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Dynamics of the Timberline in High Mountain Areas of the Nether-Polar Urals under the Influence of Current Climate Change

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Abstract—Changes in the altitudinal position of the timberline in high mountain areas of the Nether-Polar Urals and basic factors that influence such changes have been revealed on the basis of comparison of the age structure of Siberian larch (*Larix sibirica*) and arctic birch (*Betula tortuosa*) tree stands and photographs made in different years. On the mountain slopes studied, an upward shift of the timberline took place in areas covered in winter with thick snow (in the late 18th century), with Siberian larch being the pioneer species. Larch began colonizing areas with a thin snow cover in the 20th century. Birch appeared later and has since strengthened its positions. The increase in winter temperatures and precipitation facilitated the expansion of the forest.

Keywords: snow depth, timberline, tree stand structure, *Larix sibirica*, *Betula tortuosa*, climate change, Nether-Polar Urals

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International agreements of the past few decades (the United Nations Framework Convention on Climate Change, the Kyoto Protocol, and others) were a strong driving force behind studies on the responses of ecosystems to global and regional climate change. High mountain and high latitude regions are especially attractive as model systems for evaluating climatic factors and their influence on the formation and growth of forest communities (Gorchakovskii and Shiyatov, 1985).

In recent years, considerable changes have been revealed in the composition, structure, and altitudinal position of tree stands at the timberline in the Southern Urals (Shiyatov et al., 2001; Moiseev et al., 2004), Northern Urals (Kapralov et al., 2006; Moiseev, Bartysh, and Nagimov, 2010), and Polar Urals (Shiyatov, 2009; Shiyatov and Mazepa, 2007). However, no such studies have been performed in the Nether-Polar Urals. Only some earlier publications on this problem are available (Shiyatov, 1974, 1981), but they are mainly descriptive and obviously insufficient for generalizations.

We have studied the composition and structure of tree stands and local conditions in the areas they occupy in the central Nether-Polar Urals along the altitudinal gradient within the forest–tundra ecotone, and employed the rarely used method of landscape photographs made at the same sites in different years (Shiyatov, 2009).

MATERIALS AND METHODS

The Nether-Polar Urals extend from the upper reaches of the Lyapin (Khulga) River (65°40′ N) in the north to Mt. Tel'pos-Iz (64° N) in the south. The area of the mountain part of this region is 32000 km^2. The region is distinguished by the Urals' highest main mountain ranges (up to 1895 m), a broad mountain zone, and high precipitation. The climate of the region is cold and excessively humid. The annual precipitation reaches 1500 mm. Winters are cold and snowy. The duration of stable snow cover is 200 to 240 days. The rivers have a high water flow and are mostly snow-fed. Closed forests reach elevations of 550–650 m a.s.l., on average, expanding even higher (up to 750 m) along river valleys (Kemmerikh, 1961).

We studied larch and birch tree stands in the timberline ecotone, understood as the transitional mountain zone between the upper limits of closed forests and upper limits of single tree growth in the tundra. According to Gorchakovskii and Shiyatov (1985), this ecotone includes several categories of upper limits: the upper limit of closed forests (canopy closure 0.4–0.5); the upper limit of open forests (canopy closure 0.2–0.3); the upper limit of sparse tree growth (canopy closure 0.05–0.1); and the upper limit of single tree growth in the tundra (canopy closure less than 0.05).

This study was performed by the method used in the international project INTAS-01-0052. Altitudinal transects were established on slopes of different exposure. In each transect, three altitudinal levels were delimited: lower, at the upper limit of closed forests (570–620 m a.s.l.); middle, at the upper limit of open forests (630–680 m a.s.l.); and upper, at the upper limit of sparse tree growth (690–730 m a.s.l.). At each level, 22 to 26 test plots (20 × 20 m) were established, and each tree in the plots was examined to record the following parameters: height, stem diameter at the base and at a height of 1.3 m, and diameter of crown projection in two directions. In those areas of the forest–tundra ecotone in which canopy closure was smaller than 0.1, the size of test plots was increased to 0.5 ha. To estimate the age of trees, a core sample of wood was taken from each living tree with stem diameter over 3 cm; in slenderer or dead trees, cross cuts were made at the base of the stem. The annual rings in the samples were counted and dated by standard dendrochronological methods, using the master chronology for the study area (Shiyatov, 1986). The age structure of Siberian larch tree stands was assessed after combining the numbers of trees into 5-year age groups, since abundant seed production in this tree species takes place at certain time intervals (Koshkina, 2008). Specialized publications report that the arctic birch is almost invariably multistemmed, with most of stems appearing much later than the tree itself. This makes it difficult to estimate the actual age of an arctic birch tree. However, the environment-forming role of trees during the development of forest communities manifests itself mainly after the main parts of the crowns grow forth (Moiseev, Bartysh, and Nagimov, 2010). Therefore, arctic birch stems were also combined into 5-year age groups to provide the possibility of comparing the periods of colonization of formerly forest-free areas by tree stands of these species.

