Climate-Driven Dynamics of the Forest-Tundra Vegetation in the Polar Ural Mountains

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Abstract—The paper presents the results of long-term studies of the effect of climate changes on the structure, productivity, and spatial distribution of forest-tundra communities growing in the upper treeline ecotone on the east-facing macroslope of the Polar Ural Mountains, in the Sob' River basin. The study reveals variations in the stand age structure, density, productivity, and the altitude of the upper line of larch open forests and closed forests over the last 1000 years. These results were compared to long-term variations in summer temperature reconstructed using tree-ring analysis. Spatiotemporal dynamics of the forest-tundra communities was analyzed in detail in relation to the 20th century climate warming.

Most records across the Arctic show a widespread transition from cold conditions of the 19th century to warm conditions of the 20th century, with local warming of 1–3°C that average ~1.5°C across the Arctic domain [1]. The region has experienced higher warming rates over the last 30 years and the process has been accelerating at unprecedented rates over the last decade [2]. 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 temperature around the world [3–5]. 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 [6]. Warming is expected to have large effects on global vegetation and plant distribution, particularly in ecosystems at high altitudes and high latitudes, where plant growth is mainly limited by temperature [7, 8].

Today, spatiotemporal studies of forest-tundra and forest-grassland plant communities in high mountains are given considerable but deserved consideration because of the opportunity and necessity to evaluate their responses to what is widely considered to be anomalous 20th century warming [9–11]. The montane plant communities growing at high latitudes are of particular interest because of the magnitude of climate change observed in instrumental records at these locations [12]. The pace and pattern of biotic response to climate variation on scales of decades to centuries is highly relevant to understanding the potential ecological consequences of anthropogenically induced climate change [13]. Conducting such research in "natural" or largely undisturbed areas where human impact is minimal is highly desirable.

Patterns of plant population response to climate variation are most clearly observed at climatically determined ecotones, where the abiotic environment is the ultimate control over ecological processes [14]. Following Ch. Körner (1999), the term "tree-line ecotone" is taken here to represent the transitional belt of mountain vegetation situated between the upper limit of single tree growth in the tundra and the upper limit of closed forests. This ecotone is wider than the subgoltsy belt because it covers the lower part of the alpine tundra belt, where solitary woody plants are found.

In the Polar Urals, dead trees at high elevation are preserved *in situ* for more than a millennium. Numerous explorers [15–18] observed a great number of dead trees and wood remnants in various degrees of decomposition around the upper tree-line on the eastern slope of the Polar Ural Mountains. Such wood is especially abundant in the Sob' River Basin. Dead trees located above the current tree-line ecotone provide evidence of the spatiotemporal dynamics of the forest-tundra communities in the recent past. The paleoecological record preserved in these dead trees is highly resolved, both spatially and temporally, providing a unique opportunity to reconstruct the precise history of actual changes in the structure of forest-tundra stands [19–21].

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 [22–25], and tree-line as well as forest-tundra ecotones in North America, Scandinavia, Siberia, and Urals have been shifting north- and upwards [4, 21, 26–29]. Simi-

larly, dendroecological studies show that trees at high latitudes and altitudes of the northern hemisphere have been growing better during the last decades [30]. There are, however, also reports on decreasing tree growth in the drier regions of Interior Alaska [31] and Middle Siberia [32].

One such promising area is the Polar Ural Mountains. Important note has to be made with respect to the choice of the field site location. The eastern macroslope of the Polar Urals represents a pristine environment where tundra, forest, and shrub ecosystems have not been exposed to significant anthropogenic impact and show no signs of forest fires in more than 1000-year long tree-ring records [19, 21, 33, 34]. These ecosystems experience the effect of natural disturbance factors; these are mainly related to climate variability/change. Furthermore, the routes of seasonal migration of reindeer herders go around this area because of the danger related to crossing of the Sob' River and the railroad. Most backpackers, who travel to the Rai-Iz range, approach it from the western and northern slopes because of the proximity to railroad stations. From the eastern side, it is only possible to reach the foothills of the mountains using an all-terrain vehicle. Consequently, the proposed field monitoring area represents an ideally suited location for studies of climate impacts on pristine tundra, forest, and forest-tundra communities of the subarctic region.

This paper demonstrates how the age structure of forest-tundra stands within the former and current tree-line ecotone and the morphogenesis of Siberian larch in the Polar Urals have changed over the last millennium.

OBJECTS AND METHODS

This paper presents the results of long-term studies on climate-driven dynamics of various forest-tundra communities growing in the upper treeline ecotone on the east-facing macroslope of the Polar Urals, in the Sob' River basin. We define the term "upper treeline ecotone" as a transitional belt of montane vegetation between the upper line of closed forests and the upper line of tundra with scattered individual trees. The lower limit of the ecotone is located at 140–230 m asl and the upper one at 270–560 m asl. The ecotone is mainly populated by pure larch (*Larix sibirica* Ldb.) communities of various densities. The lower ecotone is covered with larch open forests and larch closed forests with an admixture of *Picea obovata* Ldb. and *Betula tortuosa* Ldb.

The studies began in 1960s and are still going on [19, 21, 35]. The study area is a promising model for studying climate-driven dynamics of forest-tundra vegetation. It is located at the latitude of the Arctic Circle and has highly variable climatic conditions with climatic events of various duration [35]. The forest-tundra vegetation within the upper treeline ecotone did not ex-

perience wildfires, nor suffered considerable anthropogenic impact. Wildfires did not occur there for at least the last 1500 years, during which 4–5 generations of larch trees followed. This is indicated by the absence of charred dead tree remnants and charcoal on soil. However, we did find charcoal in soil at a depth of 25–30 cm on a sample plot chosen within the contemporary ecotone. The presence of the charcoal provides evidence that wildfires occurred within the contemporary ecotone during the Holocene thermal maximum, when the upper treeline was advancing uphill. Today wildfires occur only at lower hypsometric levels, within the mountain-taiga belt, and do not reach the subgoltsy belt.

