

## Climate Changes and Tree Stand Dynamics at the Upper Limit of Their Growth in the North Ural Mountains

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**Abstract**—The composition and structure of tree stands near the timberline have been studied on different slopes and at different elevations in the Tylaisko-Konzhakovsko-Serebryanskii Massif, the North Urals. It has been found that the upper limits of tree stands with different degrees of canopy closure have risen considerably (by about 100 m of elevation) since the mid-19th century, although the formation of these stands started as early as the late 18th century. Woodless areas in the eastern part of the massif started to be colonized by *Larix sibirica* in the late 18th to early 19th centuries; those in the western part, by *Picea obovata* in the mid-19th century; and in the southern part, by *Betula tortuosa* in the late 19th century. Analysis of meteorological data provides evidence for warming and increasing humidity of the climate since the late 19th century. Favorable climatic changes that facilitated the expansion of the forest have taken place both in the summer (prolongation of the growing period) and in winter seasons (increase of air temperature and precipitation). The observed differences in the composition and dynamics of tree stands between the studied areas of the mountain range are most probably explained by different requirements of tree species for the depth of snow cover and the degree of soil freezing.

**Keywords:** timberline ecotone, tree stand structure, climate warming and increasing humidity, snow cover, air and soil temperatures.

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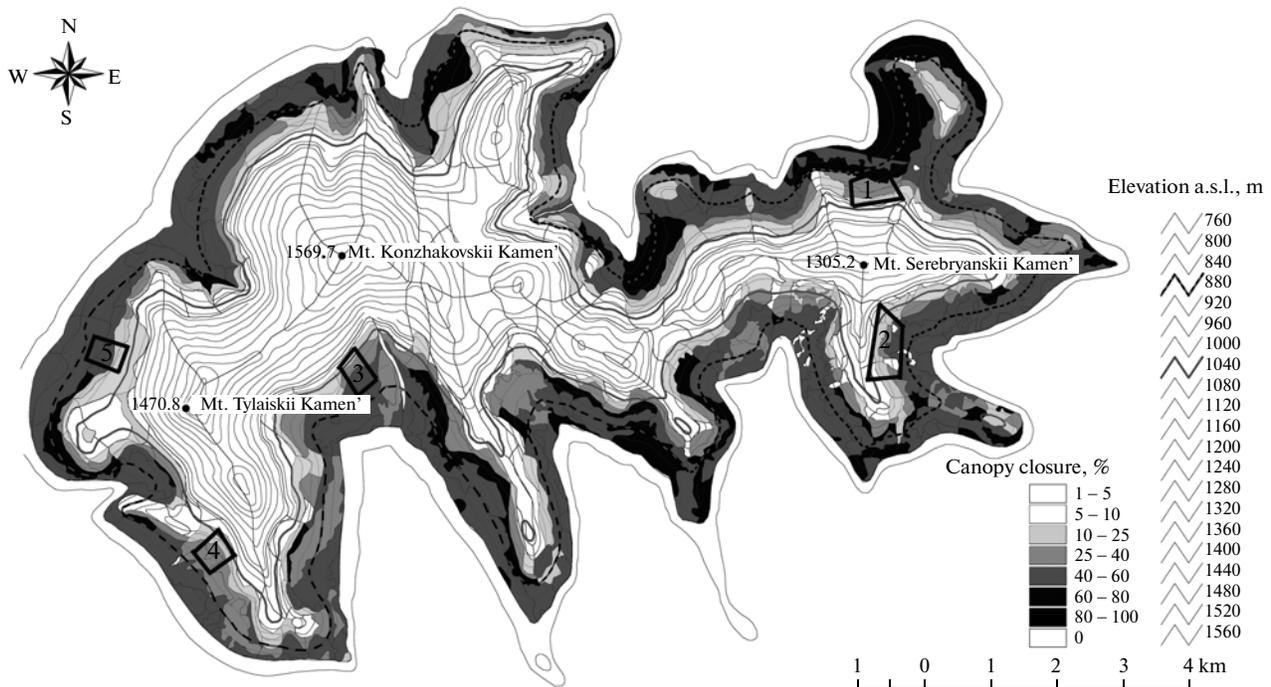
Intensification of forest regeneration and increase in tree stand density near the timberline during the 20th century were recorded in different regions of the world (for review, see Harsch et al., 2009). The upper limits of closed and open forests were found to shift to higher elevations over the past 60–80 years in the South Urals (Moiseev et al., 2004) and in the Polar Urals (Shiyatov et al., 2005). Kapralov et al. (2006), who analyzed photographs of the landscape and descriptions of tree stands made in 1956 and 2005, concluded that the upper limit of open forests in the North Urals (Tylaisko-Konzhakovsko-Serebryanskii Massif) has risen over the past 50 years (on average, by 40 m of elevation), and their composition and structure have changed. However, it is not yet completely clear when these changes started (50, 100 years ago or earlier), what has happened with the upper limits of other types of tree vegetation (closed forests, isolated trees, and groups of trees), and what role in these processes has been played by local habitat conditions and climate changes over the past few centuries. To find answers to these questions, we studied the composition and structure of tree stands and site conditions

along altitudinal gradients in the forest–tundra ecotone of this mountain massif.

### STUDY AREA AND METHODS

The study was carried out on slopes of the Tylaisko-Konzhakovsko-Serebryanskii Massif (59°30'–59°40' N, 59°00'–59°20' E), in the southern area of medium-high Northern Ural ranges forming a partially isolated mountain node at the boundary between the Northern and Middle Urals, which consists mainly of pyroxenites, dunites, and gabbro. The climate in this area is cold and excessively humid. The average temperatures of January and July are –16.8 and 17.0°C; annual precipitation is 500–700 mm in the mountain taiga belt but considerably higher in belts lying at higher elevations, reaching 1200 mm. Summers are relatively short and moderately warm, winters long and cold, with early snow cover establishment. The massif extends latitudinally for 20 km, and its western and eastern slopes markedly differ in the degree of climate continentality.

The mountain forest belt, with the prevalence of dark coniferous forests dominated by the Siberian



**Fig. 1.** Locations of altitudinal transects on slopes of the Tylaisko-Konzhakovsko-Serebryanskii Massif: (1, 2) larch forests; (3) birch forests; (4, 5) spruce forests.

spruce (*Picea obovata* Ledeb.), Siberian fir (*Abies sibirica* Ledeb.), and Siberian pine (*Pinus sibirica* (Rupr.) Mayr.), reaches the elevation of 900 m above sea level. The subgoltsy belt, occupied by the same tree species, lies at higher elevations (up to 1000–1050 m). On slopes of Mount Serebryanskii Kamen', the taiga dominants in this belt are joined by the Siberian larch (*Larix sibirica* Ledeb.), which forms sparse stands. The white birch, widespread in mountain forests, is replaced here by the closely related arctic birch (*Betula tortuosa* Ledeb.). The upper parts of the mountains (above 1000–1050 m) are dominated by forest tundras and screes of large boulders (“kurums”).