In the southeastern part of Issledovatel'skii Ridge (the Kobyla-Yu River basin), we established three altitudinal transects in 2007 (Fig. 1): two on the northeastern slope of Mt. Khus'-Oika (transect 1 in a birch tree stand and transect 2 in a larch tree stand) and one (transect 3) on the southeastern slope of Mt. Ner-Oika. Transect 4 was established in 2009 on the northern slope of Mt. Sale-Pasne-Ner in areas exposed to extreme wind pressure. On the whole, morphological parameters of 2019 trees were measured (age was estimated for 1500 trees) and 2138 young trees in the undergrowth were examined in test plots with a total area of 6.56 ha.

Changes in the climate of the study area were estimated from measurements taken at the Troitsko-Pechorskoe weather station, where the longest series of records are kept (since 1880). The correctness of our calculations is supported by the fact that the time courses of temperatures recorded at the Troitsko-Pechorskoe station and weather stations situated closer to the study area (Pechora, Saranpaul', Ust'-Shchugor, and Ust'-Tsil'ma) strongly correlate with each other: the coefficient of determination (R^2) for different months varies from 72 to 94%.

The following parameters were recorded for assessing biotopic conditions for tree stands in the transects: elevation a.s.l., slope exposure and angle, soil moisture, and snow depth in late winter. The accumulation of snow in the test plots and adjacent areas was studied in late March 2010: its level was marked with paint on was tree stems, and the height of the marks was measured in summer.

Forest sites were photographed from approximately the same points as previously (more than 40 years ago). A total of over 100 photographs were taken in various areas of the Nether-Polar Urals (valleys of the rivers Naroda, Khobe-Yu, Shchekur'ya, Kobyla-Yu, Lunvozh-Synya, and Sed'-Yu, and environs of Torgovoe Lake).

RESULTS

Description of local biotopic conditions in altitudinal transects. The soils in both transects established in the timberline ecotone on the northwestern slope of Mt. Khus'-Oika are of mesic type. The slope angle decreases by a factor of 3 from the lower to middle level and increases by a factor of 2 from the middle to upper level (Table 1). The snow depth in transect 1 slightly increases with a decrease in elevation; in transect 2, it remains almost unchanged between the lower and middle levels but increases twofold from the middle to upper level. This snow accumulation pattern is explained by specific mesotopographic features in different areas of this slope.

The soils in all altitudinal levels of the transect on Mt. Ner-Oika are also of mesic type. The slope on which this transect was established is part of a watershed range, and its angle increases with elevation from 10° to 25°. Large amounts of snow are transferred in winter from west to east over the pass lying above, and this snow is largely retained by tree stands at the upper level. As a result, the snow depth increases with elevation.

On Mt. Sale-Pasne-Ner, all areas affected by strong wind pressure are situated on mountain passes. The slope angle is at most 5°. In terms of moisture regime, the soils are of temporarily dry type. The snow depth slightly decreases with elevation (from 0.5 to 0.2 m).

On the whole, the altitudinal levels of the transects (despite their similarity in absolute elevation) differ in biotopic conditions, especially snow depth. Therefore, we divided all areas of the slopes into two categories: high-snow areas (with a background snow depth of 1.0 to 2.0 m in late winter) and low-snow areas (with a background snow depth of up to 0.5 m).

Composition and structure of tree stands and reconstruction of their formation at the timberline. The results of calculations show that in transect 1, on the northeastern slope of Mt. Khus'-Oika, the arctic birch is the dominant tree species in tree stands at the lower and upper levels (no tree stands have been found at the middle level) (Table 2). Its dominance over the Sibe-

