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Recent drought stress leads to growth reductions in *Larix sibirica* in the western Khentey, Mongolia

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Abstract

Trends in air temperature and precipitation in the forest-steppe ecotone of the western Khentey, northern Mongolia were studied and related to stem increment and shoot water relations in Mongolia's most common tree species, Siberian larch (*Larix sibirica*). The area has been subject to a significant increase of summer temperature and a decrease of summer precipitation during the last 47 years. Tree-ring width series from >400 larch trees show a strongly decreasing annual increment since the 1940s. The onset of this decrease is independent of the age of the trees and, therefore, can be attributed to the increasing aridity in the 20th century. Simultaneously to the declining annual increment, regeneration of Siberian larch decreased as well; today regeneration is virtually lacking in the larch forests on mountain slopes of the western Khentey. Measurements of shoot water potentials during the growing season exhibited daily minimum water potentials close to the point of zero turgor for extended periods. The drought stress indicated by these results is in line with the current low annual increment. Trees in the forest interior were more severely stressed and grow more slowly than trees at the forest line to steppe. This is attributable to the recent increase in aridity, as the stand density and probably also the trees themselves in the forest interior are adapted to moister conditions, whereas the trees at the forest edge have always been exposed to a more extreme microclimate. The progressing increase in aridity during the 21st century that is predicted for the western Khentey, suggests a future decline of larch forests. A widespread increase of aridity predicted for most parts of the Mongolian forest belt, suggests even a supra-regional decline of larch.

Keywords: climate change, drought stress, forest-steppe ecotones, semi-arid north-eastern Asia, shoot water potentials, Siberian larch, tree-ring width

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Introduction

Mongolia, a country of 1.5 million km^2, is among the earth's regions where (1) a particularly high increase of temperature was observed already during the late 20th century and (2) global change studies predict particularly high increases of temperature in the 21st century. Summer temperature is projected to increase by 2 °C and winter temperature by 1 °C within the next 80 years (Sato & Kimura, 2006). Within the last 60 years, Mongolia's annual temperature increased by 1.7 °C (Batima *et al*., 2005). This is much more than the global average increase of 0.7 °C during the past 100 years (Trenberth *et al*., 2007). The late 20th century warming in Mongolia already results in the melting of glaciers (Kadota & Davaa, 2005). Increasing temperatures in Siberia reduced the intensity of cold fronts and thereby the intensity of springtime storms, which are a typical feature of the Mongolian climate (Hayasaki *et al*., 2006; Sato & Kimura, 2006). Permafrost, which currently has a large extension in Mongolia's forest soils (Etzelmüller *et al*., 2006) is predicted to retreat from Mongolia during the 21st century (Stendel & Christensen, 2002; Böhner & Lehmkuhl, 2005).

The vegetation of Mongolia follows a latitudinal zonation with forests in the most humid northern parts and steppe, semidesert and desert in the center and the south (Hilbig, 1995; Vostokova & Gunin, 2005). Around 80% of Mongolia's forest is built by Siberian larch (*Larix sibirica* Ledeb.) (Savin *et al*., 1978; Tsogtbaatar, 2004), which is one of northern Asia's most important tree species (Koizumi *et al*., 2003). It has its southern distribution limit in Mongolia, as growth further in the south is hampered by drought (Gunin *et al*., 1999; Dulamsuren *et al*., 2009a). At the borderline between forests and steppe, Siberian larch is limited to the relatively moist north-facing slopes, whereas south-facing slopes and dry valleys are covered with grasslands. Since the southern limit of Siberian larch and other conifer species occurring in Mongolia, including Siberian fir (*Abies sibirica* Ledeb.) and Siberian spruce (*Picea obovata* Ledeb.), migrated through Mongolia

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during the Holocene as a response to variations in aridity (Dinesman *et al*., 1989; Tsedendash, 2007), the question arises as to whether increasing aridity due to global warming will reduce the forested area of Mongolia in the near future.

The present study aims at testing the hypothesis that the late 20th century warming caused a recent degradation of the growth conditions for Siberian larch in Mongolia. The study is composed of three parts: (1) temperature and precipitation trends during the late 20th century were analyzed, (2) tree-ring analyses were applied to test the hypothesis that recent drought stress led to reduced rates of growth and regeneration in Siberian larch, and (3) water relations were studied in some of the trees used for wood core sampling to test the hypothesis that trees currently suffer from drought stress.

Materials and methods

Study area

The study was conducted in the western Khentey Mountains in northern Mongolia, an area selected as a case example for extensive ecological study of the Mongolian mountain taiga (Dulamsuren *et al*., 2005a–c, 2008, 2009a-c, 2010; Dulamsuren & Hauck, 2008; Hauck *et al*., 2008; Schlütz *et al*., 2008). The western Khentey Mountains were chosen, because they (1) presently belong to the moistest areas of Mongolia, (2) are known to have undergone a marked late 20th century warming, and (3) are projected to receive significantly less precipitation than today in future (Sato & Kimura, 2006; Sato *et al*., 2007a). Field work was carried out in Mandal county (Mandal somon) near Khonin Nuga Research Station (49°04′48″N, 107°17′15″E). The research station is located 130 km north of Ulan Bator in a valley, where the Rivers Sharlan Gol and Khongiyn Gol unite and become the River Eroo, a tributary of the Orkhon River. Elevation of the study area ranges from 900 m a.s.l. in the river valleys up to 1600 m on the mountain tops. Geologically, the Khentey mainly consists of Proterozoic and Paleozoic rocks, especially of granite. Permafrost is found under forests on northern slopes. The study sites for the present investigation were located near Khonin Nuga Research Station on northwest-facing slopes of the Sharlan Valley (49°6′N, 107°19′E) (in the following called site A) at an elevation of 1010–1072 m, Mt. Bayantogol (49°5′N, 107°17′E) (site B) at 1020–1120 m and Mt. Baziin Am (49°3′N, 107°15′E) (site C) at 990–1090 m; the sites were up to 6.5 km apart.

The climate of the Khentey Mountains is characterized by the Asiatic anticyclone in winter, which typically has its center southwest of Lake Baikal and causes dry and cold winters with mean January temperatures below −20 °C and extreme values between −45 and 50 °C (Dulamsuren & Hauck, 2008). In summer, warm air masses from the south flow into northern Mongolia resulting in the formation of cyclones when they meet the cold air from Siberia (Sato *et al*., 2007b). Mean July temperature is around 17 °C with daily maxima of 40 °C (Dulamsuren & Hauck, 2008).

