

Expanding forests and changing growth forms of Siberian larch at the Polar Urals treeline during the 20th century

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Abstract

The ongoing climatic changes potentially affect plant growth and the functioning of temperature-limited high-altitude and high-latitude ecosystems; the rate and magnitude of these biotic changes are, however, uncertain. The aim of this study was to reconstruct stand structure and growth forms of *Larix sibirica* (Ledeb.) in undisturbed forest–tundra ecotones of the remote Polar Urals on a centennial time scale. Comparisons of the current ecotone with historic photographs from the 1960s clearly document that forests have significantly expanded since then. Similarly, the analysis of forest age structure based on more than 300 trees sampled along three altitudinal gradients reaching from forests in the valleys to the tundra indicate that more than 70% of the currently upright-growing trees are <80 years old. Because thousands of more than 500-year-old subfossil trees occur in the same area but tree remnants of the 15–19th century are lacking almost entirely, we conclude that the forest has been expanding upwards into the formerly tree-free tundra during the last century by about 20–60 m in altitude. This upward shift of forests was accompanied by significant changes in tree growth forms: while 36% of the few trees that are more than 100 years old were multi-stem tree clusters, 90% of the trees emerging after 1950 were single-stemmed. Tree-ring analysis of horizontal and vertical stems of multi-stemmed larch trees showed that these trees had been growing in a creeping form since the 15th century. In the early 20th century, they started to grow upright with 5–20 stems per tree individual. The incipient vertical growth led to an abrupt tripling in radial growth and thus, in biomass production. Based on above- and belowground biomass measurements of 33 trees that were dug out and the mapping of tree height and diameter, we estimated that forest expansion led to a biomass increase by 40–75 t ha⁻¹ and a carbon accumulation of approximately 20–40 g C m⁻² yr⁻¹ during the last century. The forest expansion and change in growth forms coincided with significant summer warming by 0.9 °C and a doubling of winter precipitation during the 20th century. In summary, our results indicate that the ongoing climatic changes are already leaving a fingerprint on the appearance, structure, and productivity of the treeline ecotone in the Polar Urals.

Keywords: biomass, carbon sequestration, climate change, growth form, morphogenesis, Polar Ural, Siberia, treeline, tree ring, tundra

Received 9 July 2007 and accepted 11 October 2007

Introduction

The mean global temperatures of the last decade have been the warmest for the last 1000 years, and projections suggest a further increase in the average surface tem-

perature around the world (Briffa *et al.*, 1995; IPCC, 2001; Esper *et al.*, 2002). In the arctic and alpine regions, the estimated temperature anomalies for the past 100 years were twice as large as those averaged for the northern hemisphere (Kelly *et al.*, 1982). Warming is expected to have large effects on global vegetation and plant distribution, particularly in ecosystems at high

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altitudes and high latitudes, where plant growth is mainly limited by temperature (Vaganov *et al.*, 1999; Kittel *et al.*, 2000; Becker & Bugmann, 2001; Shiyatov & Mazepa, 2007).

Historic photographs as well as satellite remote sensing surveys documented that high-latitude ecosystems have changed considerably during the last century: in tundra regions of northern Alaska and central Russia, the abundance of shrubs has increased strongly (Myneni *et al.*, 1997; Shvartsman *et al.*, 1999; Silapaswan *et al.*, 2001; Sturm *et al.*, 2005), and treeline as well as forest–tundra ecotones in North America, Scandinavia, Siberia, and Urals have been shifting north- and upwards (Kullman, 2002; Moiseev & Shiyatov, 2003; Shiyatov, 2003; Esper & Schweingruber, 2004; Lloyd, 2005). Similarly, dendroecological studies show that trees at high latitudes and altitudes of the northern hemisphere have been growing better during the last decades (Paulsen *et al.*, 2000; Esper *et al.*, 2002). There are, however, also reports on decreasing tree growth in the drier regions of Interior Alaska (D'Arrigo *et al.*, 2004) and Middle Siberia (Vaganov *et al.*, 1999). In contrast to the growth of individual trees, little is known about the impact of climatic changes on the growth forms and growth strategies of trees. At the fringe of their distribution, boreal trees grow in a number of growth forms (creeping, single-, and multi-stem), and they are able to adapt their growth form to environmental changes (Gorchakovskiy & Shiyatov, 1985; Weisberg & Baker, 1995; Pereg & Payette, 1998; Goroshkevich & Kustova, 2002; Holtmeier, 2003). However, there is no quantitative understanding on the development and the timing of these growth forms, and to date only few attempts have been made to link the dynamics of growth forms to the changes in climatic conditions (Goroshkevich & Kustova, 2002).

Forest expansions into former tundra could induce positive and negative feedbacks of ecosystems with climate (Chapin *et al.*, 2000). While increasing tree biomass sequesters carbon from the atmosphere and thus would lead to a negative feedback, decreasing albedo through increasing tree cover would amplify atmospheric heating, particularly during the snow-covered season. For arctic Alaska, Chapin *et al.* (2005) estimated that the potential heating effect by expanding forests exceeds the climatic effects induced by a doubling of atmospheric CO₂. However, treeline advances and forest establishment lag behind anthropogenic climatic change, and rates of change differ strongly among sites, which add great uncertainties in predicting the feedbacks between terrestrial ecosystems and climate (Chapin *et al.*, 2005; Lloyd, 2005).

The remote Polar Urals are an ideal place for studying the response of ecosystems to climatic change, as they have been impacted by humans only negligibly and show no signs of forest fires in more than 1000-year long

tree-ring records (Mazepa, 2005; Shiyatov *et al.*, 2005). The aim of our study was to estimate how the forest–tundra ecotone of the remote Polar Ural Mountains and the morphogenesis of Siberian larch have changed during the last centuries. Our specific objectives were

- (1) to quantify the distribution and biomass of different growth forms along altitudinal gradients across the treeline ecotone,
- (2) to reconstruct how forest structure and growth forms have changed in time and space,
- (3) to estimate how changes in the forest–tundra ecotone have affected carbon storage, and
- (4) to examine if these changes are driven by observed climatic change.

