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Structure and Dynamics of Tree Stands at the Upper Timberline in the Western Part of the Putorana Plateau

A. A. Grigor'ev[a, *], **N. M. Devi**[a], **V. V. Kukarskikh**[a], **S. O. V'yukhin**[a, b],
A. A. Galimova[a], **P. A. Moiseev**[a], **and V. V. Fomin**[a, b]
[a]*Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia*
[b]*Ural State Forestry Engineering University, Yekaterinburg, 620100 Russia*
**e-mail: grigoriev.a.a@ipae.uran.ru*

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Abstract—Analysis of the age structure of Dahurian larch (*Larix gmelinii* Rupr.) forests in the western part of the Putorana Plateau (Sukhie Gory Range) and comparison of diachronous topographic maps and satellite images have revealed changes in the altitudinal position of the upper boundary of tree vegetation. The most significant changes occurred on south- and southwest-facing slopes. Correlations of trunk diameters with the phytomass of trees and its fractions have been found. The course of changes in the structure and phytomass of tree stands in the upper timberline over the past centuries has been reconstructed. Forest expansion has been facilitated by the general change in climate conditions (warming) in the study area.

Keywords: Dahurian larch, upper timberline ecotone, phytomass of trees and stands, climate changes, Putorana, Subarctic

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The determination and quantitative assessment of the transformation and biological productivity of mountain forest ecosystems are among important ecological problems, with their relevance significantly increasing in the context of current climate change. According to the data of the Intergovernmental Panel on Climate Change [1], the temperature near the earth surface during each of the past three decades was higher than in any previous decade since 1850.

It is common knowledge that tree vegetation growing under extreme conditions (in particular, at the upper timberline) is sensitive to environmental changes and, therefore, has an indicator role [2]. Extensive studies on revealing and assessing changes in the composition, structure, and altitudinal position of tree stands at the upper timberline have been carried out in many regions of the world in recent decades [3]. Analysis of literature sources has shown that these processes are associated with changes in climate factors acting in different combinations. In relatively dry high-mountain areas with little snow, this process leads to an increase in summer [4–6] or winter [7] precipitation; in addition, if temperatures are too high, the level of tree regeneration decreases, because soil moisture is insufficient for successful emergence and survival of seedlings. In areas with high precipitation levels (e.g., on the Pacific coast in the northwest of the United States), trees colonize subalpine meadows during periods when the snow cover is relatively thin and thaws earlier, which results in an increased duration of the growing season [8, 9]. On the contrary, in regions where the levels of soil moisture on slopes differ depending on orographic conditions, tree regeneration is intensified during discrete or overlapping periods with different moisture conditions [10, 11]. Periods of intense regeneration in areas where the amount of precipitation and snow depth are at a medium level (e.g., in zonal forest–tundra communities) coincide with periods of general warming; however, regeneration is locally intensified when snow depth increases, since the snow protects undergrowth against extremely low winter temperatures [12–14].

In the subarctic regions of Russia, where the effect of thermal regime on the growth of woody plants is more significant, in-depth studies aimed to reveal assess changes in the structure of tree stands at the upper timberline were carried out only in the Polar Urals [15–18]. In the central zone of the Subarctic, studies of this kind were performed mainly in the plain part (near the village of Khatanga, Ary-Mas tract) [19]. Based on satellite- and land-survey materials, the authors revealed an increase in the area of closed forests, as well as the expansion of larch to the tundra zone, i.e., to the Ary-Mas tract (the world's northernmost forest massif). Similar results were also obtained in the mountain part of Anabar Plateau in the upper reaches of the Kotuy River [20]. Studies on assessing the altitudinal position of the timberline and the ecological and biosphere role of tree stands formed in previously woodless areas in the mountain part of the Putorana Plateau are few, since this area is hardly accessible [21, 22], and the amount of available data is obviously insufficient for any general conclusions.

We hypothesized that the altitudinal position of tree stands at the upper timberline in the western part of the Putorana Plateau (where studies of this kind have not yet been performed) and the patterns of their formation and phytomass accumulation are characterized by specific features conditioned by the strong influence of Atlantic air masses coming mainly from the west (compared to the northern and central areas of the plateau). To test this hypothesis, we studied the structure, productivity, and altitudinal position of tree stands with different degrees of closure in the transitional zone between closed forests and mountain tundras on the slopes of the Sukhie Gory Range (at the eastern part of Lake Lama) and evaluated specific features of local conditions in their habitats.

OBJECTS AND METHODS

The Sukhie Gory Range adjoins the southern shore of Lake Lama in the western part of the Putorana Plateau. This is one of the most hardly accessible and poorly studied regions in the north of Russia (69.4460° N, 90.5230° E; 69.3400° N, 90.9460° E) (Fig. 1). The Putorana Plateau is in the northwest of Central Siberia. Extending from 89° to 101° E and from 60° to 71° N, it occupies an area of about 284000 km^2 [23]. This is the largest monolithic mountain range in the Russian polar region, with almost the entire its area lying north of the Arctic Circle. With respect to the geological and geomorphological features, it is a flat-topped basalt crystalline massif (plateau) with elevations averaging 900–1200 m and reaching a maximum of 1701 m a.s.l. in the central part (Mt. Kamen mountain). Multiple uplifts on the Putorana Plateau have generated deep radial tectonic fractures in this area in the form of narrow gorges and canyons with the trappean structure of slopes.

The Putorana Plateau is in the subarctic climate belt, at the boundary between the Atlantic and Siberian regions, in the continuous permafrost zone. The climate is excessive continental [24], and the amount of precipitation is significantly higher than anywhere else in the north of Eastern Siberia . The upper timberline is formed by Dahurian larch (*Larix gmelinii* Rupr.) and lies in the interval of 200 to 900 m a.s.l., depending on regional and local habitat conditions.