The vegetation of the study area was currently surveyed by Dulamsuren *et al*. (2005a, b). The western Khentey is the region with the highest tree diversity in Mongolia (Tsedendash, 1995; Gunin *et al*., 1999; Dulamsuren *et al*., 2005a). Forests at the forest-steppe border line are so-called light taiga forests, which are dominated by *L. sibirica*, *Betula platyphylla* (at disturbed sites) and (locally) *Pinus sylvestris*. These forests are restricted to the more humid north-facing slopes, whereas south-facing slopes are covered with different types of montane meadow steppe, mountain steppe, and small savanna-like *Ulmus pumila* stands (Dulamsuren *et al*., 2005b, 2009b).

Analysis of climate trends from weather data

Weather stations which have been recording data continuously for more than a few decades are rare in Mongolia. The nearest permanent weather station to the study area with a continuous data set is located 87 km NW of Khonin Nuga Research Station (Station 'Eroo') at an elevation of ca. 900 m (49°48′N, 106°42′E). From this weather station, data of air temperature and precipitation are available since 1961.

Field and laboratory work for tree-ring analysis

Wood cores were sampled at sites A, B, and C in September 2007. Six plots of $50 \times 50\,\mathrm{m}^2$ per site were nonrandomly selected in a minimum distance of 30 m from the forest line to the steppe and of 100 m from one another. In these plots, wood cores of all conifers ($N = 410$; 97% of them belonging to *L. sibirica*) were collected with an increment borer of 5 mm of the inner diameter. Conifers other than *L. sibirica* included *A. sibirica*, *Pinus sibirica*, and *P. sylvestris*. A survey of the number of trees investigated on the individual plots and the age structure of the sampled stands is compiled in Table 1. *B. platyphylla* co-occurred in varying proportions with *L. sibirica* and the other conifer species, but was not included in the study, as this pioneer tree is of little interest for the dendroecological analysis. Tree-ring samples of conifers other than larch were only used to describe the age structure of the stands (Table 1). In addition to the trees growing inside the forest, single trees located immediately at the forest line were sampled in one oblong plot per site (Table 1). The length of these plots varied between 50 and 100 m. At 1 m above the ground, the increment borer was driven into the wood parallel to the contour lines of the mountain slopes to avoid compression wood in the cores. All sample plots were searched for seedlings and saplings below 1 m height to collect stem cross-sections. These samples were used for the determination of the age structure. Additional data, including trunk diameter, social rank, and fire traces, were recorded in the field.

Wood cores were mounted on wood strips; the core surfaces were cut lengthwise with a scalpel, and the contrasts between annual tree rings were brought out with chalk. Annual tree-ring width was measured with a precision of 10 μm on a movable object table, the movements of which are electronically

Table 1 Sample plots used for dendroecological analyses at sites A–C including sample sizes and age of sample trees ($N = 410$) in the forest interior (plot numbers 1–6) and forest edge (FE)

			Cambial age (years)			Age class (years)		
Plot	Tree species	*N*	Mean	Min.	Max.	>90	50–90	<50
Site A (143 trees)								
1	*Larix sibirica*	17	62 ± 4	55	106	2	14	1
2	*Larix sibirica*	14	90 ± 6	50	112	10	3	1
3	*Larix sibirica*	7	74 ± 9	48	102	3	3	1
4	*Larix sibirica*	26	72 ± 4	36	115	4	19	3
	Pinus sibirica	5	65 ± 2	62	69	0	5	0
5	*Larix sibirica*	19	63 ± 2	32	74	0	17	2
	Pinus sylvestris	3	59 ± 4	52	66	0	3	0
6	*Larix sibirica*	11	72 ± 7	51	122	3	8	0
	Pinus sibirica	8	58 ± 3	46	65	0	8	0
	Pinus sylvestris	2	59 ± 3	56	61	0	2	0
	Abies sibirica	1	58	58	58	0	1	0
FE	*Larix sibirica*	30	81 ± 6	50	161	12	17	1
Site B (166 trees)								
1	*Larix sibirica*	30	62 ± 3	38	140	1	26	3
2	*Larix sibirica*	10	107 ± 9	63	159	8	2	0
3	*Larix sibirica*	27	98 ± 4	52	155	21	6	0
4	*Larix sibirica*	28	62 ± 2	42	79	0	24	3
5	*Larix sibirica*	22	63 ± 1	56	76	0	22	0
6	*Larix sibirica*	15	64 ± 4	30	116	1	13	1
FE	*Larix sibirica*	34	57 ± 2	18	80	0	29	5
Site C (101 trees)								
1	*Larix sibirica*	5	126 ± 34	48	211	3	1	1
2	*Larix sibirica*	9	164 ± 4	140	182	9	0	0
3	*Larix sibirica*	7	157 ± 11	92	173	7	0	0
4	*Larix sibirica*	16	50 ± 1	42	59	0	7	9
5	*Larix sibirica*	18	47 ± 1	32	54	0	6	12
6	*Larix sibirica*	16	62 ± 7	41	166	1	13	2
FE	*Larix sibirica*	30	70 ± 8	26	196	9	7	14

transmitted to a computer system equipped with TSAP-WIN software (Rinntech, Heidelberg, Germany).

Evaluation of tree-ring data

Evaluation of tree-ring data was also conducted with TSAP-WIN software. The tree-ring series were controlled for missing rings and false rings during crossdating, as especially the failure of tree rings is not rare in the semiarid environment of Mongolia at the drought limit of forests. Crossdating was based on the use of two parameters: coefficient of agreement ['Gleichläufigkeit' (GL)] (Eckstein & Bauch, 1969) and *t*-values (Baillie & Pilcher, 1973). The GL- and *t*-values measure the similarity between tree-ring series in the high- and low-frequency domain, respectively. Trees of the same site were pooled by calculating mean values of the annual increment. Tree-ring series used for the calculation of means had GL >65% (GL was >80% in 44% of the sample trees) and *t*-values >3.5 (>6 in ca. 90% of samples). Trend lines were calculated using moving 5-years averages. The course of a tree-ring series is primarily influenced by climate and tree age (Fritts, 1976; Cook, 1985; Bräuning, 1999). Other influences, including stand-internal disturbances (e.g. the natural death of a neighboring tree) and stand-external disturbances (e.g. insect infestations, fire) (Dulamsuren *et al.*, 2010) or tree-specific characters caused by genetic variations or the small-scale variation of site parameters were minimized due to the large sample size and the collection of wood cores on three mountain slopes. The coherence within a tree-ring chronology was measured by the expressed population signal (EPS) (Wigley *et al.*, 1984); a chronology is considered to be reliable if the EPS exceeds the 0.85-threshold. Except for the few middle-aged trees available at site C where the EPS amounted to 0.83 in the forest interior and 0.71 at the forest line, the EPS is >0.85 for all other tree-ring chronologies.

