

Effect of Climatic Changes on the Formation of Siberian Spruce Generations in Subgoltsy Tree Stands of the Southern Urals

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Abstract—The correlation between climatic changes and the numbers of trees in the generations of Siberian spruce (*Picea obovata* Ledeb.) in subgoltsy tree stands of the Southern Urals was analyzed over the past 200 years. The results showed that the most abundant generations appeared in 1809–1816, 1821–1827, 1839–1845, 1850–1867, 1875–1887, 1891–1896, 1900–1904, 1911–1918, 1923–1932, 1944–1952, 1958–1966, and 1975–1995. Their formation proved to be related to the improvement of thermal conditions of the warm season during the five to seven years before and after the emergence of trees and conditions of the cold season in the year of their emergence, as well as to the periods of increased snow depth in late April in the years 27–32 of tree growth.

Key words: timberline, forest regeneration, climatic changes, *Picea obovata*, the Southern Urals.

Due to considerable warming in many parts of the world in the 20th century, the international scientific community has devoted increasing attention to studies on the responses of ecosystems and their individual components to climatic changes. The most sensitive ecosystems are those located in high mountains and at high latitudes, as their existence depends strongly on such changes. This well-known fact has been confirmed by the results of studies on the processes of forest renewal at altitudinal and polar forest limits in different regions of the world, including Canada (Kearney, 1982; Lavoie and Payette, 1992), the United States (Denton and Karlen, 1977; Jacobos and Romme, 1993; Taylor, 1995; Weisberg and Baker, 1995; Woodward *et al.*, 1995; Lloyd and Graumlich, 1977), northern Europe (Kullman, 1986; Kullman and Engelmark, 1977), Russia (Shiyatov, 1967, 1983, 1993), and New Zealand (Wardle and Coleman, 1992). These data provide evidence that changes in the structure of plant communities within the forest–tundra ecotone are strongly dependent on variation in certain climatic parameters. According to some authors (Kearney, 1982; Jacobos and Romme, 1993; Taylor, 1995; Woodward *et al.*, 1995), the corresponding processes depend mostly on climatic changes in the summer period and, in particular, on average summer temperature and precipitation rate. Other authors have noted that the growth of trunks and whole trees depends on the weather in the cold period of the year and, in particular, on the parameters such as snow depth, air temperature, and wind velocity, which determine the degree of soil freezing and frost damage to plant parts located above the snow surface (Lavoie and Payette, 1992; Weisberg and Baker, 1995; Kullman and Engelmark, 1997).

Analyzing the available meteorological data on the Southern Urals and publications on the climatogenic dynamics of communities within the forest–tundra ecotone and specific biological features of Siberian spruce, we have hypothesized that the formation of spruce generations in the subgoltsy tree stands depends on temperatures and precipitation rates in both warm and cold seasons, as these parameters determine the proportion of viable seeds and plant mortality at different developmental stages of age generations. Thus, the number of seedlings in some habitat in a certain year depends on the number of viable seeds coming to the soil, and this number, in turn, depends on conditions for flower bud formation and seed maturation in the previous several years (Kearney, 1982; Jacobos and Romme, 1993). The density of young undergrowth in the first years of life depends not only on the total number of seedlings, but also on specific weather conditions in the preceding period (Cui and Smith, 1991; Soll, 1994). The undergrowth rising above the average level of the herb–dwarf shrub layer suffers from rapid weather changes in the snowless period, whereas the impact of these changes on the ground vegetation layer is alleviated by its specific phytocenotic environment. Hence, unfavorable conditions for plants in the following years lead to increased mortality in this age group (Shiyatov, 1965).

Conditions for the young plants whose apical shoots rise above the average snow level in winter are also of considerable importance, as snow transfer by wind in the 50-cm surface air layer leads to their desiccation and mechanical damage (Shiyatov, 1965; Lavoie and Payette, 1992). Hence, snow depth, wind velocity, and temperature in the cold season determine plant mortality in the corresponding age group. Mortality among

the plant of older generations is lower, as they are at the peak of their development. However, their tolerance to adverse climatic factors decreases with age, and the following long cold periods (no less than 20–30 years) lead to their gradual elimination from the tree stand (Shiyatov, 1993).