The species composition of the stands in the upper treeline ecotone is simple—they are composed mainly of *Larix sibirica*. This makes studying their dynamics easier. Moreover, a wealth of data on species composition and structure of forest vegetation has been accumulated for the study area during the last 40–50 years, enabling us to evaluate past changes from direct evidence.

The study area is located on the east-facing macroslope of the Polar Urals, in the Sob' River basin (66°46′–66°55′N, 65°22′–65°49′E). The largest in area and the highest in altitude is the Rai-Iz peridotite massif extending almost latitudinally from the Sob' River in the east to the Makar-Ruz' River in the west. The northern part of the massif has several peaks rising to 1260–1290 m asl. Gabbro mountains of various heights extend along the southern extremity of the massif. The highest are Chernaya Mountain, 1030 m, and Malaya Chernaya Mountain, 594 m. There is a chain of gentle-sloped hills (300–460 m in height), extending along the southeast-facing slopes of the Rai-Iz massif and Chernaya Mountain. The north- and east-facing slopes of the Rai-Iz massif are framed with the schist mountains Slantsevaya, Yar-Keu, and Pour-Keu, 400–880 m in height.

The study area is characterized by a great deal of well-preserved standing and fallen deadwood within both the contemporary stands and lower alpine tundra belt (Fig. 1). This indicates that vegetation had been growing at higher hypsometric levels in the past. Dating the emergence and death time of the trees with dendrochronological methods enables us to analyze stand age structure and productivity for time periods greater than the longest biological age of larch trees (400–450 years). As dead tree remnants are preserved *in situ*, we are also able to reconstruct with great accuracy altitudinal and horizontal shifts of the upper treeline of forest-tundra communities.

Two permanent altitudinal transects were established within the upper treeline ecotone to reconstruct climate-driven dynamics of vegetation over long time periods.
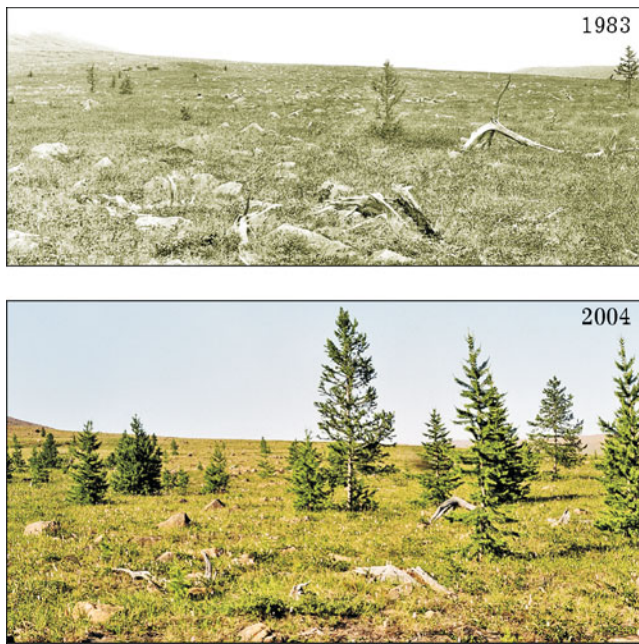
Fig. 1. Photographs taken in the same middle part of Transect 2 in 1983 and 2004, showing abundant old woody remnants and contemporary uphill-dispersing larch.

Transect 1 was established in 1960 on the east-facing macroslope of a 312.8-m-high hill, its top being 4 km to the east of Chernaya Mountain, in the interfluve between the Engayu and Kerdomanshor rivers. The transect lies on old moraine deposits, along the prevailing wind direction. The upper transect is strongly windswept; hence most trees thereon are multistemmed. The transect crosses the middle and lower parts of the upper treeline ecotone, from the upper line of larch sparse growth to the upper line of closed larch forest with spruce admixture. The upper transect lies at 265 m asl and lower at 190 m asl, crossing three forest strips and two treeless strips each 60–100 m wide. The strips are treeless due to 5–6 m-thick snowdrift that melts up by as late as mid July and thereby reduces growing season. The transect has a length of 860 m, a width of 80 m upslope and 40 m downslope, and a total area of 5.6 ha (Fig. 2). The upper left-hand corner is at 66°48′57′′N and 65°34′09′′E. A 20 by 20 m-side grid was established on Transect 1 and marked with stone piles in the grid corners. A 1:100 scale map of the transect was drawn. Twenty five plant communities, >4500 live trees, including saplings, and 769 standing and fallen dead trees were marked on the map. All living trees and saplings were numbered and their morphometries (basal diameter and diameter at breast height, stem height in single-stemmed and height of all stems in multistemmed trees, the height of the beginning of the crown and its diameter) were measured.

In 1999 and 2000, all living trees and large saplings were retallied and their morphometries were re-

measured at Transect 1 for deeper understanding of the processes that took place in the forest-tundra vegetation in the 20th century. Each standing and fallen dead tree was cross-sectioned to estimate calendar lifespan. In the upper transect, more than 500 living trees were cored at breast height and at the trunk base.