Spatial and temporal changes in the altitudinal position of the upper timberline (UTL)—the upper boundary of sparse forests with a crown closure of 35–40%—were determined and quantitatively assessed by constructing a digital elevation model (DEM) for the study area in the ARC/INFO geographical information system (ESRI Inc., United States) using the TOPOGRID algorithm. The model was based on geoinformation isoline layers and elevation, water flow, and lake marks (coordinates of the left upper and right lower angles of the study area: 66°45′ N, 90°52′ E; 66°34′ N, 90°95′ E, $S = 5.49$ km^2; see Fig. 2). These layers were created by digitizing scanned images of maps available from the State Center for Geoinformation Systems (scale 1 : 25000). Two linear vector geoinformation layers characterizing the UTL position in 1956 and 2017 were created using topographic maps of 1956, recent satellite images with submeter spatial resolution, and field survey data.

The values of vertical and horizontal shifts were estimated using the previously developed technique [15, 25, 26]. The value of the altitudinal position of the UTL was determined by imposing the rasterized boundary line on the digital elevation model (DEM). A DEM cell with a certain elevation value corresponded to each cell of the boundary. Thus, the altitudinal position of the boundary was characterized by a set of cell distribution statistics (Table 1). Changes in the value of the altitudinal boundary position (altitudinal shift) were estimated from the difference between statistics values, e.g., the median or mean value, or the difference between the current altitudinal position of the UTL and its former position. The rate of altitudinal shift was calculated as the ratio of its value to the time interval. To estimate the value and rate of the horizontal shift from the boundary line, we calculated a raster with cells containing the values of Euclidean distance from the line at the beginning of the study period. A rastered UTL line at the end of the study period was imposed on this raster. The value of the horizontal shift was estimated using statistics of the distribution of its values, and the rate of the shift was determined by dividing its values by the value of the time interval (see Table 1).

In summer 2017, two altitudinal transects were established in the upper timberline ecotone (UTLE) on southwest-facing slopes of the Sukhie Gory Range: one in an insular forest area at 2 km from Lake Lama (69°39′ N, 90°75′ E), and the other, in a continuous forest massif at 6 km from Lake Lama (in the upper reaches of the Yuzhny Neralakh River). The UTLE is understood as a transitional belt in mountains between the upper boundary of closed forests and the lower boundary of sparse tree growth in the tundra [27].

Three altitudinal levels were distinguished in each transect: the lower level at the upper boundary of closed forests, the middle level at the upper boundary of sparse forests, and the upper level at the distribution limit of tree groups in the tundra. Three sampling plots 20 × 20 m in size were established at each level, where the exact locations of trees, their diameters at the base and at breast height (1.3 m), crown diameters in two mutually perpendicular directions, and their age and life state were determined. To determine tree age, core samples of wood were taken or, if trunk diameter was

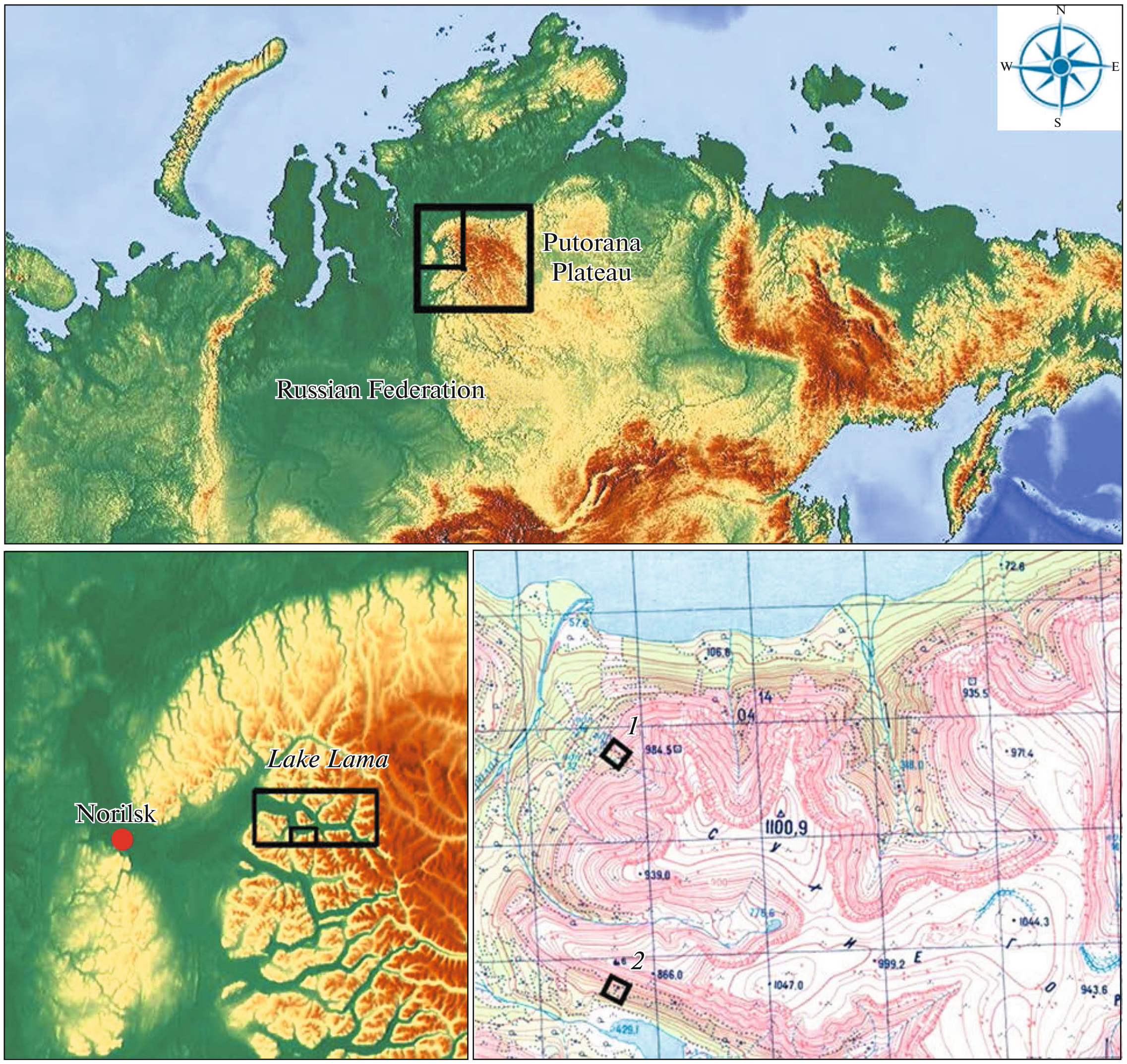

Fig. 1. Schematic map of the study area: (*1, 2*), locations of altitudinal transects.

less than 3 cm, transverse saw cuts were made at the tree base. Each sample was glued onto a wooden base, smoothed out with a sharp blade, and pigmented with toothpowder for better visualization of tree rings.