The composition and structure of tree stands were studied along five altitudinal transects established on slopes of different exposure over the period from 2002 to 2007 (Fig. 1). The transects were positioned in the *upper timberline ecotone*, i.e., in the transitional mountain belt between the upper limits of closed forests and of isolated tree growth in the tundra. The ecotone includes several categories of the upper limits of forest vegetation, according to Gorchakovskii and Shiyatov (1985): *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 line of the contact between the uppermost forest phytocenoses and adjoining non-forest phytocenoses (forest areas are defined as those where the tree layer is distinct, trees are two to three times as high as the shrub layer, their canopy closure is at least 0.1, and the average size of the area is at least five times greater than the average height of the tree layer); *the*

*upper limit of sparse tree growth* (canopy closure 0.05–0.1), the shortest line connecting the uppermost locations of small groups of trees, together with young tree growth and species typical of the lower layers of forest phytocenoses under their crowns; *the upper limit of single tree growth* (canopy closure less than 0.05), the shortest line connecting the uppermost single trees of any growth form (single-stemmed, multistemmed, or prostrate) in the mountain tundra or meadows.

In each transect, three altitudinal levels were delimited: lower, at the upper limit of closed forests (880–930 m a.s.l.); middle, at the upper limit of open forests (931–980 m a.s.l.); and upper, at the upper limit of sparse tree growth (980–1040 m a.s.l.). Three to six 20 × 20-m test plots were established at each level. The elevation and geographic coordinates of each plot were determined using a GPS receiver. Each tree (single-stemmed) or stem (in multistemmed trees) in the plots was examined to record the following parameters: species, exact location, growth form (single-stemmed, multistemmed, or prostrate), height, stem diameter at the base and at breast height, diameter of canopy projection in two directions, and canopy projection length. These parameters were then input into the Microsoft Office Excel 2003 spreadsheet and processed statistically. The proportions of individual tree species in the stands were estimated from the sum of cross-section areas of their stems.

To estimate the time of tree (stem) establishment in the plots, a core sample of wood at a height of 25 cm or lower was taken from each living tree with stem diam-

eter over 3–4 cm; in dead trees, cross cuts were made. Cross cuts at the root collar were also taken from every second young tree with height over 0.2 m but trunk diameter smaller than 3–4 cm. In the laboratory, each core sample was fixed in a wooden holder, smoothed with an office knife and a razor blade, and rubbed with tooth powder to make tree rings more contrasting.

For most of wood samples, visual dating by standard dendrochronological methods was sufficient, since the width and variation of tree rings allowed direct comparison of the results with the master chronologies compiled by Shiyatov (1986). In doubtful samples, annual wood increments were measured using a LINTAB-III device, and the formation for the central tree ring was finally dated with the TSAP-3.0 program.

If the core sample did not reach the center of tree stem, then the date of central ring formation was estimated as follows: first, the radius of the arc formed by the earliest (closest to the center) annual ring was determined by comparing it with arcs of circles with different radii drawn on transparent film; then, annual rings were counted in the earliest part of the sample equal to the above radius, and this number was added to the number rings observed and dated in the sample.

Since the age of young trees higher than 0.2 m but less than 3–4 cm in diameter was determined in cross cuts made at the root collar (0 cm), estimations of this parameter were especially reliable. Using data on the age and height of such trees, we calculated the regression equation for the dependence between these parameters and, using this equation, calculated the time when each of older trees reached the height at which core samples were taken. Adding this calculated value to the estimated age of the sample, we determined the age at the level of the root collar for each tree with diameter over 3–4 cm.

A total of 66 sampling plots with a total area of 2.64 ha were established in the five transects. Morphometric parameters were determined in 6780 stems of single-stemmed and multistemmed trees, and the year of establishment was estimated for 2828 of them.

It is well known that almost all tree species of the temperate zone bear abundant seeds at certain intervals (in spruce and larch species, 3–6 years). Therefore, new tree generations appear only after must years, whereas seedlings emerging during intervals between these years take no part in the formation of tree stands, since they are small in numbers and perish before reaching the reproductive age (Koshkina et al., 2008). Because of possible errors in determining the age of trees with an eccentric pattern of radial growth and variation in the time required for young trees to reach the height at which wood samples were taken (5–25 cm), our estimations of tree age are accurate to about 1–3 years. Therefore, with regard to our own and published data (Turmasova, 1991; Basov, 2000) on must years (for spruce in the North Urals these were the years 1934, 1937, 1941, 1947, 1952, 1955, 1961,

1964, 1970, 1973, 1977, 1981, 1987, 1991, 1996, 2000, and 2004), we pooled the numbers of trees by five-year periods, each including two years before and two years after the year next to a bumper year. Abundant seed yields are usually confined to one year in the first and one year in the second half of each decade (for instance, 1934 was a bumper year for spruce between 1931 and 1935, and 1937 was such a year between 1936 and 1940); hence, the values pooled over 5 years, even for the period prior to 1934, can be used for characterizing the numbers of trees that appeared after the bumper year of a certain half-decade (1921–1925, 1916–1920, 1911–1915, etc.) and survived to this day. The age of arctic birch trees is often difficult to estimate, since all of them are multistemmed and most of stems are formed much later than the tree itself appears. However, an important factor in the formation of forest communities is the timing of growth of tree crowns, which play the principal edificatory (environment-forming) role in the life of ground vegetation layer. Thus, for comparison with periods of tree stand formation by other tree species, we similarly combined the numbers of birch stems into five-year groups.

Hourly temperature measurements were made from July 2004 to September 2005 with nine TBI32-20+50 StowAway Tidbit data loggers installed in tree crowns (2 m above the soil surface) in the upper, middle, and lower parts of the timberline ecotone on the southeastern and the northern slopes of Mount Serebryanskii Kamen'. These data were used to calculate monthly average temperatures. In 2007, the depth of snow cover was measured in 52 test plots studied previously and in adjacent areas. Measurements in biotopes with medium or small amounts of snow were made with a 2-m surveying rod (in 100 points per plot); in biotopes with large amounts of snow, its level was marked on tree trunks with paint, and the height of the marks was measured in summer. Simultaneously, the temperature of the upper 5-cm soil layer under snow was measured at 48 points.