Since both the variation of climate and the age-related growth trends are relevant for our study, different procedures were applied to extract this information from the tree-ring chronologies. The interannual (high-frequency) variation of climate was extracted by removing the age-related information from the tree-ring width series. This is principally achieved by dividing the observed tree-ring width (r_i) through the expected annual increment. The expected annual increment declines throughout the lifetime of a tree for two reasons: (1) the same amount of wood has to be distributed around a larger circumference of the trunk from year to year; (2) trees tend to grow faster during the first decades of their lifetime and slow down afterwards. Finding the correct function for the age-related growth trend (for estimating the expected growth rate) is easier in semiarid environments, including our study area, than in well water-supplied regions, as the stand density in semiarid woodlands is relatively low and, thus, the individual trees are less influenced by changes in the stand structure than in dense and moist forests (Cook, 1985). Therefore, the same type of standardization (i.e. of removing the age-related trend) could be applied for all tree-ring chronologies studied. The annual tree-ring index (z_i) of year i was calculated with the equation $z_i = 100 \times r_i/m_i$ with m_i being the 5-years moving average of year i.

Pointer years (Schweingruber *et al.*, 1990) describing intervals of exceptionally favorable or unfavorable growth conditions were identified by calculation the growth deviation δz_i with the equation $\delta z_i = z_i - ([z_{i-1} + z_{i-2} + z_{i-3} + z_{i-4} + z_{i-5}]/5)$ (Neuwirth *et al.*, 2004). The resulting δz_i was divided by the standard deviation for all tree-ring widths of the entire chronology and multiplied by 100 to calculate the relative intensity of growth deviation in the year i (Bräuning, 1999). The mean of pointer year intensities across the three study sites was calculated to obtain a site-independent climate signal.

Long-term (low-frequency) climate trends can be identified by removing the annual variation of climate from the tree-ring series and conserving the age-related trend (Sarris *et al.*, 2007). If the annual increment is not related to the calendar year, but to tree age, a mean age-related growth curve [regional growth curve (RGC); Briffa *et al.*, 1992; Helama *et al.*, 2004; Naurzbaev *et al.*, 2004] can be established for a given site, largely independently of the annual variation of climate. Climate trends can be deduced from the RGC by comparing it with tree-ring series from trees of different age. We prefer the comparison of several (partial) RGC for trees of different age classes with one another, because the comparison of an individual growth curve to the RGC calculated for all trees might blur existing trends, as the individual tree-ring series is also included in the RGC. Age is generally specified as the age of the oldest tree ring ('cambial age') at the sampling height of 1 m; ca. 10 (at most 20) years should be added to deduce tree age from these age specifications (Körner *et al.*, 2005; Sankey *et al.*, 2006). Age classes include trees with a cambial age >90 years ('old trees'), between 50 and 90 years ('middle-aged trees') and trees <50 years ('young trees'). In addition to the comparison of RGC for trees belonging to different age classes, linear regressions were calculated for the original tree-ring data of old and middle-aged trees using XACT 8.03 software (SciLab, Hamburg, Germany). The slopes of the regression lines calculated for the first 55 tree rings were compared.

Shoot water relations in L. sibirica

Measurements of the shoot water potential in Siberian larch were made at site B in the growing season of 2006. Sample trees were nonrandomly selected according to diameter (ca. 30 cm), height (ca. 20 m), and the availability of foliated twigs, all of them falling in the age class of 50- to 90-year-old trees (cambial age). The plant water status was assessed by measuring shoot water potentials (Ψ) once a month each on three trees at the forest line to the steppe and in the forest interior. The measurements were done on rainless days with clear sky in five sun-exposed shoots of 10 cm length per tree. South-facing, 2-year-old twigs at a height of 1.5–2.0 m were selected for the measurements. The shoot water potential was determined with a Model 1000 Pressure Chamber Instrument (PMS Instrument Company, Albany, OR, USA; Scholander *et al.*, 1964; Dulamsuren *et al.*, 2009a). Monthly measurements were limited to the recording of the predawn (Ψ_p) and midday (Ψ_m) water potentials. In addition, pressure–volume curves were established in triplicate every month to determine the point of zero turgor (Ψ_0). Ψ_0 is the maximum value of Ψ, from which on irreversible damage due to cytorrhysis is possible. However, the point of cytorrhysis can be below Ψ_0 if the elasticity of the cell wall allows negative turgor values (Rhizopoulou, 1997). Twigs used for the determination of Ψ_0 were recut underwater and saturated with water in a glass wrapped in plastic foil for 12 h. Ψ_0 is relatively little affected by the length of the saturation phase before the measurements (Parker & Pallardy, 1987). Ψ_0 was deduced from plots of $-1/\Psi$ vs. the relative water content of the sample. In addition to the monthly measurements of Ψ_p and Ψ_m, the diurnal variation of Ψ was measured in the mid of the growing season. These measurements were conducted each on three trees in the interior and at the edge of the forest on 2 days in July and August 2006.

Air temperature and relative humidity needed for the calculation of the dew point temperature and, with it, of the atmospheric vapor pressure deficit (VPD) were measured with a HOBO weather station (Onset, Bourne, MA, USA), which was mounted on a meadow steppe in front of the forest line at site B at an altitude of 1060 m. The weather station was equipped with a H21 data logger and a set of HOBO Smart Sensors including a sensor for measuring air temperature and relative air humidity at 1 m above the ground (temperature/RH sensor S-THA). Data were recorded every 10 min and are means of 10 subsequent measurements (Dulamsuren & Hauck, 2008).

Statistics

Arithmetic means ± SE are given throughout the paper. Data were tested for normal distribution with the Shapiro–Wilk test. Pairwise comparisons of means were made with Student's *t*-test. Statistical analyses were computed with SAS 6.04 software (SAS Institute Inc., Cary, NC, USA).