Tree rings were calculated and core samples were dated in the laboratory by conventional methods [28, 29]. All wood samples were measured using a semiautomatic LINTAB 5 system. False and missing rings were revealed by constructing a generalized tree-ring chronology based on wood core samples (40 pcs.) that were specially taken from old trees in the study area. Trees no more than 1.5 m high and 30 years old were classified as undergrowth. When core samples did not reach the trunk center, the year of central ring formation was determined by calculating missing rings using a transparent film with circles of different sizes drawn on it. Data on the age of undergrowth with a height of over 0.2 m and a diameter of less than 3–4 cm were most reliable, since it was determined from saw cuts made at the root collar level. Based on these data, we derived the equation of regression between the age and height of these trees, which allowed us to calculate corrections for determining more exactly the age of each studied tree with a diameter of over 3–4 cm. It should be noted that tree vegetation growing in both altitudinal transects has not been exposed to forest fires and other deleterious factors over the past 400 years, since we found no fire marks (burns) in saw cuts and core samples; we also did not observe a significant number of dry trees during the establishment of sampling plots. In total, an area of 0.72 ha was surveyed, where morphometric parameters and age were determined in 495 trees and 91 undergrowth units .

To assess microclimate conditions in transect I, six autonomous thermal sensors DS1921 Thermochroni-Button™ were placed in each sampling plot to measure air and soil temperatures. In April 2018 (during maximum snow accumulation), snow depth was measured

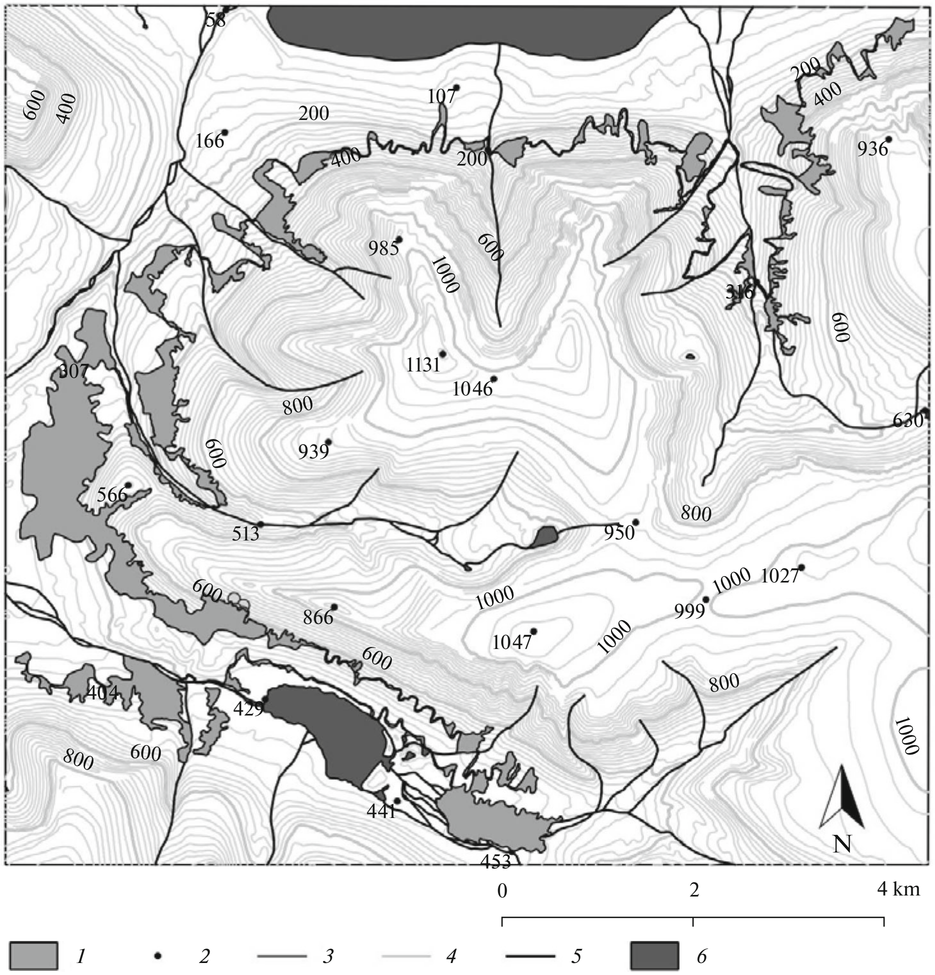

Fig. 2. Spatiotemporal changes in the altitudinal position of the upper boundary of sparse forests in the Sukhie Gory Range in the western part of the Putorana Plateau in 1956 to 2017: (*1*) zone of boundary shift; (*2*) elevation marks, m; (*3*) altitude isolines at 100-m intervals; (*4*) altitude isolines at 20-m intervals; (*5*) rivers and streams; (*6*) lakes.

in sampling plots and adjacent sites. To this end, tree trunks were stained at the snow surface level and, in summer, the height of the stain mark above the soil surface was measured.

