Tree Stands and Their Productivity Dynamics at the Upper Growing Limit in Khibiny on the Background of Modern Climate Changes

P. A. Moiseev^a, *, A. A. Galimova^a, M. O. Bubnov^a, N. M. Devi^a, and V. V. Fomin^a, b

^aInstitute of Plant and Animal Ecology, Ural Bran Ekaterinburg, 620144 Russia ^bUral State Forestry University, Ekaterinburg, 620100 Russia *e-mail: moiseev@ipae.uran.ru Received September 12, 2018; revised February 25, 2019; accepted March 1, 2019

Abstract—Within the ecotone of the upper limit of woody vegetation on the southeastern macroslope of the Khibiny Mountain ridge (Kola Peninsula), the spatial and age structure, as well as features of the phytomass accumulation of spruce-birch stands, were studied. Analysis revealed that there was a manifold increase in the density and productivity of forest stands in the last century, and the upper border of the woodlands and dense forests has moved considerably higher into the mountains. All of this happened against the background of an increase in early summer temperatures and a longer growing season in the area in the 20th century. Our data will help simulate the response of mountain ecosystems in the region to future climate change.

Keywords: upper limit of woody vegetation, dynamics of stands, phytomass of trees and stands, climate change, Khibiny, Subarctic

DOI: 10.1134/S1067413619050084

INTRODUCTION

At the present stage of research, the carbon-insulating role of terrestrial ecosystems, especially forest communities, is widely discussed due to the increase in the concentration of carbon dioxide (CO₂) in the last century, which is, according to many scientists, the main greenhouse gas contributing to the increase in the temperature of the Earth's atmosphere. The length of the forest border in the mountainous regions of the world is tens of thousands of kilometers they have shifted up the slopes by hundreds of meters and in many regions due to climate change [1, 2]. This increased the forest cover area by thousands of square kilometers. Despite this, quantitative studies of the features of phytomass accumulation and its dynamics in stands at the upper limit of their growth are extremely rare: in the Urals [3], the Rocky Mountains [4], and Tibet [5]. In particular, in the southern Urals, we previously [3] found that, from 1910 to 2013, against the background of an increase in early summer (0.6°C) and winter (1.8°C) temperatures and an increase in the amount of solid precipitation, the aboveground phytomass of birch and spruce stands on the slopes of the Iremel Massif increased closed forests on average from 0.3 to 95.8 t/ha on the modern upper forest border, up to 45.8 t/ha on the woodlands border, and up to 4.3 t/ha on the border of tree groups.

In recent decades, significant changes in the composition, structure, and high-altitude position of stands at the upper limit of their growth in Fennoscandia were also revealed [6–9]. On the slopes of the Kola Peninsula mountains, such studies were conducted only on the valley of the Tulyok River (Khibiny) at an elevation of 27-29 m since 1958 [10]. This is confirmed by the occasional observations of the staff of Moscow State University and Polar Geophysical Institute in the valleys of the Yumye-Gorr River (western slopes of the Khibiny Mountains). Based on a comparison of the images of vegetation in historic photographs by V. Ramsay (1890s), they concluded that there was displacement of the upper border of birch crooked forest to a height of 100–120 m [11, 12]. Therefore, we conducted quantitative studies of the age, morphometric parameters, growth, and productivity of both individual trees and entire stands on the slopes of the Khibiny in the ecotone of the upper limit of woody vegetation to create a basis for the development of a model of carbon deposition in regional forest communities during climatogenic changes.

EXPERIMENTAL

The study area is Khibiny Massif (the highest point is the mountain of Yudychvumchorr, which is 1200.6 m above sea level). It is located in the band of the highest central hills of the Kola Peninsula (Fig. 1), which is characterized by significant heights (up to 900-1200 m above sea level) and large amplitudes (up to 800 m), a complex geological structure, humid climate (to 1200 mm per year), and pronounced, high-

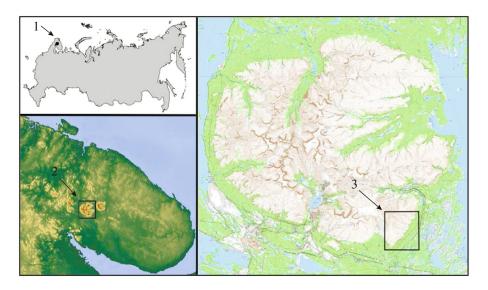


Fig. 1. Location of the study area in the Russian Federation (1), Kola Peninsula (2), and Khibiny Mountain Ridge (3).

altitude landscape zoning [11]. The ecotone of the upper boundary of woody vegetation (EUBWV), which, according to P.L. Gorchakovskii and S.G. Shiyatov [13], is considered a transitional zone in the mountains between the upper limits of the distributions of closed forests and individual trees in the tundra, is confined to heights from 300 to 600 m above sea level in the Khibiny. The tree stands growing there are mainly formed by the twisting birch (*Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman) and the Scots pine (*Pinus sylvesris* L.) with an admixture of the Siberian spruce (*Picea obovata* Ledeb.).

The values of the coordinates of the upper left and lower right corners of the intensive study area on the southeastern slope of the Khibiny (with the conventional name "Koashva") are 67.629° N, 33.979° E and 67.549° N, 34.135° E. In the course of research in the geological information system ARC/INFO (ESRI Inc., USA) with the use of the TOPOGRID algorithm, a digital elevation model (DEM) of the area was constructed based on geographic information layers of contours, elevation, water flows, and lakes (Fig. 2). These layers were created via the digitization of scanned images of sheets of Gosgistsentr maps (scale 1:25000) obtained from the public web resource loadmap.net. Three linear vector geographic information layers were created with topographic maps of 1956 and 1986 and modern satellite images of high spatial resolution, as well as field survey data. They characterize the location of the upper forest boundary in the past (1956 and 1986) and present (2017).

The values of vertical and horizontal shifts were estimated with the method developed by the authors [14, 15]. To obtain the elevation values of the upper forest boundary, the previously rasterized boundary line was superimposed on the relief digital elevation model. Each cell of the border matches the cell size of

the DEM 30×30 m with a certain height value: 3302 cells in 1956, 3322 in 1986, and 5260 in 2017. Thus, the boundary height position was characterized by a set of statistics of cell height distribution (Table 1). The difference between values of a statistic, such as median or mean, the current height of the upper forest boundary, and its position in the past were used to estimate the change in the boundary height position (altitude shift). The rate of altitude shift was calculated as the ratio of the shift value to the time interval.

A raster, the cells of which contain Euclidean distance values, was calculated to estimate the magnitude and rate of the horizontal shift from the boundary line at the beginning of the study period. It is superimposed with the rasterized line of the forest upper boundary at the end of study period. The value of the horizontal shift was calculated from the statistics of its values distribution, and the rate was calculated by dividing the shift values by value of the time interval (Table 1).