Materials and methods

Study area

The study was conducted on the eastern slope of the Polar Urals, Russia (66°49'N, 65°35'E) at the foot of the Rai-Iz massif (Fig. 1). Climatic data of the Salekhard meteorological station (55 km south-east of the study site) show a mean annual temperature of –6.4 °C (1883–2000). The coldest month is January (–24.0 °C) and the warmest is July with +14.1 °C. The growing season lasts about 60 days, from mid-June to early August. Mean annual precipitation amounted to 415 mm in the period of 1891–2000. Prevailing winds are from the west (Shiyatov & Mazepa, 1995). The vegetation in the remote study area has never been influenced by humans (Shiyatov *et al.*, 2005) and was not influenced by fire, at least not during the last millennium (Mazepa, 2005). The treeline ecotone reaches from 140 to 270 m a.s.l. and is dominated by Siberian larch (*Larix sibirica* Ledeb.) in association with Siberian spruce (*Picea obovata* Ledeb.) and mountain birch (*Betula tortuosa* Ledeb.). The understorey vegetation consists of different tree shrubs (*Betula nana* L., *Salix phylicifolia* L.), dwarf shrubs (e.g. *Vaccinium uliginosum* L., *Empetrum hermaphroditum* Hagerup., *Dryas octopetala* L., *Arctous alpina* L.), and herbs (e.g. *Bistorta major* S. F. Gray, *Thalictrum alpinum* L., *Solidago lapponica* With). In the ground layer, mosses (*Dicranum majus*, *Aulacomium palustre*, *Hylocomium splendens*) and lichens (*Cetraria islandica*, *Cladina arbuskula*) prevail (cf. Peshkova & Andreyashkina, 2006).

In the present study, we evaluated the dynamics of stand structure and tree growth forms along three altitudinal transects (eastern, north-eastern, south-eastern slopes) reaching from the closed larch forest to the tundra with isolated trees. The three transects covered an altitudinal range of approximately 100 m and stretched over a distance of 0.77–1.85 km. On each

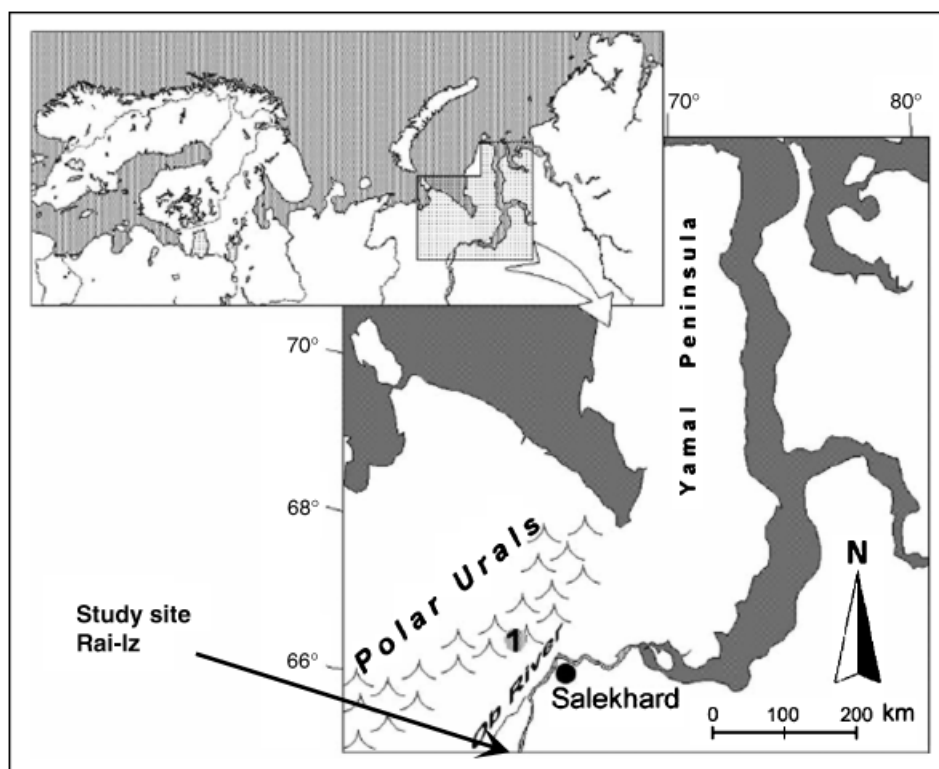


Fig. 1 Location of the study area in the Polar Urals.

Table 1 Characteristics of tree stands along the altitudinal transects in the Polar Urals

	Transect (slope)	Tundra – species line	Sparse tree growth	Open forest	Closed forest
Altitude (m a.s.l.)	East	299	nd	220	183
	Northeast	265	nd	240	220
	Southeast	265	240	235	197
Number of plots	East	12	nd	12	12
	Northeast	12	nd	12	12
	Southeast	20	28	20	4
Tree density (trees ha ⁻¹)	East	17	nd	475	450
	Northeast	142	nd	875	350
	Southeast	105	114	565	2350
Saplings (n ha ⁻¹)	East	82	61	178	37
	Northeast	0	nd	45	55
	Southeast	nd	nd	nd	nd

nd, not determined.

transect, we established numerous 10 m × 10 m plots in four typical categories of the forest–tundra ecotone (Shiyatov *et al.*, 2005): (1) *tundra with isolated trees*, the species line (> 50 m distance between trees, 44 plots); (2) *sparse tree growth* (20–50 m between trees, 28 plots); (3) *open forests* (7–20 m between trees, 44 plots); and (4) *closed larch forests* with few Siberian spruces (*P. obovata* L.) (< 7 m between trees, 28 plots). The main characteristics of the three altitudinal transects are shown in Table 1.

Reconstruction of forest structure

Approach. Our approach to reconstruct stand structure of the forest–tundra ecotone was first to map and measure morphometric variables of trees and second to determine tree ages using dendrochronological methods. A prerequisite for the reconstruction was that the current tree generation was the first one (i.e. that there was no antecedent living tree generation). Because thousands of more than 500-year-old dead tree

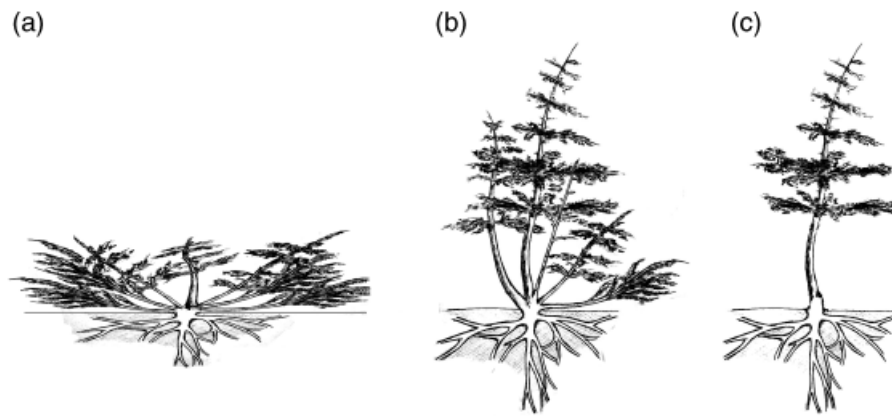


Fig. 2 Growth forms of Siberian larch: (a) creeping, (b) multi-stem and (c) single-stem.

stems occur on the slopes (Shiyatov, 2003; Mazepa, 2005), but tree remnants of the 15–19th century are lacking almost entirely, the age and distribution of the current living tree generation must reflect the expansion of a ‘new’ forest in space and time.