The material for studying phytomass stocks and structure was collected in 2017 on the southern slope of the Sukhie Gory Range, near sampling plots on the transects, following the procedure developed under INTAS International Project no. 01-0052 [30]. Primary data on the phytomass of 40 model Dahurian larch trees were obtained under field conditions distinguishing the following fractions: the phytomass of

Table 1. Characteristics of altitudinal position and altitudinal and horizontal shifts of the upper boundary of sparse forests with a closure of 35–40% on slopes of the Sukhie Gory Range (the western part of the Putorana Plateau)

Statistics	Altitudinal position of the boundary, m		Altitudinal shift		Horizontal shift	
	1956	2017	Value, m	Rate, m/year	Value, m	Rate, m/year
Mean value	345.3	409.1	63.8	1.0	177	2.9
Standard error	104.7	101.2	–	–	202	3.3
Error of mean	1.2	1.0	–	–	2	–
Minimum	98.2	125.9	27.7	0.5	0	0
Median	338.2	424.4	86.2	1.4	99	1.6
Maximum	583.7	662.1	78.4	1.3	1020	16.7

trunk, branches, needles, roots, and generative organs. We took 858 saw cuts and weighted samples to determine dry matter contents in all the fractions. These data served as a basis for calculating tree phytomass in absolutely dry state and deriving equations for the correlation of the dry weight of different fractions with the same morphometric parameter, namely, the trunk base diameter. These correlations proved to be very high ($R^2 = 0.92–0.99$). Based on factual measurements of morphometric tree parameters and core samples from sampling plots along transects I and II, we carried out tree-ring analysis to reconstruct the diameters of all trees that were growing in these areas as of 1800, 1850, 1900, 1950, 2000, and 2017. The correlations and reconstructed data on trunk diameters made it possible to calculate the stocks of aboveground phytomass per unit area and estimate the rate of its accumulation over the past 200 years.

RESULTS

Altitudinal Position of the Upper Timberline and Quantitative Estimate of Its Displacement over the Past 60 Years

Using the methods described above, we compared the current altitudinal position of the UTL (stands with a closure of 35–40%) with that shown on topographic maps of 1956 and found that it markedly shifted higher to the mountains over the past 60 years: on average for all the plots, for more than 64 m vertically and 177 m horizontally (Table 1, Fig. 2). Analysis of the current altitudinal position of the UTL in selected slope areas least influenced by adverse nonclimatic factors (high stoniness, steepness, and moisture) showed that its mean values in this region of the Putorana Plateau increase in a series from northern slopes (348 ± 65 m a.s.l.) to eastern (461 ± 45 m), western (537 ± 92 m), and southern slopes (610 ± 60 m) (Fig. 3). The most significant altitudinal shifts of forest boundaries over the past 60 years were revealed for slopes facing south (111 ± 74 m) and west (86 ± 62 m); medium shifts, for eastern slopes (78 ± 50 m); and minimum shifts, for northern slopes (59 ± 56 m). As can be seen, when areas obviously influenced by nonclimatic factors are excluded from analysis of UTL dynamics, the average rate of upward shift in the upper forest limit increases from 1.0 to 1.4 m/year, which indicates a significant adverse effect of these factors.

Composition, Structure, and Reconstruction of the Formation of Tree Stands at the Upper Timberline

The results of calculations showed that the mean and maximum morphometric parameters of tree stands in both transects consistently change (decrease) as elevation increases (i.e., as the conditions for their growth deteriorate) (Table 2). Thus, the average trunk base diameter decreases by a factor of 2–4; diameter at breast height, a factor of 2.5–5; trunk height, a factor of 3–3.5; and crown diameter, by a factor of 2–2.5. Of particular interest is the gradual decrease in the average age in the direction from the lower to upper part of the transect: from 89 to 43 years in transect I and from 177 to 49 years in transect II. The maximum values of morphometric parameters are 2–4 times lower in the upper part of the UTLE than in its lower part. On the whole, the most significant changes in the morphometric parameters of tree stands are observed in the transitional zone between the middle and upper parts of the ecotone: they are 1.5–2 times higher at the lower and middle levels of transect II than at these levels of transect I, which is explained by specific features of the sampled tree stands (as noted above, transect II was in a continuous forest massif).

The crown cover of tree stands also consistently decreases with an increase in elevation, especially in the transitional zone between the middle and upper parts of the ecotone. The highest density is characteristic of forests in the middle part of the UTLE in both altitudinal transects.

It was of special interest to reconstruct the colonization of slopes by larch, which is currently dominant, based on analysis of the age structure of tree stands (Figs. 4a, 4b). It was found that the establishment of single larch trees at the lower level of transect I (see Fig. 4a) was occurring during the period from the mid-17th century to the late 18th century, with only 3% of currently growing trees having appeared in this area over 150 years (the figure presents the data only since 1800). The periods of large-scale establishment of larch at this level were 1870 to 1910 and 1950 to 2000 (30 and 45% of trees, respectively). The middle level began to be colonized only in the second half of the 19th century, and mass regeneration of larch in this area began in the 1920s and has continued since then (93% of the currently growing trees have emerged between 1920 and 2010). At the upper altitudinal level, single larch trees were emerging since the late 19th century, but their large-scale establishment started only in the 1950s.

The processes of larch stand formation in transect II followed a different scenario. At the lower altitudinal level, the first trees appeared in the early 17th century, and the process of larch establishment during the subsequent 400-year period was uniform, without distinct regeneration peaks, except for a slight increase in the proportion of newly established trees by the late 20th century (17% of the currently growing trees appeared from 1600 to 1700; 22%, from 1700 to 1800, 24%, from 1800 to 1900, and 37%, from 1900 to 2000). At the middle altitudinal level, the first larch trees appeared only in the second half of the 18th century, and their large-scale establishment began only after the 1950s (74% of currently growing trees). At the upper altitudinal level of transect II, colonization by singe larch trees continued from the 1830s to the 1950s (in total, 16% of trees). Active larch regeneration in

