix sibirica* in the Mongolian forest–steppe mediated by changes in age and stand structure.**

Abstract Climate warming increasingly limits the productivity of boreal forests via increased drought stress, especially at the southern fringe of the biome. The southernmost boreal forests are exposed to more intensive human disturbance than most forests at more northern latitudes. We asked the question of how forest use through logging and moderate forest grazing interferes with the climate response of the annual radial stem increment. We conducted a case study in *Larix sibirica* stands of the Mongolian forest–steppe involving two neighboring forest regions (20 km distance) differing in logging and grazing

Communicated by S. Leavitt.

✉ Markus Hauck
  mhauck@gwdg.de

✉ Choimaa Dulamsuren
  dchoima@gwdg.de

1   Plant Ecology, Albrecht von Haller Institute for Plant
    Sciences, Georg August University of Göttingen, Untere
    Karspüle 2, 37073 Göttingen, Germany

2   Genetic Resources Institute, Azerbaijan National Academy of
    Sciences, Ave 155. Azadlıg, 1106 Baku, Azerbaijan

3   Agroecology, Mongolian University of Life Sciences, Khan-
    Uul, Zaisan, Ulan Bator 17024, Mongolia

4   Geography and Geoecology, Mongolian Academy of
    Sciences, Baruun Selbe 15, Chingeltei, Ulan Bator 15170,
    Mongolia

intensity. One site was subjected to heavy logging until 25 years ago and low intensity of livestock grazing; another site was exposed to moderate selective logging and higher, but still moderate livestock numbers. While the differences in grazing had no detectable effect, former heavy logging led to younger and more even-aged forest stands. Forests at both sites showed recent increases in missing-ring frequency, which probably indicated increased drought vulnerability. Climate-response analysis indicated that heavy logging 25 years ago was associated with high sensitivity of stemwood formation to high summer (especially June) temperatures. These findings suggest that: (1) recent logging under the conditions of climate warming has increased the sensitivity of tree growth to temperature in these southern boreal forests; (2) high replication at the stand level is needed to avoid bias in dendrochronological analyses in regions exposed to spatially heterogeneous logging intensities.

Introduction

The boreal forest region differs from other forest biomes of the Northern Hemisphere by its cold climate and the limited amount of conversion of forest into agricultural land. During the short growing season, the productivity of boreal forests is usually limited directly by low summer temperatures, or indirectly via nutrient shortage due to slow organic matter decomposition (Jarvis and Linder 2000). Only recently, parts of the boreal forest turned from temperate and nitrogen limitation to water limitation as a

result of climate warming-induced drought (Buermann et al. 2014). The forest–steppes at the continental southern margins of the boreal forest in Inner Asia and at the northern fringe of the Great Plains in North America differ from most of the central boreal forest belt insofar that drought has always been a key factor limiting tree growth (Gunin et al. 1999; Huang et al. 2010). Moreover, the forest–steppe located at the northern fringe of the temperate grassland belt has a long tradition of human land use, mainly by mobile and sedentary pastoralists in Inner Asia (Outram et al. 2009) and a shorter history of livestock management in North America (Johnston 1970). Traditional forest use in the forest–steppe ecotone is usually not stand-replacing, as is modern forestry in most of the central boreal forest belt (Östlund et al. 1997; Hansen et al. 2013). Rather, timber harvest is dominated by haphazard selective logging, a practice that is continued in large parts of Inner Asia (Lkhagvadorj et al. 2013a; Dulamsuren et al. 2014). Fire is an additional important factor that affects forest stand dynamics and increases in significance due to rising temperatures and increased human activities (Park et al. 2009; Hessl et al. 2012).

Woodlands at the southern edge of the boreal forest belt have recently attracted increased attention in both Eurasia (Dulamsuren et al. 2013; Liu et al. 2013) and North America (Michaelian et al. 2011; Peng et al. 2011). This is because global warming-related drought has progressively reduced forest productivity and tree regeneration and is the cause of elevated tree mortality in the majority of studied places. Nonetheless, even within the southernmost fringe of the boreal forest, contrasting examples have also been found where forests perform increasingly better due to climate warming, since temperature and not water is limiting at high elevation (D'Arrigo et al. 2000; Chen et al. 2012) or due to local increases in precipitation (Dulamsuren et al. 2010; Peng et al. 2011). The climatically induced spatial variation in trends of forest productivity, regeneration and tree mortality is additionally complicated by changes in the stand structure due to logging and forest grazing. These types of land use affect the competition for light, water and nutrients between trees by reducing stand density (Dulamsuren et al. 2014) and influencing the heat transfer to the soil and thus trigger the melt of permafrost (Park et al. 2009). Furthermore, reduced competition by the ground vegetation as a result of high grazing pressure was found to facilitate seedling establishment. However, livestock grazing suppresses sapling growth and increases the saplings' mortality due to mechanical damage and feeding (Khishigjargal et al. 2013).

Tree-ring studies analyzing the climate response of annual stemwood formation seek to eliminate as much of the non-climatic variation from the tree-ring signal as possible to identify the climatic key effectors for the trees'

productivity and to use this information for climate reconstruction (Briffa et al. 1996; Briffa 1999). While this practice is mandatory for the study of variations in climate, it reduces the options for analyzing the effects of external disturbances, including land use. We were interested in the combined effect of climate, selective logging and forest grazing on the age structure and stem increment of forests in the forest–steppe ecotone and thus used a combined approach with filtered and unfiltered tree-ring data. Therefore, we carried out a case study in the Mongolian forest–steppe ecotone at the southern edge of the Eurosiberian boreal forest to investigate the variability of age structure, stem increment, and tree mortality at a small spatial scale of some 20 km in stands of the same tree species with known differences in land use history. At two locations, stands of *Larix sibirica* forest were studied with replicate plots differing in (1) the logging intensity until Mongolia's transition from planned to market economy in 1990, and (2) past and present density of livestock. The first site (site A) was exposed to higher logging intensity until 1990 as well as to lower past and present grazing pressure by livestock than the second site (site B; Table 1). At both sites, we distinguished plots at the lower forest border adjacent to steppe grassland from plots in the forest interior, since the forest edge is usually exposed to higher intensities of selective logging and livestock grazing (Khishigjargal et al. 2013; Lkhagvadorj et al. 2013a, b; Dulamsuren et al. 2014). With our study, we tested the hypotheses that (1) trees at the more heavily logged site A are less evenly distributed across age classes than trees at site B, (2) mean sensitivity of tree-ring series to climate is higher at the less severely logged and thus less disturbed site B, (3) stem increment at both sites is significantly limited by summer drought, and (4) trees at both sites exhibit increasing missing-ring frequency since the late twentieth century. A major objective of these investigations was to analyze how severely spatial heterogeneity in land use practices interferes with the climate response of forest productivity and forest health. As another outcome of our study, we expected information on how strongly low replication on the stand level might bias the conclusions drawn from dendrochronological climate-response studies in the forest–steppe ecotone.

Materials and methods

Study area

Our study was carried out at the southern fringe of the Eurosiberian boreal forest in the forest–steppe of northwestern Mongolia, ca. 630 km west of Ulan Bator and 550 km southwest of Lake Baikal. Mongolia's forest–

Table 1 General characteristics of study sites A and B in the Khangai Mountains, near Tosontsengel, Mongolia

	Site A	Site B
Logging intensity	High intensity until 1990 (selective logging and clear-cuts) Low-intensity selective logging after 1990	Low-intensity selective logging until and after 1990
Livestock grazing	Low	Moderate
Latitude	48°29–31′N	48°20–22′N
Longitude	97°52–54′E	97°41–47′E
Elevation (m a.s.l.)	1975–2109	1917–2027

steppe is strongly dominated by Siberian larch (*Larix sibirica* Ledeb.); the species covers 75–80% of Mongolia's boreal forest (Tsogtbaatar 2004; MNE 2012). The study was conducted in the northern Khangai Mountains, a large mountain range of central and western Mongolia, which represents a large proportion of Mongolia's forest–steppe landscape. The landscape is typically a vegetation mosaic of forests on north-facing slopes and grasslands on south-facing slopes and in dry valleys. The grasslands are home to pastoral nomad families that hold mixed flocks of livestock, including goats and sheep (most animals), cattle, yak, horses, and occasionally camels (Lkhagvadorj et al. 2013b). This livestock is not herded much and browses the forest, particularly forest edges, in addition to the grassland. Grazing intensity can considerably vary with the spatial distribution of nomad camps and water access, which thus differentially affects biodiversity (Hauck and Lkhagvadorj 2013; Hauck et al. 2014) and forest regeneration (Khishigjargal et al. 2013).