Sampling and field work. The relative fraction (%) and characteristics of the different larch growth forms (Fig. 2) in all the four forest–tundra communities were determined on all plots of the three altitudinal transects during the summers of 2002, 2003, and 2004. In each of the plots, all trees and saplings taller than 20 cm were counted and mapped. For all trees, we recorded basic morphometric parameters such as growth form, tree height, stem diameter, crown length, and density as well as the mean distances between trees.

The age structure of the forest stands was estimated by sampling all trees of the plots along the east and north-east transect and 15% of all the trees at the south-east transect, reflecting the full spectrum of tree sizes and ages. Tree cores were taken at base height from the single-stemmed trees, while stem slices were cut at the base of the horizontal stem from creeping and multi-stemmed trees. In total, we sampled 263 single-stemmed and 63 multi-stemmed trees. In order to determine when multi-stemmed trees changed from creeping to upright growth, we cut disks of 23 tree clusters along the south-east transect with 2–17 stems at the base of their horizontal creeping stems and again at the base of the vertical stem.

Biomass of each growth form was estimated using model trees ($n = 33$). Model trees were dug out including the full rooting system, and the different compartments such as roots, stems, branches, needles, and cones were counted, measured, weighted, and subsamples were taken to the laboratory to dry them at 105 °C. The biomass of each plot was then estimated by calculating allometric functions between the measured compartment biomasses and tree height and diameter,

followed by multiplying these amounts with the mapped tree heights and diameters. Carbon storage in the biomass was calculated by multiplying biomass with 0.5.

Dendrochronological analysis

Tree or shoot age was assessed from stem disks or tree cores using standard dendrochronological methods. Tree-ring width was measured using a binocular microscope and a mechanic measure table (LINTAB, F. Rinn SA, Heidelberg, Germany). Ring widths were recorded using the TSAP program v3.5 (Time Series and Presentation Program, Rinn, 1998, <http://www.rinntech.com/>). All samples were first cross-dated visually and then checked using the software package COFECHA (Holmes, 1995), which statistically matched the undated samples against the dated larch chronology from the Polar Urals published by Shiyatov (1995). Other statistical analyses were conducted using STATISTICA 6.0.

Results

Current forest stands

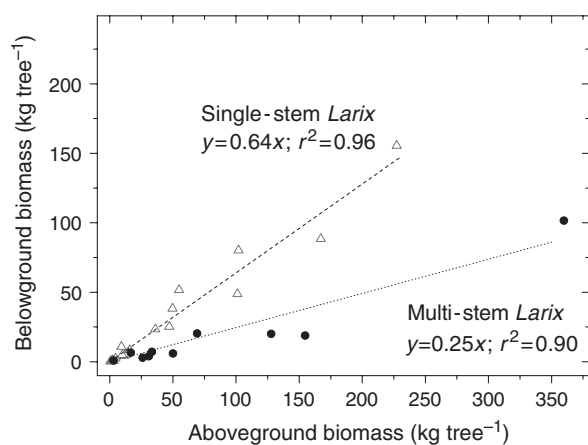
As expected, current canopy cover increased from 1% in the tundra with isolated trees to 87% in the closed forest. Tree density increased analogously (Table 1), but it differed between the three slopes. The closed forest on the south-eastern slope had a much higher tree density than the forests on the other two slopes, where trees were taller and older (Table 1). On all transects, single-stemmed larch trees were dominating with more than 80% of the tree stems (Table 2). Tree clusters with up to 20 stems per cluster (presumably representing one tree individual) occurred on all transects.

For single-stemmed larch, stem diameter, stem height, and crown diameter increased from the tundra

Table 2 Basis growth parameters of single- and multi-stemmed larch trees along three altitudinal gradients in the Polar Urals

	Transect (slope)	Tundra – species line		Sparse tree growth		Open forest		Closed forest	
		Single-stems	Multi-stems	Single-stems	Multi-stems	Single-stems	Multi-stems	Single-stems	Multi-stems
Stand	East	100	0	–	–	96 ± 3	4 ± 2.9	92 ± 4	8 ± 4
composition (%)	Northeast	75 ± 13	25 ± 13	–	–	84 ± 4	16 ± 4	62 ± 10	38 ± 10
	Southeast	43 ± 16	57 ± 16	71 ± 11	29 ± 11	81 ± 5	19 ± 5	87 ± 4	13 ± 4
Stem diameter at base (cm)	East	5.5 ± 1.5	–	–	–	12.8 ± 1.0	11.3 ± 1.6	19.6 ± 1.4	17.9 ± 4.3
	Northeast	3.9 ± 0.6	4.0 ± 0.5	–	–	5.3 ± 0.4	8.2 ± 0.7	25.1 ± 2.5	25.0 ± 2.0
Stem height (m)	Southeast	6.6 ± 0.5	10.0 ± 0.6	4.5 ± 0.4	8.5 ± 0.6	8 ± 0.6	14 ± 0.7	12.0 ± 0.7	11.0 ± 1.1
	East	1.8 ± 1.1	–	–	–	5.3 ± 0.3	4.3 ± 0.5	8.7 ± 0.6	5.9 ± 1.6
Crown diameter (m)	Northeast	1.1 ± 0.2	1.8 ± 0.2	–	–	2.2 ± 0.2	3.3 ± 0.3	8.8 ± 0.7	7.5 ± 0.6
	Southeast	2.1 ± 0.2	3.7 ± 0.2	1.4 ± 0.1	3.1 ± 0.2	2.7 ± 0.2	4.4 ± 0.2	4.8 ± 0.2	4.0 ± 0.3
Crown diameter (m)	East	1.3 ± 0.2	–	–	–	1.8 ± 0.1	1.5 ± 0.2	2.7 ± 0.2	2.3 ± 0.4
	Northeast	0.7 ± 0.1	0.7 ± 0.2	–	–	1.0 ± 0.1	1.7 ± 0.1	3.5 ± 0.3	2.9 ± 0.3
	Southeast	1.1 ± 0.1	3.0 ± 0.3	0.7 ± 0.1	1.9 ± 0.3	1.4 ± 0.1	2.6 ± 0.2	2.4 ± 0.1	3.0 ± 0.4

Means ± standard errors.