In July 2017, to study the structure of forest stands at three altitudinal profiles on different local exposure areas (S, SE and E) of the southeastern slope of the Kitchepakh Mountain, 18 sampling plots measuring 20 × 20 m: 2 were laid at the bottom (320–340 m above sea level), average (350–380 m above sea level), and upper (410–450 m above sea level) parts of the ecotone of the EUBWV (Figs. 2, 3). On each sampling plot for a single tree (single-stem and multistem forms) the type, location, trunk height graded by a 6-meter pole, and the trunk diameter (at the base and height of the chest) were determined via measurement of the perimeter with measuring tape, as well as the diameter of the crown projection in two directions and the life state.

To determine the calendar time of the appearance of living trees (single-trunk growth form) or trunks

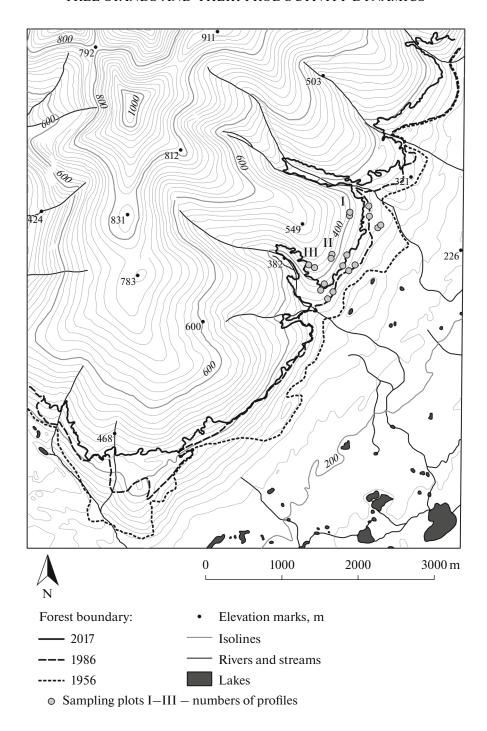


Fig. 2. Upper limit of rarefied forests with a density of 35–40% on the southeastern slope of Kitchepakhk Mountain (Khibiny) in 1956, 1986, and 2017.

(multitrunk growth form) with a diameter of > 3-4 cm, brown wood samples were taken at a height of up to 40 cm, and a disk was cut from the dried samples. A transverse disk was taken from each second young tree >0.2 m high but with a diameter at the trunk base of <3-4 cm at the level of the root neck. Each transverse disc and drilling sample (previously fixed in a wooden holder) was cut in the laboratory with a cutting tool,

and a tooth-shock was then rubbed onto the cleaned surface to increase the contrast of the annual rings. After that, the width of the annual rings was measured for all wood samples at the LINTAB-III installation, and the year of the formation of the most central annual ring was finally dated with the TSAP 3.0 software.

If the taken kerns did not reach the trunk center of, then, to determine the time of the formation of the

Table 1. Characteristics of the altitude position and shift of the upper boundary of rarefied forests with a density of 35–40%
in the southeastern macro slope of the Khibiny (Kola Peninsula) for the period from 1956 to 2017

		Statistics							
Characteristics	Years	mean value	standard deviation	mean error	minimum	median	maximum		
Altitude position	1956	304.5	39.2	0.7	249.1	293.1	397.9		
of the boundary, m	1986	360.7	42.5	0.8	276.5	351.2	472.6		
	2017	392.4	38.7	0.5	315.8	390	478.2		
Altitude shift,	1956-1986	56.2/1.9	_	_	27.4/0.9	58/1.9	74.7/2.5		
m/shift rate, m/year	1986-2017	31.7/1.0	_	_	5.6/0.2	38.8/1.3	39.4/1.3		
	1956-2017	87.9/1.4	_	_	66.7/1.1	80.3/1.3	96.9/1.6		
Horizontal shift,	1956-1986	165.7/5.5	118.3	2.1	_	155/5.2	478.9/16		
m/shift rate, m/year	1986-2017	240.2/7.7	236.9	3.3	_	160.1/5.2	1036.2/33.4		
	1956-2017	421.4/6.9	278.4	3.8	_	326.1/5.3	1413.2/23.2		

central ring, the radius of the arc formed by the earliest (closest to the center) annual ring was first determined by comparison with the lines of circles of different sizes deposited on transparent film. The number of annual rings on the earliest part of the core equal to the calculated radius was then calculated and added to the number of identified and dated annual rings in the sample [3]. We did not apply the calculation of the correction using the age curve, since the test comparisons of the ring number on 77 birch kerns that reached the center on the segment from 0 to 2.5 mm (the average arc radius of the last full ring at 133 cores that did not reach the center) and from 2.6 to 5 mm did not show significant differences in ring number (6.3 ± 3.1) and (6.2 ± 2.9) mm, respectively).

Since the undergrowth age of >0.2 cm and a diameter of <3-4 cm was determined by the cuts taken at the root-neck level, it was most reliable. The regression equation between these parameters was calculated from the age of such trees and the height of their trunks. The corrections were calculated with the equation to determine a more accurate age of each tree with a diameter of >3-4 cm.

In accordance with the distribution order of the trunks of firs and birches by diameter at each altitude level in 2017, a systematic sample of model trees was formed in the immediate vicinity of sampling plots to determine the taxation indicators and stand phytomass. Model trees (10–30 specimens) were selected by mean diameter, height and size of the crown for the thickness step within the entire range of variation in the diameter of trunks in the forest stand.

The phytomass was determined in 11 single-trunk firs and 53 trunks of multitrunk birch individuals with subdivision into the following fractions: wood and bark of the trunk, wood and bark of the branches, needles, or leaves, and dead branches. The trunk phytomass in the bark was determined by direct weighing in the field with an accuracy of 50 g, for which the trunk

was cut into 1 m sections. The dry content in both wood and bark was determined in discs sawn from the ends of cut sections. Wood and bark from the discs were weighed on site with an accuracy of 0.1 g and then sent to the laboratory for further drying and measurement of their mass in a completely dry state.

In the determination of the phytomass of the crown and its structural parts, all branches from the trunk were cut off and divided into three sections according to the location in the crown (upper, middle, and lower parts). The total mass of each section of the crown was measured by direct weighing in the field, and the crown was then divided into leaved and leafless parts. A sample of up to 20-30% by weight of the total was taken from the leaved part. The needles (leaves) in the sample were separated from the branches and weighed. The leafless branches were weighed separately, and a sample of 5–10% of their weight was taken from them to determine the proportion of wood and bark in the branches. A 20-g sample was taken for subsequent drying in the laboratory to measure absolutely dry matter in the needles (leaves) from each section of the crown. All samples were dried in a drying cabinet (shsp-0.25-100) at a temperature of 106°C to a completely dry state and weighed. The obtained ratios between the raw canopy weight (in the field) and the absolutely dry state were used to calculate the phytomass of different fractions of model trees in the absolutely dry state. To determine the dry matter in all fractions, 848 sawmills and weight samples were taken, and the phytomass of trees in absolutely dry state were calculated from the obtained weight propor-

The trunk diameters were calculated for each year in the tree's life based on drilling samples of wood (kerns); the width of each annual ring was measured and the calendar year of their formation was determined by standard dendrochronological methods. In the calculations, it was accepted that growth of the