The climate in the Mongolian forest–steppe is highly continental and is imprinted by the stable Siberian High Pressure Cell in the cold winter and warm, short summers. The maximum annual precipitation of roughly 200–300 mm in most forest–steppe regions is mostly delivered in summer. The dominant bedrock type in the study region is siliceous rock, including granite and metamorphic rock (e.g., schist). The prevailing forest soils are Cambisols and Leptosols. The study area is located in the zone of discontinuous permafrost (Sharkhuu and Sharkhuu 2012).

Study sites and sample plot selection

The study sites were located in the Zavkhan province of Mongolia ca. 70–90 km southwest of the city of Tosontsengel (48°45′N, 98°16′E, 1700 m a.s.l.) at the border of the Tosontsengel and Ider administrative subunits of the Zavkhan province. Site A was located at 48°29–31′N, 97°52–54′E with plots distributed over an area of ca. 5 km², whereas plots at site B were located at 48°20–22′N, 97°41–47′E and were distributed over an area

of ca. 10 km² (Fig. S2; Table 1). The mean elevation of sample plots at site A (2026 m a.s.l., range 1975–2109 m a.s.l.) was 60 m higher than at site B (1966 m a.s.l., range 1917–2027 m a.s.l.). Climatically, the 60-m altitudinal distance implies a mean annual temperature 0.4 °C lower at site A if a temperature lapse rate of 6.5 °C km^{-1} is assumed. Site A was exposed to high logging intensity (selective logging and clear-cuts) due to a saw mill in Tosontsengel which operated until 1990 and was then abandoned as a result of the transformation of Mongolia's economy from planned to market economy. Afterward, site A was subjected to unplanned occasional selective logging by the local population, as was site B before and after 1990. Site A was traditionally exposed to lower livestock grazing pressure than site B, because site B is located within a settlement area of pastoral nomads. There are no systematic differences in the fire regime of the two sites; variation in fire history in the Mongolian forest–steppe is usually on a small spatial scale due to the widespread logging and grazing influence and the isolated character of forest fragments (Hessl et al. 2012). Potential local variation in the fire history is overcome by high replication in our study.

A total of 17 plots per site or 34 plots for the entire study were investigated. Eleven replicate plots were selected in the forest interior at each site. Six of the 11 interior plots were randomly selected for establishing six additional neighboring plots occupying the forest edge position (Fig. S1 in the Electronic Supplementary Material). The plot size was 20 m × 20 m. All data on the age and stand structure provided in the paper refer only to the forest stands where both forest interior and forest edge plots were selected to allow direct comparison between habitats. On these 24 plots (6 plots in the forest interior and 6 plots in the forest edge per site), a total of 729 *L. sibirica* trees was sampled. Plots in the forest interior were located 50–100 m behind the forest line; plots at the forest edge had the outer limit at the mostly sharp lower (not temperature driven) forest line at the border to steppe grassland. Each plot (or interior–edge plot pair, respectively) was located in a separate forest. Forests were selected using the rather

regular distribution of forest and grassland in the Mongolian forest–steppe with the forests occurring as isolated patches on north-facing slopes. This way, neighboring forests were selected within each site (Fig. S1). Plot location within a forest was selected randomly. As an exception from random selection, moist depressions were avoided, because they differ in tree growth characteristics from well-drained slopes.

Climate data

Air temperature and precipitation data were available from two manual weather stations run by Mongolia's meteorological agency. The weather station Ider (48°13′N, 97°22′E) is located ca. 30 km (site B) to 50 km (site A) southwest of our sample plots, whereas the weather station Tosontsengel is located ca. 80 km northeast of our plots. The Ider station is thus closer to our plots, but the weather station in Tosontsengel had a better data quality. Weather data in Tosontsengel cover the period from 1964 (precipitation: 1968) to 2012, whereas data from Ider were available from 1973 to 2010. In Tosontsengel, weather recording was disrupted in 1971 causing 2.9% of missing values in the data set. The quality of the data set in Ider was much worse with 11.8 and 12.3% of missing values in the temperature and precipitation data, respectively. While missing temperature data for Ider could be reconstructed with the data from Tosontsengel using linear regression for monthly mean values ($r = 0.67$–0.92, $P < 0.001$), this was not possible for precipitation. We therefore used the data from Tosontsengel for the analysis of the climate response of tree-ring width. Mean annual, July, and January temperatures in Tosontsengel were −5.8, 14.8, and −31.2 °C, respectively, and mean annual precipitation was 224 mm. The less reliable data from Ider suggested somewhat lower precipitation and higher temperatures, especially in winter.

Field and laboratory work for tree-ring analysis

Fieldwork was carried out in August 2012. On the 34 plots, which were all monospecific stands of *L. sibirica*, all trees (ca. 1000 individuals) with a stem diameter (at 1.3 m height) of ≥3 cm were included in wood-core sampling for tree-ring analysis. In addition to these samples from the 20 m × 20 m plots, living old trees located outside the plots were sampled as reference samples to establish long tree-ring chronologies. A total of 140 such trees were additionally sampled; data from these trees were not included in the analysis of age and stand structure. All cores were collected with a 5-mm increment borer (inner diameter). The cores were taken at 1.3 m above the ground in a direction parallel to the contour lines of the mountain slopes to avoid compression wood. Additional data, such as trunk circumference, density of branches, dominance (dominant, subdominant and suppressed), and fire traces, were recorded in the field.

The wood cores were mounted on wooden strips and the top of the core was shaved off with a microtome blade to make the growth rings visible; the contrast between annual tree rings was enhanced by dusting the surface with chalk dust. The tree-ring width was measured with a precision of 10 μm on a movable object table (Lintab 5, Rinntech, Heidelberg, Germany), the movements of which are electronically transmitted to a computer system equipped with Time Series Analysis and Presentation (TSAP)-Win software (Rinntech).

Evaluation of tree-ring data

The TSAP-Win software was also used for the evaluation of the tree-ring data. Trees were categorized into four age classes including 'very old trees' (>160 years), 'old trees' (101–160 years), 'middle-aged trees' (61–100 years), and 'young trees' (≤60 years). Age specifications represent the age of the cambium at 1.3 m above the ground. Tree age is higher than cambial age at 1.3 m, since the tree needs several years to reach that height. Based on the experience from other studies, tree age can be roughly estimated by adding 10 years to the cambial age (Körner et al. 2005; Sankey et al. 2006). The age of the very old trees (>160 cambial years) is partly underestimated by our method because in 4.6% of these trees the pith was rotten in the center and the relevant wood cores were thus incomplete. Nevertheless, we kept these very old trees in our analysis, because this inaccuracy did not affect any of our conclusions.

The tree-ring series were controlled for missing and unrecognized false rings during cross-dating. Trees with similar growth trends were pooled separately into groups for calculating the mean values of annual increment. Merging of tree-ring series to a chronology was based on the coefficient of agreement ['Gleichläufigkeit' (GL), Eckstein and Bauch 1969] and (standard) t values. The GL and t values measure the similarity between tree-ring series in the high- and low-frequency domain, respectively. Calculation of mean values was considered to be permitted for series with GL > 65% ($P ≤ 0.05$) and $t > 3$; with this approach, ca. 95% of the individual tree-ring series could be incorporated in mean curves for annual stem increment. Trend lines were calculated using 5-year moving averages.

Tree-ring series were representative of the studied stands as shown by the calculation of the expressed population signal (EPS) using sums of squares of within-core variation and error sums of squares calculated in a two-way analysis of variance (ANOVA) (Wigley et al. 1984). The EPS calculated separately for the individual plots exceeded

the 0.85 threshold in all cases; in most forest edge plots, however, this threshold was not reached before the late twentieth century (Table S1).

Original tree-ring series were standardized to extract the climate information and to remove the age-related trend in the data, which is the result of declining productivity at high tree age and the mere geometrical fact that, with increasing stem diameter, the wood is distributed over a larger circumference and thus leads to thinner tree rings (Fritts 1976; Cook 1985; Bräuning 1999). Standardization was achieved by calculating the annual tree-ring index (z_i) of year i, which was derived from the equation $z_i = w_i/m_i$, where w_i is observed tree-ring width and m_i is the moving 5-year average of year i (Dulamsuren et al. 2010). The large sample size in our study reduced the effect of stand-internal disturbances (e.g., the natural death of a neighboring tree) and stand-external disturbances (e.g., insect infestations, fire) or the influence of small-scale variation of site parameters on the tree-ring index.