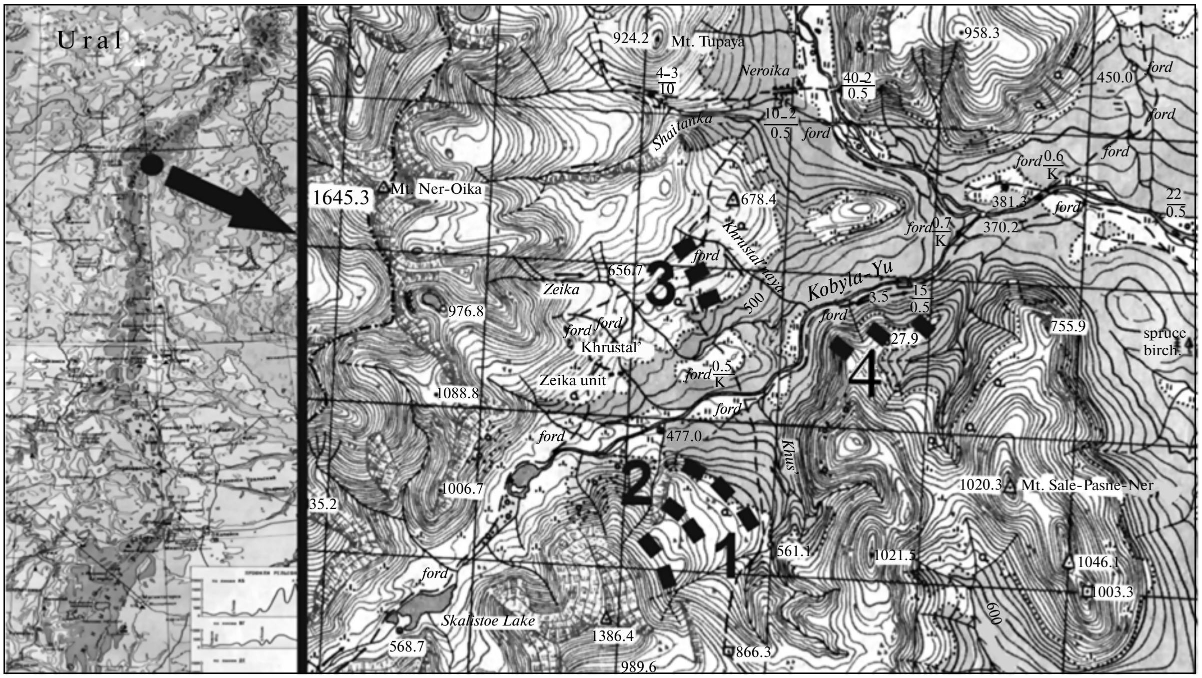

Fig. 1. Study area: 1–4, transect numbers; filled rectangles, test plots.

rian larch is especially well manifested in the number of stems. The young growth includes not only birch and larch but also Siberian stone pine (Table 3). At the upper level, the young growth is dominated by birch (57%), while at the lower level it is dominated by larch (48%). The proportion of Siberian stone pine at the upper level (22%) is considerably higher than at the lower level (8%). The morphometric parameters of

Table 1. Characteristics of local biotopic conditions along altitudinal transects

Altitudinal level	Elevation a.s.l., m	Exposure	Slope angle, degrees	Soil moisture	Average snow depth, cm
High-snow areas of Mt. Khus'-Oika (transect 1)					
Upper	705	NW	10–15	Mesic	104 ± 2.3
Lower	600				141 ± 2.5
High-snow areas of Mt. Khus'-Oika (transect 2)					
Upper	705	NW	10–15	Mesic	50 ± 1.6
Middle	650		5–10		150 ± 3.2
Lower	600		10		115 ± 2.0
High-snow areas of Mt. Ner-Oika					
Upper	700	SE	15–25	Mesic	162 ± 6.56
Middle	650		15–20		148 ± 3.59
Lower	600		10–15		105 ± 4.2
Low-snow areas of Mt. Sale-Pasne-Ner					
Upper	700	Pass	5–10	Temporarily dry	20 ± 1.3
Middle	625		0–5		35 ± 1.9
Lower	570		0–5		50 ± 1.1

Table 2. Proportions of larch (L), birch (B), and Siberian stone pine (SP) in the composition of tree stands at different altitudinal levels of the transects, %

Altitudinal level	Habitat	High-snow							Low-snow	
	Massif	Khus'-Oika (1)		Khus'-Oika (2)		Ner-Oika			Sale-Pasne-Ner	
	Tree species	L	B	L	B	L	B	SP	L	SP
Upper	by completeness	42	58	97	3	94	6	0	100	0
	by density	20	80	73	27	42	58	0	100	0
Middle	by completeness	–	–	99	1	100	0	0	100	0
	by density	–	–	89	11	100	0	0	100	0
Lower	by completeness	47	53	89	11	94	2	4	82	18
	by density	16	84	51	49	77	13	10	70	30

Table 3. Abundance of young growth of larch (L), birch (B), and Siberian pine (SP) per ha at different altitudinal levels of the studied transects

Habitats		Thick snow cover									Thin snow cover		
Massif		Khus'-Oika (1)			Khus'-Oika (2)			Ner-Oika			Sale-Pasne-Ner		
Tree species		L	B	SP	L	B	SP	L	B	SP	L	B	SP
Altitudinal level	upper	20	52	20	24	29	0	77	33	8	6	0	25600
	middle	–	–	–	1322	13	158	139	0	182	23	0	15200
	lower	150	138	25	223	100	67	17	0	150	221	150	17500

larch and birch stands in areas dominated by birch markedly change with elevation (Table 4). Thus, the average values of tree diameter, height, and age increase from the upper to the lower level by a factor of 1.5–3, tree stand density increases by a factor of 8–11, and the total area of crown projections increases by a factor of 14–18.