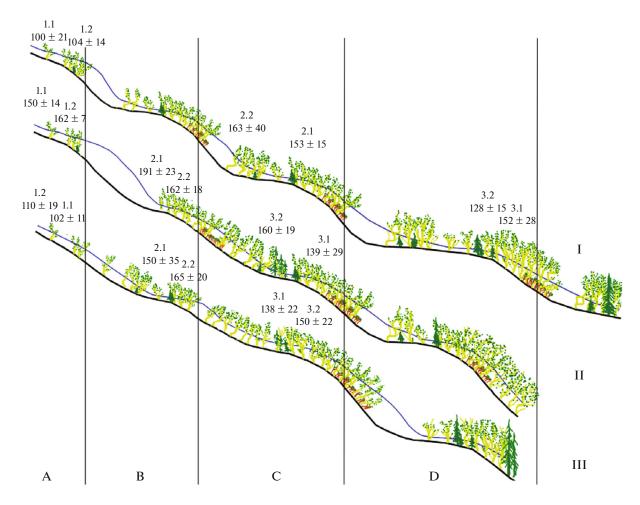


Fig. 3. Scheme of stand distribution and snow masses along the elevation gradient on the studied profiles on the southeastern slope of Kitschepakhk (Khibiny): I-III-profile numbers; vertical lines and letters indicate upland terraces (A-D); Arabic numerals indicate the names and places of sampling sites and the height of snow on them, cm, in March 2018 (mean \pm standard deviation).

trunk by a separate radius at the site of kern removal is synchronous with the increase in mean trunk diameter calculated from the perimeter of its surface with a measuring tape. The radius distance was calculated by the addition of the sizes of all annual rings from the kern to the annual ring formed by a certain calendar year, including the last one [16–19].

The calculations were made according to the formula $D_{\text{in year N}} = (L_{\text{in year N}}/L_{\text{in 2017 year}}) \times D_{\text{measured in 2017 year}}$ where $D_{\text{in year N}}$ are the calculated tree diameters in a given calendar year N (e.g., 1935); $L_{\text{in year N}}$ and $L_{\text{in 2017 year}}$ are the distance along the kern from the core to the annual ring from a given calendar year N and in the final year 2017, respectively; $D_{\text{measured in 2017 year}}$ is the actual trunk diameter in the year of measurement, 2017.

Based on the actual (2017) and calculated (for previous years of tree growth) data on the diameters of individual tree trunks on the surveyed sampling plots and identified close links between the aboveground phytomass of trees and their trunk diameters, the

reserves of the aboveground phytomass per unit of the area and the rate of its accumulation for different types of stands over the last 165 years were estimated. The tree heights were calculated with the identified allometric dependencies between the height (y) and trunk diameter (x), having the form $y = 13.43x^{0.67}$ and $y = 17.46x^{0.78}$ for birch and spruce, respectively.

From July 2017 to July 2018, a stand-alone Thermochron iButton™DS1921 thermal sensor was placed at each site to measure the temperature of the air, crown surfaces, and tree trunks at a height of 2 m from the land surface to the crown, with or without direct sunlight. One weather station was installed in the lower part of the eastern profile (Profile I) and the middle part of the southern profile (Profile III). During the same period, it measured the temperature and humidity of the air, the amount of liquid precipitation, and photosynthetically active radiation (PAR). Thermal sensors (Thermochron iButton™ DS1921) were placed in the upper, middle, and lower parts of

the EUBWV near the sites along the line from top to bottom for 5 m in the soil at a depth of 10 cm. The mean temperatures of individual days and months were calculated based on the obtained data, as well as the transitions through the threshold values and the dates of snowfall.

In March 2018, the depth of snow cover was measured to assess the snow accumulation in 18 previously studied sampling plots: with a 1.5-meter pole in the upper part of the EUBWV (30 per sampling plot) and by the painting of all tree trunks in the middle and lower parts at the snow level with subsequent measurement of the height of the marks in summer.

RESULTS

Dynamics of the Upper Limit of Rarefied Forests in the Last 60 Years. Analysis of the modern altitudinal position of the upper border of forests with a density of 35–40% on plots of different exposures identified for this area of the Khibiny revealed an increase in its mean value, starting from the northeastern slopes (337 \pm 28 m above sea level) to the eastern (361 \pm 13 m), southeastern $(407 \pm 35 \text{ m})$, southern $(427 \pm 17 \text{ m})$, and southwestern $(460 \pm 36 \,\mathrm{m})$. The methods described above were used to compare the modern high-altitude position of the upper boundary of light forests with a density of 35–40% and those marked on topographic maps in 1956 and 1986. It showed that there was a significant advance of woody vegetation higher in the mountains in this area over the past 60 years: on average, 88 m vertically and 421 m horizontally (Table 1, Fig. 2). At the same time, the most significant boundary shifts were found on the slopes with SE, S, and SW exposures (average heights of 107, 105, 99 m, respectively), medium shifts were found on E slopes (average 90 m), and minimal shifts were found on NE slopes (average 70 m).

Modern Structure of Stands on the Studied Profiles. Comparison of the characteristics of forest stands within EUBWV (Table 2) showed a 1.2- to 1.8-fold decrease in the mean values of morphometric tree parameters with increasing elevation above sea level. At the same time, the number of live birch trunks taller than 20 cm and the proportion of dead and damaged trunks in the total sample are reduced more significantly. The proportion of trunks in multitrunk birches in the forest stand structure exceeds an average of 60%. There is a notable participation of spruce in the stands (20-60%) at some sites only in the lower part of profiles (Table 2); at other levels, its proportion does not exceed a few percent. In addition to spruce and birch, there is Scots pine (*Pinis sylvestris* L.) in the stands, but its participation does not exceed 0.1%.

As shown in Fig. 3, the closeness of tree stands varies with altitude in the studied profiles extremely unevenly, which is associated with a pronounced terrace structure of slopes characteristic for the whole mountain massif of Khibiny. The step height and ter-

race width are extremely variable and vary from several to tens and sometimes hundreds of meters. It should be noted that there are often thickets of curved aspens, *Populis tremula* L. in the upper parts of the steps with a height of no more than 2 m.

History of the Forest Stands. Analysis of the data on the distribution of birch trees by periods of appearance on the sites of Profile I (Fig. 4) showed that the appearance of the oldest currently growing trees in the lower part of EUBWV (322 to 324 m above sea level) dates back to the 1890s, but their number is very small (about 0.1%). Almost all of the trees appeared during the 20th century. The most active seed regeneration of both birch and spruce was here, between 1960 and 2000. In the period of 1905–1960, the increase in stand density at this level was facilitated by the emergence of new vertical trunks of multitrunk trees. In the middle part of the profile (345–356 m above sea level), the oldest living trees are also less than 135 years old. Most trees appeared there, as in the lower part, in the second half of the 20th century. Throughout nearly all of the dispersal period, a significant contribution to the increase in stand density at this level was realized by the emergence of a large number of new vertical shoots in multitrunk trees, more than half of the total. No birch trees older than 95 years were found in the upper part of the profile (407–411 m above sea level), and most trunks appeared in the period after 1970.