The relationships between the annual tree-ring index and climate parameters (i.e., monthly mean temperature and monthly precipitation in the year of and prior to tree-ring formation) were analyzed separately for the different age classes using multiple regression analysis and including the complete period covered by the weather data record at the weather station in Tosontsengel. Multiple regression analysis was computed with SAS 9.4 software (SAS Institute Inc., Cary, North Carolina, USA). Standardized β coefficients were used to quantify the effect of temperature and precipitation in individual months in the climate-response analysis. Climate-response analysis was restricted to the tree-ring series of such forest stands where pairs of plots from the forest interior and forest edge were available ($N = 6$) to enable direct comparison between these habitats.

To detect long-term (low-frequency) trends in annual radial stem increment as caused, for instance, by long-term changes in climate, regional growth curves (RGC) were established. In an RGC, the original (non-standardized) annual stem increment is related to tree age instead of the calendar year (Sarris et al. 2007; Dulamsuren et al. 2010). This procedure removes the inter-annual (high-frequency) variation in annual stem increment, but keeps the low-frequency variability, including the age-related trend. Changes in long-term site conditions that control the annual wood production can be inferred from the RGCs from different tree age classes by comparing the increment at the same cambial age. Comparing data from the same cambial age allows detecting long-term trends not related to tree age. The RGCs were only calculated for the two age classes that were occupied by most of the sample trees, i.e., old and middle-aged trees. Only subdominant trees were integrated in the RGCs, as dominant trees usually have

better access to water than other trees. Suppressed trees were excluded, because their productivity is strongly affected by competition for light with other trees.

Mean sensitivity and autocorrelation coefficients (Fritts 1976) were calculated with TSAP-Win from raw increment data over the whole lifespan of each sample tree. Mean sensitivity is a measure for the inter-annual variation of tree-ring width and thus the putative influence of climate, which is usually the most strongly varying influential parameter between consecutive years; mean sensitivity is calculated as the difference in the tree-ring width of consecutive years divided by the mean tree-ring width of the 2 years. The first-order autocorrelation coefficient quantifies the dependence of tree-ring width on the stem increment in the previous year; first-order autocorrelation is the strength of the linear correlation of the tree-ring width in a given year with the tree-ring width in the previous year calculated for all consecutive years of a tree-ring series. High mean sensitivity in combination with low first-order autocorrelation coefficients is an indication of a large influence of short-term climatic variability on stemwood formation.

Statistics

Arithmetic means ± standard errors are presented throughout the paper. Data were tested for normality with the Shapiro–Wilk test. Pairwise differences (of non-normally distributed data) were tested for significance with Mann–Whitney's U test. Multiple comparisons were done using Duncan's multiple range test. Two-way analysis of variance (ANOVA) was calculated to quantify the effect of site location and habitat and the interaction between these parameters on age and stand structure. Degrees of freedom (df) for multiple tests are specified for model and error ($df_{\text{model,error}}$). All statistical tests were computed with SAS 9.4 software.

Results

Temperature and precipitation trends

The mean annual temperature at the Tosontsengel weather station has increased by 2.4 or 0.50 °C decade^{-1} from 1964 to 2012 (Fig. 1a). In contrast to the mean annual temperature, the mean annual precipitation has remained unchanged since the 1960s (Fig. 1b). Significant increases in temperature occurred in all months except for December and January (Fig. 1c). The increases in monthly mean temperatures from February to November had slopes of similar magnitude. However, the temperature trends in the recent decades were of higher significance from July to

Fig. 1 Climate trends in Tosontsengel (48°45′N, 98°16′E, 1700 m a.s.l.), northwestern Mongolia: **a** increase in mean annual temperature ($y = 0.05x − 104.55$, $r = 0.54$, $P \leq 0.001$), **b** mean annual precipitation (no linear trend) and **c**, **d** trends for monthly, **c** mean temperature and **d** precipitation
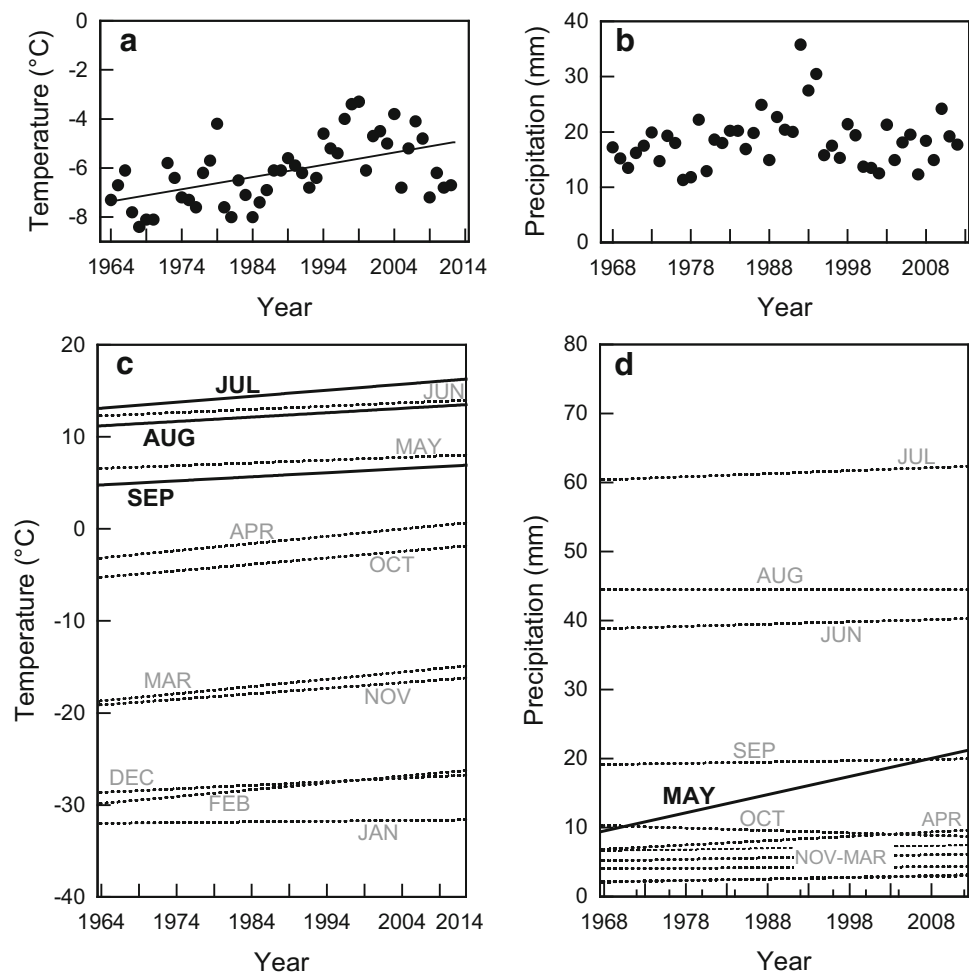
September ($P \leq 0.001$) than in the rest of the year and most pronounced in July ($r = 0.60$), which is the warmest month of the year. As with mean annual precipitation, most months did not show any significant trend for change in the amount of precipitation over time (Fig. 1d). Only in May, at the start of the growing season, precipitation showed a significant increase ($r = 0.32$, $P = 0.01$). This increase was partly compensated by a weak insignificant trend for decreasing precipitation in autumn, thus explaining the constant mean annual precipitation (Fig. 1b).

The qualitatively less reliable data from the weather station Ider showed an increase in temperature by 2.1 or 0.57 °C decade^{-1} from 1973 to 2010 (data not shown). For monthly mean temperatures, significant increases ($P \leq 0.05$) occurred from March to May and July to November. As in Tosontsengel, the most significant temperature trend over time was found for July ($r = 0.70$, $P < 0.001$). The mean annual precipitation remained constant from 1973 to 2010 (not shown). In the individual months, there were significant increases in precipitation in May ($r = 0.48$, $P = 0.002$) and from December to February ($r = 0.40–0.56$; $P \leq 0.005$). These increases

were associated with weak insignificant trends for declining precipitation from June to September and in April.