**Fig. 3** Relationship between above- and belowground biomass for single- and multi-stemmed trees.

to the closed forest (Table 2). In contrast, for multi-stemmed trees maximum morphometric parameters occurred in the open forest, whereas they decreased towards the tundra as well as towards the closed forest. Smaller average stem diameters, stem heights, and crown diameters in the area of sparse tree growth were caused by the large fraction of saplings (26%).

The relationship between above- and belowground biomass differed significantly for single- vs. multi-stemmed trees (Fig. 3). Multi-stemmed trees had only 20% of their total biomass in roots, while the roots of single-stemmed trees comprised as much as 40% of the total biomass. Relative stem biomass was significantly greater for multi-stemmed trees (Table 3). As expected,

Table 3 Biomass in stems, branches, needles, and roots of multi- and single-stemmed larches in the tundra at the upper growth limit and in the closed forest

	Tundra – species line (t biomass ha ⁻¹)		Closed forest (t biomass ha ⁻¹)	
	Single-stems	Multi-stems	Single-stems	Multi-stems
Stems	0.199 ± 0.120	1.93 ± 0.79	21.3 ± 7.2	9.0 ± 4.4
Branches	0.052 ± 0.030	0.61 ± 0.24	5.0 ± 1.6	2.7 ± 1.3
Needles	0.024 ± 0.010	0.19 ± 0.07	1.5 ± 0.4	0.7 ± 0.3
Roots	0.131 ± 0.080	0.83 ± 0.34	16.2 ± 5.6	3.8 ± 1.8

Means ± standard errors.

total carbon stocks in tree biomass increased from <5 tC ha⁻¹ in the tundra to 40 tC ha⁻¹ in the closed forest (Fig. 4).

Treeline ecotone changes in the past

The comparison of the current forest–tundra ecotone with historic photographs taken in 1962 provided clear evidence on the significant expansion of the forested area during the last decades (Fig. 5). Similar changes have been observed across large areas on the eastern slope of the Polar Urals (Shiyatov *et al.*, 2005). Moreover, tree age structure along the three transects showed that 67% of the trees emerged after 1930 (Fig. 6). Only 28% of the trees had established before 1900, mostly in the valley bottoms. Thus, the slopes were almost treeless 100 years ago. In all transects, single-stemmed trees were much younger than the multi-stemmed ones. Seventy percent of the analyzed 263 single-stemmed

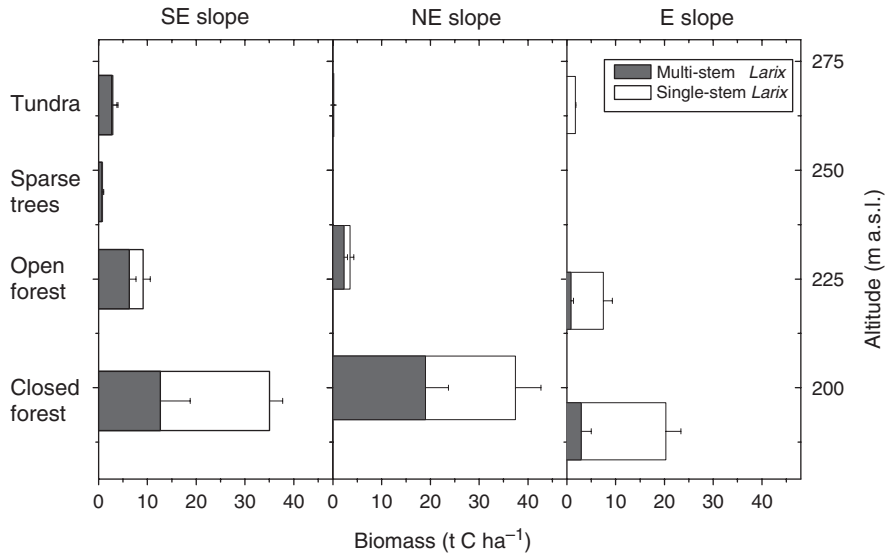


Fig. 4 Changes in biomass of single- and multi-stemmed trees along three altitudinal gradients in the Polar Urals.

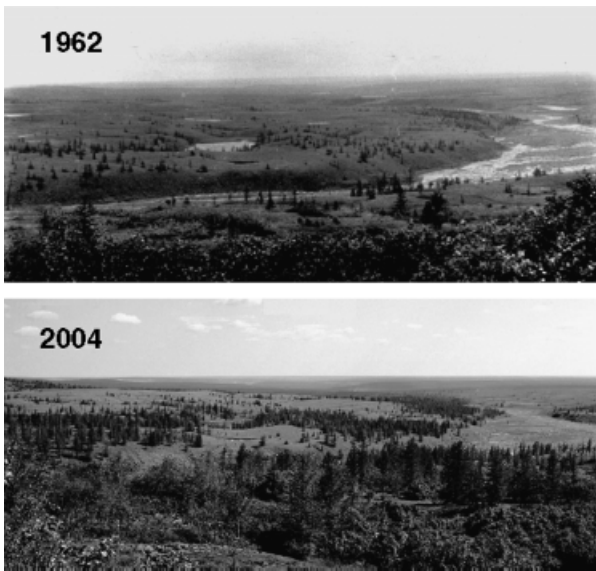


Fig. 5 Forest-tundra ecotone on the eastern slope of mountain Malaja Chernaya (Polar Urals) in 1962 and 2004 (photos Stepan Shiyatov).

trees appeared during the last 60 years, while few multi-stemmed trees were up to 300 years old and had a mean age of 140 years. In the closed forest of the eastern slope, single-stemmed trees were up to 300 years old, but they grew all in the valley bottom. The age of single-stemmed trees decreased with altitude. In the tundra and the area of sparse tree growth, 87% of the trees had emerged after 1970. In contrast, the age of multi-stemmed trees did not change with altitude. Our analysis of tree ages do not reflect tree establishment during the last two decades because we only sampled trees taller than 20 cm, which were 10–30 years old. This