To verify the above hypothesis, we studied the structure of subgoltsy tree stands (within a 100- to 150-m altitudinal zone below the timberline) in the Southern Urals and analyzed the results for correlations between the numbers of trees in spruce generations and changes in the aforementioned climatic parameters during the past centuries.

MATERIAL AND METHODS

Studies were performed on Mount Dal'nii Taganai (1146 m a.s.l.; 55°22'11" N, 59°54'28" E) and the Iremel' Mountain Range (1586 m a.s.l.; 54°30'–34' N, 58°49'–54' E) located in the northern and central parts of the Southern Urals, respectively. On their slopes, several altitudinal vegetation belts can be distinguished: dark conifer–broadleaf forests with the areas of *Pinus sylvestris* stands (up to 700 m a.s.l. on Mount Dal'nii Taganai and up to 900 m on Mount Bol'shoi Iremel'), the mountain forest belt (up to 950 and 1200 m a.s.l.), the subgoltsy belt (up to 1000–1050 and 1400 m a.s.l.), and the mountain tundra belt (up to 1146 and 1586 m a.s.l., respectively). Siberian spruce (*Picea obovata* Ledeb.) and birch *Betula tortuosa* Ledeb. are the main tree species forming the timberline. In places, other species (*Larix sibirica* Ledeb., *Pinus sylvestris* L., and *Abies sibirica* Ledeb.) occur above the upper forest limit.

According to data from the Taganai-Gora weather station, which is located slightly above the timberline on Mount Dal'nii Taganai, monthly average temperatures in this area are $10.4 \pm 1.9^\circ\text{C}$ in June, $12.3 \pm 1.8^\circ\text{C}$ in July, and $10.6 \pm 1.9^\circ\text{C}$ in August; the sum of above-zero daily temperatures varies from 1100 to 1850°C; annual precipitation varies from 600 to 1300 mm; and the average snow depth in late April is about 123 cm. The warm season is characterized by considerable cloudiness, frequent fogs, and long periods of inclement weather. The monthly average wind velocity reaches a peak in the cold season, when the winds blowing at the mountaintops often exceed 25–30 m/s.

On the northwestern slope of Mount Dal'nii Taganai, five circular test plots (radius 12.6 m, 500 m²) were established in 1999, and five more plots (radius 8 m, 200 m²) were established in 2001 along an altitudinal gradient of 950 to 1090 m a.s.l. On the southwestern slope of Mount Malyi Iremel' 18 square test plots (20 × 20 m) were established along an altitudinal gradient of 1250 to 1360 m a.s.l. in July 2002.

In each plot, characteristics of individual trees and saplings higher than 20 cm were recorded. They included location (azimuth and distance from the center

of the plot); plant height and trunk diameters at the base and breast height; crown length; shape, and diameter of crown projection; and vitality. Simultaneously, the samples of wood from each trunk with a diameter exceeding 5 cm were taken with a corer at a height of 20–30 cm (on Mount Iremel', this was done in two diagonally adjacent 10 × 10-m plots). Every second tree higher than 0.2 m but less than 5 cm in diameter was used to make saw cuts at the root collar and at a height of 25 cm. Saplings lower than 20 cm were counted either in 32 1 × 1-m squares (Iremel) or throughout the plot.

The year of formation of the oldest tree ring in each of 779 trunks (523 from Taganai and 256 from Iremel') was determined by cross-dating cores and saw cuts. If the corer reached the center of the trunk, then the age of the tree at a height of 20–30 cm from the trunk base was assumed to be equal to the difference between the year of sampling and the year of the oldest tree ring formation. If the corer did not reach the center because of eccentricity of the trunk growth or a focus of rot, then the distance to the center was first calculated from the radius of a template circumference that fitted the shape of the arc formed by the oldest tree rings of the core sample. In this case, the number of years in the last segment of the sample equal to the calculated radius was taken to be the number of years that had to be added to obtain the age at a height of 20–30 cm.

The average age at which young trees reached the height of sampling (20–30 cm) was calculated from the difference between the numbers of tree rings in saw cuts made at the root collar and at a height of 25 cm in 77 trunks with a base diameter of less than 5 cm. This age was 10 ± 2 years. By adding this value, we calculated the age at the level of the root collar for each tree thicker than 5 cm in diameter. Due to probable errors in determining the age of trees with an eccentric pattern of trunk growth at a height of 20–30 cm (by core samples that did not reach the center) and differences in the period required for growing to a height of 25 cm, the calculated age of trees in the undergrowth was not always accurate to one year. However, it was close to the real age, and we considered it possible to use these data (smoothed using a five-year sliding mean) for revealing correlations between the number of trees that appeared in a certain year and changes in climatic parameters.