Analysis of the data shown in Fig. 2a provides evidence that colonization of this slope area by larch started in the mid-19th century and progressed with time: 11% of present-day living trees appeared during the period from 1855 to 1860; 40%, from 1875 to 1920; and 43%, from 1920 to 1965. At the upper level, the first trees appeared during the second quarter of the 20th century, and active colonization of this level has continued since then: 53% of present-day living trees appeared between 1920 and 1965, and the remaining 47% appeared between 1965 and 2000. The period of abundant restocking by birch at the lower level continued from 1920 to 1965, when 75% of the present-day living trees appeared there (Fig. 2b). Colonization of the upper level by birch began only in the second half of the 20th century (98% of present-day living trees appeared from 1965 to 2000). Although birch lagged behind larch in the timing of abundant tree establishment at this level, its current density is several times higher than that of larch, as at the lower level.

In transect 2 on Mt. Khus'-Oika, tree stands at all levels are dominated by larch (Table 2), with birch being markedly inferior in both total stem cross-section area and tree density. In the young growth, larch is dominant only at the upper and middle levels (Table 3). Changes in the morphometric parameters of tree stands in areas dominated by larch in transect 2 show the same trends as in transect 1. Differences are especially conspicuous upon transition between the upper and middle levels (Table 4). The colonization of the lower level by larch started in the early 18th century (Fig. 3a), 10–15% of present-day living trees appeared by the end of that century, and abundant tree establishment took place in 1920 to 1965. The colonization of the slope by birch started in the early 20th century, and this process appears to be still underway: 42 and 56% of present-day living trees appeared during the periods from 1920 to 1965 and from 1965 to 2000, respectively. The formation of larch tree stands at the middle level followed a similar scenario but with a peak shifted to the period after 1920. Abundant colonization of this level by birch took place during the second half of the 20th century, when 75% of present-day living trees appeared. Larch began to colonize the upper level markedly later (in the early 20th century), and the majority of trees in present-day sparse stands (40–50 trees per

Table 4. Average taxonometric parameters of larch and birch stands at different altitudinal levels of the transects

Altitudinal level	Average parameters of trees				Area-related parameters	
	Diameter, cm	Height, m	Age, years	Crown diameter, m	Density, ind./ha	Total canopy closure, m^2/ha
Larch stands						
High-snow areas of Mt. Khus'-Oika (transect 1)						
upper	6.0 ± 0.6	3.4 ± 0.2	44 ± 2	2.0 ± 0.2	38	134
lower	14.6 ± 1.2	7.7 ± 0.5	99 ± 6	2.6 ± 0.3	319	2495
High-snow areas of Mt. Khus'-Oika (transect 2)						
upper	3.7 ± 0.3	2.8 ± 0.1	42 ± 2	1.7 ± 0.1	51	134
middle	13.0 ± 0.4	6.6 ± 0.2	71 ± 2	2.7 ± 0.1	456	3347
lower	13.3 ± 0.5	7.4 ± 0.2	90 ± 2	2.5 ± 0.1	625	3830
High-snow areas of Mt. Ner-Oika						
upper	12.2 ± 1.4	5.3 ± 0.5	58 ± 4	3.7 ± 0.4	48	451
middle	16.3 ± 0.7	8.2 ± 0.3	83 ± 3	3.6 ± 0.1	279	3423
lower	18.4 ± 1.1	10.2 ± 0.5	94 ± 5	3.7 ± 0.2	413	5184
Low-snow areas of Mt. Sale-Pasne-Ner						
upper	3.4 ± 0.5	2.7 ± 0.3	79 ± 5	2.2 ± 0.1	28	66
middle	3.9 ± 0.3	2.8 ± 0.1	57 ± 2	1.6 ± 0.1	49	127
lower	2.8 ± 0.3	2.5 ± 0.1	45 ± 2	1.4 ± 0.1	196	365
Birch stands						
High-snow areas of Mt. Khus'-Oika (transect 1)						
upper	3.2 ± 0.21	2.8 ± 0.09	30 ± 0.8	1.8 ± 0.08	154	462
lower	6.3 ± 0.29	4.8 ± 0.16	58 ± 1.1	2.0 ± 0.07	1669	6578
High-snow areas of Mt. Khus'-Oika (transect 2)						
upper	1.2 ± 0.21	2.0 ± 0.10	29 ± 2.0	1.1 ± 0.14	19	23
middle	4.5 ± 0.49	3.4 ± 0.22	34 ± 2.3	1.7 ± 0.11	54	139
lower	4.5 ± 0.24	4.1 ± 0.12	45 ± 1.4	1.7 ± 0.05	598	1629
High-snow areas of Mt. Ner-Oika						
upper	2.6 ± 0.26	2.5 ± 0.13	30 ± 1.4	1.7 ± 0.11	77	118
lower	6.9 ± 0.73	6.1 ± 0.77	49 ± 3.6	2.8 ± 0.24	96	451

hectare) appeared only after 1970. The establishment of birch at this level began only in the late 20th century.