Analysis of the data on tree distribution by periods of occurrence on Profile-II sites shows that the age of oldest living birches in the lower part of this profile (333–335 m above sea level) does not exceed 125 years; for spruce, it does not exceed 200 years. Most birch trees appeared there in the 20th century, and the most active renewal was between 1900 and 1950; it then decreased by two times on average. The increase in stand density at this level was also facilitated by the emergence of a significant number of new vertical shoots in multitrunk trees (\approx 40% of the total). The terrace spruce is more visible on leveled areas in forest stands: its coverage reaches 60% in some places. The spruce renewal occurred there in parallel with the appearance of birches throughout the 20th century. In the middle part of the profile (360–381 m above sea level), the very first birch trees of those now growing appeared in the first half of the 19th century. As in the lower part, active renewal occurred between 1920 and 1950, as well as in 1960–1980. In the upper part of this profile (425–442 m above sea level), the first birch trees growing there began to appear only in the 1920s, and its active settlement took place after 1950. Spruce began to appear much earlier, in the 1840s.

Analysis of the data on tree distributions by the periods of occurrence on Profile-III plots revealed that the age of the oldest living birches and spruces in its lower part (339–347 m above sea level) is about 160 years. The most active birch renewal was between 1905 and 1940, and it declined markedly in the subse-

Table 2. Characteristics of the forest stands on the study areas of the research profiles on southeastern slope of the Kitchepakhk Mountain (Khibiny) in 2017 (mean value \pm standard deviation)

Elevation Sum of crown projections,		Number of trees per hectare				Trunk diameter		T 11 11			
above sea level, m	projections, at the height spruce 1.3 m, cm		-	Trunk height, m		Age, years					
icvei, iii	birch	spruce	<1.5 m	>1.5 m	<0 m	in average	max	in average	max	in average	max
Altitude profile I											
407	372	0	325	300	0	4.7 ± 1.8	8.3	1.6 ± 0.6	2.6	51 ± 19	93
411	629	0	100	225	0	4.9 ± 3.7	11.8	1.8 ± 1.2	4.4	56 ± 18	94
345	6809	0	100	1100	0	7.5 ± 3.2	17.8	2.7 ± 0.8	3.9	88 ± 23	133
356	6094	0	350	1875	0	5.7 ± 0.7	16.9	2.2 ± 1.0	4.8	52 ± 19	119
322	6492	91	725	1500	75	6.4 ± 4.9	21.7	2.1 ± 1.1	5.5	55 ± 27	129
324	4519	833	575	3300	650	4.6 ± 2.7	17.5	1.9 ± 0.9	5.0	44 ± 12	101
						9.6 ± 5.7	28.7	2.5 ± 1.8	6.8	49 ± 21	95
Altitude profile II											
442	515	73	250	250	100	4.9 ± 3.3	11.5	1.5 ± 0.7	2.6	49 ± 14	67
425	407	233	25	250	50	5.7 ± 1.9	9.1	1.8 ± 0.5	2.6	61 ± 18	94
381	4046	0	75	675	0	6.8 ± 3.2	14.3	2.1 ± 0.9	4.7	79 ± 29	122
360	5526	0	25	825	0	10.3 ± 4.2	20.9	2.4 ± 0.9	4.4	85 ± 36	194
333	6918	1	25	825	25	7.3 ± 3.2	15.3	2.5 ± 1.1	6.6	79 ± 27	121
335	2125	3187	25	400	850	8.6 ± 4.2	16.9	3.0 ± 1.2	5.2	85 ± 20	114
						8.4 ± 4.9	34.5	2.8 ± 1.9	7.6	93 ± 41	201
			•	•	Altitud	e profile III					
448	2589	79	125	475	25	4.5 ± 2.7	13.7	1.2 ± 0.5	2.3	62 ± 23	109
445	1638	0	0	300	0	8.8 ± 4.5	18.8	1.8 ± 0.5	2.5	92 ± 31	173
371	6718	0	100	1150	0	6.6 ± 2.9	12.7	2.4 ± 0.8	3.8	81 ± 25	135
379	6749	0	100	850	0	7.0 ± 3.6	15	2.3 ± 0.7	3.6	72 ± 30	124
339	5237	897	50	750	225	9.9 ± 5.5	29.6	3.0 ± 1.3	5.7	88 ± 28	146
						8.1 ± 3.3	25.5	3.3 ± 2.0	7.0	97 ± 37	158
347	7101	411	0	1025	100	8.2 ± 4.6	22.3	2.7 ± 1.1	5.0	93 ± 36	161

Standard font are features for curved birch; bold indicates characteristics for Norway spruce.

quent period. Throughout the dispersal period on this level, the increase in stand density was facilitated by the emergence of new vertical shoots in multitrunk trees (more than 70% of the total). In the middle part of the profile (371–379 m above sea level), the very first trees of those currently growing appeared at the end of the 19th century, and the periods of active dispersal were dated to 1905-1960 and 1970-1990. About 70% of the trunks that appeared in the period before 1960 belong to clumps of multitrunk trees. The later increase in stand density was equally due to the appearance of both single trunks and additional trunks of multitrunk trees. In the upper part of the profile (445–448 m), the first birch trees growing there began to appear in 1840s, but the periods of active dispersal were extended to a later period: by 1920-1960 and 1970-1990.

Phytomass of Model Trees. The trunk phytomass is predominant in the fractional phytomass structure in both studied species, but its contribution in the spruce and birch differs by 1.5–2 times. In the spruce the trunk phytomass contributed on average 41% of the total aboveground tree phytomass; in the birch, the figure is 68%. The part of branches in the composition of aboveground phytomass in both species does not differ and averaged 25–26%. The greatest differences are noticeable in a comparison of these types of phytomass in photosynthesizing organs: the birch-leaf phytomass is only 5% of the total aboveground tree phytomass at 34%, which is attributable to the spruce-needle phytomass.

Equations for the mass of different fractions with a single morphometric index, the trunk-base diameter, were developed for each species based on the results.

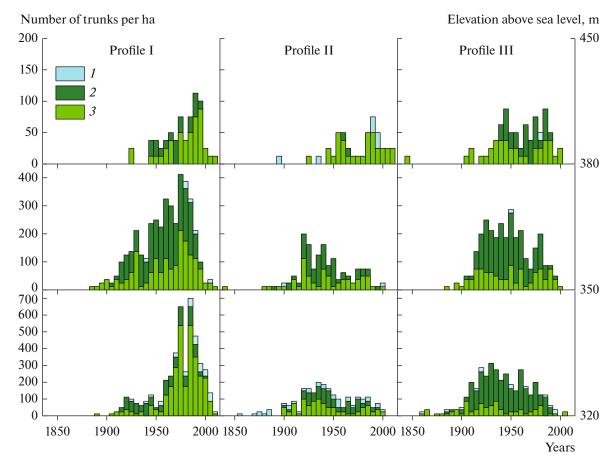


Fig. 4. Age structure of wood stands at different elevations of the studied profiles on the southeastern slope of Kitchepakhk Mountain (Khibiny) (number of trunks that appeared in separate 5-year intervals, e.g., the period between 1901 and 1905 corresponds to the symbol 1905): *I*—spruce; *2*—main (oldest) trunks of birch; *3*—additional birch trunks.