Transect 2 was established in 1983 on the gentle southeast-facing slope of the Rai-Iz massif, within an about 40-ha former larch open forest, extinct by the late 19th century (Fig. 1). The type of the upper timberline on this slope is thermally determined, and the stand must have declined only due to climate cooling [16]. Transect 2 lies across the upper part of the upper treeline ecotone, where young larch open forest and solitary trees in tundra are growing. Moreover, the uppermost extremity of the transect extends into the lower alpine tundra belt, where dead tree remnants are preserved. Transect 2 has a length of 430 m and a width of 20 m. It upper extremity lies at 340 m asl and lower extremity at 280 m asl. The upper left-hand corner is at 66°51′19′′N, 65°38′57′′E. A 10 by 10 m grid was established on Transect 2. Two hundred fifty two dead trees in various degrees of decomposition were mapped within the transect. Each dead tree was cross-sectioned to date its calendar lifespan. We also mapped and described young growth and saplings found on the transect. As soil conditions were relatively uniform within the transect (only soil stoniness increased with altitude), we did not divide it into sites. In 2004 we retallied new larch trees on the transect.

The two transects, spaced 5.5 km apart, span the width of the upper treeline ecotone and encompass various forest-tundra plant communities, from solitary trees in tundra to closed forest.

The calendar lifespan of dead trees was cross-dated by mean larch tree-ring chronology for the last 1250 years [35]. In the harsh climate, resin-containing coarse woody remnants (trunk bases and large roots) are preserved for up to 800–1300 years. As underbark ring and sapwood were not preserved in most dead trees, we added 15–20 rings to accurately date the trees' death. The pith annual rings were present in most cross-sections. However, we had to make corrections for the height the stems were cross-sectioned at and estimate the number of decomposed inner rings for some samples. As dendrochronology is a highly sensitive method, about 90% of dead tree remnants were dated (667 of 769 stems on Transect 1 and 221 of 252 stems on Transect 2). Undated were mostly small remnants with <30–40 annual rings.

We uprooted and examined 33 model larch trees (20 single-stemmed, 10 multistemmed, and 3 prostrate trees) of various ages and diameters, growing near Transect 1, to study accumulation and distribution of fractional phytomass (stems, branches, ≤1 cm roots, bark, and foliage). The trees were fractioned in situ. Each fraction was weighed and samples were taken. In
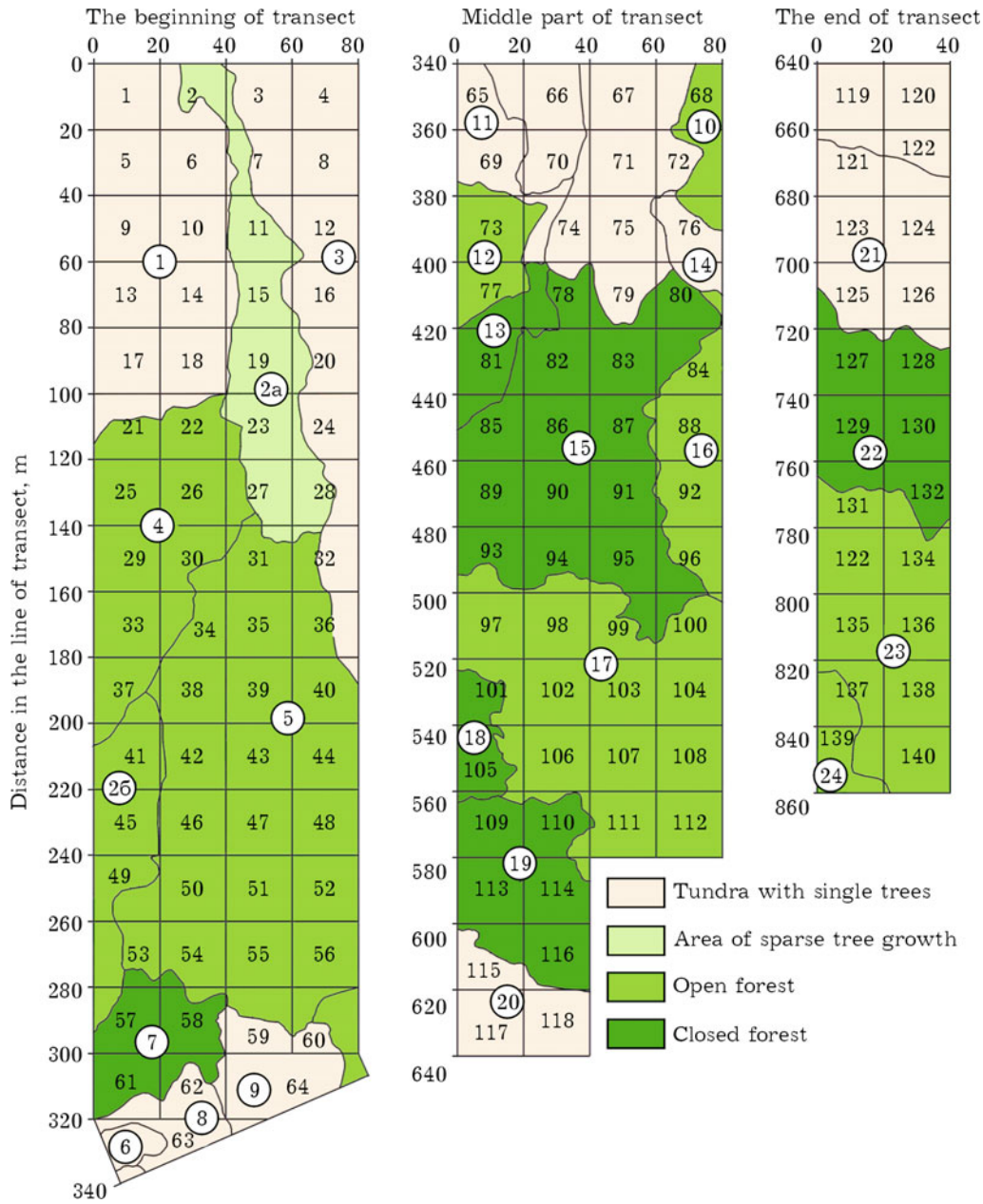
Fig. 2. Schematic map of Transect 1, showing 140 20 by 20-m grid and 25 sites (encircled numbers).

the laboratory, the samples were oven-dried and reweighed to obtain allometric ratios between stem diameter and oven-dry phytomass for each fraction. For multistemmed and prostrate larch, we used reduced diameter calculated as the total circumference of all stems and boughs at the base of an individual plant.