Climate changes over the period from 1888 to 2008 were evaluated on the basis of data from weather stations Biser (120 km southwest of the study area), Cherdyn' (180 km northwest), and Karpinsk (45 km east).

## RESULTS

**Composition and structure of tree stands.** Tree stands at all levels of transects 1 and 2 are dominated by larch (Table 1). The number of species in the stand decreases from five at the lower level to only two at the upper level, with the proportion of the larch increasing and that of other species decreasing with elevation. The composition of young tree growth markedly differs from that of the tree stand. Young growth of dark coniferous species prevails at the lower level (up to 95%). The largest proportion of birch is observed at the

**Table 1.** Proportions of different tree species in the tree stand (according to the total area of stem sections) and in the young growth (according to numbers per hectare), %

Transect	Altitudinal level														
	lower					middle					upper				
	L	S	F	P	B	L	S	F	P	B	L	S	F	P	B
Tree stand															
1	69	7	1	6	17	94	–	–	1	5	99	–	–	1	–
2	91	–	–	–	9	95	–	–	–	5	99	–	–	1	–
3	–	–	2	–	98	–	–	10	–	90	–	1	–	–	99
4	–	88	–	–	12	–	89	6	–	5	–	98	2	–	–
5	–	57	2	–	41	–	67	4	–	29	–	99	–	1	–
Young growth															
1	1	28	47	20	4	13	27	18	16	26	34	4	–	59	3
2	1	12	33	26	28	3	27	16	7	47	12	27	1	54	6
3	–	–	17	–	83	–	–	3	1	96	–	4	2	15	79
4	–	44	7	10	39	–	65	20	4	11	–	73	7	20	–
5	–	13	79	5	3	–	18	78	4	–	–	88	12	–	–

Note: L, larch; S, spruce; F, fir; P, Siberian stone pine; B, birch.

middle level. The proportions of larch and Siberian stone pine increase with elevation. At the upper level, the proportion of young larch trees is considerable (34%), but Siberian stone pine is still dominant there (59%), since large amounts of pine seeds are annually brought to this zone by nutcrackers, which store them in areas with little or no snow.

Tree stands in transect 3 consist almost entirely of birch. Its proportion is 98% at the lower level, 90% at the middle level, and 99% at the upper level. The young growth also consists mainly of birch (83% at the lower level, 96% at the middle level, and 79% at the upper level).

Tree stands at all levels of transect 4 are dominated by spruce, with the proportion of birch at the lower level being also fairly large (up to 12%). The proportion of spruce increases with elevation from 88% to 98%. The young growth is also dominated by spruce at all levels. Its proportion increases with elevation from 44 to 73%.

Tree stands at all altitudinal levels of transect 5 are also dominated by spruce, with considerable proportions of birch in the middle and lower levels (29% and 41%, respectively). The proportion of spruce markedly increases with elevation, from 57% to 99%. The young growth is dominated by dark coniferous species, fir at the middle and lower levels (78 and 79%), and spruce at the upper level (88%).

Taxonomic parameters of tree stands significantly change with elevation (Table 2). Thus, upon transition from the lower to the upper level of transect 1, the average tree age decreases by a factor of 3.4; average diameter, by a factor of 3.5; average height, by

a factor of 2.4; density, by factor of 2.1; and the sum of crown projections, by a factor of 7.6. Similar trends in these parameters are also observed in other transects.

**Reconstruction of tree stand dynamics by the timing of tree establishment.** Analysis of data on the establishment of individual trees on the slopes of Mount Serebryanskii Kamen' (transects 1 and 2) showed that mass colonization by larch at the lower level took place during two periods: from 1775 to 1815 (37% of present-day living trees) and from 1880 to 1940 (22%); at the middle level, from 1890 to 1960 (80%); and at the upper level, from 1940 to 1990 (83%) (Fig. 2a). Colonization of these transects by birch at the lower level was especially active from 1900 to 1935 (40%) and from 1945 to 1995 (52%); at the middle level, from 1945 to 1995 (83%); and the small amount of birch growing at the upper level appeared only after 1975 (Fig. 2b). The establishment of spruce at the lower level began in the early 19th century, but the greater part of trees appeared during the 20th century (Fig. 2c). At the middle level, this process began in the late 19th century but became sufficiently active only in the mid-20th century. Single spruce trees at the upper level appeared in the early 20th century, but appreciable establishment of this species took place only at the end of that century. Siberian stone pine appeared at the lower level in the early 19th century, i.e., earlier than spruce and birch but later than the larch. However, its active establishment has been taking place only in the past few decades, beginning from 1980. The same applies to the middle level, where Siberian stone pine began to appear in the first decade of the 20th century.

**Table 2.** Morphometric parameters of trees of dominant species and areal characteristics of tree stands at different altitudinal levels of the transects

Altitudinal level	Elevation a.s.l., m	Average parameters of trees of dominant species			Number of tree stems per ha	Total area of crown projections, m <sup>2</sup> /ha
		Age, years	Diameter, cm	Height, m		
Transect 1 (larch forests)						
Upper	985–1015	56 ± 3.0	4.4 ± 0.2	2.6 ± 0.1	956	1700
Middle	930–950	97 ± 2.5	7.7 ± 0.2	3.6 ± 0.1	1955	6000
Lower	880–910	191 ± 7.2	15.5 ± 0.5	6.3 ± 0.2	1980	12900
Transect 2 (larch forests)						
Upper	1030–1060	71 ± 4.0	5.7 ± 0.3	2.6 ± 0.1	400	1000
Middle	985–995	89 ± 3.4	11.7 ± 0.5	4.5 ± 0.3	1768	7900
Lower	940–960	144 ± 8.2	17.6 ± 1.0	5.9 ± 0.3	1989	8100
Transect 3 (birch forests)						
Upper	1020–1040	46 ± 2.6	2.7 ± 0.1	3.3 ± 0.2	1132	2000
Middle	960–980	66 ± 1.7	3.1 ± 0.1	4.5 ± 0.2	3725	8200
Lower	920–940	95 ± 3.1	3.9 ± 0.2	7.2 ± 0.4	2009	7300
Transect 4 (spruce forests)						
Upper	1020–1050	81 ± 6.1	6.3 ± 0.3	2.3 ± 0.1	563	1300
Middle	980–1000	136 ± 3.8	9.4 ± 0.3	3.0 ± 0.1	1300	3900
Lower	920–960	134 ± 2.4	17.5 ± 0.4	5.4 ± 0.1	1744	7600
Transect 5 (spruce forests)						
Upper	1005–1020	44 ± 1.8	3.1 ± 0.2	2.1 ± 0.1	1025	1400
Middle	950–980	89 ± 3.7	8.5 ± 0.5	3.4 ± 0.1	1238	4400
Lower	900–930	110 ± 4.9	17.0 ± 1.1	7.2 ± 0.4	1157	11000