Results

Temperature and precipitation trends

At the weather station Eroo, the annual mean (47 years, 1961–2007) of air temperature amounts to $-2.0 \pm 0.2\,^{\circ}\mathrm{C}$. Monthly mean values vary between $-27.3 \pm 0.5\,^{\circ}\mathrm{C}$ in

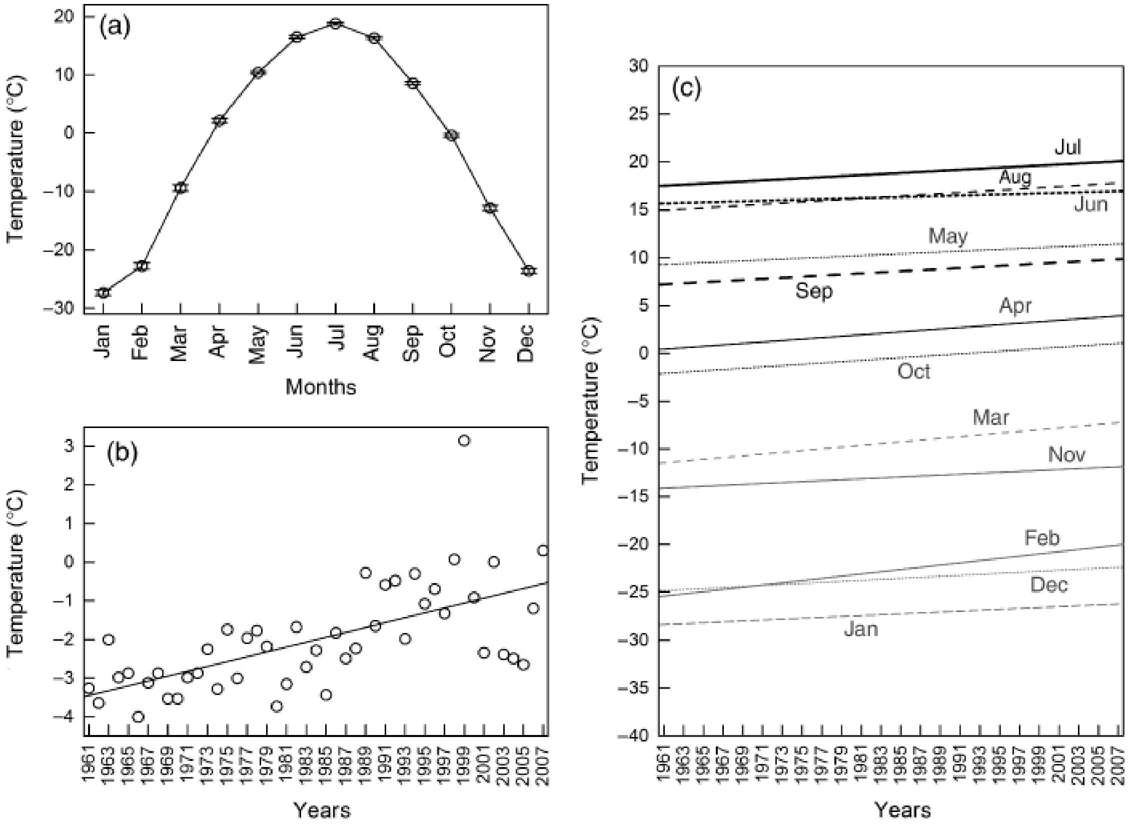

Fig. 1 Air temperature (1961–2007) at the weather station Eroo, 87 km NW Khonin Nuga Research Station. (a) Monthly mean values. (b) 45-year trend of annual mean temperature showing an increase by 2.5 °C ($r = 0.63$, $P < 0.001$). (c) 45-year trend of temperature separated by months (only regression lines plotted).

January and 18.8 ± 0.2 °C in July (Fig. 1a). The annual mean temperature exhibits an upward trend from 1961 to 2007 with an increase by 2.5 °C ($r = 0.63$, $P < 0.001$; $y = -3.51x + 0.06$) (Fig. 1b). An outlier in 1999 is remarkable, as the mean air temperature in this year (3.2 °C) exceeded the long-term mean by 5.2 °C. The unusual mean temperature for 1999 is caused by exceptionally high winter and spring temperatures. The monthly means for January to April 1999 exceed the relevant long-term mean values by 10.0 to 12.9 °C. The outlier in 1999 has no significant effect on the long-term temperature trend. Excluding the value for 1999 from the regression in Fig. 1b still yields a significant upward trend ($r = 0.67$, $P < 0.001$; $y = -3.45x + 0.06$). Significant increases of temperature ($P \leq 0.05$ in linear regression) are observed throughout the year, except for the winter months November to January and for June (Fig. 1c).

Annual precipitation from 1961 to 2007 amounted to 273 ± 11 mm. Precipitation has a marked peak in summer with a maximum of 77 ± 5 mm in July (Fig. 2a); monthly precipitation from October to April is generally <10 mm (from November to March <4 mm). Precipitation is highly variable between years with a coefficient of variation of 26% from 1961 to 2007 (Fig. 2b). Total precipitation decreased significantly since 1961 ($r = -0.45$, $P < 0.001$; $y = 330–2.35x$). Precipitation trends strongly depend on the season. Precipitation decreased in summer, but remained constant during the other seasons (Fig. 2c). The decrease was strongest (and only statistically significant) in the most rain-laden months, July ($r = -0.34$, $P = 0.009$; $y = 96.8–0.87x$) and August ($r = -0.41$, $P = 0.002$; $y = 94.8–1.02\ x$). July precipitation decreased by 50 mm from 95 mm in 1961 to 55 mm in 2007, whereas August precipitation decreased by 45 mm from 90 to 40 mm.

Years with strong growth deviations

Tree-ring chronologies in the western Khentey go back to the late 18th century (Fig. 3). The plots of tree-ring indices vs. time strongly resemble one another for the three sites suggesting that climate is responsible for most interannual variation. Years of below- and above-average increment, where the departure of the annual increment exceeded the standard deviation of the entire chronology, are frequent (Fig. 4). Pointer years