Age and stand structure of the *Larix sibirica* forests

Both the location (site A vs. B) and the habitat (forest interior vs. edge) controlled the age structure, but not the stand structure (in terms of basal area and stand density) of the investigated larch forests (Table 2). Two-way ANOVA revealed a significant effect of the location on the percentage of the trees on a plot occurring in the individual age classes. The habitat had a significant effect on the relative abundance of very old and middle-aged trees. Middle-aged trees represented the largest group of all sample trees (58%, 421 out of 729 trees), followed by old trees (28%), very old (8%) and young trees (6%). In the forest interior, very old trees were overrepresented and middle-aged trees underrepresented at site B compared to site A (Fig. 2). Furthermore, old trees showed an insignificant trend for higher relative abundance at site B. At the forest edges, the relative abundance of middle-aged trees was higher at site A than site B, whereas there was an

Table 2 Results of two-way ANOVA ($df_{model,error} = 3, 20$) analyzing the effect of location (site A vs. B) and habitat (forest interior vs. edge) on the percent of tree individuals in age classes as well as on mean and maximum tree ages, basal area and stand density

	Total			Location		Habitat		Loc. × Hab.	
	R^2	F	P	F	P	F	P	F	P
Cambial age									
>160 years	0.55	8.2	<0.001	4.2	0.05	14.8	0.001	5.5	0.03
101 − 160 years	0.28	2.6	0.08	5.2	0.03	2.5	0.13	0.0	1.00
61 − 100 years	0.60	10.0	<0.001	19.9	<0.001	13.4	0.002	1.5	0.23
≤60 year	0.20	1.7	0.20	5.0	0.04	0.0	0.89	0.0	0.89
Mean age	0.47	6.0	0.005	2.9	0.10	13.4	0.002	1.5	0.23
Max. age	0.32	3.1	0.05	2.0	0.18	7.3	0.01	0.1	0.75
Basal area	0.12	0.9	0.46	2.4	0.14	0.4	0.54	0.0	1.00
Stand density	0.03	0.2	0.88	0.3	0.61	0.3	0.58	0.1	0.77
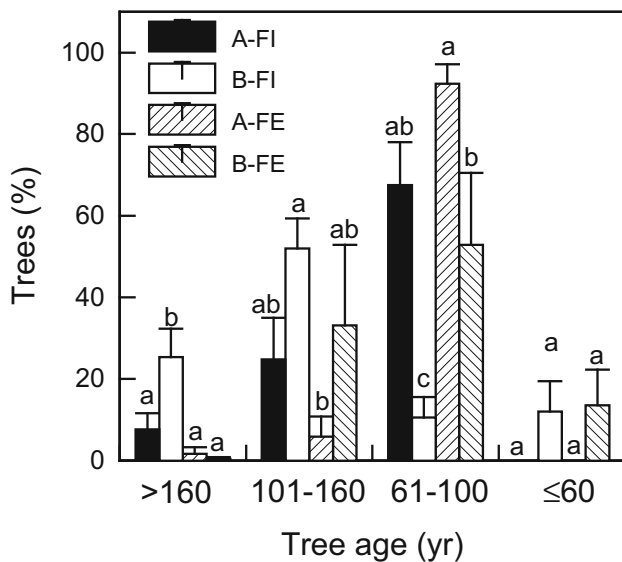
Fig. 2 Distribution of sample trees in age classes (cambial age at 1.3 m) in the forest interior (FI) and at the forest edge (FE) of sites A and B. Within the same age class, bars (±SE) sharing a common *letter* represent means that do not differ significantly ($P ≤ 0.05$, Duncan's multiple range test, $df_{model,error} = 3, 20$)

insignificant trend in the opposite direction for old trees. Very old trees were very rare at forest edges of either location. Young trees were completely absent in site A, but contributed 10% (forest interior) and 17% (forest edge) to the total tree population at site B. This difference between sites was detected as being significant in the two-way ANOVA (Table 2), but not in the subsequent Duncan's multiple range test (Fig. 2).

In terms of absolute numbers, most larch trees forming the interior forest stands at site B have established throughout the complete nineteenth and twentieth centuries (Fig. 3b). Most trees growing at the more heavily logged site A were established in the early twentieth century (Fig. 3a); tree establishment also occurred throughout the nineteenth century, but the number of tree individuals left from that time in today's forest stands at site A was small.

At the forest edges, most trees were established during the first half of the twentieth century at both sites A and B (Fig. 3c, d). At site B, some trees established earlier in the second half of the nineteenth century, whereas trees that germinated during the nineteenth century were virtually absent from site A. Trees that established before the nineteenth century are not included in Fig. 3, but occurred at both sites (a total of 8 trees in A and 2 trees in B). The oldest trees at sites A and B had a cambial age of at least 286 and 407 years, respectively.

Plot-wise mean and maximum ages were more strongly influenced by the habitat than by the location (Tables 1, 2). Trees tended to be younger at the edges than in the interior of the forests, though this difference was only significant for mean age at site B in Duncan's multiple range test. There was also a tendency for greater tree age at site B than A, but this trend was only significant for the mean age of trees growing in the forest interior.

Stand basal area and stand density did not differ between sites A and B or between forest interior and forest edge according to the results of both two-way ANOVA (Table 2) and Duncan's multiple range test (Table 3). However, there were tendencies toward higher values for both parameters at site A compared to site B and in the forest interior compared to the forest edge.

Climate response of the tree-ring index

Climate-response analysis refers to the last part of our tree-ring chronologies since 1964, in an interval of the chronologies with high sample numbers (Fig. 4). Mean sensitivity was higher and first-order autocorrelation was lower at the less intensely logged site B than at site A (Table 4). Trees from the forest interior that were more than 100 years old had a tendency to be less sensitive than other trees. Climate-response analysis revealed a trend toward weaker correlation of the tree-ring index with monthly mean temperatures and precipitation from middle-

Fig. 3 Chronology of the establishment of the present *L. sibirica* populations during the nineteenth and twentieth centuries in **a**, **b** the forest interior and **c**, **d** the forest edge of sites A (**a**, **c**) and B (**b**, **d**). The numbers of trees established before 1800 are not shown
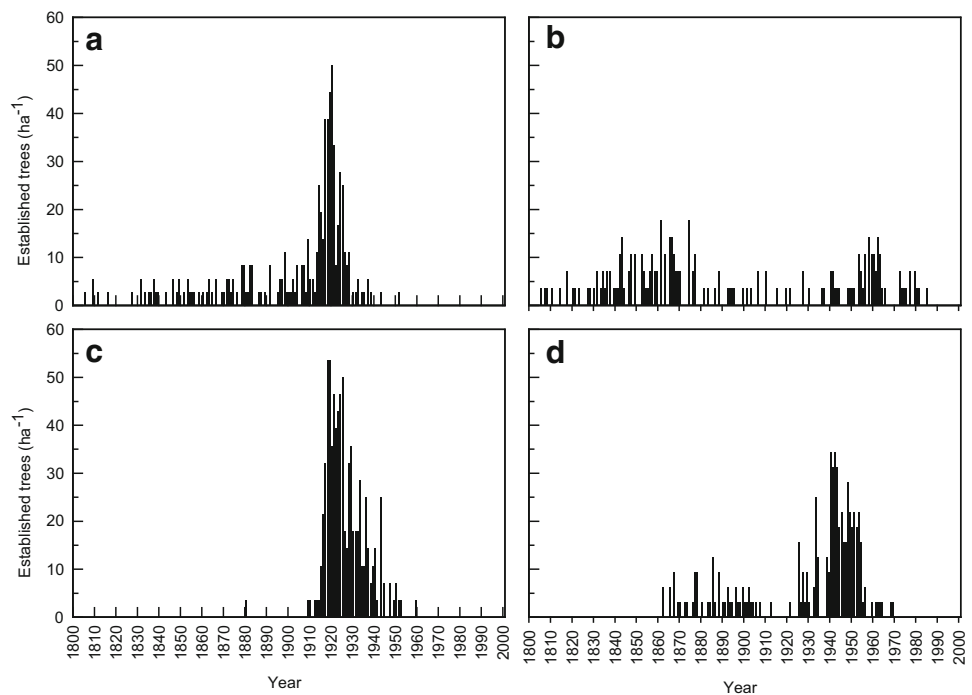
Table 3 Mean and maximum ages of *L. sibirica* trees as well as basal area and stand density in the forest interior and at the forest edge of sites A and B