Analysis of the suitability of different regression equations showed that the most accurate description of this relationship is a power function of the form $y = ax^b$

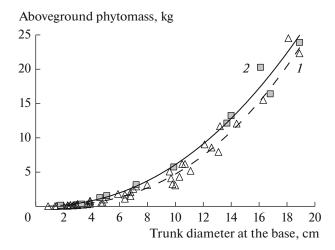


Fig. 5. Dependence of the aboveground phytomass of spruce and birch trees on their diameter at the trunk base: (I) spruce, (2) birch.

(Fig. 5). Table 3 gives the statistical parameters of the developed equations. The relationship between the presented parameters is characterized as high or extremely high, which made it possible to use these equations to calculate the phytomass of individual trees growing on sampling plots with further transition to the stand level.

Reconstruction of the Taxation Characteristics and Phytomass of Tree Stands. Analysis of the data showed that there is a gradual increase at all elevation levels in the mean tree diameter and heights, but the rate of observed changes is extremely low (Table 4). At the top level, the morphometric tree characters increased by an average of 1.9–2 times over 137 years. In the middle and lower parts of the high-rise profile, these changes are more pronounced: parameters of trees increased from three to seven times. At the middle and lower high-altitude levels, there is a higher rate of increase in the tree stand density.

Assessment of the dynamics of phytomass accumulation showed that the reserves of the top phytomass amounted to an average of 0.001 t/ha (Table 4) at the initial stage of the stand formation in the second half of the 19th century at all elevation levels. The mean

Table 3. Characteristics of the equations of the dependence of the phytomass fractions, kg, of birch and spruce trunks on the trunk-base diameter, cm, at the upper boundary of rarefied forests on the Kitchepakhk Mountain (Khibiny)

Phytomass	Species	a	b	R^2	n
Total under-	Birch	14.337	2.4939	0.9809	53
ground	Spruce	10.148	2.224	0.9881	11
Trunk	Birch	13.533	2.6095	0.9737	53
	Spruce	7.9381	2.4946	0.9714	11
Branches	Birch	1.0838	2.1377	0.8454	53
	Spruce	3.4208	2.3668	0.9877	11
Leaves	Birch	0.0878	1.8612	0.8443	53
or needles	Spruce	1.3212	1.8592	0.9633	11

rate of phytomass accumulation during this period was extremely low, reaching a maximum of 0.0004 t/ha per year in the woodlands. In the forest stands on the upper border of closed forests, there was a sharp increase in phytomass growth in 1880–1910. The annual production during that period increased by 22 times. During the 20th century, this figure increased by 280 times, reaching 0.26 t/ha per year by 2000. For the first 17 years of the 21st century, the phytomass growth rate increased by two times. The current reserves of the aboveground phytomass in the closed forest are 10.4–28.5 t/ha.

There is a similar picture in rarefied forests, but with a shift of 30 years: until 1910, the growth of stand phytomass was extremely slow; in the period 1910—1940, it was followed by a 17—fold increase in the rate of phytomass accumulation, and this figure increased by another 15 times by 1970, reaching 0.1 t/ha per year. In subsequent periods, the rate of phytomass growth increased by another nine times. At the moment, the aboveground phytomass of stands in woodlands is 3.7—9.7 t/ha.

The rate of biomass accumulation remained extremely low in the tundra with tree groups in the first half of the 20th century. By 1940, when the phytomass of these stands reached 0.004 t/ha, its growth rate increased sharply: in the period between 1940 and 1970, this indicator increased by 159 times as compared to the previous period. In subsequent years, there is no such sharp rise in the annual stand production, although the tendency of an increase in the rate of phytomass growth remains. By 2017, the reserves of phytomass of forest stands in the tundra with tree groups amounted to 0.5–1.7 t/ha.

In the analysis of the contribution of different species of woody plants to the total phytomass of tree stands, it was found that birch is dominant at the moment, although its contribution during the 20th century at different elevation levels varied differently: 100% of the stands phytomass was spruce in the closed forest until the beginning of the 20th century; in the 1940s, there

Table 4. Reconstructed and actual characteristics of stands at different types of upper boundaries on the southeastern slope of the Kitchepakhk Mountain (Khibiny)

		Years							
Characteristics	Upper boundary	reconstructed							
		1880	1910	1940	1955	1970	1985	2000	2017
Mean diameter	Groups of trees	0.02	0.03	0.01	0.01	0.02	0.02	0.03	0.04
of trunk at the base, m	Rarefied forest	0.03	0.02	0.01	0.02	0.03	0.04	0.05	0.07
	Closed forest	0.01	0.02	0.02	0.04	0.05	0.05	0.05	0.07
Mean trunk height, m	Groups of trees	0.85	1.14	0.75	0.86	0.96	1.065	1.17	1.66
	Rarefied forest	1.29	0.97	0.76	0.99	1.21	1.475	1.74	2.18
	Closed forest	0.58	0.84	1.03	1.36	1.68	1.79	1.90	2.31
Number of trunks	Groups of trees	4	4	37	148	258	450	642	667
per hectare	Rarefied forest	8	50	612	1219	1825	2356	2887	2887
	Closed forest	29	112	875	917	958	2298	3637	3775
Aboveground	Groups of trees	0.0002	0.001	0.004	0.017	0.104	0.168	0.326	0.823
phytomass, t/ha	Rarefied forest	0.002	0.010	0.064	0.286	0.795	1.834	3.836	7.412
	Closed forest	0.001	0.015	0.247	1.062	2.879	6.048	10.67	17.82
Increase of phyto-	Groups of trees	0.00001	0.00001	0.00002	0.0001	0.006	0.004	0.011	0.031
mass in previous period, t/ha per year	Rarefied forest	0.00007	0.00027	0.00062	0.0030	0.014	0.007	0.031	0.063
	Closed forest	0.00003	0.00046	0.00237	0.0131	0.023	0.014	0.053	0.096

Table 5. Mean temperature of the air and soil in the lower part of tundra zone and on the upper limits of tree stands of dif-
ferent density on the southeastern slope of the Kitchepakhk Mountain (Khibiny) from July 15, 2017, to July 13, 2018