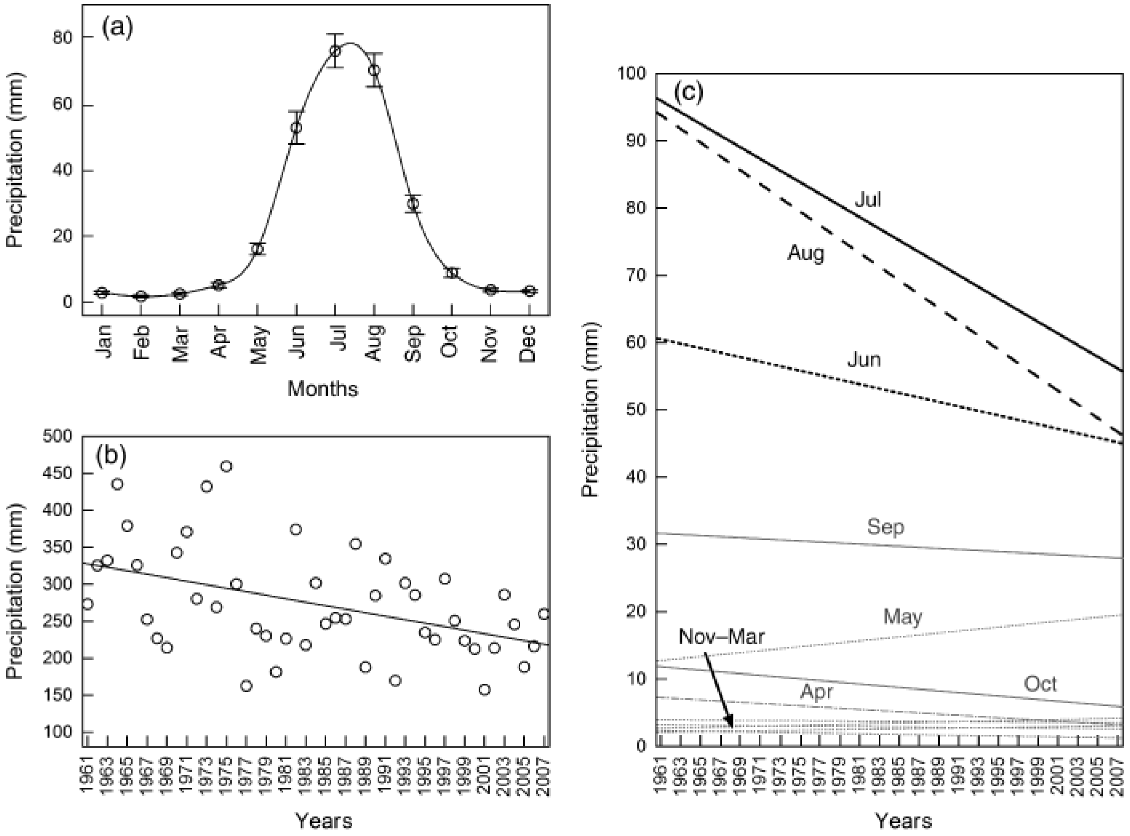

Fig. 2 Precipitation (1961–2007) at the weather station Eroo. (a) Monthly mean values showing a marked peak of precipitation in summer. (b) 45-year trend of precipitation showing a decrease by 100 mm ($r = -0.45$, $P < 0.001$). (c) 45-year trend of precipitation separated by months (only regression lines plotted).

with low tree-ring widths do not occur more frequently along with late 20th century warming. Rather, high pointer year intensities became rare from the late 1950s onwards.

Growth trends in Siberian larch

RGC show that old trees grew considerably faster than young or middle-aged trees during the first decades of their lifespan (Fig. 5). This is most pronounced at sites A and B (Fig. 5a and b). The recent decline in the annual increment at given age is also demonstrated in Table 2, where the results of linear regression of the increment during the first 55 cambial years is compared between old and middle-aged larch trees. The slopes of the linear regression lines describing the relationship between annual increment and tree age are more strongly negative in presently middle-aged than in presently old trees. A correlation of these slopes with the germination years of the individual trees exhibits that the annual increment during the first 55 cambial years declines increasingly more rapidly during the 20th century (Fig. 6).

The raw tree-ring data show that the onset of reduced annual increment of Siberian larch was in the 1940s (Fig. 7). Tree rings remained permanently narrow since two subsequent years with low increment in 1948 and 1954 (Figs 4 and 7). The decline was independent of tree age. The annual increment of the old trees even increased until the 1940s, whereas the annual increment of trees that established in the 1940s or later declined from the start (Fig. 7). Trees at the forest line to the steppe grew generally faster than trees in the forest interior, as exemplified in Fig. 8 for site B, where also the water potential measurements were carried out.

Regeneration of Siberian larch

There is no recent regeneration on the studied mountain slopes. Cones were not observed on the studied larch trees. Except for a single tree germinated in 1980, Siberian larch did not establish on the sample plots since 1970 (Fig. 9). Most larch trees presently growing on the sample plots established during the 1930s and 1940s in a period that was framed by the drought years 1929 and 1948 (Fig. 9). From the 1920s backwards to 1800, trees could regularly establish (Fig. 9).

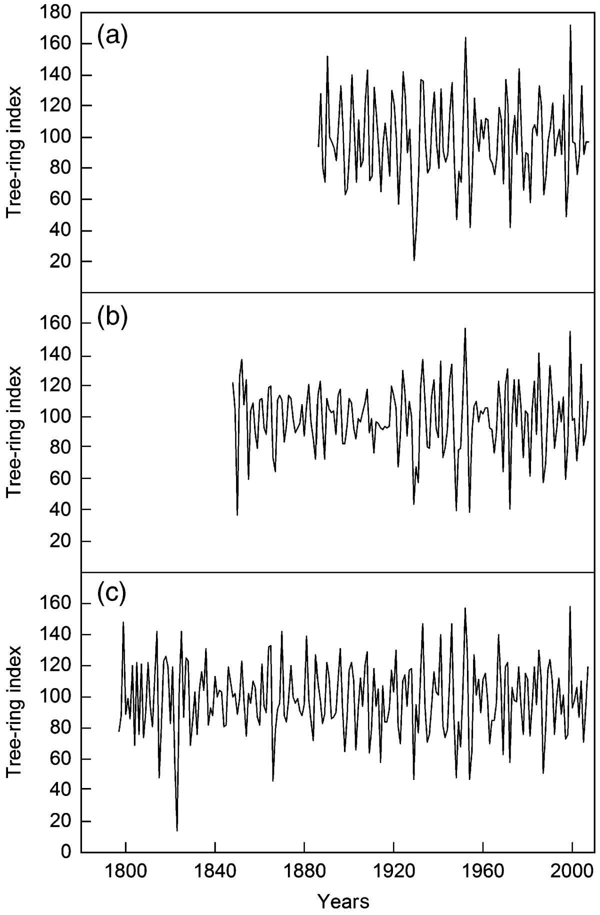

Fig. 3 Tree-ring indices at sites A (a), B (b), and C (c) calculated for old Siberian larch trees (cambial age >90 years) growing in the forest interior.

Shoot water status

During mid-summer in July and August, Ψ_m was significantly lower in the larch trees of the forest interior than at the forest edge to the steppe (Fig. 10). In contrast to the forest edge, Ψ_m of the trees in the forest interior was close to Ψ_0. Ψ_p was similarly high in trees of both sites. Diurnal courses of Ψ (Fig. 11) exhibited lower values for trees in the forest interior than at the forest line from the late morning hours to late afternoon.