	Site A		Site B	
	FI	FE	FI	FE
Mean age (years)	113 ± 4^a	91 ± 3^a	139 ± 14^b	95 ± 11^a
Max. age (years)	214 ± 18^{ab}	136 ± 27^a	272 ± 42^b	172 ± 39^{ab}
Basal area (m^{-2} ha)	62 ± 9^a	57 ± 10^a	47 ± 12^a	43 ± 7^a
Stand density (trees ha^{-1})	1196 ± 84^a	1146 ± 238^a	1154 ± 256^a	992 ± 107^a

Within a row, means ($\pm$SE) sharing a common letter do not differ significantly ($P \leq 0.05$, Duncan's multiple range test, $df_{model,error} = 3, 20$)
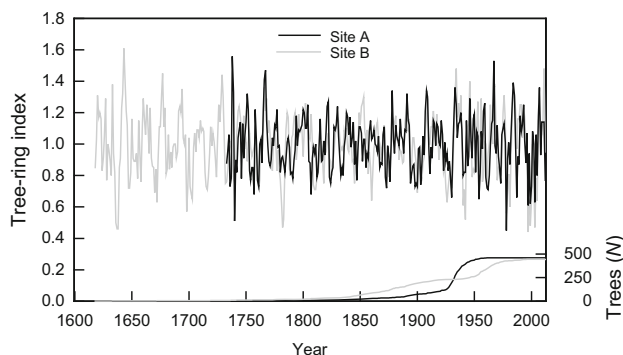
Fig. 4 Tree-ring index for *L. sibirica* from the forest interior of sites A and B

aged trees (Table 5) to old trees to very old trees at site A (Table S2), but not at site B (Table S3).

The climate-response analysis yielded similar, but weaker correlations for temperature at site B than at site A

(Tables 4, S1, S2). The tree-ring index decreased with increasing June and April temperatures of the current growing season and with increasing December and January temperatures at both sites. However, correlations in June were weaker and fewer at site B than at site A and never exceeded the level of marginal significance ($P \leq 0.10$). Positive correlation with May temperature was widespread at site A, but lacking at site B. Sporadic positive correlation of the tree-ring index was found with August temperature of the current year at both sites. On a few plots, stem increment decreased with June and July temperature of the previous summer.

Correlations between growing season precipitation and the tree-ring index tended to be stronger and more frequent at site B than A (Tables 4, S1, S2). Both sites shared sporadic positive correlations of the tree-ring index with July and August precipitation of the previous summer. At site B, positive correlations with June
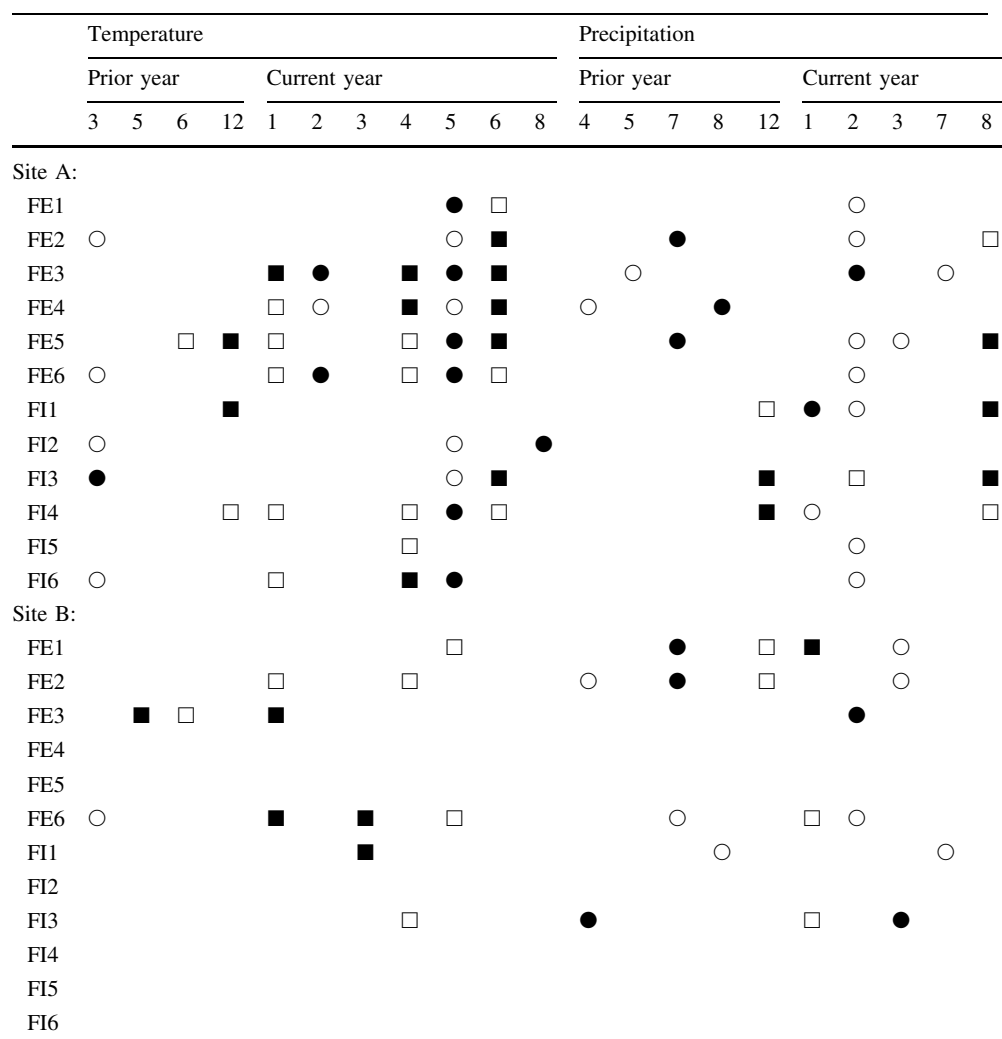
Table 4 Mean sensitivity and first-order autocorrelation coefficients of *L. sibirica* trees of different age classes from the forest interiors (FI) and the forest edges (FE) of sites A and B

	Mean sensitivity			Autocorrelation		
	Site A	Site B	P^a	Site A	Site B	P
All trees	0.34 ± 0.00	0.39 ± 0.00	***	0.77 ± 0.01	0.73 ± 0.01	***
>160 years, FI	0.26 ± 0.01	0.38 ± 0.01	***	0.77 ± 0.02	0.73 ± 0.01	*
>160 years, FE	–	0.35 ± 0.00		–	0.72 ± 0.02	
101–160 years, FI	0.27 ± 0.01	0.39 ± 0.01	***	0.81 ± 0.01	0.75 ± 0.01	***
101–160 years, FE	0.28 ± 0.01	0.37 ± 0.01	***	0.83 ± 0.02	0.76 ± 0.01	**
61–100 years, FI	0.36 ± 0.01	0.40 ± 0.01	*	0.78 ± 0.01	0.73 ± 0.02	**
61–100 years, FE	0.35 ± 0.01	0.40 ± 0.01	***	0.75 ± 0.01	0.71 ± 0.01	**
≤60 years, FI	–	0.43 ± 0.02		–	0.62 ± 0.03	
≤60 years, FE	–	0.44 ± 0.01		–	0.76 ± 0.01	

[a] Level of significance: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, (*U* test)

Table 5 Response of the tree-ring index of *L. sibirica* trees of middle-aged trees (60–99 years) from the forest interior and forest edge at sites A and B to monthly temperature and precipitation of the year of and the year prior to tree-ring formation

	Temperature											Precipitation									
	Prior year				Current year							Prior year					Current year				
	3	5	6	12	1	2	3	4	5	6	8	4	5	7	8	12	1	2	3	7	8
Site A:																					
FE1									●	□								○			
FE2	○								○	■			●					○			□
FE3					■	●		■	●	■			○					●	○		
FE4					□	○		■	○	■		○			●						
FE5		□	■		□			□	●	■			●					○	○		■
FE6	○				□	●		□	●	□								○			
FI1				■												□	●	○			■
FI2	○								○	●											
FI3	●								○	■					■		□				■
FI4				□	□			□	●	□					■	○					□
FI5								□										○			
FI6	○						□	■	●									○			
Site B:																					
FE1								□					●		□	■			○		
FE2					□		□					○	●		□				○		
FE3		■	□		■													●			
FE4																					
FE5																					
FE6	○				■		■	□					○				□	○			
FI1							■							○						○	
FI2																					
FI3								□		●							□		●		
FI4																					
FI5																					
FI6																					

Correlation significant ($P \leq 0.05$): *filled circle* positive, *filled square* negative correlation; marginally significant ($P \leq 0.10$): *open circle* positive, *open square* negative correlation. Months are identified with numbers 1–12. *FE1–6* forest edge plots no. 1–6; *FI1–6* forest interior plots no. 1–6

precipitation of the summer prior to tree-ring formation were also found. Further positive correlations were found with April and May precipitation of the previous year, which were, however, stronger at site B than at site A. Precipitation of the current summer was more often correlated with annual stem increment at site B than A. Positive correlation with current June precipitation occurred, albeit sporadically, throughout all age classes at site B, but was completely absent in the data from site A. In a few cases, the tree-ring index was positively correlated with July precipitation and negatively correlated with August precipitation at both sites. In terms of winter precipitation, tree-ring indices were inversely correlated with December precipitation at both sites, whereas positive correlation of the tree-ring index with January and February precipitation (mostly only marginally significant at $P \leq 0.10$) was limited to site A.