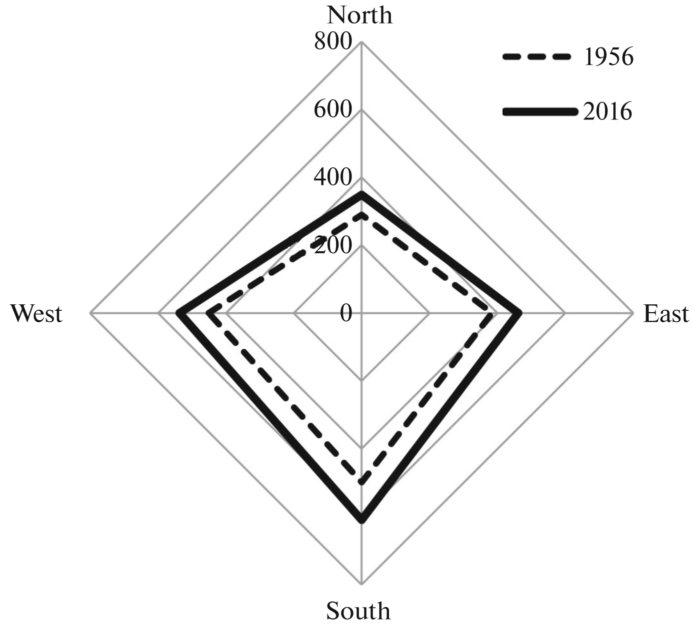

Fig. 3. Mean elevation (m a.s.l.) of the upper boundary of sparse forests with a closure of 35–40% on slopes of different aspects in the Sukhie Gory Range, the western part of the Putorana Plateau, in 1956 and 2017.

this area began in the 1960s and has continued since then (84% of trees).

Dynamics of Phytomass Accumulation in Tree Stands at the Upper Timberline

Analysis of the age structure of tree stands and the dynamics of phytomass showed that phytomass stocks in tree stands at the upper boundary of closed forests in transect I increased abruptly (by a factor of 7) during the period from 1900 to 1950 (Fig. 5, Table 3), with annual phytomass production increasing fourfold. During the subsequent period, the rate of accumulation further increased by a factor of 1.7. The current stocks of the aboveground phytomass in closed forest are 34–42 t/ha. The average rate of phytomass

Table 2. Main morphometric parameters of larch stands at different altitudinal levels of transects on slopes of the Sukhie Gory Range (the western part of the Putorana Plateau)

Morphometric parameters	Transect I			Transect II		
Part of the UTLE	Lower part	Middle part	Upper part	Lower part	Middle part	Upper part
Elevation, m a.s.l.	570	590	610	640	670	700
Mean trunk base diameter, cm	13.8 ± 1.0	8.2 ± 0.4	5.9 ± 0.5	25.5 ± 2.2	14.2 ± 1.6	6.5 ± 0.5
Maximum trunk base diameter, cm	50.0	25.5	12.7	58.0	47.0	24.0
Mean diameter at breast height, cm	9.8 ± 0.9	5.6 ± 0.3	3.5 ± 0.4	22.8 ± 1.5	10.9 ± 1.2	4.6 ± 3.8
Maximum diameter at breast height, cm	28.0	19.0	7.0	40.0	33.0	17.0
Mean height, m	5.6 ± 0.4	3.9 ± 0.2	2.0 ± 0.2	10.6 ± 0.8	5.7 ± 0.6	2.9 ± 0.2
Maximum height, m	12.5	10.0	3.8	19.0	15.0	8.1
Mean crown diameter, m	2.7 ± 0.2	2.1 ± 0.1	1.5 ± 0.1	3.2 ± 0.3	2.8 ± 0.3	1.4 ± 0.1
Maximum crown diameter, m	8.0	5.1	2.9	7.0	7.5	3.5
Mean age, years	89 ± 4	52 ± 2	43 ± 3	177 ± 14	73 ± 5	49 ± 3
Maximum age, years	211	139	119	405	242	180
Forest density, trees/ha	967	1200	275	383	400	533
Crown cover area, m^2/ha	6008	3560	527	5100	4408	1532
Undergrowth density, ind./ha	67	75	167	100	133	217

Table 3. Rate of changes in phytomass stocks in different time periods at different altitudinal levels of the transects on slopes of the Sukhie Gory Range (the western part of the Putorana Plateau), t/ha per year

Part of transect	Transect I			Transect II		
	1900–1950	1950–2000	2000–2017	1900–1950	1950–2000	2000–2017
Lower part	0.094	0.416	0.726	0.538	0.577	0.850
Middle part	0.007	0.061	0.342	0.029	0.232	0.648
Upper part	0.001	0.002	0.032	0.004	0.020	0.157

accumulation in sparse forest was 0.007 t/ha per year until 1950; in the second half of the 20th century, this parameter increased 8.7 times due to the large-scale establishment of trees. The current stocks of the aboveground phytomass in sparse forest are 4.8–12.0 t/ha and continue to increase at an average rate of 0.34 t/ha per year. The mass formation of tree stands in the upper part of the present-day ecotone began only in the second half of the 20th century. Before this period, the aboveground phytomass stock at this altitudinal level was almost zero. The average rate of phytomass accumulation between 1800 and 1950 was very low (0.0003 t/ha per year) but increased 32-fold during the subsequent period. The current values of tree phytomass stocks in the tundra with groups of trees are 0.4–0.9 t/ha.

Compared to transect I, the age and morphological structure of tree stands in transect II is different, and the current phytomass stocks are 2.6–5.5 times higher, although periods of sharp increase in the rates of phytomass accumulation coincide in both transects (Table 3). It should be noted that the highest current rate of increase in forest phytomass stocks (by a factor of 8–16 since 2000) is observed in both altitudinal transects in the upper part of the present-day ecotone. Annual production rates increase because these tree stands are at the stage of formation that coincides with the period favorable for the survival and growth of the newly developing tree generation.

Local Habitat Conditions

Analysis of data from thermal sensors showed that summer monthly average air temperatures in larch crowns at a height of 2 m tend to increase (by 0.1–0.4°C) upon transition from the lower to middle part of the UTLE due to higher crown openness and solar warming of air and plant parts; however, these temperatures remain almost the same or decrease by 0.1–0.6°C in the transitional zone between the middle and upper parts of the UTLE (Table 4). The temperatures recorded in October to April do not differ significantly.