		Air	temperature,	°C	Soil temperature, °C				
Year	Month	u	pper boundar	·y	mountain	upper boundary			
		groups of trees	rarefied forest	closed forest	tundra	groups of trees	rarefied forest	closed forest	
2017	July	15.7	16.0	16.4	10.3	10.5	11.3	12.2	
2017	August	10.8	11.2	11.4	9.4	9.8	10.4	11.1	
2017	September	6.3	6.7	6.8	6.0	6.5	7.0	7.3	
2017	October	0.5	0.9	1.2	2.6	3.1	3.6	3.5	
2017	November	-3.7	-3.5	-3.3	0.6	1.0	1.4	1.2	
2017	December	-6.3	-6.5	-6.5	0.6	0.8	1.0	0.9	
2018	January	-7.6	-7.5	-7.4	0.5	0.6	0.8	0.7	
2018	February	-8.9	-9.0	-8.8	0.3	0.4	0.6	0.6	
2018	March	-8.7	-8.2	-8.1	0.2	0.2	0.4	0.2	
2018	April	-0.3	0.4	0.6	0.1	0.2	0.3	0.3	
2018	May	7.9	8.5	8.3	0.4	1.9	2.0	3.5	
2018	June	9.6	10.3	10.4	6.1	7.1	7.9	8.8	
2018	July	16.7	17.3	17.5	10.3	10.6	11.2	12.3	

was a fourfold decrease in the contribution of spruce phytomass to the total phytomass of stands associated with the mass appearance of birch trunks. In subsequent periods the proportion of spruce phytomass remained almost unchanged in the closed forest, ranging from 23 to 25% of total phytomass reserves. In rarefied forests and tundra with tree groups, there is the opposite situation: birch was initially dominant in the phytomass, but its contribution began to decline gradually in 1970s. The decrease in the contribution of birch phytomass is more pronounced at the upper elevation level, where it ranged from 71 to 83% in different periods of the second half of the 20th century, while this figure did not decrease below 96% in the woodlands.

Local Conditions of Growing Places. Analysis of the data from temperature sensors showed that the mean monthly air temperature in the birch crowns from March to October was 0.4–0.8°C lower in the upper part of the EUBWV as compared to the lower part (Table 5) and above 0.1-0.3°C or almost equal in December-February. It is noted that autonomous weather stations and temperature sensors at the same level located in the dense crowns of spruce trees with protection from direct sunlight recorded lower rates in March-September (mean monthly air temperatures decreased by 0.8-2.9°C) than temperature sensors located in the sparse crowns of birches without protection, and they practically did not differ from each other in the cold season. This is due to the fact that the thermosensors of weather stations and temperature sensors in spruce-tree crowns protected from direct sunlight show the real temperature of the air. For uncovered sensors, the surface temperature of branches and tree trunks in the warm season in the middle of the day is usually $7-10^{\circ}$ C higher.

The results of snow measurements in March 2018 showed that the height of the snow cover varies significantly during the transition from the lower to the upper part of the EUBWV on all surveyed profiles, both in connection with the pronounced terracing of the slopes, which is observed everywhere on the flat and medium-steep sections of the Khibiny Mountains, and in connection with snow redistribution by strong mountain winds. Thus, at the transition from the lower to the medium level, the mean snow height at surveyed sites increases from 128–160 to 150–191 cm. From the medium to the upper one, it is reduced to 100–162 cm (Fig. 3), because a significant amount of snow is blown away from the higher, treeless spaces and is retained by the more closed stands of the lower levels. At the medium and lower levels, the snow is retained more than at the top because of the greater stand density. Large snow masses (up to 3–5 m) also accumulate under the steep slopes of terraces, and they usually disappear in early July. For example, in the summer of 2017, with the preceding snowy winter and cool spring, such snowfields finally melted only at the end of July.

Comparison of the data from temperature sensors located at a depth of 10 cm in the soil showed that the mean monthly temperatures in May–September are $0.8-1.7^{\circ}$ C lower in the upper part of the EUBWV than in the lower. In October–April, they differ only by $0.1-0.4^{\circ}$ C or are identical (Table 5). Analysis of the

changes in the soil temperature showed that the date of the 2018 snow melt (identified by the appearance of a pronounced diurnal temperatures change) differ between the upper and lower parts of EUBWV by 4 days (May 19 and 15, respectively) and by 15 days (June 1 and 15 May, respectively) between the alpine tundra and the lower part of EUBWV. It was also revealed that the soil at a depth of 10 cm is warmed and its temperature was above 3.2°C for 2–3 days after the snow melt within EUBWV and for 8 days in the tundra. According to G. Paulson and K. Kerner [20], the roots of woody plants begin to function only above 3.2°C. Our calculations showed that, by June 30, 2018, the sum of daily soil temperatures above 3.2°C was equal to 364 deg/day at the upper boundary (UB) of the closed forests, 288 deg/day at the UB of rarefied forests, 263 deg/day at the UB of tree groups, and 171 deg/day at the UB of mountain tundra.

DISCUSSION

We found that the highest elevation of the modern upper limit of light forests with density of 35–40% is reached in the studied area on the southwestern slopes, where it is higher than in the northeastern slopes (123 m). The maximum altitude shift (99–107 m) also occurs on the slopes of the southern exposures in the last 60 years. This is due to the well-known fact that the total radiation (direct + scattered) arriving on the open surface on slopes with different exposures differs significantly. The surface of the southern slopes of the Khibiny (Yukspor meteorological station, 910 m above sea level) with an inclination angle 10° in the real mode of cloudiness for June-August receives 34.8 kcal/cm², the western and eastern slopes receive 32.9, and the northern slope receives 30.6. The difference between the northern and southern slopes also increases with increasing surface inclination: to 6.5 kcal/cm² at 20°, to 8.8 kcal/cm^2 at 30° , and to 17.7 kcal/cm^2 at 50° [11]. It increases even more with an increase in the proportion of direct radiation of the total (a higher number of hours of sunshine), and, as our observations show, the direct rays of the sun lead to significant heating of the tree crowns and trunks, and their temperature becomes higher than the ambient temperature by $7-10^{\circ}$ in the middle of the day and by 0.8-2.9°C per month on average.

As L. Kullman and L. Oberg [9] noted, in the middle part of Scandinavia from 1915 to 2007, the upper boundary of tree groups with a height of more than 2 m with dominant birch moved higher into the mountains by 0.74 ± 0.49 m/year on relatively snow-covered slopes, while it was equal to 0.75 ± 0.58 m/year in the period from 1915 to 1975 and 0.65 ± 0.78 m/year from 1975 to 2007. For the upper reaches of the Tulyok River in the Khibiny in the period from 1958 to 2006, the shift of the upper boundary of the groups of trees with the dominance of birch was 29 m high (0.6 m/year) [10]. In our study area, the displacement of the upper bound-

ary of light forests with closeness of 35–40% in the period from 1956 to 2017 averaged 1.4 m/year on the southeastern macroslope of the Khibiny, and there was also a difference in the observation periods: 1.9 m/year in 1956–1985 and 1.0 m/year in 1986– 2017 (Table 1). Such significant differences in the shift rate (by 2 times) can be explained, in our opinion, by the fact that it is "more difficult" for trees to populate treeless tundras than to "move" along closed communities due to the use of space between already-existing groups of trees and forest islands occurring above the upper woodland boundary. This explanation is confirmed by an analysis of the age structure of stands (Fig. 4), most of which began to form in the first half of the 20th century in the lower and middle parts of the EUBWV, but they were still extremely sparse and small in height (according to our calculations, 0.76–1 m) by the time of the topographic maps production in 1956 and therefore were classified as nonforest areas. After 30 years, by 1986 (the next year of updated information on topographic maps), many new individuals appeared in the stand composition, and the crowns of adult trees also grew quite strongly due to the appearance of shoots, many of which turned into large additional trunks. This led to a sharp increase in the density of forest stands above 35–40%, as a result of which many of them have already moved into the category of forests, and the upper limit of the forest communities marked on the maps became much higher. In the subsequent period, until 2017, the processes of the emergence of new individuals and the increase in crown size in the lower and middle parts of the EUBWV began to slow down gradually due to the increasing competition. Apparently, this led to an almost twofold decrease in the rate of the increase in the upper limit of closed forests; the dispersal processes in mountain tundras, however, did not stop but proceeded less quickly. Perhaps, with further improvement of the conditions for tree growth and renewal, the generation that appeared in 1980–2000 will also quickly take up space, and the border of closed stands in the coming years will significantly move higher into the mountains.