Tree stands occupying the timberline ecotone on the southeastern slope of Mt. Ner-Oika are dominated by larch at all altitudinal levels. At the middle level, larch is the only species forming the tree stand (Table 2). Birch occurs on this slope in very small amounts at the lower level (2%) and at the upper level (6%). Siberian stone pine participates in tree stand formation only at the lower level (4%). Remarkably, the role of Siberian pine in restocking increases at the lower and middle levels (Table 3). The morphometric parameters of birch and larch also increase with a decrease in absolute elevation (Table 4). Abundant colonization of previously forest-free areas by larch followed a scenario similar to that in transect 2 on Mt. Khus'-Oika (Fig. 4a). The establishment of birch on this slope started only in the early 20th century and has continued to date (Fig. 4b).

Tree stands in the areas studied on the slope of Mt. Sale-Pasne-Ner consist mostly by larch, with an admixture of Siberian stone pine occurring only at the lower level of the transect. Birch does not contribute to tree stand formation. The density of larch trees and young growth consistently increases with a decrease in absolute elevation. This transect differs from the oth-

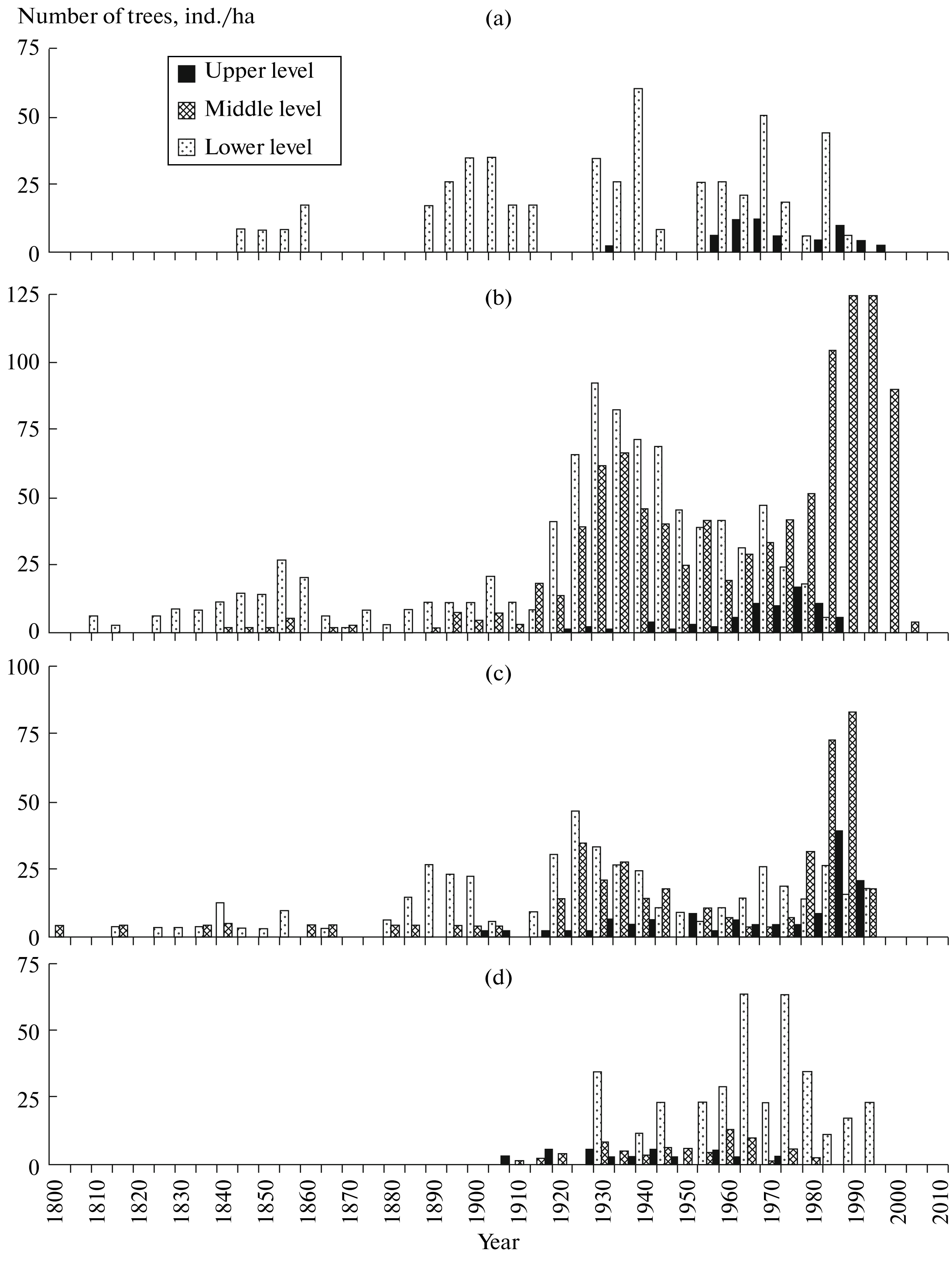

Fig. 2. Distribution of larch trees by periods of their appearance at different altitudinal levels of the transects: (a) Mt. Khus'-Oika, transect 1; (b) Mt. Khus'-Oika, transect 2; (c) Mt. Ner-Oika; (d) Mt. Sale-Pasne-Ner.

ers in a considerable amount of young growth, which, in addition, is dominated by Siberian stone pine at all levels. Figure 5 shows that the first larch trees appeared at all altitudinal levels of the transect only in the early 20th century. At present, the density of stems of multi-stemmed larch trees even at the lower level is at most 200 per hectare, and their taxonometric parameters (diameter, height, and age) are two to four times lower than in the other transects.