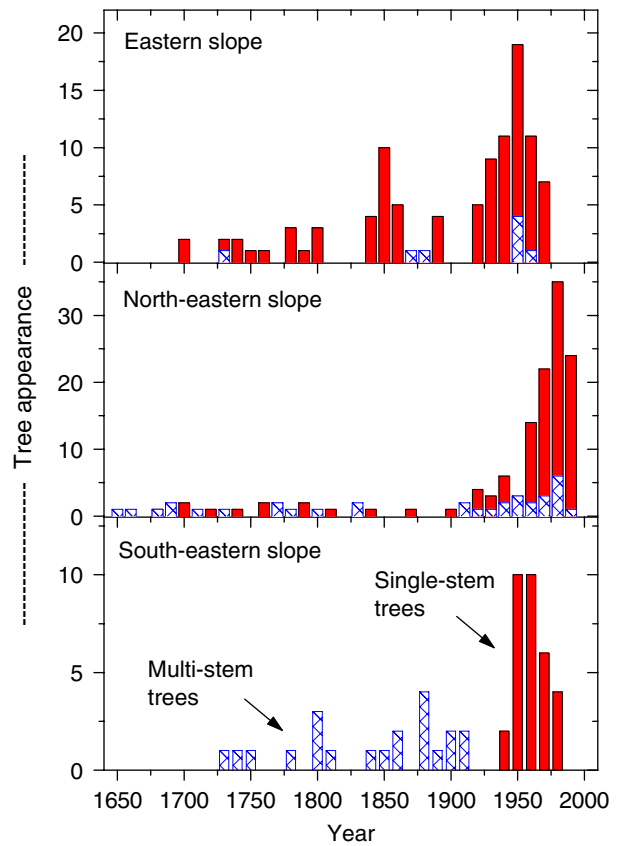


Fig. 6 Age structure of tree stands at the three altitudinal gradients. The age of multi-stemmed trees was measured at the tree base and thus, it represents tree age and not the beginning of upright growth.

time lag is also responsible for the apparent decline in tree establishment after 1970 as suggested by Figs 6 and 7. The occurrence of saplings, particularly in the

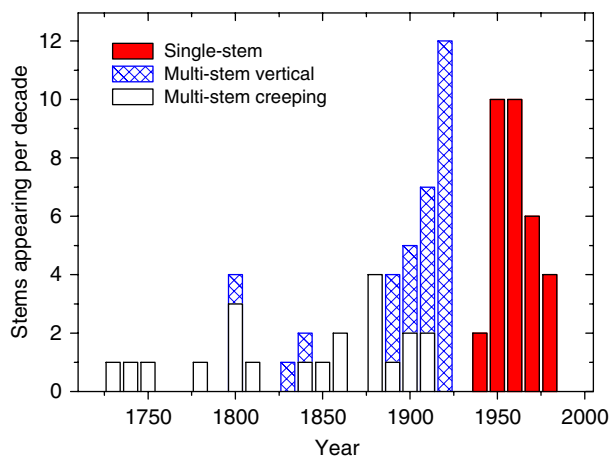


Fig. 7 Growth form changes of larch trees at the south-eastern transect.

'protected' open forest, indicates an ongoing forest expansion (Table 1).

The detailed analysis of horizontal and vertical stems of multi-stem trees showed that all the vertical stems were much younger than the horizontal ones (Figs 7 and 8). Because there were not any old vertical stems (dead or living), the vertical stems of the multi-stemmed trees must have developed from creeping trees and not from layering (enrooting of branches) of single-stemmed trees. The stem ages provide evidence on the timing of these growth-form changes: the first multi-stemmed trees appeared in the early 15th century and grew in a creeping form until the beginning of the 20th century. Vertical stems started to appear after 1900, with most of them appearing in the 1920s and 1930s (Figs 7 and 8). The change from creeping to vertical growth led to significant growth enhancements of the multi-stemmed trees, as indicated by the increases in the ring widths of the horizontal stems of multi-stemmed trees (Fig. 8). Approximately one to two decades after the stems had started to grow vertically, ring widths increased 2- to 10-fold, which were much greater than the increases in ring width of single-stemmed trees during the same period.

Climate-growth relationship

Figure 9 shows summer temperature and winter precipitation since the end of the 19th century recorded at the meteo station of Salekhard, 50 km south-east of the study area. Summer (June–August) temperatures have increased significantly during the 20th century (overall $0.9\text{ }^{\circ}\text{C } 100\text{ yr}^{-1}$, $P < 0.02$). Winter (November–March) temperatures have also increased by $1.2\text{ }^{\circ}\text{C}$ during this period, but there was no strong change between the ending of the 19th and the beginning of the 20th century

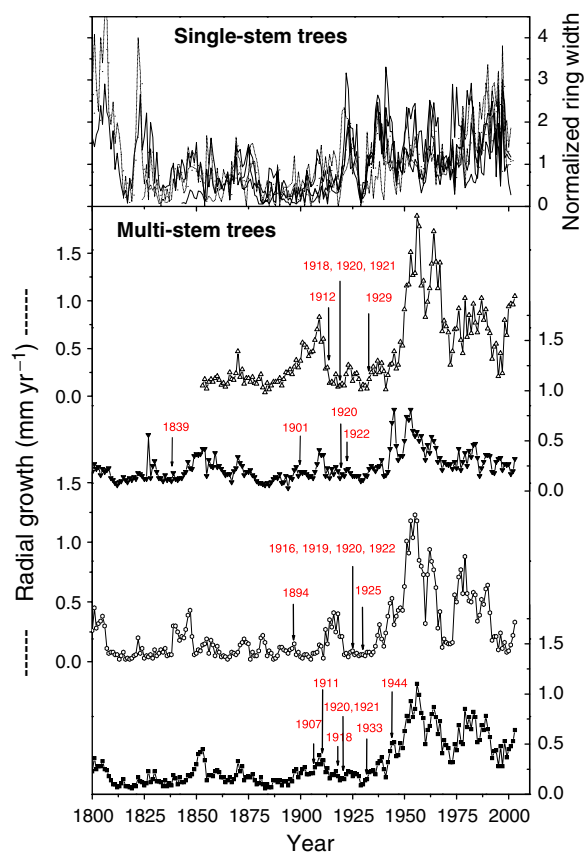


Fig. 8 Tree-ring widths of single-stemmed trees and of horizontal stems of multi-stemmed trees during the last two centuries. Each curve represents ring widths of the horizontal stem of one multi-stemmed tree cluster; the arrows indicate the beginning of vertical growth of individual stems. Annual tree ring widths of the five single-stemmed trees were normalized to mean ring widths.

as for summer temperatures. Precipitation has increased drastically. Total annual precipitation has increased from 300 mm in the year 1900 to 480 mm at present ($P < 0.001$). Winter precipitation falling as snow has more than doubled during the 20th century: it increased from a water equivalent of 50 mm in the period 1890–1910 to 120 mm in the period 1980–2000.