Secular variation of the Transect 1 tree layer productivity was estimated from the radial growth of >500 live and 667 dead trees. From these data we calculated cumulative diameter for each calendar year for each tree. If the tree samples contained decomposed parts, we fitted a circle template so as to estimate average growth

for this part of a sample. We also made corrections if a tree had eccentric or decomposed outer rings.

In 2000–2005 we described forest-tundra communities growing within the upper treeline ecotone at the foothills of Chernaya and Malaya Chernaya mountains, on the south- and north-facing slopes of the Rai-Iz massif and Slantsevaya Mountain and marked them on the 1:25 000 scale map. A total of 930 sites of 5770 ha were mapped. For each site, we determined community type. The main community types were the following: tundra with scattered individual trees, sparse tree growth, open forests, and closed forests. A community type was de-

termined from stand density estimated from average tree-to-tree distances. Forest-tundra larch communities were classified as follows: a closed forest, a community with an average tree-to-tree distance of <7–10 m; an open forest, from 7–10 to 20–30 m; a larch sparse growth, from 20–30 to 50–60 m; and tundra with scattered individual trees, >50–60 m. For each site we visually determined species composition and structure of the existing vegetation and the main microclimatic and soil conditions. Special attention was paid to the stand age structure. Moreover, we reconstructed species composition and stand structure for each site for the early 1910s and 1960s from the morphological and age structure of the stand and from descriptions and re-enumerations on the permanent sample plots and transects established in 1960–1962. Especially useful were landscape photographs of the woody vegetation, taken 40–45 years ago. The ARC/INFO (ESRI Inc., USA) and ERDAS Imagine (ERDAS Inc., USA) packages were used for drawing distribution maps of forest-tundra communities for the early and mid-20th century and the early 21st century. The mapping methodology was discussed in greater detail in [36]. A special method was used for calculation of altitudinal and horizontal shifts of the upper line of open forests and closed forests.

Climate variation analysis was based on 120-year instrumental records from the Salekhard weather station (55 km to the east of the study area) and 1252-year-long larch dendroclimatic series [35].

RESULTS AND DISCUSSION

Forest-tundra vegetation dynamics over the last 1000 years. In Figure 3, the short bars show calendar lifespan of the dead larches that had been growing within transects 1 and 2. The sloping lines are altitude above sea level at different locations on the transects. The location and age of living trees are the lines "hanging" from the upper edge of graph. Living trees were absent on Transect 2 for a long time, from the early 19th to the early 20th century, whereas they were present on Transect 1, in the middle and lower part of the upper tree line ecotone, due to more favorable mesoclimatic conditions. They were growing there for the entire study period in question, but only those growing in the upper forest strips are indicated (Fig. 2, quadrats 1–62).

Figure 3 shows that the oldest preserved tree remnants are comprised of trees that emerged in the early and mid-8th century. The remnants are few as most wood decomposed or some preserved remnants could not be dated with tree-ring analysis. Ancient wood is absent in the lower transects as decomposition rate therein is higher due to better microclimate and colonization of fallen deadwood by grasses and turf.

We were able to reconstruct the upper treeline of larch open forest over the last 1300 years by using the remnants at the highest altitudes as these remnants were well preserved on Transect 2 and the upper Transect 1

(Fig. 4). The upper line of open forest was advancing upward from 310 to 340 m asl from the early 8th to the late 12th century. During the 13th and the early 14th century, the treeline was at the highest altitude. Then mass death of trees began and the treeline was receding till the early 20th century. The receding was the most rapid in the 15th and 19th centuries. By the early 19th century, Transect 2 was devoid of living trees and the upper line of open forest receded to 280 m asl. A few larches and a prostrate spruce remained on Transect 1 at 250–265 m asl. The receding of the upper line of open forest changed over time. Moreover, the upper treeline even advanced in the second half of the 17th and most of the 18th century due to larch stands, overmatured now. The situation reversed in the 1920s, when viable young growth emerged on Transect 2 and the prostrate trees on Transect 1 changed into multistemmed. According to the 1983 records, only 16 larch saplings were recorded on the lower Transect 2, the oldest one emerged in the early 20th century. The 2004 retally showed that larch had been actively colonizing the slope for the last 20 years. The number of trees, including saplings and young growth, increased from 16 to 147 stems (Fig. 3). The two 10-year larch trees at the top of the transect emerged at 330 m asl, i.e., at the altitude where trees were growing in the 13th century. In the 20th century, the upper line of open forests at Transect 2 advanced from 280 to 310 m asl; beyond that limit only scattered solitary saplings and young growth occur. The photographs taken at the same location in the middle transect in 1962 and 2004 show that there were no larch saplings in 1962, but now a typical sparse larch growth has formed. The magnitude and rate of the shift of the upper line of open forest on the slope are available in greater detail in [21].

Changes in the structure and productivity of the forest-tundra communities paralleled altitudinal shifts of the upper line of open forests. Analysis of Fig. 3 shows that in the 12–13th centuries, when the upper line of open forest was at the highest altitude for the last 1000 years, dense forest stands were growing in the upper treeline ecotone, although deadwood has only partially been preserved. Comparison of stand densities for the two transects evidences that fact. Figure 3 indicates that at Transect 2, where conditions for wood decomposition are less favorable, stands were denser than at Transect 1. Later, Transect 1 stands were as dense only in the 17–18th centuries. Now dense productive stands are forming due to young larch growth. Stands sparsened considerably in the 15–16th and especially 19th centuries (Fig. 3).