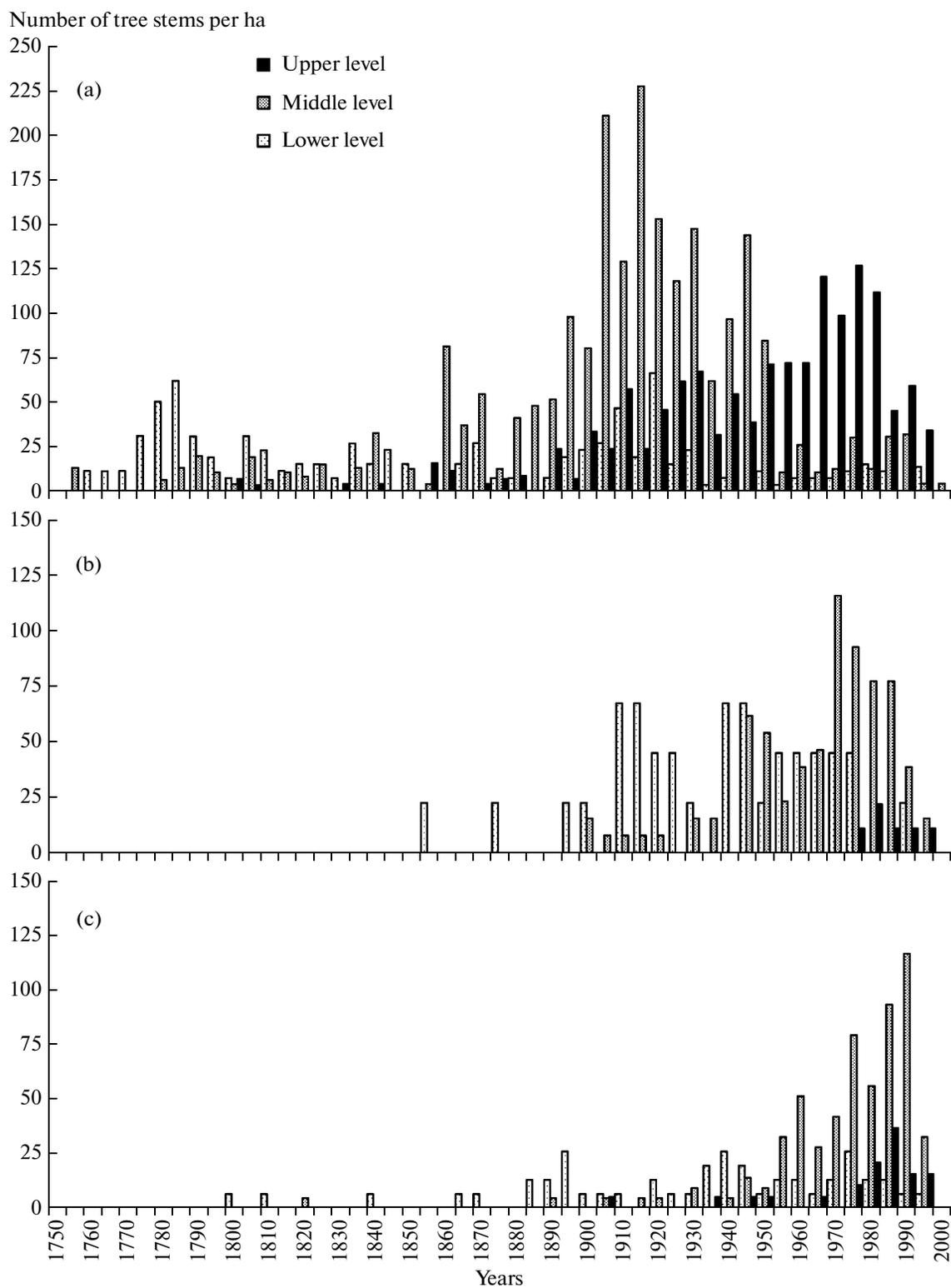
On the slopes of Mount Konzhakovskii Kamen' (transect 3), active colonization by birch at the lower level took place from 1890 to 1940 (71% of the present-day living trees); at the middle level, from 1910 to 1960 (70%); and at the upper level, from 1940 to 2000 (89%) (Fig. 3).

On the southwestern slope of Mount Ostraya Kos'va (transect 4), spruce actively colonized the lower level from 1820 to 1940, with a peak in the 1900s (87%); the middle level, from 1840 to 1940, with a peak in the 1870s (63%); and the upper level, from 1880 to 1950, with a peak in the 1920s (50%) (Fig. 4a). Colonization of the northwestern slope of Mount Konzhakovskii Kamen' (transect 5) by this species took place somewhat later than on transect 4: from 1860 to 1940 at the lower level (81%), from 1890 to 1960 at the middle level (82%), and from 1940 to 1990 at the upper level (90%) (Fig. 5a). Mass establishment of birch on these transects took place between 1880 and 1960 (Figs. 4b, 5b).