Ring widths of single-stemmed trees were found to be correlated significantly with annual precipitation ($r = 0.48$, $P < 0.001$) and with summer temperatures of the previous year ($r = 0.2$; $P < 0.02$), implying that climate was an important driver of tree growth. Tree appearance was most closely related not only to winter precipitation but also to summer precipitation (decadal means), particularly of the single-stems (Table 4). Similarly, growth form changes from creeping to upright were closely correlated with summer and winter precipitation, but they were also correlated significantly with the summer temperatures.

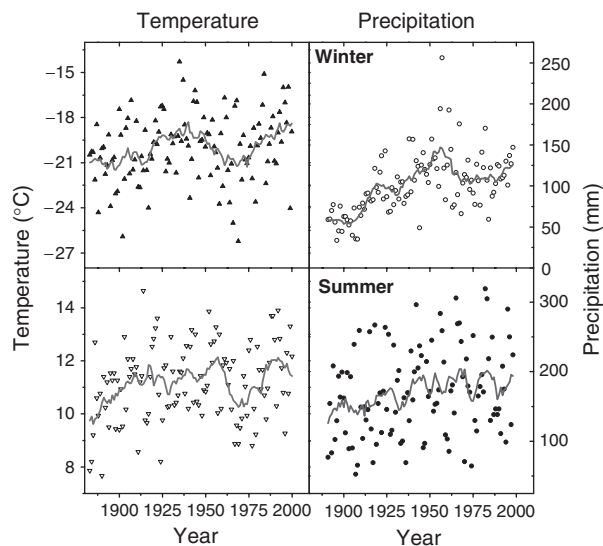


Fig. 9 Average winter and summer temperature, as well as average winter and summer precipitation at the meteorological station of Salekhard, 50 km south-east of the study area. Winter lasted from November to March; summer from June until August. Lines represent moving averages of ten years.

Discussion

Treeline advances in the Polar Ural mountains

Our results show that the forest–tundra ecotone of the Polar Urals has changed fundamentally during the 20th century. The comparison with historic photographs (Fig. 5) and an age structure analysis (Fig. 6) indicate that areas that are now covered by closed forest and have a tree density of up to 2350 trees ha^{-1} were almost treeless one century ago. Moreover, *L. sibirica*, which had been growing in a creeping form for centuries, has started to grow upright only 100 years ago (Figs 7 and 8). Today, the forest is dominated by single-stemmed trees, with 70% of the trees being <60 years old. In the same area, Shiyatov (2003) and Mazepa (2005) have found thousands of lying and upright-standing 1000-year-old subfossil trees, which all had died between the seventh and the 19th century. These remnants show (1) that climatic changes in the past had caused up- and downward shifts of the forest–tundra ecotone and (2) that subfossil wood is decomposing extremely slowly in this dry climate with extremely cold winters. Therefore, the ages and the spatial distribution of the current living tree generation mostly reflect the expansion of a ‘new’ forest in space and time. Our results show that the forests have rapidly been expanding upwards during the 20th century. If we assume that the increasing tree ages of the forest stands with decreasing altitude reflect the rate of change, this suggests that the different stages

Table 4 Relationship between tree appearance, growth form changes and climate

	Tree appearance <i>n</i> = 10–12		Growth form change (<i>n</i> = 4) Creeping-to- upright
	Single- stems	Multi- stems	
Winter temperature	0.14	0.23	0.81*
Summer temperature	0.42	0.11	0.55
Winter precipitation	0.77**	0.49	0.87*
Summer precipitation	0.71**	0.48	0.99***

Coefficients of correlations (*r*) were calculated for a decadal time scale. Winter was from November to March; summer was from June to August.

P* < 0.05; *P* < 0.01; ****P* < 0.001.

of the forest–tundra have advanced by 20–60 m in altitude over the last century. Our estimate, which is based on three altitudinal gradients covering an area of 3 km², is supported by a large-scale mapping study based on old photographs and stand structures (Shiyatov *et al.*, 2005; Shiyatov & Mazepa, 2007), which showed that forest cover increased over large areas in the Polar Urals with a mean upward shift of open forest areas by 20–50 m in altitude between 1910 and 2000. The high saplings densities in the open forest (up to 180 saplings ha^{-1} ; Table 1) indicate that forest expansion is ongoing. Similar ecosystem changes were observed at the northern treeline of Siberia, where Esper & Schweingruber (2004) reported a tree invasion into genuine treeless tundra environments during the last century. Satellite data indicate that larch forests at the mid-Siberian northern treeline have advanced northwards by 90–300 m between 1973 and 2000 (Kharuk *et al.*, 2006). For arctic Alaska, Lloyd (2005) estimated that treeline expanded by 100 m on slopes and by 2500 m on flat terrain during the last 50 years. We found a similar rate of forest expansion in the Polar Urals: on the gentle slopes, forests advanced by 100–400 m during the 20th century.

Growth form changes

The upward expansion of forests was accompanied by significant changes in tree growth forms (Figs 7 and 8). Larches that had been growing in a creeping form since the 15th century started to grow upright at the beginning of the 20th century, with up to 20 stems per tree individual. More than 90% of the trees emerging after 1950 are single-stem ones. At present, they are already dominating the forest 50 m below the species line (Table 2). The changes of multi-stemmed trees from creeping

to vertical growth led to a 2- to 10-fold increase in radial growth of the creeping stems (Fig. 8). We mainly attribute these strong increases in ring width to the higher photosynthetically active needle area from several emerging vertical stems. More favorable climatic conditions might also have contributed to the growth enhancements, but the increases in ring widths of the horizontal stems of multi-stemmed trees were much greater and more abrupt than the climatic-driven increases in the ring widths of single-stemmed trees (Fig. 8).

According to our tree-ring analysis, vertical stems of multi-stemmed larch trees emerged during a relatively short period [i.e. only a few decades (Figs 7 and 8)]. This contrasts with the behavior of 'mobile', 500-year-old tree islands in the Colorado Front Range, where windward edges are dying back and new stems are emerging over long periods on the leeward side (Marr, 1977; Benedict, 1984). Our age analysis of horizontal and vertical stems indicate that in the Polar Urals vertical growth of multi-stemmed larch is a much more recent phenomenon, and because climatic conditions have apparently been changing rapidly, multi-stemmed trees are very likely only a transitional growth form. Single-stemmed larches are dominating already now 50 m below current treeline. Therefore, when conditions are becoming slightly more favorable, larch seedlings can succeed as single stems, and they do not first grow in a creeping form before they start to grow upright. As multi-stems are a transitional growth form, they are indicators for changing growth conditions that can easily be dated using dendrochronological methods.