Tree-ring width as being dependent on time and tree age

Regional growth curves (RGC) revealed that middle-aged trees grew more slowly than old trees at the same cambial age at site A (Fig. S2a). The cumulative radial stem increment differed by ca. 20 mm at a cambial age of 75 years ($P < 0.001$, U test). At site B, middle-aged trees grew even faster than old trees, though the difference between age classes was less than 10 mm ($P = 0.004$, U test). At both sites, trees at the forest edge grew faster at the same cambial age than trees in the forest interior (Fig. S3). The original tree-ring data plotted against the calendar year for middle-aged trees representing the largest age class, however, showed that the edge trees' lead in the annual increment has decreased since the 1970s at both sites A and B (Fig. S4).
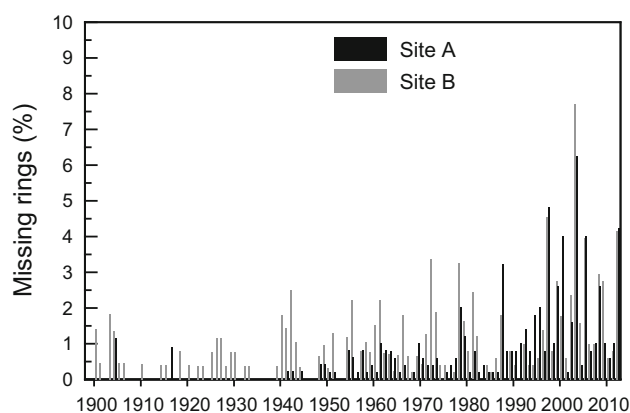
Fig. 5 Frequency of trees with missing rings from 1900 to 2012 for merged data from the forest interior and the forest edge at sites A and B

Frequency of missing rings

Missing-ring frequency increased dramatically at the end of the twentieth century and in the early twenty-first century at both sites A and B (Fig. 5). The highest percentage of missing rings in the total tree-ring series was found in 2003.

Discussion

The larch forests at site A were situated merely some 20 km from neighboring site B. Though these sites shared largely identical topography, elevation, climate, and edaphic characteristics, they clearly differed in the age structure of their forest stands. These differences are certainly the result of heavy logging during the twentieth century at site A, but only sporadic timber harvest at site B. Logging resulted in the removal of old (cambial age of 101–160 years) and very old (>160 years) *L. sibirica* trees from site A. Decreasing numbers of old trees due to timber harvest and deforestation are a global phenomenon and critical for forest biodiversity (Lindenmayer et al. 2012). The strong overrepresentation of middle-aged trees (61–100 years) at site A is the direct consequence of the removal of older trees, which opened space for the next tree generation; the presently middle-aged trees were obviously too small to be attractive for timber harvesting during the period of heavy logging until 1990. The complete lack of young trees (<60 years) at site A is probably also the result of logging, since clear-cutting reduces seed availability and in addition increases soil temperature and reduces soil moisture both immediately by heat storage in the more exposed soil surface and in the long term by the melting of permafrost (Park et al. 2009). Since permafrost is currently on retreat in the Inner Asian forest–steppe due to climate warming (Jin et al. 2007; Sharkhuu and Sharkhuu 2012), its regeneration is not likely under the present climatic conditions. The germination success and seedling survival of *L. sibirica* in the forest–steppe are hampered by high soil temperatures and low soil moisture during the growing season (Dulamsuren et al. 2008). Slower growth of middle-aged relative to old trees at the same age (Fig. S2) despite reduced competition due to logging at site A is probably also the result of warmer and drier site conditions. In contrast to site A, sporadic logging in recent decades at site B led to growth releases (Fig. S4) and even slightly higher cumulative increment at the same tree age in middle-aged than in old trees. This finding indicates that a dramatic deterioration of the water supply due to increased heat transfer to the soil and permafrost melting has apparently not occurred at the generally less intensely logged site B.

Despite the strong influence of timber harvest on the age structure of the larch stands at site A, the past logging intensity hardly exerted an effect on structural stand characteristics. Although former intense logging has replaced forest stands of heterogeneous age structure with more evenly aged stands in agreement with our first hypothesis, stand density and basal area were similar at the present stage of forest development. The dominance of middle-aged trees, however, increases homogeneity in the vertical stand structure, which was not systematically analyzed. The disturbance by former heavy logging activities was reflected by a significant reduction of mean sensitivity and an increase in first-order autocorrelation of tree-ring width. This observation is consistent with our second hypothesis. A reduction of climate sensitivity is likely to have occurred after logging as a result of growth releases due to reduced competition among the remaining trees (Martin-Benito et al. 2011; D'Amato et al. 2013; Dulamsuren et al. 2014).

The results of climate-response analysis could substantiate a high sensitivity of the tree-ring index to summer drought only at the heavily logged site A, which is only supportive of the third hypothesis for this site. Since global climate warming has caused a strong recent increase of temperature in the study area, which is, like in many regions of semi-arid Inner Asia, far above the global average (Batima et al. 2005; IPCC 2013), the susceptibility of stem increment to summer drought has apparently caused an increase in missing-ring frequency in the recent past in support of our fourth hypothesis. In contrast to the results of climate-response analysis, increased missing-ring frequencies were found at both study sites. Increased missing-ring frequency has already been observed elsewhere in the Mongolian forest–steppe (Khishigjargal et al. 2014; Khansaritoreh et al. 2017) and other parts of Inner Asia (Liang et al. 2016). Missing-ring frequency is not related to tree age (Lorimer et al. 1999; Khishigjargal et al. 2014; Liang et al. 2016) and thus attributable to climate warming. Missing rings evidence a marked reduction of vitality in these forests and clearly suggest that *L. sibirica* is primarily limited by water availability in this region and thus not by low summer temperatures and probably also not by low nitrogen availability (Chapin et al. 2010; Yarie and Van Cleve 2010). Water limitation of forest productivity was to be expected given the position of the studied forests in the forest–steppe ecotone, but this stressor is increasingly shared by boreal forests even at higher latitudes (Buermann et al. 2014; Tei et al. 2014). The observed peak in the frequency of missing ring in 2003 after three dry and warm years (Fig. 1) supports our conclusions.

An interesting detail concerning the putative increased limitation of stem increment by increased summer drought in our study area is the comparison of tree-ring series from the interior and the edges of *L. sibirica* forests (Fig. S4).

Trees at both sites showed higher radial stem increment at forest edges than in the interior in the mid-twentieth century, but similar growth rates since the late twentieth century when climate warming accelerated at the global level (IPCC 2013). Apparently, the trees profited from the lower stand density and thus lower intraspecific competition for resources at the forest edge through higher productivity in the cooler mid-twentieth century, but are now equally constrained by summer drought in both habitats. This finding could indicate that the more light-exposed, warmer and better nutrient-supplied forest edges (Dulamsuren and Hauck 2008; Hauck et al. 2012) have recently switched from the limitation by several site factors to merely water-limited systems as a result of climate warming (Chapin et al. 2010).