Allometric relationships between cumulative diameters of living and dead trees and oven-dry phytomass were used to estimate production process. Variations in the tree layer phytomass for Transect 1 over the last 800 years are shown in Fig. 5. For better comprehension and detection of long-term trends in phytomass variation, factual data before the 20th century are given using
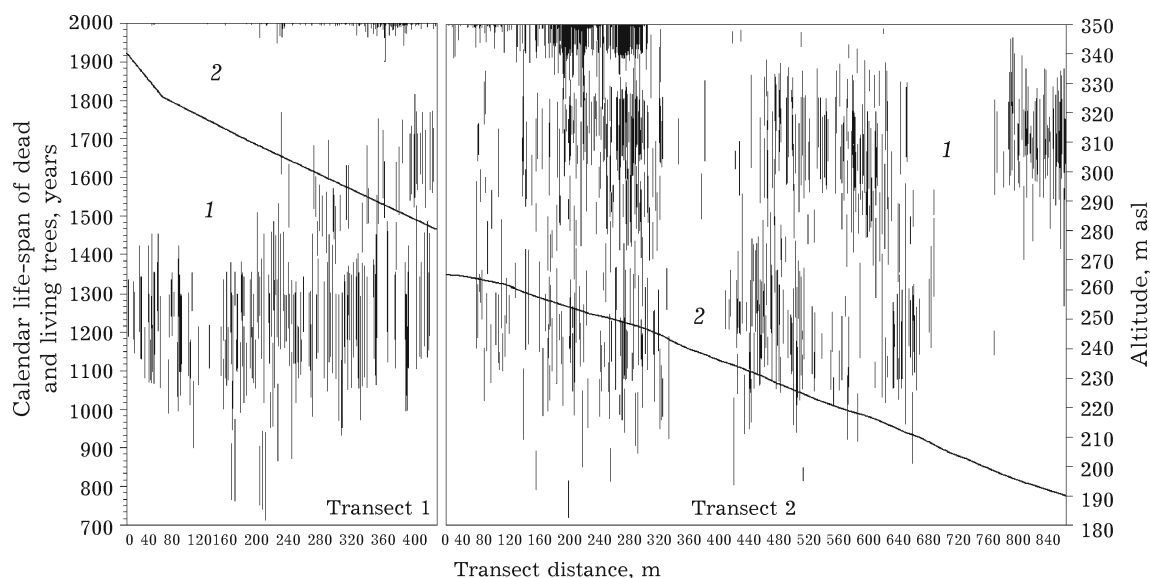
Fig. 3. Distribution of calendar lifespans of dead and living trees on transects 1 and 2 over the last 1300 years. *1*, tree lifespan; *2*, altitude asl.
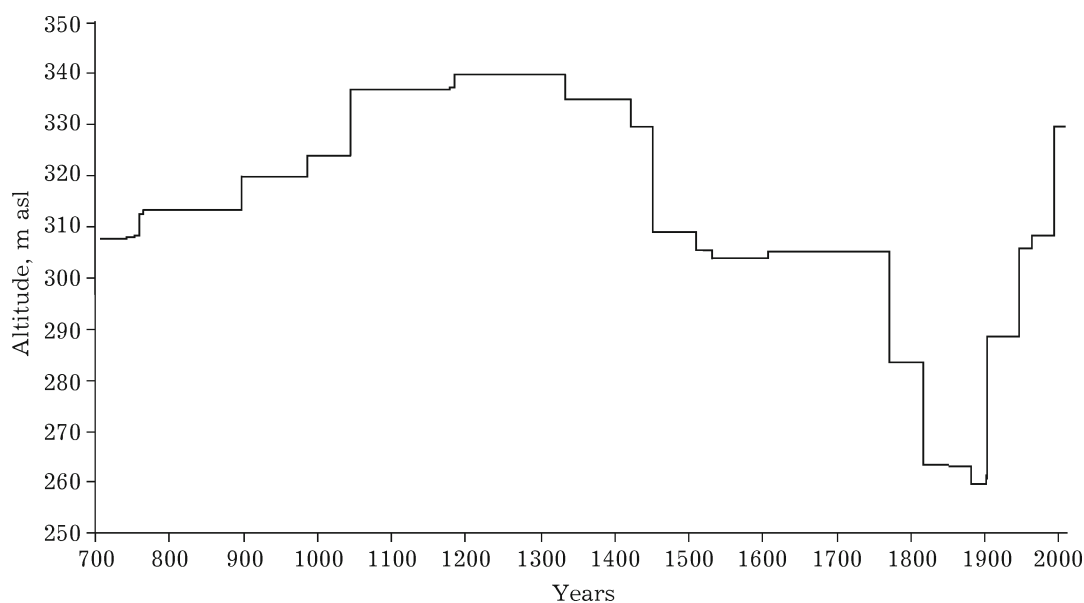

Fig. 4. Dynamics of the upper line of larch open forest over the last 1300 years.

100-year steps and the contemporary data, 40–60-year steps. The factual phytomass for each estimated period was total phytomass of contemporary living and dead trees. The figure shows 3 phytomass maxima and 2 phytomass minima for the study period. The first maximum occurred in the 13th century, the second, in the 17–18th centuries, and the third, in the 20th century. Phytomass minima occurred in the 15–16th and 19th centuries. In fact, the earliest phytomass is somewhat underestimated, at least till the 19th century, because the phytomass of completely decomposed trees and that

of small and largely decomposed remnants was not included. As mentioned above, small tree remnants with few rings are hard or impossible to date with tree-ring analysis. However, our study does not require utmost dendrochronological accuracy for so long a period.