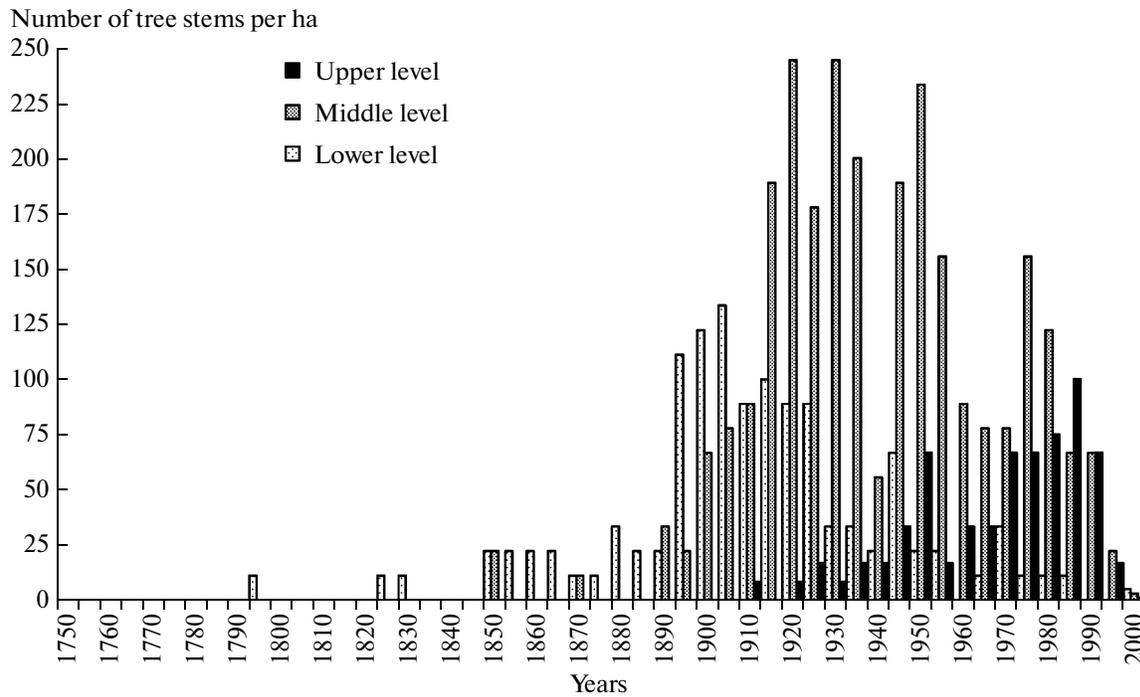
**Site conditions.** Parameters of soil moisture on transects 1 and 2, located in the eastern part of the massif, do not differ significantly between altitudinal levels: moisture supply is moderate at the lower and middle levels, and soil at the upper level may become dry during summer droughts, which are rare in this

region. Differences in monthly average air temperatures between altitudinal levels on the transects do not exceed 0.8°C, usually being about 0.3–0.5°C (Table 3). The depth of the snow cover changes slightly upon transition between the lower and middle levels (from 1.6 to 1.5 m) but markedly decreases at the upper level (from 1.5 to 0.5 m) (Table 4). Changes in the depth of snow cover are explained by the fact that considerable amounts of snow are blown away from the higher-elevation woodless areas to be retained by relatively dense tree stands at lower elevations. More snow is accumulated at the middle and lower levels than at the upper level, where tree stands are sparse. Soil temperature in the upper layer at the end of winter also decreases with elevation. The soil at the lower and middle levels cools down to only –0.7°C, compared to –5.1°C at the upper level, where snow cover is thin and provides poor heat insulation.

Transects 4 and 5 (spruce forests) are positioned in the west of the massif, where both winter and summer precipitation is higher than in transects 1 and 2; therefore, soil moisture is also higher. Despite considerable wind transfer of snow from the upper parts of the slopes, its depth is considerable at all altitudinal levels (1.15–2.0 m). The lowest winter temperature of the upper soil layer is higher (–0.7 to –1.8°C), compared



**Fig. 2.** Distribution of (a) larch, (b) birch, and (c) spruce trees according to the period of their establishment on slopes of Mount Serebryanskii Kamen' (transects 1 and 2).



**Fig. 3.** Distribution of birch trees according to the period of their establishment on the southeastern slope of Mount Konzhakovskii Kamen' (transect 3).

to the eastern transects, and also decreases with elevation.

In transect 3, located in the middle of the massif, the soils are moist at all altitudinal levels due to high precipitation. Snow cover is deep (1.7–1.8 m), regardless of elevation. The upper soil layer at all altitudinal levels cools to only  $-0.8$  to  $-0.7^{\circ}\text{C}$ .

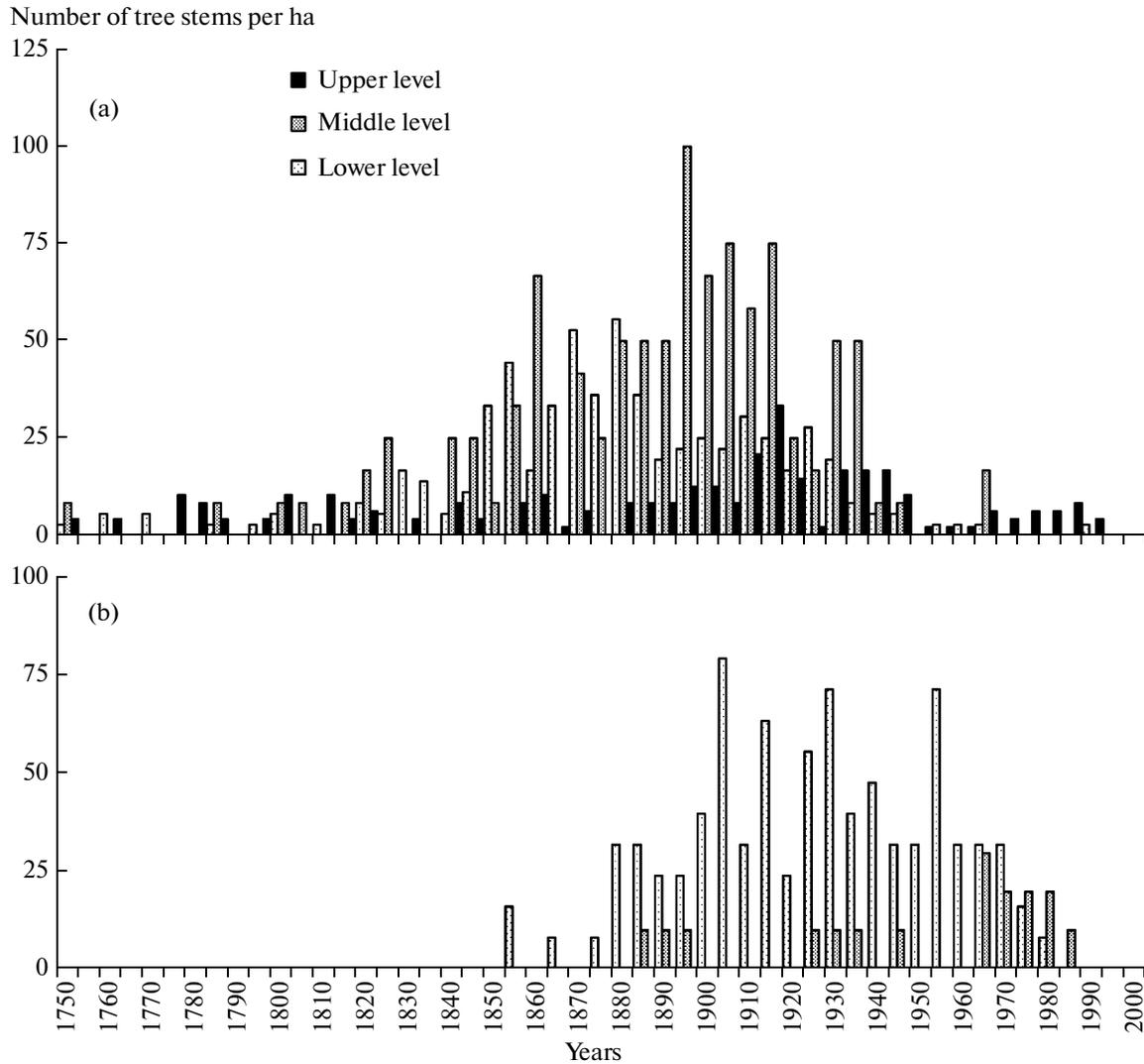
## DISCUSSION

Reconstructions of the dynamics of tree vegetation from the calendar time of tree establishment show that