Two pairs of photographs taken in different years (Figs. 4 and 5) provide a more illustrative picture of the

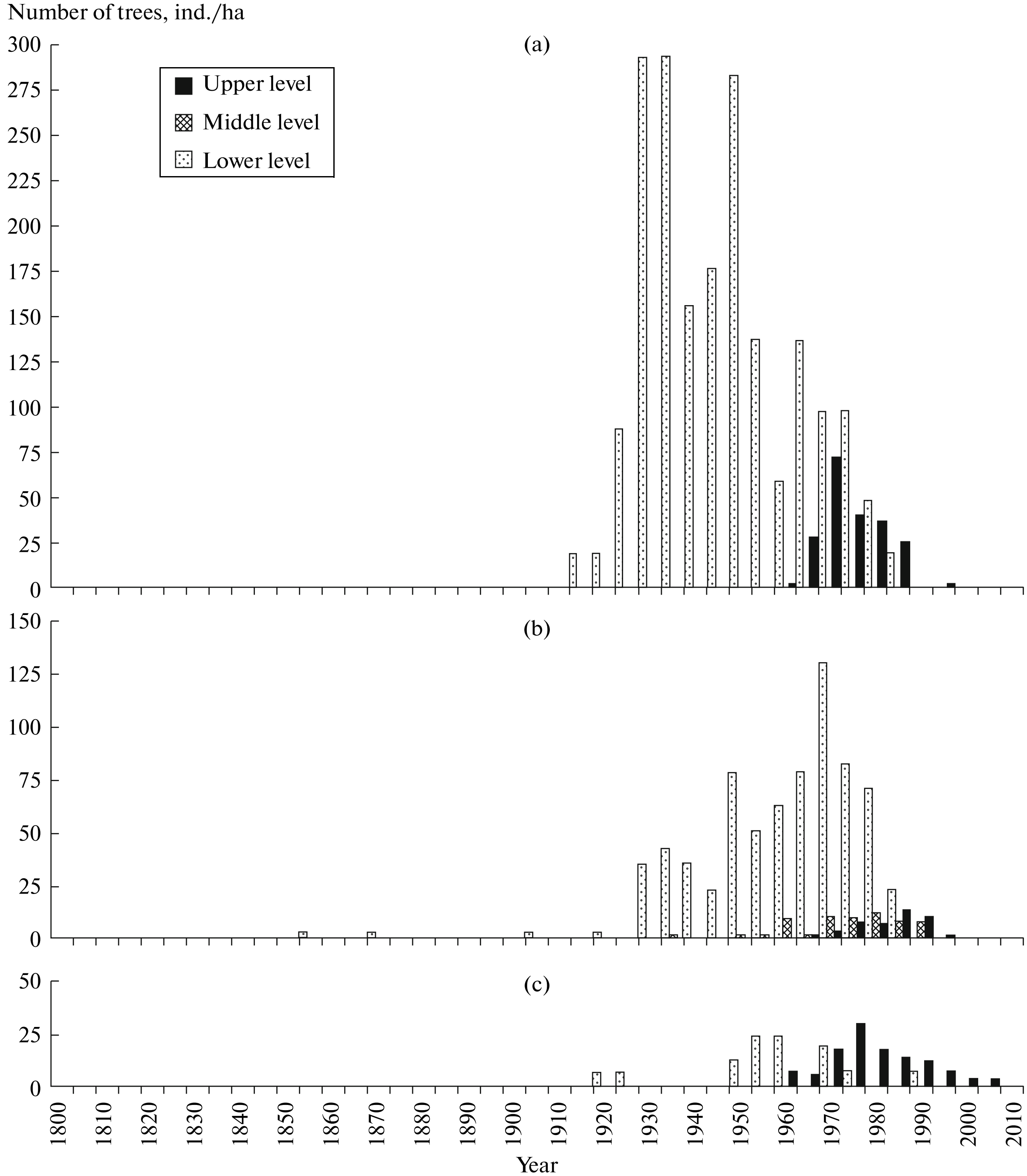

Fig. 3. Distribution of birch trees by periods of their appearance at different altitudinal levels of the transects: (a) Mt. Khus'-Oika, transect 1; (b) Mt. Khus'-Oika, transect 2; (c) Mt. Ner-Oika.

dynamics of the timberline. The first pair was taken at the northwestern slope of Mt. Khus'-Oika. In the foreground, it shows larch tree stands of the third level (transect 2) in the area where our test plots were established. In the background, there is the northern slope of Mt. Ner-Oika and, behind it, Mt. Tupaya (in the center) and the southern slope of Selener Range. Analyzing these photographs, it can be seen that in 2010, compared to 1934, single larch trees appeared in the foreground and tree stands in the background markedly increased in density. On the whole, the upper boundary of larch tree stands has shifted to higher elevations.