The most important results of the study are the revealed long-term trends in the variation of stand productivity, caused by climate change. Figure 5 confirms this by annual and secular variations (the upper curves) in the larch tree-ring indices for the study area, indicating June–July air temperature [35]. The indices were
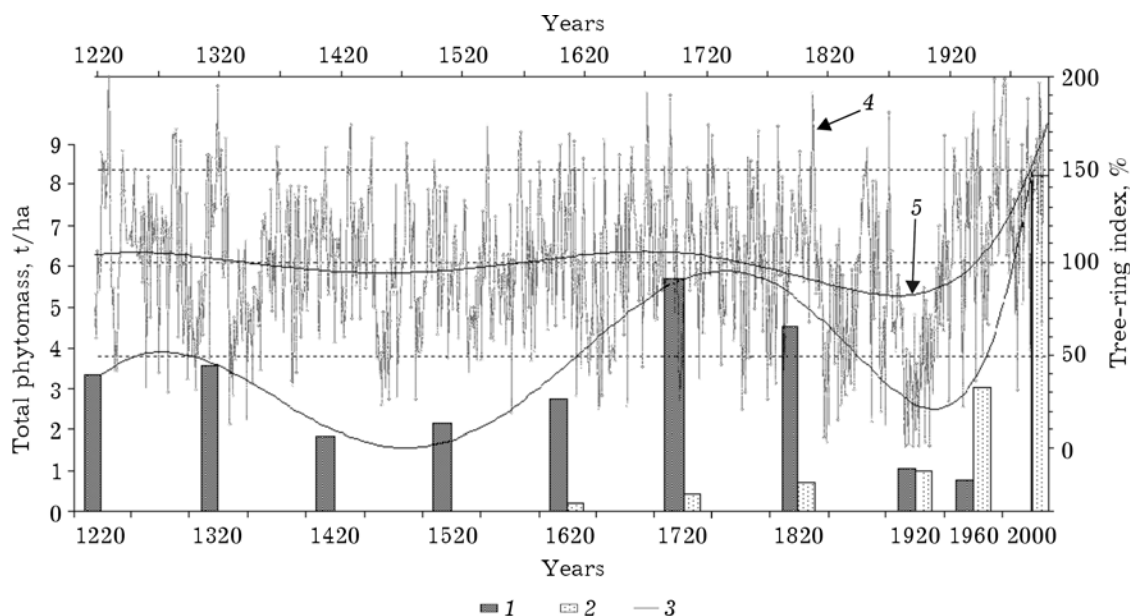
Fig. 5. Tree layer phytomass dynamics for Transect 1 over the last 800 years. *1*, phytomass estimated from dead trees; *2*, phytomass estimated from living trees; *3*, phytomass variation trend; *4*, annual fluctuations in larch radial growth; *5*, variation trend of tree-ring indices.

smoothed using the same technique as stand phytomass was. Note that the secular variations are little pronounced in the indices as we used wood samples with relatively low number of tree rings (150–350 rings) and due to standardization. Yet it is clear from Fig. 5 that the phytomass trend is in phase with the indices, which means that the processes were synchronous. As shown above, variations of the altitude of the upper treeline and those of stand density were synchronous. This indicates that the processes are interrelated and are determined by variation in a common factor, irrespective of stand location within the upper treeline ecotone and soil conditions. Such a common factor can only be a climatic one, e.g., temperature regime in June and July. There is copious direct and indirect data on the climate change, indicating similar long-term climate changes in Northern Eurasia [35]. In the 8–13th centuries, a widespread climate warming occurred, followed by cooling—the so-called Little Ice Age. There are different opinions as to when the cooling began and ended. Our data indicate that in the Polar Urals it began in the late 13th century and ended in the early 20th century. Judging by the annual growth, structure, productivity, and spatial distribution of the forest-tundra stands, the coldest period was the 19th century.

Forest-tundra vegetation dynamics in the 20th century. We paid special attention to the 20th-century changes caused by the contemporary warming that began in the 1920s and is still going on to better understand and quantify the effect of climate change on the forest-tundra vegetation.

Figure 6 shows the distribution of various forest-tundra communities in the early 1910s and 2000s, and the table summarizes variations in absolute and relative areas for the early 1910s, 1960s, and 2000s. These data indicate considerable transformations and spatial redistributions of various community types within the upper treeline ecotone. Woody vegetation expanded considerably, which was expressed in considerable increase in open and closed forests and in decrease by nearly 1000 ha in the area of tundras with single trees. Sparse larch growth area varied in a special way: in the first half of the 20th century, it increased abruptly from 662 to 1015 ha, whereas in the other half, it decreased abruptly, being now only 113 ha greater than that at the beginning of the period in question. This happened because the sparse larch growth changed to open and closed forests. Open forest area changed more or less smoothly, from 640 ha in the early 20th century to 1066 ha now. Closed forest area experienced the most drastic rise: in the early 1910s, 19 small closed forests totaled 69 ha, whereas now the closed forest area comprises 623 ha of the ecotone area. While in the 1910s the area of sparse tree growth, open forests, and closed forests totaled 1371 ha, or 24% of the mapped area, in the 1960s it increased to 2110 ha (37%), and now it is 2464 ha (43%). In other words, the forest-covered area of the ecotone nearly doubled.

The upper lines of sparse tree growth, open forests, and closed forests advanced uphill on many slopes. The advance of the upper line of sparse tree growth averaged 26 m and that of closed forests 35 m. The horizontal shift averaged 290 and 520 m, respectively [36].