Biomass changes

Our biomass estimates for the different growth forms indicate that multi-stemmed trees had significantly smaller root-to-shoot ratios than single-stemmed ones (Fig. 3). The 36% of single-stem biomass in roots correspond fairly well with the 27% root fraction estimated by Bernoulli & Körner (1999) at upper treeline in Switzerland. However, in the Polar Urals, multi-stemmed trees had only 18% of their biomass in roots. This lower investment in roots may suggest that nutrients and water were not strongly growth limiting. Also, multi-stemmed trees may require less below-ground biomass for the mechanical stabilization of upright growth, as the tree stems that are growing side by side may be protecting one another.

Overall, carbon stocks in biomass have increased from $3 \pm 1 \text{ tC ha}^{-1}$ in the tundra to $38 \pm 4 \text{ tC ha}^{-1}$ in the closed forest (Fig. 4). Our age structure analysis indicates that these biomass changes occurred during the last century, which suggests that approximately 20–

$40 \text{ g C m}^{-2} \text{ yr}^{-1}$ had been sequestered in tree biomass of expanding forests in the valleys, and $<5 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the tundra with sparse tree growth. Intuitively, one would assume that the striking forest establishment in formerly tree-free tundra would cause a significant sequestration of carbon in its biomass. However, the carbon accumulation rates are smaller than in managed (but faster growing) forests of the temperate zone. For instance, Janssens *et al.* (2003) estimated that the mean C uptake by Europe's forest amounts to $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ although the greatest fraction of net growth is removed through harvest. We therefore conclude that the current upward expansion of forest at the altitudinal treeline has been of minor importance for C sequestration to date, as trees grow quite slowly under these conditions. However, the appearance, structure and very likely also the functioning of these ecosystems change fundamentally.

Treeline changes driven by increased winter precipitation?

Because the study areas in the Polar Urals have hardly been affected by humans (Shiyatov *et al.*, 2005), we attribute the upward shift of forest and the change in growth forms primarily to the distinct climatic changes during the last century. Temperature records from the nearby Salekhard weather station show that mean summer temperatures have increased from $<10^\circ\text{C}$ before 1900 to more than 11°C after 1920, and precipitation has increased from 300–480 mm from 1900 until 2000 (Fig. 9). Tree-ring studies in the Polar Urals and Northern Siberia have found that radial growth is closely related to summer temperature, in particular to early summer temperature (Vaganov *et al.*, 1999; Esper *et al.*, 2002). Here, the ring widths of single-stemmed trees were found to be correlated most closely with temperatures of the previous summer (Fig. 8). We, however, suggest that for the change in growth form and for tree establishment (and thus tree survival), changes in winter conditions are likely to have been significant as well. Tree appearance and growth form changes were correlated significantly with winter precipitation (Table 4), which has roughly doubled at the beginning of the 20th century (Fig. 9): it increased from 56 mm yr^{-1} in 1891–1910 to 102 mm yr^{-1} in 1921–1940 and to 128 mm yr^{-1} in 1941–1960. Similar increases during the 20th century were measured across Russia, Canada, and Alaska (Groisman *et al.*, 1994; Vaganov *et al.*, 1999; Sturm *et al.*, 2005). Snow cover plays a key role in the protection of young trees from frost and wind damage (Holtmeier, 2003). Because trees affect snow accumulation, the increase in snowfall might have induced a positive feedback with more snow allowing trees to grow better, and

bigger trees promoting the accumulation of additional snow. Moiseev *et al.* (2004) observed a similar upward expansion of forests into former tundra areas in the Southern Urals, which they related to increases in winter precipitation. At northern treeline in Canada, Pereg & Payette (1998) also found that changes in the growth forms of black spruce from creeping to vertically growing trees were correlated with increasing snow depth. For northern Alaska, where shrub abundance has been strongly increasing during the last decades, Sturm *et al.* (2005) proposed positive feedbacks loop between snow depth and plant growth: more snow and, as a consequence, higher soil temperatures in winter promote microbial activity, which leads to more plant-available nitrogen and better plant growth, which in turn enhances snow accumulation. In contrast to these positive effects on tree establishment, tree-ring records across northern Siberia indicate that the increasing snowfall has probably reduced wood production by delaying snow melt and thus, the beginning of cambial activity (Vaganov *et al.*, 1999; Kirilyanov *et al.*, 2003). This suggests that the increasing winter precipitation observed in northern regions could have contrasting effects on the growth of young vs. older trees.

Conclusions

Historic photographs and tree age structure analyses indicate that remote areas of the forest–tundra ecotone in the Polar Urals have changed significantly during the 20th century. The distribution of Siberian larch has been shifting upwards by 20–60 m in altitude, and today young larch trees are growing in formerly treeless tundra. Since 1900, growth forms of larch have started to change from creeping growth that prevailed over centuries to upright growth as multi-stemmed trees. At the same time, single-stemmed trees have commenced to establish. At present, the single-stemmed larches are dominating the forest 50 m below the species line. The expanding forest led to an increase of biomass by 40–75 t ha⁻¹ and a carbon sequestration of approximately 20–40 g C m⁻² yr⁻¹ during the last century, which is, however, small compared with temperate forests. The forest expansion and change in growth forms coincided with a significant warming in summer and a doubling of winter precipitation, thus drastically changing snow conditions. In summary, our study shows that the ongoing climatic changes are altering the composition, structure, and growth forms of Siberian larch in undisturbed treeline ecotones of the Polar Urals.

Acknowledgements

This work was supported by the Russian Foundation for Basic Research, project no. 04-04-48687 and the INTAS grants nos. 01-0052 and 04-83-3788.