The data from thermal sensors installed in soil at a depth of 10 cm showed that the monthly average temperatures were 2.4–6.3°C lower in the lower than in the upper part of the UTLE in June–July and, on the contrary, 2.9–13.7°C higher in the lower than in the upper part in October–April (Table 4). The significant differences in average temperature values are explained by significant soil shading by larch crowns (50–60%) and alder crowns in the lower part of the UTLE in summer months and by more effective protection from cold in winter due to deeper snow cover: 91 vs. 54 cm (in windblown areas, at most 39 cm) in the upper part of the UTLE.

DISCUSSION

The results of our research show that forests in the western part of the Putorana Plateau expanded higher to the mountains during the 20th century, with their productivity increasing during this period. This process had certain distinctive features depending on the type of forest massif. The colonization of higher hypsometric levels by larch started in the second half of the 20th century and has continued since then (Fig. 4), which is confirmed by the consistent decrease in the average age of trees currently growing in the study area (Table 2) and by differences between the degrees of its coverage by closed forests shown on historical topographic maps and in recent satellite images (Fig. 2).

It has been found that the upper timberline on the Sukhie Gory Range is the highest on south-facing slopes (610 ± 60 m a.s.l.) and the lowest on north-facing slopes (348 ± 65 m a.s.l.). In our opinion, these considerable differences are explained by higher warming and earlier snow thawing on southern slopes, due to which the growing season is longer than on northern slopes, and by higher heat supply to these habitats in summer. This contributes to better survival of tree sprouts and seedlings, as well as to the development of tree stands in general.

Differences in the average altitudinal position of the upper timberline on eastern and western slopes (461 vs. 537 m a.s.l.), which are more or less equally insolated and warmed in summer, may be due to the fact that the prevailing southwesterly and westerly winds in winter account for higher snow accumulation on eastern slopes. As a consequence, the snow thaws later, and the growing period is shorter than on western slopes. This also follows from the data on altitudinal UTL shifts on slopes of different aspects: similar to the altitudinal position of the UTL, their mean values gradually decrease from southern slopes (111 ± 74 m)

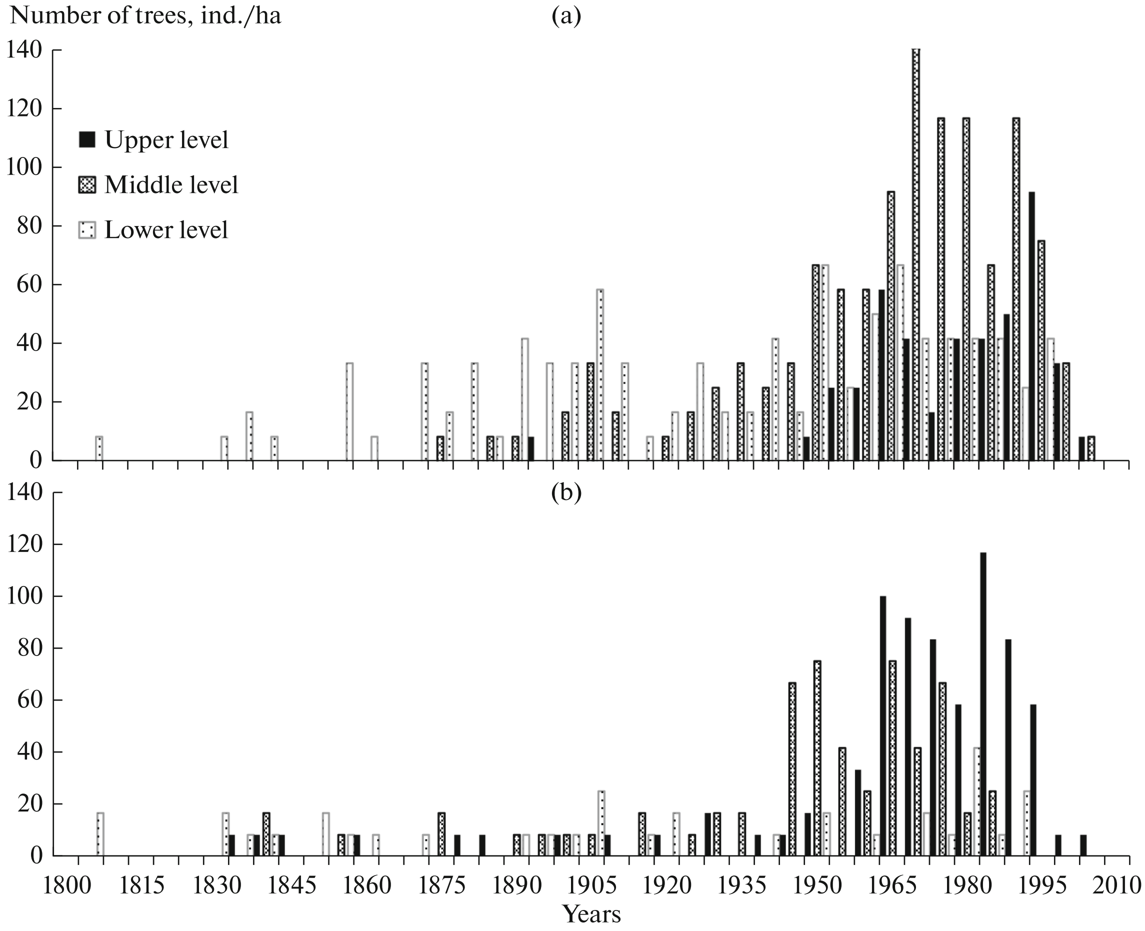

Fig. 4. Numerical distribution of trees by the periods of their appearance in altitudinal transects established on the southern slopes of the Sukhie Gory Range in the western part of the Putorana Plateau: (a) transect I, (b) transect II.

to western (86 ± 62 m), eastern (78 ± 50 m), and northern slopes (59 ± 56 m).