The increase in the open and closed forest areas was paralleled by a considerable increase in height and diameter growth. Annual radial growth over the last
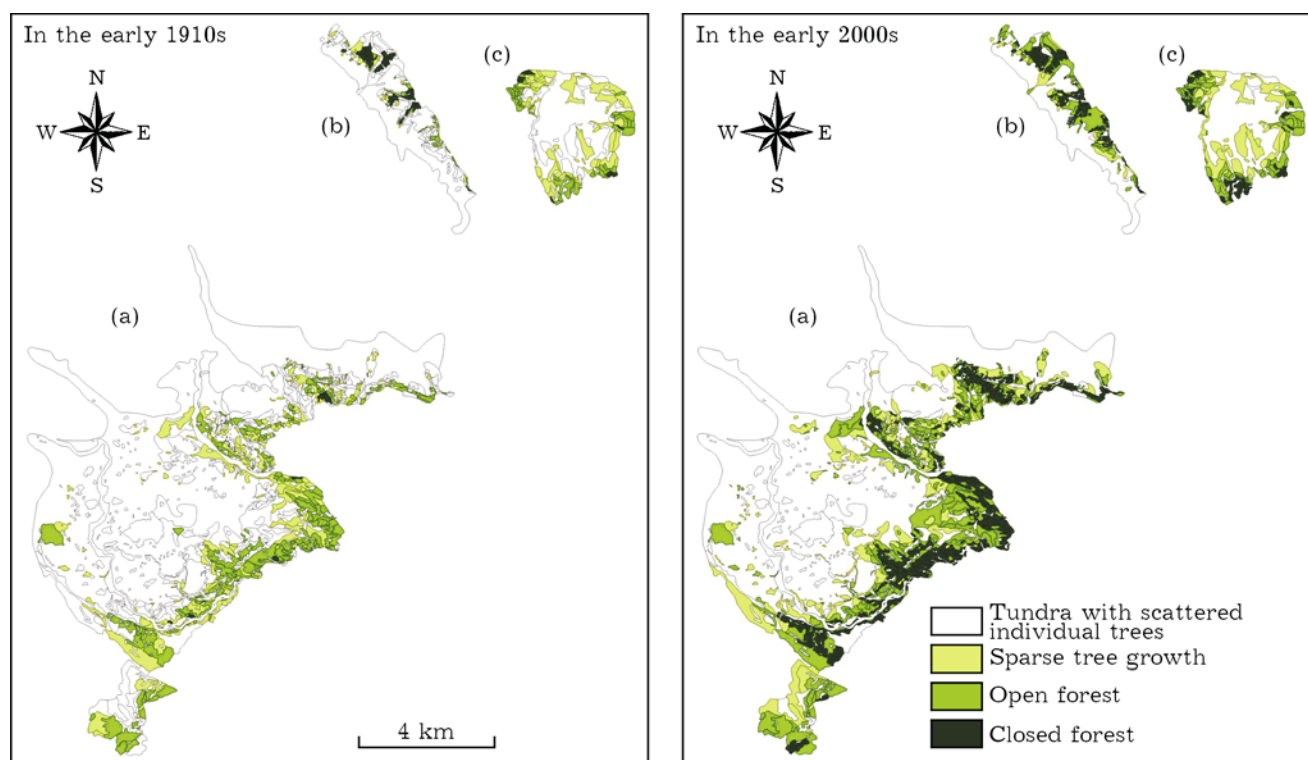
Fig. 6. Distibution of various forest-tundra communities in the upper treeline ecotone in the early 1910s and 2000s. (a), the area of the Rai-Iz massif; (b), the Slantsevaya Mountain area; (c), the area of Chernaya and Malaya Chernaya mountains.

70–90 years averaged 0.83 mm, whereas over the preceding 60–80 years it was about 4 times lower (0.21 mm). Annual height growth of single-stemmed larch trees nearly doubled after 1920s, from 3.2 to 6 cm on average. In prostrate and multistemmed larches, it increased 4–5 times, from 0.4–1.2 to 1.9–5.2 cm, respectively. Interannual variation of radial growth decreased, which was caused mainly by fluctuations in summer temperatures (sensitivity coefficient declined from 0.6 to 0.4), indicating better conditions for tree growth.

In the second half of the 20th century, stand productivity also increased. We estimated changes in phytomass, number of trees, stand volume, and stand density over the last 40 years on Transect 1. Figure 7 shows the estimates of the changes for each of the 25 sites within the transect. There is a clear 2–5-fold increase in phytomass, density, and degree of closeness of the stands on most of the sites over such a short period. The variables increased even more for some sites that were almost treeless in the 1960s.

The phytomass of the tree layer varies along the altitudinal gradient of Transect 1 from 7 t/ha to 30 t/ha. The above-ground : below-ground phytomass ratio is 3.4 : 1 in the upper transect, 1.9 : 1 in the middle transect, and 1.7 : 1 in the lower transect.