Discussion

Drought is a major stressor for conifers at the southern fringe of the Siberian taiga in central and north-eastern Asia (Gunin *et al.*, 1999). Tense water relations are the rule for Siberian larch during extended parts of the short growing season in the Mongolian forest-steppe ecotone (Dulamsuren *et al.*, 2009a). The annual stem increment of *L. sibirica* in northern Mongolia (Dulamsuren *et al.*, 2010) as well as that of *L. gmelinii* in southern Siberia (Sidorova *et al.*, 2009) were shown to decrease with increasing aridity during the growing season. This implies that pointer years with markedly high or low tree-ring widths reflect years with low or high aridity, respectively, during the growing season. Increased aridity due to increased summer temperatures and decreased precipitation in the western Khentey compounds drought stress and thereby reduces wood formation. Larch trees of all age classes were subject to reduced stem growth in the late 20th century. This suggests that global warming is the main driving force triggering the recent changes in tree-ring width (Sarris *et al.*, 2007). Strongly reduced tree-ring widths explain the scarcity of high pointer year intensities in the late 20th century implying that the current inter-annual variation of climate is already beyond favorable growth conditions for Siberian larch, even in relatively cool and moist years. The coolest and moistest years in

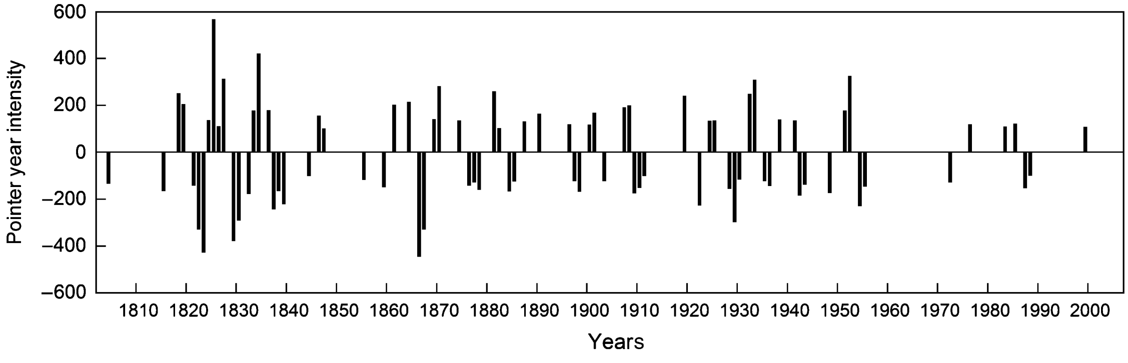

Fig. 4 Pointer year intensities (mean values of sites A, B, and C) exceeding the threshold of ±100.

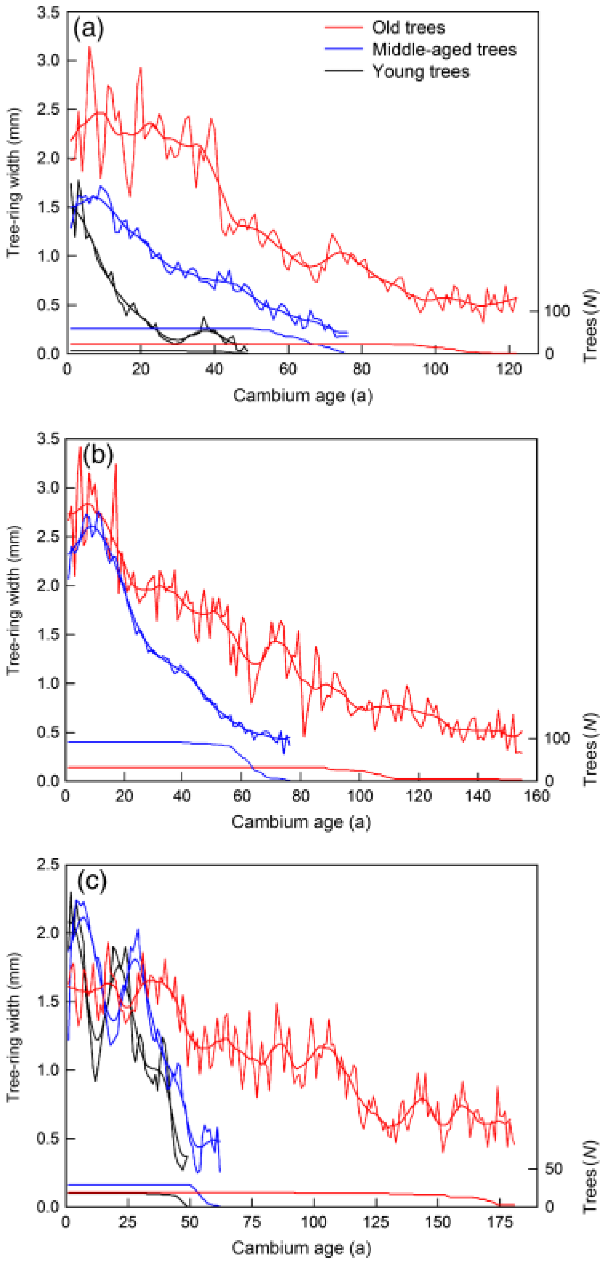

Fig. 5 Regional growth curves (RGC) for old (>90 years), middle-aged (50–90 years), and young (<50 years; if applicable) Siberian larch trees from the forest interior at sites A (a), B (b), and C (c).

the most recent decades are in the range of years with average temperature or precipitation at the beginning of weather recording in the study area (Figs 1b and 2b).

More severe drought stress in trees from the forest interior than in trees from the forest line to the steppe seems to contradict our conclusions, as the forest line has a hotter and drier microclimate than the forest interior (Bannikova, 2003; Dulamsuren & Hauck, 2008). This more severe drought stress was indicated by lower shoot water potentials and lower tree-ring widths in interior than edge trees. Furthermore, Dulamsuren *et al.* (2009a) found higher stomatal conductance in the larch trees from the forest edge than from the interior. There are two possible explanations for these observations which would be consistent with the conclusion that increased drought stress due to global warming was the cause for the reduced tree-ring widths in the trees from either habitat. Firstly, trees from the forest line could be better adapted to drought, as they were always exposed to a more extreme microclimate than trees of the forest interior. This would be plausible as adaptiveness to microclimate in conifers is already determined during seed formation (Greenwood & Hutchinson, 1996; Rehfeldt *et al.*, 1999). Secondly, the current stand density in the forest interior was developed under lower evaporative demand of the atmosphere than today, resulting in fierce competition of the trees for water with increased aridity. There is no reason to assume that stand density increased during the late 20th century, because regeneration ceased after the 1950s. Furthermore, the area was subject to a short period of logging after 1978 (Schlütz *et al.*, 2008). The effect is visible in a short increase of annual tree-ring width in the 1980s (Fig. 7). If increased stand density, rather than global warming, was crucial for the growth declines in the late 20th century, then logging should have led to a permanent recovery of the annual tree-ring widths onto early 20th century levels. Compared with the interior, competition for water is less severe at the forest line, as other factors than microclimate, including herbivory, also cause a low stand density (Dulamsuren *et al.*, 2008; Hauck *et al.*, 2008). Already Allen & Breshears (1998) and López *et al.* (1998) highlighted the significance of tree density for drought resistance of forests on the stand level in forest communities regularly suffering from water constraints.