the upper limits of tree vegetation (from the limit of closed forests to the limit of sparse tree growth) in all the transects have shifted upslope during the past centuries. The start and the course of this process were largely determined by local conditions in areas colonized by trees as well as by the tree species. This process started first on Mount Serebryanskii Kamen', with larch being the pioneering tree species. The present-day upper limit of closed forests on the northern slope of this mountain lies 50 m lower than that on the southeastern slope, although there is no significant difference in the timing of colonization between the

**Table 3.** Monthly average air temperatures ( $^{\circ}\text{C}$ ) at different altitudinal levels of transects 1 and 2 (slopes of Mount Serebryanskii Kamen') in 2004 and 2005

Altitudinal level	2004							
	7	8	9	10	11	12		
Upper	$17.3 \pm 0.1$	$9.3 \pm 0.1$	$4.1 \pm 0.1$	$-4.3 \pm 0.1$	$-9.0 \pm 0.1$	$-13.0 \pm 0.1$		
Middle	$17.2 \pm 0.1$	$9.5 \pm 0.1$	$4.3 \pm 0.1$	$-4.1 \pm 0.1$	$-8.8 \pm 0.1$	$-13.1 \pm 0.1$		
Lower	$16.9 \pm 0.1$	$9.6 \pm 0.1$	$4.5 \pm 0.1$	$-3.9 \pm 0.1$	$-8.5 \pm 0.1$	$-13.1 \pm 0.1$		
Altitudinal level	2005							
	1	2	3	4	5	6	7	8
Upper	$-10.2 \pm 0.1$	$-12.8 \pm 0.1$	$-11.8 \pm 0.1$	$-1.2 \pm 0.2$	$9.1 \pm 0.2$	$9.1 \pm 0.1$	$15.1 \pm 0.2$	$11.3 \pm 0.1$
Middle	$-10.3 \pm 0.1$	$-12.8 \pm 0.1$	$-11.4 \pm 0.1$	$-1.2 \pm 0.1$	$9.2 \pm 0.2$	$9.4 \pm 0.1$	$15.2 \pm 0.1$	$11.7 \pm 0.1$
Lower	$-10.0 \pm 0.1$	$-12.6 \pm 0.1$	$-11.2 \pm 0.1$	$-2.0 \pm 0.1$	$9.1 \pm 0.2$	$9.4 \pm 0.1$	$14.9 \pm 0.1$	$11.7 \pm 0.1$



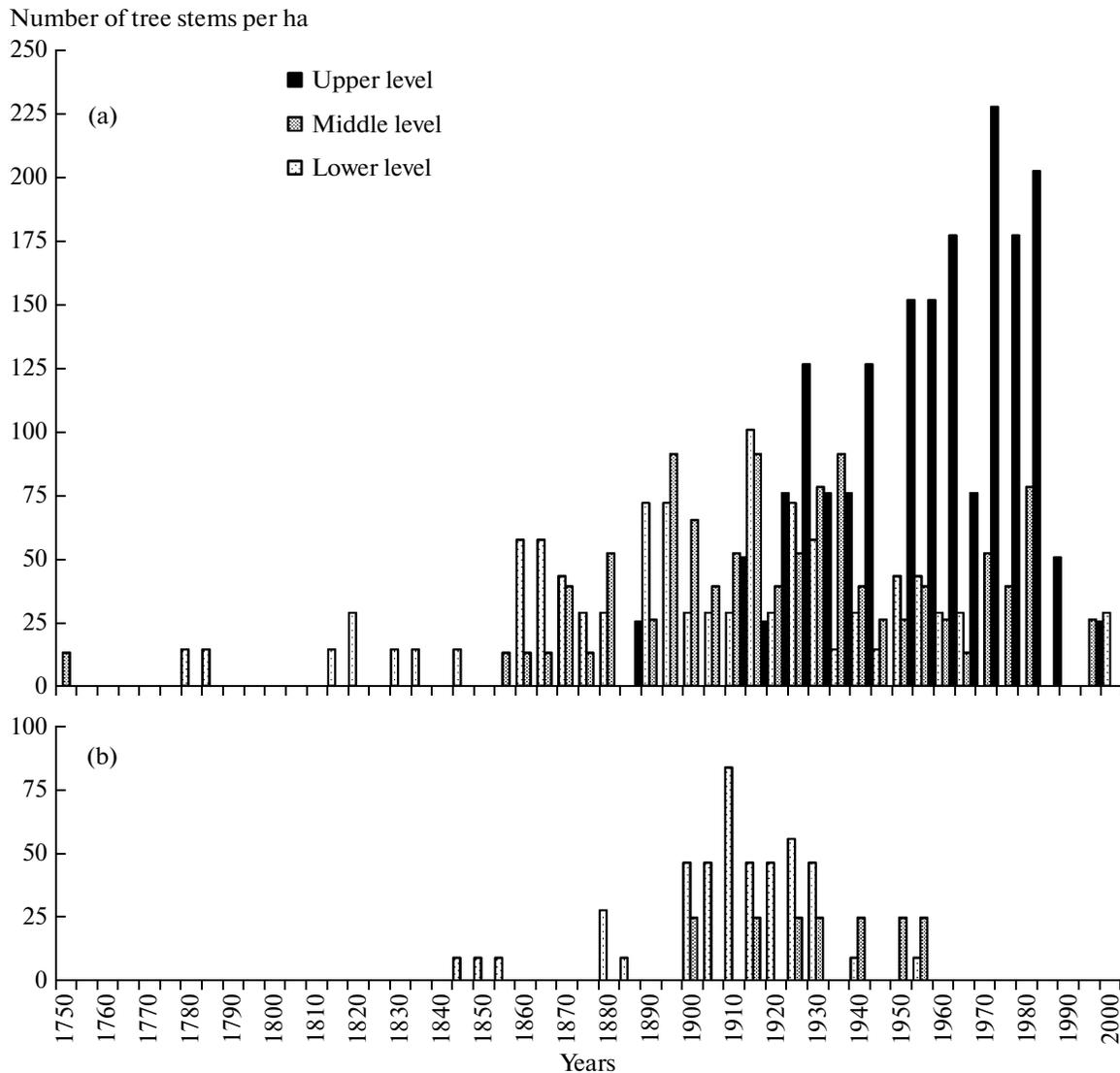
**Fig. 4.** Distribution of (a) spruce and (b) birch trees according to the period of their establishment on the southwestern slope of Mount Ostraya Kos'va (transect 4).