The second pair of photographs was taken on a gently sloping mountain terrace on the southern slope of Salener Range, 6 km from the village of Neroika.

Fig. 4. Photographs of the northwestern slope of Mt. Khus'-Oika taken in 1934 by A.N. Aleshkov (1937) and in 2010 by P.A. Moiseev.

Despite the relatively short period of time between the two photographs (on the time scale of this study), visible changes have occurred in the vegetation. The terrace in the background was almost treeless (except for single larch trees) In 1970, but a large (though sparse) larch forest has grown there by 2011. Another conspicuous feature is the increased density and productivity of larch tree stands shown in the foreground.

DISCUSSION

The results of our study show that, beginning from the 18th century, the timberline in the Nether-Polar Ural Mountains was shifting to higher elevations. The fact that the age of present-day larch and birch tree stands consistently decreases with an increase in elevation and differences in vegetation visible in photographs taken in different years confirm this conclusion. The rate of forest expansion to formerly treeless areas largely depends on local biotopic conditions, including snow depth and, therefore, the temperature regime of soils in winter. Thus, the rise of the timberline began in high-snow areas of Mts. Khus'-Oika and Ner-Oika, whereas the establishment of trees in low-snow areas on Mt. Sale-Pasne-Ner began 100 years later. This is explained by the fact that conditions at high elevations are extreme for the survival and growth of young trees, the most vulnerable link in the process of tree stand formation. Young trees are especially sensitive to frost heaving, cold injury, snow abrasion, and frost desiccation; this is why protection by snow cover is necessary for them.

Fig. 5. Photographs of the southern slope of Salener Range taken in 1970 by S.G. Shiyatov and in 2011 by A.A. Grigor'ev.

According to Goryaeva (2008), deep snow is one of the factors that have a positive effect on the emergence and survival of self-sown trees in the timberline ecotone. Snow accumulation in the forest depends on tree stand composition, canopy closure, and height of the tree–shrub and herb–dwarf-shrub layers, as well as on terrain topography. The timing and depth of soil freezing and thawing determine the soil temperature regime and the starting date of the growing season (Shiyatov, 1969; Korepanov, 1989). In mountain tundras, the life of plants with woody stems is strongly associated with snow cover, which protects them from cold injury and wind desiccation. The renewal buds on shoots that extend above the average snow level usually die in winter, while shoots covered by snow remain viable and successfully develop and branch repeatedly, resulting in a prostrate growth form (Gorchakovskii, 1970). In areas where snow accumulation is especially

Table 5. Changes in climatic parameters over the period from 1888 to 2000 according to data from weather stations Troitsko-Pechorskoe, Pechora, and Saranpaul'

Station	Periods compared, years	Month													
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	June–Aug.	Nov.–Mar.
Air temperature, °C															
Saranpaul'	1961–2000	–23.4	–20.6	–10.9	–3.7	3.9	12.1	16.3	12.3	6.1	–2.9	–14.4	–20.4	13.5	–17.9
	1888–1920	–24.0	–20.8	–13.8	–3.5	3.8	12.0	16.1	12.6	6.2	–3.7	–15.6	–21.8	13.6	–19.2
	Differences	0.6	0.2	2.9	–0.2	0.1	0.1	0.1	–0.4	–0.1	0.8	1.2	1.4	0.0	1.3
Pechora	1961–2000	–19.9	–17.0	–9.1	–3.3	3.5	11.7	16.0	11.9	6.3	–1.6	–10.6	–15.9	13.2	–14.5
	1888–1920	–20.3	–17.6	–12.3	–3.3	3.2	11.3	15.6	12.3	6.3	–2.5	–12.0	–18.0	13.1	–15.8
	Differences	0.5	0.6	3.2	0.0	0.2	0.4	0.4	–0.4	0.0	0.8	1.4	2.2	0.1	1.3
Troitsko-Pechorskoe	1961–2000	–18.3	–15.6	–7.3	–0.5	6.0	12.9	16.3	12.3	6.7	–0.8	–9.3	–14.7	13.9	–13.0
	1888–1920	–18.9	–15.9	–9.6	–0.5	5.7	12.8	16.0	12.8	6.8	–1.6	–10.5	–16.7	13.9	–14.3
	Differences	0.6	0.4	2.3	0.0	0.2	0.2	0.3	–0.5	–0.1	0.8	1.2	2.0	0.0	1.3
Precipitation, mm															
Troitsko-Pechorskoe	1961–2000	43	33	30	37	52	63	71	77	61	67	54	48	212	208
	1921–1960	24	16	19	23	42	59	64	57	62	47	30	26	181	114
	1889–1918	26	17	19	24	45	56	63	69	59	45	33	30	190	128
	Differences	17	15	11	13	7	7	8	8	2	22	21	19	22	80