The better current performance at the forest edge than in the forest interior does not mean that the trees at the forest edge would have the potential to encroach onto the steppe. Since the steppes of the western Khentey are limited to south-facing slopes, whereas the larch taiga grows on north-facing slopes (Dulamsuren *et al.*, 2005a, b), the microclimate in front of the forest line changes rapidly to more xeric conditions with increasing distance from the forest (Dulamsuren & Hauck, 2008). Therefore, individual larch trees, which were able to establish some 10 m in front of the closed forest regularly suffer from drought stress (Dulamsuren *et al.*, 2009a). The establishment of seedlings under the current climatic conditions is virtually impossible, as shown in sowing and planting experiments

Table 2 Mean slopes of the linear regression lines calculated for the annual increment versus time for the first 55 cambial years of Siberian larch trees belonging to two age classes in the forest interior of light taiga forests or at the forest line to the steppe

	Slope			*N*		Year of oldest tree-ring†	
Site	Old‡	Mid	*P**	Old	Mid	Old	Mid
Forest interior							
Site A	−1.89 ± 0.47	−2.72 ± 0.18	0.04	19	55	1886–1914	1927–1953
Site B	−2.86 ± 0.27	−4.05 ± 0.18	<0.001	33	85	1849–1923	1929–1952
Site C	−0.94 ± 0.36	−2.88 ± 0.27	<0.001	20	11	1797–1916	1946–1953
Forest edge							
Site A	−2.02 ± 0.53	−3.82 ± 0.61	0.04	12	13	1847–1920	1938–1953
Site B	−2.02 ± 0.53‡	−4.59 ± 0.33	<0.001	12	25	1847–1920	1938–1953
Site C	0.36 ± 0.57	−1.56 ± 0.62	0.02	7	11	1890–1911	1943–1953

*Results of *t*-test.

†As trees with the first tree-ring formed at least 85 years ago were absent from the forest edge at site B, data from the forest line at site A were used for a comparison with middle-aged trees at site B.

‡Old, old trees (cambial age >90 years); Mid, middle-aged trees (50–90 years).

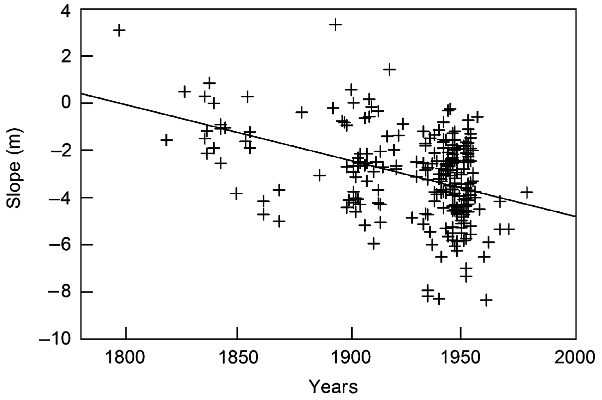

Fig. 6 Slope of the linear regression calculated for the increment in Siberian larch vs. time during the first 55 cambial years plotted against the year of the oldest tree-ring in the sampling height at 1 m above the ground. Sample trees from the forest interior of sites A, B, and C of relevant age are pooled ($r = -0.42$, $P < 0.001$, $y = 42.6–0.02\ x$, $N = 241$).

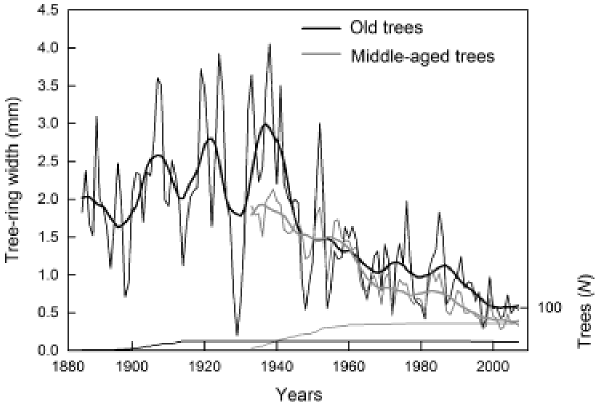

Fig. 7 Tree-ring widths of Siberian larch from the forest interior of site A. Old trees (cambial age >90 years) show an overall trend for annually increasing growth until the 1940s and reduced afterwards. Middle-aged trees (50–90 years) exhibit a negative trend for annual increment right from the beginning in the 1940s.

(Dulamsuren *et al.*, 2008) and by the absence of recent young growth.

Drought-induced growth reductions are unlikely to result in changes of the distribution of Siberian larch on the short run, because the competition by other trees is low (Dulamsuren *et al.*, 2005a). The lack of recent regeneration, however, is an acute threat for the larch forests, as they might fail to compensate for losses from fire, insect herbivory or natural mortality (Tsogtbaatar, 2004). Based on our longstanding field experiences in the western Khentey, seedlings and saplings of Siberian larch are generally virtually absent from the mountain slopes of the entire area. They do occur in the floodplains of river valleys and in high-elevation forests, which are also a habitat of Siberian larch (Dulamsuren *et al.*, 2005a). This means that present larch regeneration is limited to the moistest sites of the area and suggests that its lack at the other sites is due to increased aridity. This conclusion agrees with experimental results from the area that rates of germination and seedling performance in Siberian larch are inversely correlated with soil temperature and soil drought (Dulamsuren *et al.*, 2008). The marked peak in regeneration from the late 1920s to the late 1940s coincides with high annual increment of already established trees and with above-average precipitation throughout north-eastern Asia (Quian & Zhu, 2001; Zhang *et al.*, 2003). Livestock grazing is not likely to have caused the observed changes in the regeneration patterns. The study area is traditionally avoided by nomads and, with it, a rare

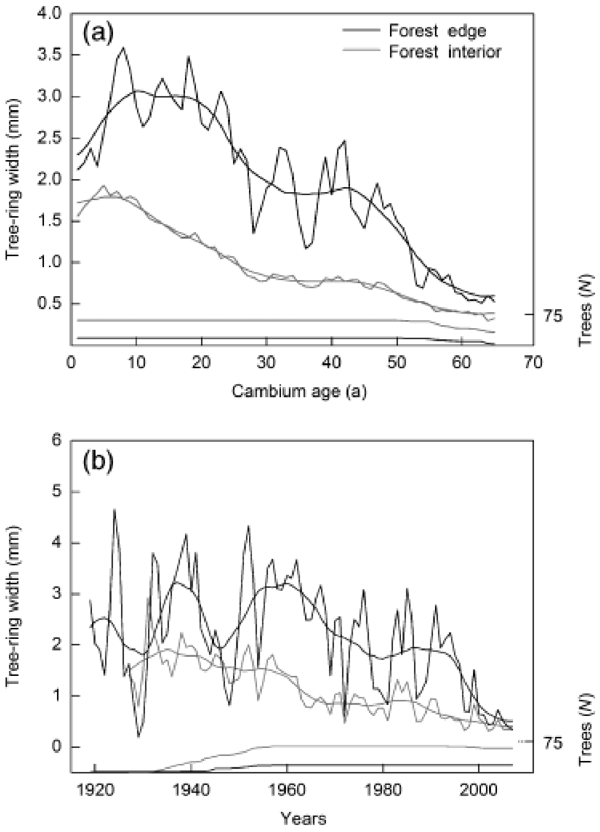

Fig. 8 Regional growth curves (RGC) (a) and tree-ring series related to the calendar year (b) for middle-aged (50–90 years) trees of Siberian larch at the forest line to the steppe and in the forest interior of site B.