slopes. On the southwestern slope of Mount Ostraya Kos'va and on the northwestern slope of Mount Tylaiskii Kamen', dominated by spruce, this process started later. Birch tree stands on the southeastern slope of Mount Konzhakovskii Kamen' were the latest to form. It is noteworthy that the role of birch in tree stand formation throughout the recent forest–tundra ecotone of the massif has been increasing since the late 19th century.

Data from the Karpinsk weather station (Fig. 6) show that monthly average air temperatures in the warm season have been changing in different directions since the mid-19th century: temperatures in May and June increased by 0.4–1.2°C, whereas that in August, decreased by 0.1°C, thereby prolonging the growing season (by 3–6 days) and improving heat supply during this season. The annual amount of precipitation has also increased, but mainly on account of

precipitation in July to September. Monthly average temperatures in winter and early spring (November–March) have changed more significantly, increasing by 1.5–5.1°C; consequently, the average temperature of the cold season has become 3.5°C higher. The amount of solid precipitation, which had been increasing since the mid-19th century, decreased by the 1930s and then started increasing again, reaching the previous level by the early 21st century. As a result, winters have become warmer and more snowy, providing better conditions for tree survival during the cold period of the year, especially for relatively large young trees as the most vulnerable link in the process of tree stand formation.

Strong winds (over 10–15 m/s) at high elevations cause desiccation and snow abrasion of leaves, buds, and shoots emerging above the snow surface. As a result, trees at the upper limit of their growth annually



**Fig. 5.** Distribution of (a) spruce and (b) birch according to the period of their establishment on the northwestern slope of Mount Tylaiskii Kamen' (transect 5).

loose 4–10% of their assimilatory organs (Cairns, 2001). If snow depth is insufficient, the soil strongly freezes, which leads to frost heaving (for 5–6 cm; Sovershaev, 1961) and cracking of upper soil layers, with consequent serious damage to fine roots. According to Tierney et al (2001), a drop in soil temperature below  $-4^{\circ}\text{C}$  and soil freezing to a depth of 25–30 cm lead to a twofold increase in the proportion of dead fine roots (from 14 to 28%) and disturb symbiotic relationships between plant roots and mycorrhizal fungi, which markedly reduces the capacity of plants for absorbing nitrogen- and phosphorus-containing mineral substances from the soil. Soil moisture freezing into ice crystals reduces the activity of cryophilic bacteria in winter (Mikan et al., 2002) and retards the release of additional amounts of mineral nutrients (supplementary to those available in summer). After

deep freezing in winter, soil thawing takes more time and soil temperature in summer is lower (the difference between soil temperatures at the upper and middle levels is  $1.5\text{--}3^{\circ}\text{C}$ ), with a consequent decrease in the activity of soil bacteria and retarded turnover of mineral substances (Kammer et al., 2007). All these factors (losses of assimilatory structures and fine roots in winter and impairment of mineral nutrition) markedly affect net photosynthesis, assimilation of nutrients, and, finally, the growth and seed production of trees.

Special studies (Osokin, 2001) have shown that the depth of soil freezing may vary by a factor of two to three depending on conditions, timing, and rate of snow accumulation. Changes in the regime of snow accumulation in the study area during the latter half of the 20th century are generally favorable. For instance,

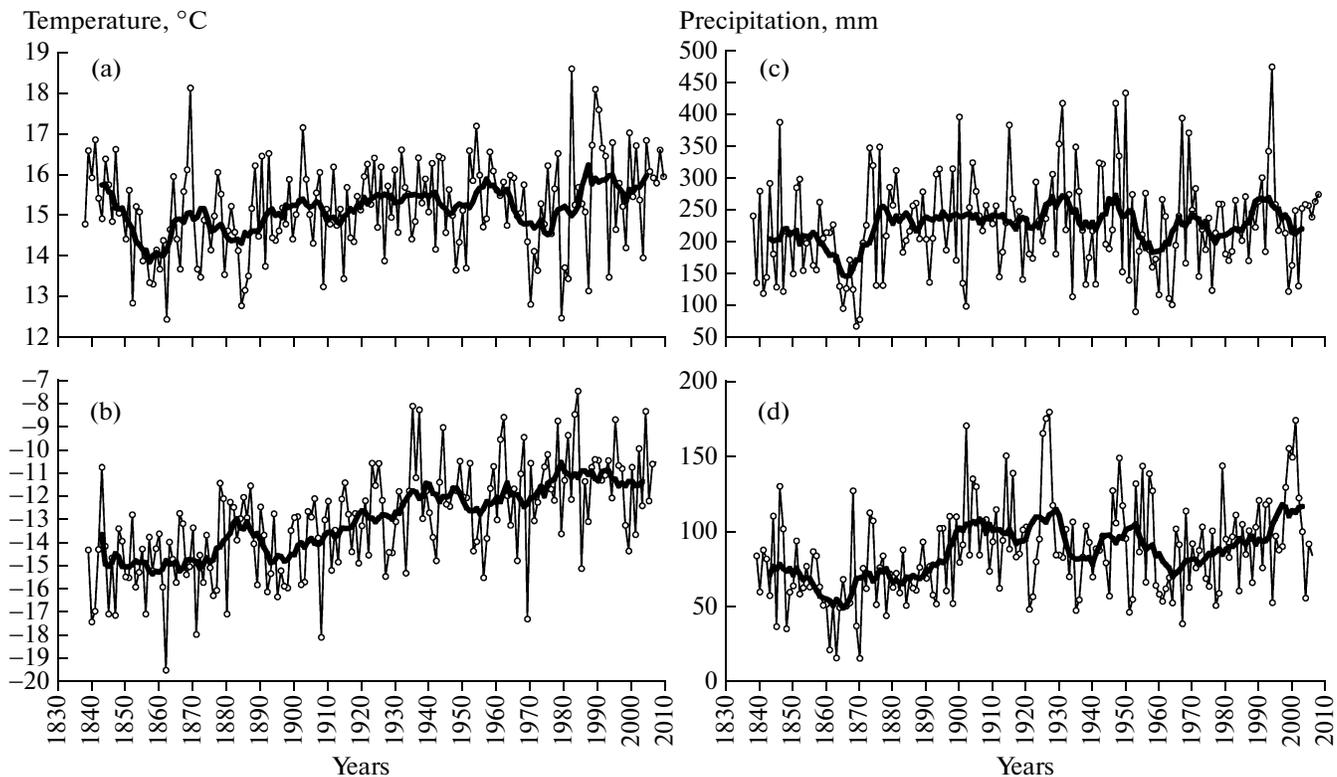
**Table 4.** Average snow depths and soil temperatures in the upper layer along the transects in March 2007