abundant, its melting is usually delayed, resulting in a shorter growing period and higher soil moisture. As a consequence, the early phenophases of plants start later and take longer (Gorchakovskii and Shiyatov, 1971). If snow cover is thin, soil moisture at the frost boundary freezes into large ice crystals, which grow and mechanically displace soil particles. Thus, frozen soil increases in volume, resulting in so-called frost heaving (Sovershaev, 1965). As noted by Molchanov (1950), not only snow cover but also forest litter can effectively protect the soil from freezing: no living soil cover is found in areas exposed to high winds on Mt. Sale-Pasne-Ner. If soil temperature falls below 4°C and the soil freezes to a depth of 25–30 cm, the proportion of dead fine roots increases from 14 to 28% and the symbiotic interactions of roots with mycorrhizal fungi become disturbed, which leads to a significant decrease in the amounts of nitrogen and phosphorus absorbed from the soil (Tierney et al., 2001).

Soils in slope areas were snow depth is small to medium are known to freeze deeper and thaw later, which leads to lower soil temperatures in the summer months and, consequently, lower activity of bacteria and retarded turnover of mineral nutrients (Kammer, Hagedorn, and Shevchenko, 2009). Water crystallization into ice particles upon a strong drop in soil temperature inhibits the winter activity of cryophilic bacteria and retards the release of extra portions of mineral nutrients, additional to those released in summer (Mikan, Schimel, and Doyle, 2002). All these factors (the partial loss of the assimilation system and fine roots, impairment of mineral nutrition) have a considerable effect on net photosynthesis, accumulation of nutrients, and, as a result, growth and seed production of trees.

Different tree species require different amounts of snow. Our studies have shown that the most favorable conditions for larch are formed in transect 1 on Mt. Khus'-Oika and in the transect on Mt. Ner-Oika, where larch is dominant in the tree stand and actively spreads to higher elevations. Moreover, the amount of larch trees in transect 2 on Mt. Khus'-Oika is considerably greater than in the transect on Mt. Ner-Oika (on a steeper slope, more strongly affected by the wind). In transect 2 on Mt. Khus'-Oika, the establishment of larch began 40 years later. A greater role in the rise of the timberline in this transect is played by birch, since moist and weakly freezing soils and a relatively short growing season in high-snow areas are favorable for this species (Kullman, 2001). Kapralov (2007), who studied the spatiotemporal dynamics of the timberline in the Northern Urals, also found that high-snow areas where other tree species become less competitive for various reasons (a reduced growing period, excessive pressure of the snow mass, or its mechanical impact on the stem and shoots) are especially favorable to the arctic birch. On the whole, the role of birch in the formation of tree stands at the timberline has been increasing since the early 20th century. A similar trend in the Northern Urals (Tylaisko-Konzhakovsko-Serebryanskii Massif) was noted by Bartysh (2008), who attributed it to the increase in winter precipitation that began in the late 19th century.

In the areas studied on Mt. Sale-Pasne-Ner, conditions are unfavorable for the growth and development of tree stands (thin snow cover, strong winds, insufficient soil moisture). Our study has shown that only Siberian larch can survive there. This is explained by the fact that this species can live on cold soils, survive low winter temperatures, modify its growth form, and develop a secondary root system (Shiyatov et al., 2000). The large amounts of young Siberian stone pine trees found on Mt. Sale-Pasne-Ner is explained by dispersal of Siberian pine tree seeds into mountain tundras by the nutcracker. In typical biotopes of the timberline ecotone, Siberian stone pine can form small vertical stems (the lower level) only if the climate becomes more favorable or the depth of snow cover increases (Kapralov et al., 2006).

Comparison of average air temperatures and precipitation levels recorded at the Troitsko-Pechorskoe weather station during two periods (from 1888 to 1920 and from 1961 to 2000) has shown that the climate of the study area has become warmer (by 0.6–0.8°C) and more humid (annual average precipitation increased by almost 30%). The strongest rise in the surface air temperature and precipitation has been recorded in the winter months (from November to March). The temperature and precipitation regimes of the summer months (from May to September) have changes to a lesser extent.

Thus, the climate of the study area has become warmer and more humid over the past 120 years. The surface air temperatures have risen especially strongly in the winter months. These changes provided for the observed expansion of tree vegetation to higher elevations, into mountain tundras. This is confirmed by differences in the vegetation pattern observed in photographs taken in different years and by changes in the age structure of tree stands along the altitudinal gradient.

The rates of the upward expansion of trees on different slopes are not equal and depend on local biotopic conditions. The species forming the tree stands (Siberian larch and arctic birch) differ in their requirements for snow depth and temperature regime of soils in winter. The rise of the timberline first started in high-snow areas (in the late 18th century), with Siberian larch being the pioneer species. The establishment of larch in low-snow areas began only in the 20th century. Birch spread to higher elevations later (in the early 20th century) and has since strengthened its positions at these elevations.

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