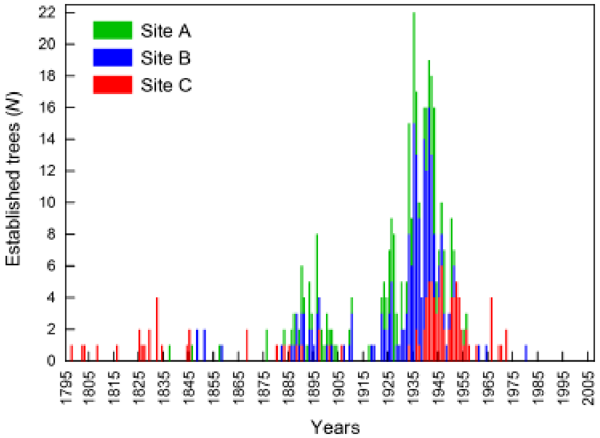

Fig. 9 Regeneration of Siberian larch in the forest interior at sites A, B, and C.

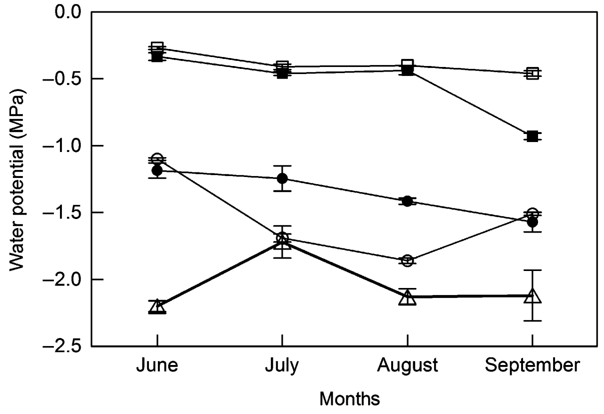

Fig. 10 Seasonal variation of shoot water potentials in Siberian larch in the interior of light taiga forest (120 m behind the forest line) and at the forest edge towards the steppe. Ψ_m, forest interior (open circles); Ψ_m, forest edge (filled circles); Ψ_p, forest interior (open squares); Ψ_p, forest edge (filled squares); Ψ_0 (triangles); $N = 3$.

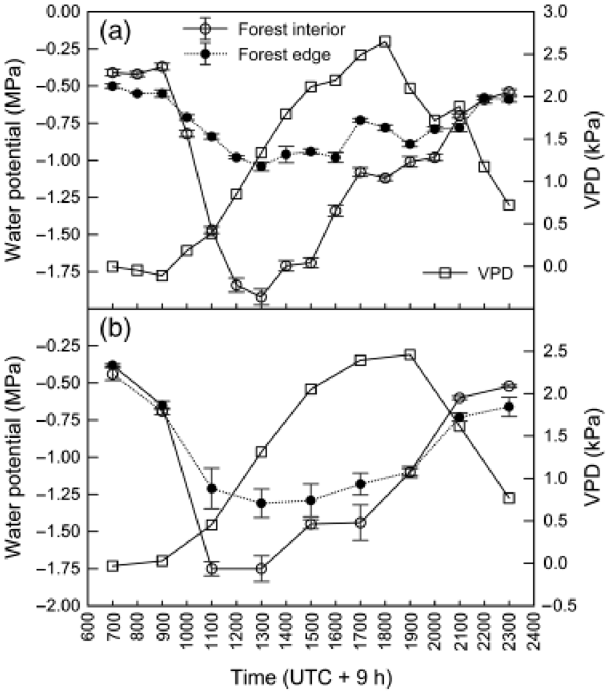

Fig. 11 Diurnal variation of shoot water potentials (Ψ) in Siberian larch in the interior of light taiga forest (120 m behind the forest line) and at the forest edge towards the steppe on (a) July 31, 2006 and (b) August 23, 2006 ($N = 3$).

exception within Mongolia (Schlütz *et al.*, 2008). The peak in regeneration in the 1930s and 1940s for climatic reasons also doubt inferences of Sankey *et al.* (2006), who attributed a simultaneous peak of larch regeneration at Lake Khovsgol, north-western Mongolia to grazing patterns rather than climate. Lacking regeneration on the mountain slopes of the western Khentey is correlated with the lack of cones since many years (personal observations). Hence, forest fires cannot play a major role at inhibiting regeneration by killing seedlings and saplings. Rather, prolonged warming apparently strongly reduced the ability of Siberian larch to invest carbon in reproduction.

Conclusions

In contrast to alpine forest lines where trees benefit from global warming because their growth is limited by low temperatures (Jacoby *et al.*, 1996; Moiseev, 2002; Yu *et al.*, 2005), Siberian larch at the lower forest line to the steppe is likely to be negatively affected by increasing aridity. A marked response of larch to precipitation has already been shown for other forests in Eurasia in non-tree line situations (Oleksyn & Fritts, 1991; Velisevich & Kozlov, 2006). Far from the forest line, changes in growth due to changes in precipitation can at most cause shifts in the tree-species composition of forests (Tchebakova *et al.*, 2005), whereas at the geographical drought limit of forests, as in the western Khentey, reduced growth and regeneration are likely to cause a retreat of the forest. Since increasing aridity is widespread in the northern Mongolian forest belt (Batima *et al.*, 2005; Nandintsetseg *et al.*, 2007) and projected to progress during the 21st century (Sato & Kimura, 2006; Sato *et al.*, 2007a), the area covered by Siberian larch will probably be reduced in the future. This will have not only far-reaching consequences for Mongolia's biodiversity (Dulamsuren *et al.*, 2005a) and the capacity to store water or carbon (Ma *et al.*, 2003; Luyssaert *et al.*, 2008), but is also likely to have significant socio-economic implications, as Mongolia's economy largely depends on the sustainable exploitation of the country's natural resources (Erdenechuluun, 2006).

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