Although stem increment at both sites was limited by summer drought, the sites exhibited a consistent difference in the details of climate response of tree-ring width. Sensitivity of stemwood formation to summer drought may manifest in correlations of tree-ring width with both summer temperature (negative correlation) and precipitation (positive correlation) (D'Arrigo et al. 2004; Wilmking and Myers-Smith 2008; Dulamsuren et al. 2011; Tei et al. 2014). While the tree-ring index in the formerly heavily logged site A decreased with June temperature, but was never correlated with precipitation, the tree-ring index at site B increased with June precipitation (Tables 4, S1, S2). Correlations with June temperature occurred only sporadically at site B and were merely marginally significant ($P \leq 0.10$). Even the correlations of the tree-ring index with June precipitation at site B were less frequent than the correlation of tree-ring index of middle-aged trees with June temperature at site A. Since the environmental conditions were comparable between sites A and B and the geographic separation between these sites was small, it is plausible to assume that the different age structure of the *L. sibirica* stands was the key factor that controlled the trees' sensitivity to temperature and precipitation in summer. Middle-aged tree populations are generally more productive than stands that are dominated by old and senescent trees (Schulze et al. 1999; Bond-Lamberty et al. 2004; Girardin et al. 2011). The higher productivity is usually associated with higher water consumption (Bond-Lamberty et al. 2009; Jassal et al. 2009) and constraints due to water shortage increase with stand density (Smith and Long 2001). Therefore, it is plausible to assume that growth of the dominantly middle-aged forests at site A is more sensitive to increases in the atmospheric vapor pressure deficit. Increased summer temperatures under the semi-arid climate of the Inner Asian forest–steppes cause elevated saturation deficits and thus should lead to reduced stomatal conductance and carbon assimilation (Li et al. 2006; Dulamsuren et al. 2009). Correspondingly, increasing

summer temperatures at constant precipitation were shown to cause reductions in the annual stem increment in *L. sibirica* forests in the forest–steppe of eastern Kazakhstan (Dulamsuren et al. 2013). These findings from Kazakhstan suggest decreasing wood formation and probably net primary production by a trend of increasing atmospheric saturation deficits due to climate warming. The positive correlations of the tree-ring index with June temperature combined with a growing frequency of missing rings suggests a similar mechanism in the forests at site A dominated by middle-aged trees, especially since the most relevant correlations were found for middle-aged trees.

The sporadic increases of the tree-ring index with increasing June precipitation and decreasing June temperature at site B with a higher share of old and very old (or in other words overmature and thus less productive) trees could be the result of weaker limitation of net primary production by summer drought than at site A. The assumed weaker drought impact is explicable by lower water consumption of a less productive canopy. Furthermore, permafrost degradation after clear-cut in the formerly more heavily logged site A could cause the presently higher susceptibility of the forests at site A to summer drought than at site B, since soil layers influenced by permafrost can reduce the susceptibility to summer drought by supplying water in addition to the current precipitation (Sugimoto et al. 2003; Li et al. 2006). Unfortunately, we do not have data on the local permafrost distribution in our study regions.

The positive correlation of the tree-ring index with the mean temperature of May, the month when snowmelt typically takes place, at site A, but not at site B, could also be the result of an improved water budget at site A, since high temperatures at snowmelt foster wood formation by increasing the trees' water supply (Sugimoto et al. 2003; Tei et al. 2014). On the other hand, high water consumption in spring through evapotranspiration can also aggravate drought stress later in summer, as the soil water reserves are consumed earlier (Buermann et al. 2013; Parida and Buermann 2014). Earlier rapid spring onset is often combined with superficial snowmelt over the frozen soil and leads to higher water loss by surface runoff than in late springs (Barnett et al. 2005), thereby further aggravating summer water shortage. Apparently, trees at site B were not severely limited by summer drought until the recent decades. This is suggested by the fact that presently middle-aged trees at site B reveal faster growth than that formerly seen in the old trees when they had the same age. In the recent past, the missing-ring frequency as an indicator of drought-related stress has increased, even at site B.

The existing differences in the livestock grazing pressure between sites A and B were apparently not effective at influencing the age structure of the studied *L. sibirica* stands,

since young trees were found at the more intensely grazed site B, but not at site A. The impact of livestock grazing must therefore be subordinate compared to the effect of timber harvest. The livestock grazing pressure in our study region, the western Khangai Mountains, is generally moderate (Hauck and Lkhagvadorj 2013; Lkhagvadorj et al. 2013a, b). Heavy livestock grazing can exert a significant influence on the age structure of forest stands in the forest–steppe by suppressing regeneration (Sankey et al. 2006). The effect on the recent regeneration was not investigated in our study, since a detailed analysis from a heavily grazed region of the Mongolian forest–steppe already showed that grazing facilitates seedling establishment through the reduction of competition by opening gaps in the ground vegetation (Khishigjargal et al. 2013). However, the abundance and vitality of sapling-sized trees is reduced, since these trees are the preferential food of goats (Khishigjargal et al. 2013), which increasingly dominate the Mongolian livestock (Lkhagvadorj et al. 2013a, b). Despite the proximity of the study sites and the replicate plots, the effects of disturbances (e.g., fire, insect infestations) might have differed between individual plots in the centuries covered by our tree-ring data. Such potential differences might explain parts of the within-site variability found in the results of the climate-response analysis.

Conclusions

Differences in the logging history of *L. sibirica* forests in close proximity (ca. 20 km) with comparable site conditions exerted strong influences on the age structure of these forest stands. This difference was the probable cause of deviations in the climate response of the tree-ring index between site A that was heavily logged until 25 years ago and site B that was continuously used for moderate selective logging. The more heavily logged site A was apparently more susceptible to increased summer temperatures and thus drought than site B. The observed differences in the results of the climate-response analysis on a small spatial scale demonstrate the importance of high replication on the stand level for the generalizability of dendrochronological results in the Inner Asian forest–steppe, which is characterized by high spatial heterogeneity in terms of forest structure and land use intensity. Our results also suggest that heavy logging might aggravate the detrimental impact of climate warming on forests in the drought-prone forest–steppes of Inner Asia.

References

Barnett TP, Adam JC, Lettenmaier DP (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303–309

Batima P, Natsagdorj L, Gombluudev P, Erdenetsetseg B (2005) Observed climate change in Mongolia. Assess Impact Adapt Clim Change Work Pap 12:1–26

Bond-Lamberty B, Wang C, Gower ST (2004) Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Glob Change Biol 10:473–487

Bond-Lamberty B, Peckham SD, Gower ST, Ewers BE (2009) Effects of fire on regional evapotranspiration in the central Canadian boreal forest. Glob Change Biol 15:1242–1254

Bräuning A (1999) Zur Dendroklimatologie Hochtibets während des letzten Jahrtausends. Dissert Bot 312:1–164

Briffa KR (1999) Interpreting high-resolution proxy climate data—the example of dendroclimatology. In: Storch H, Navarra A (eds) Analysis of climate variability. Springer, Berlin, pp 77–94

Briffa KR, Jones PD, Schweingruber FH, Karlén W, Shiyatov SG (1996) Tree-ring variables as proxy-climate indicators: problems with low-frequency signals. In: Jones PD, Bradley RS, Jouzel J (eds) Climatic variations and forcing mechanisms of the last 2000 years. Springer, Berlin, pp 9–41

Buermann W, Parida BR, Jung M, Burn DH, Reichstein M (2013) Earlier springs decrease peak summer productivity in North American boreal forests. Environ Res Lett 8(024027):1–10

Buermann W, Parida BR, Jung M, MacDonald GM, Tucker CJ, Reichstein M (2014) Recent shift in Eurasian boreal forest greening response may be associated with warmer and drier summers. Geophys Res Lett. doi:10.1002/2014GL059450

Chapin FS, McGuire AD, Ruess RW et al (2010) Resilience of Alaska's boreal forest to climatic change. Can J For Sci 40:1360–1370

Chen F, Yuan YJ, Wei WS, Fan ZA, Zhang TW, Shang HM, Zhang RB, Yu SL, Ji CR, Qin L (2012) Climatic responses of ring width and maximum latewood density of *Larix sibirica* in the Altay Mountains reveals recent warming trends. Ann For Sci 69:723–733

Cook ER (1985) A time series analysis approach to tree ring standardization. PhD thesis, University of Arizona, Tucson

D'Amato AW, Bradford JB, Fraver S, Palik BJ (2013) Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. Ecol Appl 23:1735–1742

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

D'Arrigo RD, Kaufmann RK, Davi N, Jacoby GC, Laskowski C, Myneni RB, Cherubini P (2004) Thresholds for warming-induced growth decline at elevational tree line in Yukon Territory, Canada. Glob Biogeochem Cycl 18(GB3021):1–7