Picea obovata Ldb. is regenerating in the lower ecotone, in the larch-dominated stands. The data on spruce expansion into the larch stands and the upward shift of the upper line of spruce growth were obtained

Distribution and percentages of forest-tundra communities

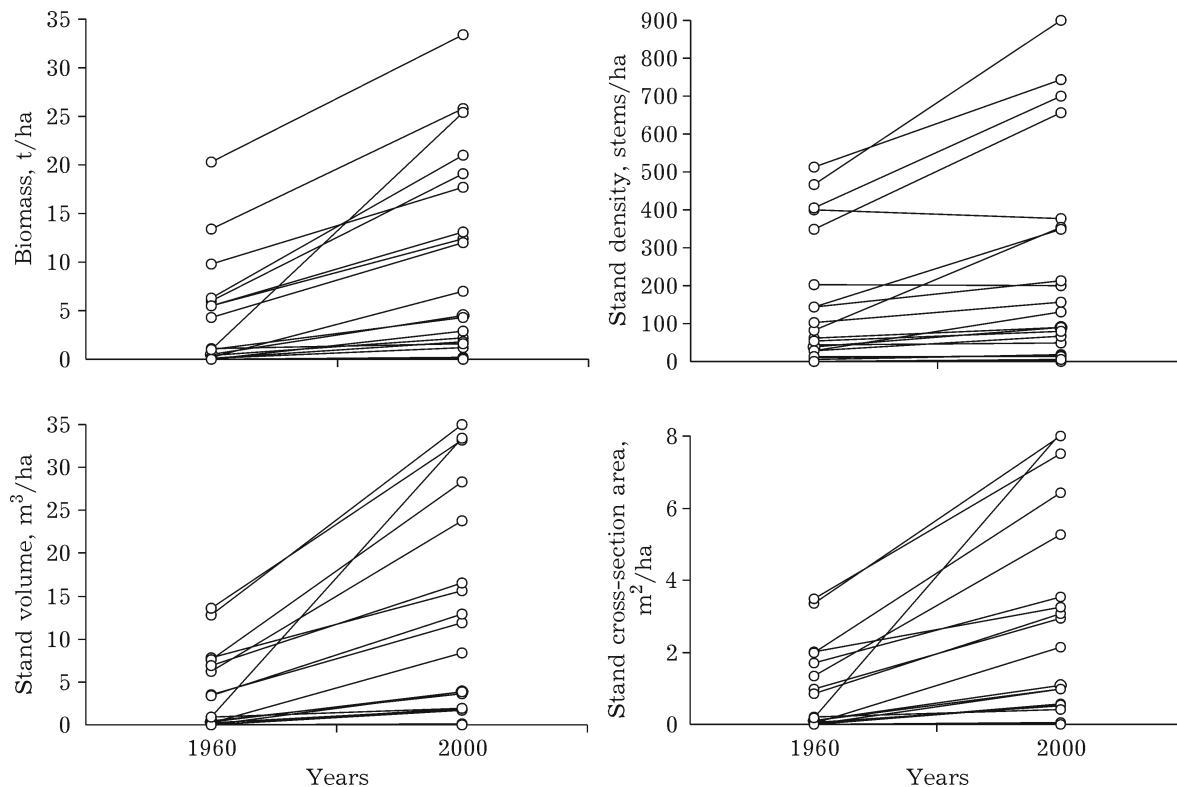| Forest-tundra community	Early 1910s		Early 1960s		Early 2000s	
	ha	%	ha	%	ha	%
Tundra with scattered individual trees	4399	76	3660	63	3306	57
Sparse tree growth	662	12	1015	18	775	14
Open forest	640	11	790	14	1066	18
Closed forest	69	1	305	5	623	11
Total	5770	100	5770	100	5770	100

Fig. 7. Taxation parameter changes in the 25 sites on Transect 1 from 1960 to 2000.

only in 2006 on a specially designated transect. These data are not considered in this study.

We think that the intensive expansion of woody vegetation in the 20th century was caused by the increase in summer and winter temperatures. This assumption is confirmed by instrumental records for the last 120 years, obtained from the Salekhard weather station. The data showed that since 1920s climate has been warming and humidifying. Average summer temperature (June–August) was 10.7°C in 1883–1920, 11.4°C in 1920–2004, i.e., it increased by 0.7°C, and average winter temperature (November–March) increased by 1.1°C, from −20.8 to −19.7°C. Total summer precipitation increased by 32 mm, from 147 to 179 mm, and total winter precipitation, by 46 mm, from 67 to 113 mm. According to summer temperatures reconstructed from larch annual ring widths in different parts of Siberian Subarctic region [35], in the 20th century, the Polar Urals experienced the greatest climate warming compared to the West Siberia north and the Taimyr Peninsula. An important role for the expansion of woody vegetation was played by earlier onset of the growing season, indicated by considerable increase in May temperature. While in the 1883–1920 period it averaged −2.4°C, in 1920–2004 it averaged −1.1°C, i.e., the May temperature increased by 1.3°C. Given that summer altitudinal gradient for the Polar Urals is 0.7°C, the upper treeline should be shifted about 100 m upward.

The contemporary warming appears to compare to that in the 12–13th centuries. On most slopes, however, woody vegetation has not reached its climatically determined limit and the altitudes it reached in the 13th century. The main reason is poor transport of seeds upslope to tundra sites in the upper part of the upper treeline ecotone. In this region larch seeds disperse a year after cone formation [33]. During the winter the seeds remain in the cones; the cones open and disperse the seeds as soon as it is sunny and warm. The dispersal usually occurs in June and July, when there is no snow cover. Heavy larch seeds are not dispersed farther than 40–60 m from a parent tree; only few are dispersed farther uphill. That is why many habitats suitable for woody vegetation are still either treeless or sparsely colonized. From this perspective it is possible to explain why the tundra areas are colonized most densely and sparse forests change to denser ones in the lower part of the upper treeline ecotone that receives the greatest seed stock, apart from more hospitable microclimatic and soil conditions.

CONCLUSIONS

Analysis of the obtained data shows that the Polar Urals, and especially its east-facing macroslope, are a promising area for studies of climate-driven dynamics of forest-tundra vegetation. In this area forest-tundra

communities are constantly transforming and their upper treelines are changing due to climate changes. The processes are very slow and lagging and this should be taken into consideration when building models of forest ecosystem dynamics under changing climatic conditions. The quantitative data showing responses of various components of the forest-tundra communities to changes in climatic factors can be used for building such models.

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