Comparison of data on the phytomass reserves of forest stands within the EUBWV for the Kitchepakhk Mountain in Khibiny and those obtained by us earlier for snowy areas of the Urals with a predominance of birch showed that they are 1.5–3 times lower on some of those same types of upper bounds. Thus, in our research area in the Khibiny (67.6° N), the phytomass reserves are on average 17.8 t/ha on the UB of dense forests, 7.4 t/ha on UB of light forests, and 0.8 t/ha on the UB of tree groups. On the southern slope of Konzhakovskii Kamen' (northern Urals, 59.63° N), they are 59.5, 36.4, and 3.1 t/ha, respectively [21]. In the more northern regions of the northern Urals, they are equal to 38.0, 21.6, and 2.3 t/ha on the slopes of mountains in the region of the Molebnyi Kamen' Ridge (61.21° N) and 28.5, 7.3, and 0.7 t/ha, respectively, on Yaruta

Mountain (63.34° N) (unpublished data). We assume that the observed decrease in phytomass reserves from south to north is related to the general latitudinal reduction in the duration of the vegetation period (7–10 days), even though that the main factor determining the altitudinal position of EUBWV in each region remains the temperature regime of summer months [20]. Since the Khibiny Mountains have the northernmost geographic position, the phytomass reserves are much lower as compared to other areas.

The expansion of woody vegetation in the Khibiny Mountains that occurred over the last century on slopes of different exposures, steepness, stoniness, moisture, and snow indicates that the impact on these processes, which are factors that are common to the whole territory, in our opinion, can only be climatic. Analysis of the data of Kandalaksha hydrometeorological station, which is located 67 km to the southwest and has the longest continuous series of observations on the Kola Peninsula, showed that the mean air temperatures in March–June increased by 0.9–1.3°C in the period from the beginning of the 20th century and by 0.2, 0.3 and 0.7°C in July, September, and October; in August, it decreased by 0.3°C. As a result, in May-September, the increase averaged 0.5°C. In November-February, the air temperatures of individual months decreased by 0.2-1.4°C, which led to a general decrease in the mean temperature of this period of the year by 0.9°C. According to the weather station located on the Lovchorr Mountain (1091 m above sea level) in Khibiny near Kirovsk, the mean long-term temperatures in 1991–2010 became higher than those in 1961–1990 by 0.9°C in November–March, by 0.4°C in April—May, by 0.6°C in June—August, and by 0.7°C in September—October [12].

As shown above, warming occurred in the last 100 years, especially at the beginning and end of the growing season (May–June and September). This led to a noticeable increase in the duration of the growing season, especially in connection with its earlier beginning, which is extremely important for the development of woody plants during their intensive growth. Thus, only between 1961-1990 and 1991-2010 was there an increase in periods with temperatures above 5 and 10°C of 4 and 9 days, respectively [12]. With regard to the precipitation regime, a small decrease in the mean amount of precipitation was observed on the Kola Peninsula from the beginning of the 20th century until the middle of 1940s. In the 1950–1960s, it reached the highest values, followed by a decline until the early 1990s. Small growth was observed in recent decades. V.I. Demin [12] noted that, in general, only a very small centennial trend of an increased amount of precipitation is noticeable.

General analysis of the changes in local conditions with altitude showed (Table 5 and Fig. 3) that, at the transition from the border of closed forests to tundra (elevation of only 80–120 m), the air temperature

decreases by 0.4–0.8°C, and the soil temperature by 0.8–1.7°C. As a result, the duration of the growing season is reduced by 4 days, and the soil heating and heat supply (the sum of daily soil temperatures above 3.2°C) at the beginning of the growing season decreases by almost 1.5-2 times. Therefore, even a relatively minor increase in the mean temperature $(0.9-1.3^{\circ}\text{C})$ in the last century and the shift in the timing of the start of the growing season (by about 7 days) to earlier dates could contribute to a considerable acceleration of growth, the regeneration of arboreal species, and a shift of the high-altitude borders of closed stands. This is confirmed by the close correlation between the number of birches appearing in the upper (109 \pm 24 cm) EUBWV with relatively little snow and the mean monthly temperatures of May-June for five years during the entire period between 1911 and 1995 ($R^2 = 0.46$). For the middle and lower, more snowy (160 \pm 32 and 141 \pm 24 cm, respectively) parts of the EUBWV in the period from 1911 to 1935, when the average annual precipitation was close to the mean values, there are the strongest connections between the number of birches appearing and the June temperatures ($R^2 = 0.76$). In the period from 1941 to 1965, the mean annual precipitation reached their maxima in the 20th century [12], with mean temperatures of May–July ($R^2 = 0.61$), and in the period 1966–1995, when there was a decrease in moisture with mean temperatures of July–September ($R^2 = 0.78$). In the last 20-25 years, the connections have been extremely weak with temperatures of any summer month, which is explained by a decrease in the reforestation level in the lower parts of EUBWV due to increased competition with an increase in the stand density.

Studies by American colleagues on the Pacific coast of the northwest of the United State in the areas with relatively large amounts of precipitation revealed [22, 23] that, against the background of a general increase in the temperature of the summer months, the dispersal of trees in subalpine meadows is timed to the periods of decrease in the height of the snow cover, during which there is an earlier snow melt, resulting in an increased duration of growing season. In mountainous areas of the United States, where orographic conditions determine different degrees of slope moistening and local habitats, intensive renewal is observed in different or overlapping periods that differ in the degree of moistening [24, 25]. The importance of research on the snow cover on slopes for the stand dynamics is confirmed by observations of the snow distribution and the dates of its disappearance in the surveyed areas of the Khibiny slopes. In places of accumulation of large amounts of snow and, consequently, its longer occurrence, the stand density, even in the lower part of the EUBWV, is extremely low, or there is no woody vegetation at all (Fig. 3). This is clearly evident when modern satellite images of the Khibiny area in the Google Earth software are considered. They clearly show a large heterogeneity in the stand distribution within epy transition zone between closed forests and mountain tundra.