The expansion of tree vegetation in the western part of the Putorana Plateau during the past centuries has occurred on slopes of different aspects and angles, with different levels of stoniness, moisture, and snowiness, which indicates that some factors common to the entire study area have had an effect on these processes. In our opinion, these may be only climatic factors. Analysis of data from the Dudinka weather station located 180 km west of the study area, which has the longest series of observations in this region of the Subarctic (since 1906), showed that, from the early 20th to the early 21st century, the average air temperatures increased by 1.5–2.5°C in early summer (June–July) and only by 0.2–0.4°C in August–September. As a result, the average increase over the warm period of the year (June–September) was only 1.1°C. In October–May, average air temperatures of November and February decreased by 0.5–1.3°C, while those of all other months increased by 0.6–2.4°C, with the average temperature over the cold season rising by 0.9°C. The amount of precipitation in summer months varied during the 20th century, showing a general tendency toward a slight decrease (5%). On the contrary, the amount of solid precipitation in winter showed a clear trend to increase (by 30% since 1936); consequently, the maximum snow cover depth increased significantly, from 40 to 75 cm. Analysis of meteorological data indicates a general rise in air temperature over the past 110 years, especially at the beginning of the growing season (June–July). On the whole, climate changes led to a significant prolongation of the growing season (by 4–7 days) due to its earlier onset, as well as to an increase in heat supply, which is extremely important for the growth and development of trees (especially during the intense growth period); they also provided more favorable conditions for the survival of trees during the cold period of the year (an increase in air and soil temperature).

In the upper part of the UTLE, soil temperature in summer and winter months was lower than air temperature by only a few degrees and showed similar daily dynamics. This implies high soil heating in summer and cooling in winter, which is extremely unfavorable for the survival of tree sprouts and seedlings. in

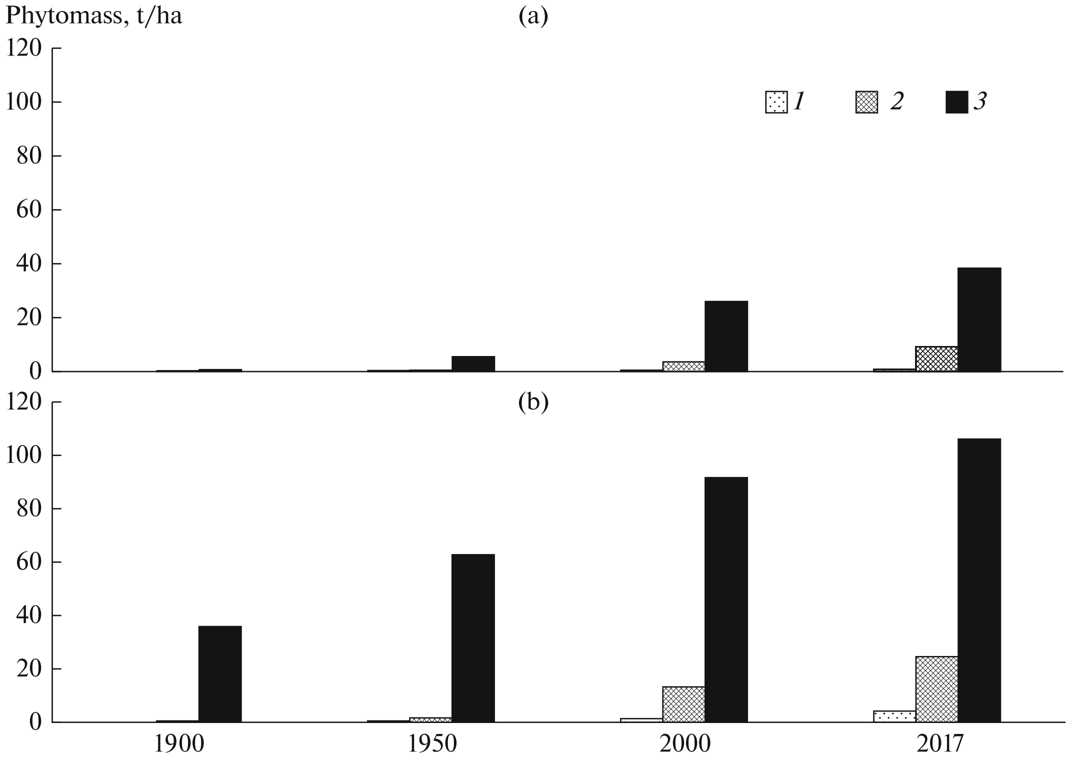

Fig. 5. Dynamics of tree phytomass stocks at different altitudinal levels of transects on southern slopes of the Sukhie Gory Range in the western part of the Putorana Plateau: (a) transect I, (b) transect II; (*1*–*3*) altitudinal levels: (*1*) upper level, (*2*) middle level, (*3*) lower level.

the lower part of the UTLE, in contrast, daily changes in air temperature are smoothed. As a result, soil temperatures decrease in summer due to shading by tree crowns and significantly increase in winter due to the protective effect of snow cover. Conditions for the development of undergrowth and seedlings are currently optimal in the middle part of the UTLE, where soils are warmed better than in the lower part but do not dry up in summer and are cooled to a lesser extent in winter than soils in the upper part of the ecotone.

The important role of summer heat supply in the dynamics of tree stands at the upper limit of their distribution in the western part of the Putorana Mountains is confirmed by high correlations between the numbers of larch trees that appeared in the upper and lower parts of the UTLE during 5-year intervals in the period of 1915 to 2005 and the average temperatures of the warmest month of the year (July). It should be particularly noted that the number of larch trees that appeared in the upper part of the UTLE during a given 5-year interval (between 1915 to 2005) was more dependent on temperatures of the previous interval ($R^2 = 0.53$) than of the current interval ($R^2 = 0.27$). As in the upper part, regeneration of tree stands in the middle part of the UTLE between 1915 and 1975, when the number of larch trees showed a clear trend to increase (Fig. 4), was more dependent on temperatures in the 5-year period preceding the appearance of trees ($R^2 = 0.63$) than on temperatures in the current period ($R^2 = 0.16$). Conversely, the numbers of larch trees appearing between 1980 and 2005 showed higher dependence on temperatures during the period of their establishment ($R^2 = 0.62$) than during the preceding period ($R^2 = 0.16$).