Dulamsuren Ch, Hauck M (2008) Spatial and seasonal variation of climate on steppe slopes of the northern Mongolian mountain taiga. Grassl Sci 54:217–230

Dulamsuren Ch, Hauck M, Mühlenberg M (2008) Insect and small mammal herbivores limit tree establishment in northern Mongolian steppe. Plant Ecol 195:143–156

Dulamsuren Ch, Hauck M, Bader M, Osokhjargal D, Oyungerel Sh, 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, Khishigjargal M, Leuschner HH, Leuschner C (2010) Diverging climate trends in Mongolian taiga forests influence growth and regeneration of *Larix sibirica*. Oecologia 163:1091–1102

Dulamsuren Ch, Hauck M, Leuschner HH, 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 Ch, Wommelsdorf T, Zhao F, Xue Y, Zhumadilov BZ, 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

Eckstein D, Bauch J (1969) Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. Forstwiss Centralbl 88:230–250

Fritts HC (1976) Tree rings and climate. Academic Press, London

Girardin MP, Bernier PY, Gauthier S (2011) Increasing potential NEP of eastern boreal North American forests constrained by decreasing wildfire activity. Ecosphere 2(25):1–23

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

Hansen MC, Potapov PV, Moore R et al (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853

Hauck M, Lkhagvadorj D (2013) Epiphytic lichens as indicators of grazing pressure in the Mongolian forest–steppe. Ecol Indic 32:82–88

Hauck M, Javkhlan S, Lkhagvadorj D, Bayartogtokh B, Dulamsuren Ch, Leuschner C (2012) Edge and land-use effects on epiphytic lichen diversity in the forest–steppe ecotone of the Mongolian Altai. Flora 207:450–458

Hauck M, Dulamsuren Ch, Bayartogtokh B, Ulykpan K, Burkitbaeva UD, Otgonjargal E, Titov SV, Enkhbayar T, Sundetpaev AK, Beket U, Leuschner C (2014) Relationships between the diversity patterns of vascular plants, lichens and invertebrates in the Central Asian forest–steppe ecotone. Biodivers Conserv 23:1105–1117

Hessl AE, Ariya U, Brown P, Byambasuren O, Green T, Jacoby G, Kennedy Sutherland E, Nachin B, Maxwell RS, Pederson N, De Grandpré L, Saladyga T, Tardif JC (2012) Reconstructing fire history in central Mongolia from tree-rings. Int J Wildland Fire 21:86–92

Huang J, Tardif JC, Bergeron Y, Denneler B, Berninger F, Girardin MP (2010) Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. Glob Change Biol 16:711–731

IPCC (2013) Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Jarvis P, Linder S (2000) Constraints to growth of boreal forests. Nature 405:904–905

Jassal RS, Black TA, Spittlehouse DL, Brümmer C, Nesic Z (2009) Evapotranspiration and water use efficiency in different-aged Pacific Northwest Douglas-fir stands. For Ecol Manag 149:1168–1178

Jin H, Yu Q, Lü L, Guo D, He R, Yu S, Sun G, Li Y (2007) Degradation of permafrost in the Xing'anling Mountains, northeastern China. Permafr Periglac Process 18:245–258

Johnston A (1970) A history of rangelands of western Canada. J Range Manag 23:3–8

Khansaritoreh E, Dulamsuren Ch, Klinge M, Ariunbaatar T, Bat-Enerel B, Batsaikhan G, Ganbaatar Kh, Saindovdon D, Yeruult Y, Tsogtbaatar J, Tuya D, Leuschner C, Hauck M (2017) Higher climate warming sensitivity of Siberian larch in small than large forest islands in the fragmented Mongolian forest steppe. Glob Change Biol 23:3675–3689

Khishigjargal M, Dulamsuren Ch, 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

Khishigjargal M, Dulamsuren Ch, Leuschner HH, 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

Körner C, Sarris D, Christodoukalis D (2005) Long-term increase in climatic dryness in the East-Mediterranean evidenced for the island of Samos. Reg Environ Change 5:27–36

Li SG, Tsujimura M, Sugimoto A, Sasaki L, Yamanaki T, Davaa G, Oyunbaatar D, Sugita M (2006) Seasonal variation in oxygen isotope composition of waters for a montane larch forest in Mongolia. Trees 20:122–130

Liang EY, Leuschner C, Dulamsuren Ch, Wagner B, Hauck M (2016) Global warming-related tree growth decline and mortality on the north-eastern Tibetan Plateau. Clim Change 134:163–176

Lindenmayer DB, Laurance WF, Franklin JF (2012) Global decline in large old trees. Science 338:1305–1306

Liu H, Williams AP, Allen CD, Guo D, Wu X, Anenkhonov OA, Liang EY, Sandanov DV, Yin Y, Qi Z, Badmaeva NK (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 (2013a) Pastoral nomadism in the forest–steppe ecotone of the Mongolian Altai under a changing economy and a warming climate. J Arid Environ 88:82–89

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

Lorimer CG, Dahir SE, Singer MT (1999) Frequency of partial and missing rings in *Acer saccharum* in relation to canopy position. Plant Ecol 143:189–202

Martin-Benito D, Kint V, del Río M, Muys B, Cañellas I (2011) Growth completion and productivity: past trends and future perspectives. For Ecol Manag 262:1030–1040

Michaelian M, Hogg EH, Hall RJ, Arsenault E (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Glob Change Biol 17:2084–2094

MNE (2012) Forest resources of Mongolia. Mongolia Ministry of Environment and Green Development, Government Agency of Forests, Ulan Bator (in Mongolian)

Östlund L, Zackrisson O, Axelsson A-L (1997) The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Can J For Sci 27:1198–1206

Outram AK, Stear NA, Bendrey R, Olsen S, Kasparov A, Zaibert V, Thorpe N, Evershed RP (2009) The earliest horse harnessing and milking. Science 323:1332–1335

Parida BR, Buermann W (2014) Increasing summer drying in North American ecosystems in response to longer nonfrozen periods. Geophys Res Lett. doi:10.1002/2014GL060495

Park YE, Lee DK, Stanturf JA, Woo SY, Zoyo D (2009) Ecological indicators of forest degradation after forest fire and clear-cutting in the Siberian larch (*Larix sibirica*) stand of Mongolia. J Korean For Soc 98:609–617

Peng C, Ma Z, Lei X, Zhu Q, Chen H, Wang W, Liu S, Li W, Fang X, Zhou X (2011) A drought-induced pervasive increase in tree mortality across Canada's boreal forest. Nat Clim Change 1:467–471

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

Sarris D, Christodoukalis D, Körner C (2007) Recent decline in precipitation and tree growth in the eastern Mediterranean. Glob Change Biol 13:1187–1200

Schulze E-D, Lloyd J, Kelliher FM (1999) Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink—a synthesis. Glob Change Biol 5:703–722

Sharkhuu N, Sharkhuu A (2012) Effects of climate warming and vegetation cover on permafrost of Mongolia. In: Werger MJA, van Staalduinen MA (eds) Ecological problems and livelihoods in a changing world. Springer, Dordrecht, pp 445–472

Smith FW, Long JN (2001) Age-related decline in forest growth: an emergent property. For Ecol Manag 144:175–181

Sugimoto A, Naito D, Yanagisawa N, Ichiyanagi K, Kurita N, Kubota J, Kotake T, Ohata T, Maximov TC, Fedorov AN (2003) Characteristics of soil moisture in permafrost observed in East Siberian taiga with stable isotopes of water. Hydrol Process 17:1073–1092

Tei S, Sugimoto A, Yonenobu H, Ohta T, Maximov TC (2014) Growth and physiological responses of larch trees to climate changes deduced from tree-ring widths and $\delta^{13}C$ at two forest sites in eastern Siberia. Polar Sci 8:183–195

Tsogtbaatar J (2004) Deforestation and reforestation needs in Mongolia. For Ecol Manag 201:57–63

Wigley TML, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J Clim Appl Meteorol 23:201–213

Wilmking M, Myers-Smith I (2008) Changing climate sensitivity of black spruce (*Picea mariana* Mill.) in a peatland-forest landscape in Interior Alaska. Dendrochronologia 25:167–175

Yarie J, Van Cleve K (2010) Long-term monitoring of climatic and nutritional affects on tree growth in interior Alaska. Can J For Sci 40:1325–1335