CONCLUSIONS

Thus, our studies demonstrated that the structure and productivity of trees at the upper limit of their growth have changed significantly in recent centuries against the background of an increase in early summer (0.9–1.3°C) temperatures on the Kola Peninsula and the earlier beginning of the growing season. The upper limit of forest stands with a density of 35-40% has risen in the past 60 years, an average of 88 m height, and the aboveground phytomass of the tree stands on the three surveyed profiles in the southeastern slope of the Kitchepahkh (Khibiny) increased from the beginning of the 20th century, from an average of 0.01 to 17.8 t/ha at an elevation of 320–340 m above sea level (current upper limit of closed forests) up to 7.4 t/ha at an elevation of 350–380 m (upper limit of rarefied forests) and up to 0.8 t/ha at an elevation of 410–450 m (upper boundary of tree groups in the tundra). The results of our study significantly clarify the overall picture of carbon deposition in regional forest communities and contribute to the development of a quantitative model simulating the response of mountain ecosystems in the region to future climate change.

FUNDING

The study was supported by the Russian Science Foundation, project no. 17-14-01112.

COMPLIANCE WITH ETHICAL STANDARDS

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.

REFERENCES

- 1. Harsch, M.A., Hulme, P.E., McGlone, M.S., et al., Are treelines advancing? A global meta-analysis of treeline response to climate warming, *Ecol. Lett.*, 2009, vol. 12, no. 10, pp. 1040–1049.
- 2. Holtmeier, F.-K., *Mountain Timberlines: Ecology, Patchiness, and Dynamics, Berlin: Springer, 2009.*
- 3. Moiseev, P.A., Bubnov, M.O., Devi, N.M., et al., Changes in the structure and phytomass of tree stands at the upper limit of their growth in the Southern Urals, *Russ. J. Ecol.*, 2016, vol. 47, no. 3, pp. 219–227.
- 4. Grafius, D.R. and Malanson, G.P., Biomass distributions in dwarf tree, krummholz, and tundra vegetation in the alpine treeline ecotone, *Phys. Geogr.*, 2015, vol. 36, no. 4, pp. 337–352.
- 5. Xin, L., Yu, N., Gao-Qiang, K., et al., Contrasting changes in above- and belowground biomass allocation

- across treeline ecotones in southeast Tibet, *J. Mountain Sci.*, 2016, vol. 13, no. 2, pp. 2036–2045.
- 6. Kullman, L., Tree limit dynamics of *Betula pubescens* ssp. *tortuosa* in relation to climate variability: Evidence from central Sweden, *J. Veg. Sci.*, 1993, vol. 4, no. 6, pp. 765–772.
- 7. Kullman, L. and Engelmark, O., Neoglacial climate control of subarctic *Picea abies* stand dynamics and range limit in Northern Sweden, *Arct. Alp. Res.*, 1997, vol. 29, no. 3, pp. 315–326.
- 8. Hofgaard, A., Dalen, L., and Hytteborn, H., Tree recruitment above the treeline and potential for climate-driven treeline change, *J. Veg. Sci.*, 2009, vol. 20, no. 6, pp. 1133–1144.
- 9. Kullman, L. and Öberg, L., Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: A landscape ecological perspective, *J. Ecol.*, 2009, vol. 97, no. 3, pp. 415–429.
- 10. Mathisen, I.E., Mikheeva, A., Tutubalina, O.V., et al., Fifty years of tree line change in the Khibiny Mountains, Russia: Advantages of combined remote sensing and dendroecological approaches, *Appl. Veg. Sci.*, 2014, vol. 17, no. 1, pp. 6–16.
- 11. Prirodnye usloviya Khibinskogo gornogo massiva: Ucheb. pos. (Natural Conditions of the Khibiny Mountains: A Textbook), Myagkov, S.M., Ed., Moscow: Mosk. Gos. Univ., 1986.
- 12. Demin, V.I., Basic climatic tendencies in the Kola Peninsula over the period of instrumental meteorological observations, *Tr. Kol'sk. Nauch. Tsentra Ross. Akad. Nauk*, 2012, vol. 3, no. 10, pp. 98–110.
- Gorchakovskii, P.L. and Shiyatov, S.G., Fitoindikatsiya uslovii sredy i prirodnykh protsessov v vysokogor'yakh (Phytoindication of Environmental Conditions and Natural Processes in High Mountain Regions), Moscow: Nauka, 1985.
- 14. Shiyatov, S.G., Terent'ev, M.M., Fomin, V.V., et al., Altitudinal and horizontal shifts of the upper boundaries of open and closed forests in the Polar Urals in the 20th century, *Russ. J. Ecol.*, 2007, vol. 38, no. 4, pp. 223–227.
- 15. Fomin, V.V., Klimatogennaya i antropogennaya prostranstvenno-vremennaya dinamika drevesnoi rastitel'nosti vo vtoroi polovine XX veka (Climatogenic and Anthropogenic Spatiotemporal Dynamics of Woody Vegetation in the Second Half of the 20th Century), Yekaterinburg: Inst. Ekol. Rast. Zhiv., Ural Ord. Ross. Akad. Nauk, 2009.
- 16. Bakker, J.D., A new, proportional method for reconstructing historical tree diameters, *Can. J. For. Res.*, 2005, vol. 35, no. 10, pp. 2515–2520.
- 17. Poulter, B., Bouriaud, O., Szejner, P., et al., A tree-ring perspective on the terrestrial carbon cycle, *Oecologia*, 2014, vol. 176, no. 2, pp. 307–322.
- 18. Babst, F., Bouriaud, O., Papale, D., et al., Above-ground woody carbon sequestration measured from tree rings is coherent with net ecosystem productivity at five eddy-covariance sites, *New Phytol.*, 2013, vol. 201, no. 4, pp. 1289–1303.
- Babst, F., Bouriaud, O., Alexander, R., et al., Toward consistent measurements of carbon accumulation: A multi-site assessment of biomass and basal area incre-

- ment across Europe, *Dendrochronologia*, 2014, vol. 32, no. 2, pp. 153–161.
- 20. Paulsen, J. and Korner, C., A climate-based model to predict potential treeline position around the globe, *Alp. Bot.*, 2014, vol. 124, no. 1, pp. 1–12.
- 21. Nagimov, Z.Ya., Moiseev, P.A., Bartysh, A.A., et al., The structure and phytomass of birch stands at the upper treeline in the Northern Urals, *Lesnoi Vestn.*, 2008, vol. 3, pp. 61–67.
- 22. Franklin, J.F., Moir, W.H., Douglas, G.W., et al., Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon, *Arct. Alp. Res.*, 1971, vol. 3, no. 3, pp. 215–224.
- 23. Taylor, A.H., Forest expansion and climate change in the Mountain Hemlock (*Tsuga mertensiana*) Zone, Lassen Volcanic National Park, California, U.S.A., *Arct. Alp. Res.*, 1995, vol. 27, no. 3, p. 207.
- 24. Rochefort, R.M. and Peterson, D.L., Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park, Washington, U.S.A., *Arct. Alp. Res.*, 1996, vol. 28, no. 1, pp. 52–59.
- 25. Woodward, A., Schreiner, E.G., and Silsbee, D.G., Climate, geography, and tree establishment in subalpine meadows of the Olympic Mountains, Washington, U.S.A., *Arct. Alp. Res.*, 1995, vol. 27, no. 3, pp. 217–225.

Translated by S. Kuzmin