It is well known that favorable or unfavorable conditions in the period preceding the appearance of trees determine the number of viable seeds, while conditions during the period of their establishment and in the first years of their life have influence on the number of sprouts and survival of seedlings. Significant differences in these characteristics by time periods in the middle part of the UTLE indicate that the number of seed-producing trees per unit area increased by 1975 to the level at which the amount of viable seeds produced by them no longer limited the rate of forest regeneration processes in this zone, yielding the leading role to factors determining success in seed germination and seedling survival. Correlations with temperatures in the period of tree establishment and the preceding period in the lower part of the UTLE proved to be lower or absent both before and after 1975 (the highest correlations with temperatures in the preceding period before 1975 is relatively weak, $R^2 = 0.19$). In our opinion, this is explained by a decrease in the level of forest regeneration in this area in the second half of the

Table 4. Mean air and soil temperatures in the lower part of the tundra belt and at the upper boundaries of tree stands with different degrees of closure on the southern slope of the Yuzhny Neralakh River (Sukhie Gory Range, Putorana Plateau) from August 1, 2017, to August, 2018

Year	Month	Air temperature, °C			Soil temperature, °C			
		Upper boundary			Mountain tundra	Upper boundary		
		open stands	sparse forest	closed forest		open stands	sparse forest	closed forest
2017	August	8.7	8.9	8.8	9.2	9.0	9.6	9.2
2017	September	1.5	1.8	1.8	2.1	2.1	3.3	2.9
2017	October	–6.6	–6.6	–6.7	–4.0	–2.8	0.2	0.1
2017	November	–16.9	–16.9	–17.1	–14.7	–7.5	–1.7	–1.1
2017	December	–16.9	–16.8	–16.9	–14.9	–8.6	–2.9	–2.3
2018	January	–21.0	–21.4	–21.4	–21.5	–18.2	–5.5	–4.5
2018	February	–20.0	–20.3	–20.3	–19.8	–16.7	–6.2	–5.3
2018	March	–19.6	–19.3	–19.6	–20.3	–19.1	–7.9	–7.1
2018	April	–10.2	–9.5	–9.8	–12.2	–13.2	–6.9	–6.0
2018	May	–2.6	–2.0	–2.4	–0.9	–5.2	–2.6	–1.9
2018	June	15.9	16.0	15.4	14.2	13.2	9.5	6.9
2018	July	9.6	10.2	9.8	11.5	10.8	10.4	8.6

20th century due to significant intensification of intraspecific competition for resources and by a decrease in soil temperatures because of increasing forest closure in this part of the forest–tundra ecotone.

Based on the comparison of satellite images of the central part of the Putorana Plateau (68°19′ N, 94°33′ E), Im and Kharuk [21] found that the rise of annual average temperature during the last 30 years of the 20th century contributed to the altitudinal expansion of tree vegetation for no more than 15 m a.s.l. Based on comparative analysis of Quickbird and Hexagon satellite images, they estimated the appearance of new trees between 1976 and 2005 in the central part of the Putorana Plateau on a southwest-facing slope at an elevation of 670 ± 40 m a.s.l., taking into account trees no less than 2.5 m high with a crown diameter over 1 m. These authors found that approximately three new trees per hectare appeared over the 30-year period. Our results show that the number of trees with the same morphometric parameters that appeared over the same time interval was no less than 40 ind./ha in transect I and 90 ind./ha in transect II; in addition, the rate of altitudinal shift in the upper timberline was markedly higher (1.0 vs. 0.3 m/year). Im and Kharuk also found that the highest elevation of the forest boundary corresponds to the 930 m a.s.l. mark, with the minimum size of the detected tree crown being 1 m. The highest elevation of the forest boundary in the study area is significantly lower (700 m a.s.l.), and the corresponding elevation in the northwestern part of the Putorana plateau (the Avam River valley) is only 390 m a.s.l. [22]. In our opinion, differences in the altitudinal position of the upper forest boundary between the western and central parts (by 230 m) are determined by the strong influence of Atlantic air masses in the western part of the Putorana Plateau and, consequently, by high precipitation in this area, which is also characteristic of other areas with different levels of soil moisture on the slopes, e.g., the Ural Mountains [31]. Climate on the northern macroslope of the Putorana Mountains is determined by a significant effect of cold Arctic air masses; therefore, the UTL in more southern areas of this mountain region lies at higher positions.

Kirdyanov et al. [22] showed that it is ongoing climate changes that lead to the expansion and upslope advance of forests. According to their data, larch regeneration in the middle and upper parts of the UTLE was most abundant in the second half of the 20th century, i.e., in the same period as in our altitudinal transects. On the whole, the aforementioned authors attribute the observed dynamics and increase in tree stand productivity at the upper timber line with general climate warming in the Subarctic.

Studies performed by different research groups in other subarctic regions provide evidence for a climate-induced increase in forest productivity in the second half of the 20th century and, on the other hand, for a drop in the rates of phytomass accumulation in the early 21st century [32–34]. The results of our research are indicative of consistent increase in the rates of phytomass accumulation (Table 3, Fig. 5), which is particularly noticeable in the upper part of the current ecotone.

Therefore, the increase in early summer temperatures (by 1.5–2.5°C) and duration of the growing season (by 4–7 days) and also in winter temperatures and amount of solid precipitation in the western part of the Putorana Plateau during the past centuries have led to changes in the altitudinal position (by 64 m) and productivity of tree stands at the upper timberline. The most significant forest expansion to higher elevation has occurred on slopes of southern and southwestern aspects in the second half of the 20th century.

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The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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