Altitudinal level	Transect					
	1 and 2 (larch forests)		4 and 5 (spruce forests)		3 (birch forests)	
	Snow depth, cm	Soil temperature, °C	Snow depth, cm	Soil temperature, °C	Snow depth, cm	Soil temperature, °C
Upper	0.57	-5.1	1.15	-1.8	1.71	-0.8
Middle	1.54	-0.7	1.67	-0.8	1.72	-0.8
Lower	1.56	-0.7	2.00	-0.6	1.82	-0.7

the amount of precipitation in the first half of winter has increased considerably, so that snow cover starts forming on not yet frozen soil and rapidly increases in depth; as a result, soils are less vulnerable to freezing. The survival of young trees strongly depends on climatic conditions in the period when they emerge from protective snow cover to the zone of snowdrift (60–100 cm above the snow surface). Due to damage of shoots and buds by snow abrasion, desiccation, and freezing, many plants fail to pass this threshold and perish (Shiyatov, 1965). In warm and snowy winters, roots are damaged to a lesser extent, the turnover of mineral nutrients accelerates, the soil freezes less deeply and thaws more quickly in spring; in combination with the prolonged growing period, this provides

for more active growth and lignification of young shoots. As a result, young trees more successfully survive the conditions of the snowdrift zone in the next winter.

As shown above, site conditions on the transects largely depend on the distance from the western edge of the massif: the closer this edge, the higher the soil moisture and the deeper the snow cover (Table 4). This is explained by the fact that humid air masses brought by the prevailing westerly winds are largely retained on the slopes and spurs of mounts Tylaiskii Kamen' (1470.8 m a.s.l.) and Konzhakovskii Kamen' (1569.7 m a.s.l.), which form the higher western and central parts of the massif, while the eastern part



**Fig. 6.** Air temperatures in (a) June–August and (b) November–March and precipitation in (c) June–August and (d) November–March according to data from the Karpinsk weather station over the period from 1838 to 2008 (bold line shows trend).

(Mount Serebryanskii Kamen', 1305.2 m a.s.l.) remains in a kind of "arid shadow."

Spruce, a moisture-loving species, suffers when the soil freezes. This is why spruce forests are confined to the lower part of the massif, where they occupy areas with moist soil and deep snow cover (1.15–2.0 m), which protects the soil from freezing. Transects 4 and 5 differ considerably in periods of their colonization by forest vegetation and in the species composition of tree stands. Mount Ostraya Kos'va (transect 4) was colonized by spruce earlier than was Mount Tylaiskii Kamen' (transect 5). This is explained by more favorable site conditions on the former transect. The small amount of birch trees at the lower level of transect 4, compared to the lower level of transect 5, is probably consequence of greater snow accumulation, poorer slope drainage, and, therefore, higher soil moisture.

Transect 3 is occupied by pure birch stands, while young spruce growth is almost absent, although local conditions are quite favorable for its formation (protection from the birch canopy, sufficient soil moisture, and deep snow preventing soil freezing). This situation can be explained by the fact that, due to the pattern of snow accumulation (a lot of snow falls and accumulates at all levels) and terrain topography (the higher the elevation, the steeper the slope), snow cover periodically slips downslope, bending flexible birch trees to the ground and breaking spruce trees. As a result, birch trees partly unbend in summer, but spruce trees die. A similar phenomenon was described in Japan (Kimiko, 2003). In a coniferous–deciduous mixed forest growing in the zone where a steep slope levels off, snowslides account for the prevalence of *Fagus crenata*, a deciduous species with flexible stem, over *Cryptomeria japonica*, a coniferous species with fragile stem. Trees of the latter species are subject to breakage and uprooting, which is rarely observed under different conditions.

Larch forests grow in the eastern part of the massif and are confined to the northern and southeastern slopes of Mount Serebryanskii Kamen'. Site conditions in this area are more severe: snow cover is thin, soil moisture is lower, and the temperature regime is relatively harsh. For instance, snow depth at the upper level of the altitudinal transects averages no more than 30–60 cm. Only larch can survive under such conditions. Spruce and birch occur only at the middle and lower levels of the transects, where snow cover is deeper due to wind transfer from higher elevations and the soil freezes to a lesser extent. Both birch and spruce poorly tolerate soil freezing. Weih and Karlsson (2002) performed experiments with mountain birch seedlings in the Subarctic (Swedish Lapland) to compare the effects of soil freezing in two variants: to  $-1.7^{\circ}\text{C}$  and to  $-10.5^{\circ}\text{C}$ . The results showed that soil freezing to low temperatures may cause increased root damage, stimulating the growth of substitute roots and reducing the capacity for nutrient assimilation and the rate of growth in summer, which eventually has an adverse

effect on the survival of birch seedlings. Thus, increasing winter precipitation in the study region improves the position of birch in tree stands throughout the mountain massif.

Thus, the data presented above show that the upper limits of tree stands with different degrees of closure have markedly shifted upslope (by about 100 m of elevation) since the mid-19th century, although the formation of these stands started as early as the late 18th century. For instance, larch in the eastern part of the massif started colonizing woodless areas in the late 18th to early 19th centuries; spruce in the western part, in the mid-19th century; and birch in the southern part, in the late 19th century. Forest expansion was facilitated by prolongation of the growing period and development of less severe winter conditions for tree survival and growth (higher air and soil temperatures and more abundant solid precipitation). Differences in the species composition of tree stands and in the pattern of forest expansion between the slopes can be explained by local features of site conditions such as the degree of mesoclimate continentality, snow depth, soil moisture, and the degree of soil freezing.

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