References

- Becker A, Bugmann H (2001) *Global Change and Mountain Regions: The Mountain Research Initiative*. IGBP Report 49. IGBP Secretariat, Stockholm, Sweden.
- Benedict JB (1984) Rates of tree-island migration, Colorado Rocky Mountains, USA. *Ecology*, **65**, 820–823.
- Bernoulli M, Körner C (1999) Dry matter allocation in treeline trees. *Phyton*, **39**, 7–11.
- Briffa KR, Jones PD, Schweingruber FH, Shiyatov SG, Cook ER (1995) Unusual twentieth-century summer warmth in the 1000-year temperature record from Siberia. *Nature*, **376**, 156–159.
- Chapin FS III, McGuire AD, Randerson J *et al.* (2000) Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology*, **6**, 211–223.
- Chapin FS III, Sturm M, Serreze MS *et al.* (2005) Role of land-surface changes in arctic summer warming. *Science*, **310**, 657–660.
- D'Arrigo RD, Kaufmann RK, Davi N, Jacobi GC, Laskowski Ch, Myreni RB, Cherubini P (2004) Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. *Global Biogeochemical Cycles*, **18**, GB3021, doi: 10.1029/2004GB002249.
- Esper J, Cook ER, Schweingruber FH (2002) Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science*, **295**, 2250–2253.
- Esper J, Schweingruber FH (2004) Large-scale treeline changes recorded in Siberia. *Geophysical Research Letters*, **31**, L06202, doi: 10.1029/2003GL019178.
- Gorchakovskiy PL, Shiyatov SG (1985) *Phytoindication of the Environmental Conditions and Natural Processes in the Alpine Terrain*. Nauka, Moscow.
- Goroshkevich SN, Kustova EA (2002) Morphogenesis of the creeping life form of Siberian cedar at the upper limit of proliferation in West Sayan Mountains. *Russian Journal of Ecology*, **4**, 243–249.
- Groisman PY, Kokpaeva VV, Belokrylova TA, Karl TR (1994) Area-averaged precipitation over the main part of the former USSR. In: *Trends '93: A Compendium of Data on Global Change* (eds Boden TA, Kaiser DP, Sepanski RJ, Stoss FW), pp. 906–910. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge ORNL/CDIAC-65.
- Holmes RL (1995) *Dendrochronological Program Library (Computer Program)*. Laboratory of Tree Ring Research, The University of Arizona, Tucson, AZ.
- Holtmeier F-K (2003) *Mountain Timberlines. Ecology, Patchiness, and Dynamics*. Kluwer, Dordrecht.
- IPCC (2001) *Synthesis Report. Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (ed. Watson RT). EarthPrint, Stevenage.

- Janssens IA, Freibauer A, Ciais Ph *et al.* (2003) Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO₂ emissions. *Science*, **300**, 1538–1542.
- Kelly PM, Jones PD, Sear CB, Cherry BSG, Tavakol RK (1982) Variations in surface air temperature: part 2. Arctic regions. 1881–1980. *Monthly Weather Review*, **110**, 71–82.
- Kharuk VI, Ranson KJ, Im SN, Naurzbaev MM (2006) Forest-tundra larch forests and climatic trends. *Russian Journal of Ecology*, **37**, 291–298.
- Kittel TGF, Steffen WL, Chapin FS (2000) Global and regional modelling of arctic-boreal vegetation distribution and its sensitivity to altered forces. *Global Change Biology*, **6**, 1–18.
- Kirdyanov A, Hughes M, Vaganov E, Schweingruber F, Silkin P (2003) The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. *Trees – Structure and Function*, **17**, 61–69.
- Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, **90**, 68–77.
- Lloyd AH (2005) Ecological histories from Alaskan tree lines provide insight into future change. *Ecology*, **86**, 1687–1695.
- Marr JW (1977) The development and movement of tree islands near the upper limit on tree growth in the Southern Rocky Mountains. *Ecology*, **58**, 1159–1164.
- Mazepa VS (2005) Stand density in the last millennium at the upper timberline ecotone in the Polar Ural Mountains. *Canadian Journal of Forest Research*, **35**, 2082–2091.
- Moiseev PA, Shiyatov SG (2003) Vegetation dynamics at the tree-line ecotone in the Ural Highlands, Russia. *Ecological Studies*, **167**, 423–435.
- Moiseev PA, Van der Meer M, Rigling A, Shevchenko IG (2004) Effect of climatic changes on the formation of Siberian spruce generations in subgoltsy tree stands of the Southern Urals. *Russian Journal of Ecology*, **35**, 135–143.
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.
- Paulsen J, Weber UM, Korner C (2000) Tree growth near treeline: abrupt or gradual reduction with altitude? *Arctic, Antarctic, and Alpine Research*, **32**, 14–20.
- Pereg D, Payette S (1998) Development of black spruce growth forms at tree-line. *Plant Ecology*, **138**, 137–147.
- Peshkova NV, Andreyashkina NI (2006) Indicatory aspect of the geographic analysis of plant communities with respect to floristic composition on mountain slopes differing in expose (the Polar Urals). *Russian Journal of Ecology*, **37**, 103–108.
- Rinn F (1998) *TSAP V 3.5: Computer Program for Tree-Ring Analysis and Presentation*. Frank Rinn Distribution, Germany.
- Silapaswan CS, Verbyla DL, McGuire AD (2001) Land cover change on the Seward Peninsula: the use of remote sensing to evaluate the potential influences of climate warming on historical vegetation dynamics. *Canadian Journal of Remote Sensing*, **27**, 542–554.
- Shiyatov SG (1995) Reconstruction of climate and the upper timberline dynamics since AD 745 by tree ring data in the Polar Ural mountain. In: *Proceedings of the SILMU Conference: International Conference on Past, Present and Future Climate, Helsinki* (ed. Heikinheimo P), pp. 144–147. Publication of the Academy of Finland 6, Helsinki, Finland.
- Shiyatov SG (2003) Rates of change in the upper tree-line ecotone in the Polar Ural mountains. *Pages News*, **11**, 8–10.
- Shiyatov SG, Mazepa VS (1995) Climate. In: *The Nature of Yamal* (ed. Dobrinsky LN), pp. 32–68. Nauka Publishers, Ekaterinburg, Russia.
- Shiyatov SG, Mazepa VS (2007) Climatogenic dynamics of forest-tundra vegetation at the Polar Urals. *Lesovedenie*, **6**, 37–48.
- Shiyatov SG, Terent'ev MM, Fomin VV (2005) Spatiotemporal dynamics of forest-tundra communities in the Polar Urals. *Russian Journal of Ecology*, **36**, 69–75.
- Shvartsman YG, Barzut VM, Vidyakina SV, Iglovsky SA (1999) Climate variations and dynamic ecosystems of the Arkhangelsk region. *Chemosphere: Global Change Science*, **1**, 417–428.
- Sturm M, Schimel J, Michaelson G *et al.* (2005) Winter biological processes could help convert Arctic tundra to shrubland. *BioScience*, **55**, 17–26.
- Vaganov EA, Hughes MK, Kirdyanov AV, Schweingruber FH, Silkin PP (1999) Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, **400**, 149–151.
- Weisberg PJ, Baker WL (1995) Spatial variation in tree seedling and krummholz growth in the forest – tundra ecotone of Rocky Mountain National Park, Colorado, U.S.A. *Arctic and Alpine Research*, **27**, 116–129.