We used the data on monthly and daily average temperatures (T_{ma} and T_{da}) and monthly precipitation (P) recorded at weather stations Taganai-Gora (T_{ma} in 1932–1988 and P in 1936–1987), Zlatoust (T_{ma} in 1837–1915 and 1926–1999, and P in 1876–1917 and 1926–1996), and Ufa (T_{ma} in 1891–1994 and T_{da} in 1900–1995). Strong correlations between the monthly average temperatures recorded at these stations and the use of regression equations allowed us to calculate monthly average temperatures in 1837–1931 and daily average temperatures in 1900–1995 at the Taganai-

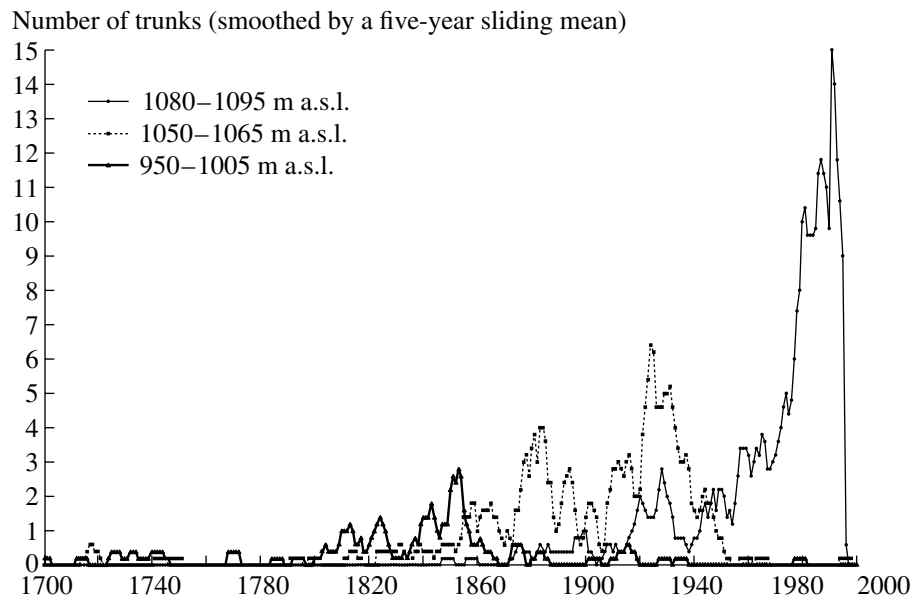


Fig. 1. Age structure of tree stands at different altitudinal levels on the northwestern slope of Mount Dal'nii Taganai.

Gora station. On this basis, the sums of above-zero temperatures over the corresponding periods were calculated.

RESULTS AND DISCUSSION

Comparing characteristics of tree stands in the plots located on the southwestern slope of Mount Dal'nii Taganai, we found that morphometric parameters of trees gradually increased (eventually, by a factor of 4–5) with a decrease in elevation (Table 1). The number of living spruce trees higher than 20 cm (older than 8–10 years) decreased tenfold (from 3600–3950 to 360–400 per hectare), whereas the proportion of dead and damaged trees increased. The total area of crown projections increased by a factor of 1.5–2 in the middle part of the transect (from 5420 to 11670 m²/ha) and then decreased to 5725 m²/ha at its lower end. The density of undergrowth lower than 20 cm in the upper and lower parts of the transect reached 2400–2500 ind./ha, but such plants were virtually absent from its middle part. The proportion of birch was greater (35%) in the plots located at higher elevations. In other plots, birch was either absent or its proportion varied from 4 to 19%, although its contribution to the total area of crown projections reached 30% in some plots. In addition to spruce and birch, the stands at the timberline contained rowan (*Sorbus aucuparia* L. ssp. *sibirica* (Hedl.) Krylov), Scotch pine, and larch, but their proportion did not exceed 1–2%. These species were absent from the remaining part of the transect, except for a few larch trees in the lowest plot.

Tree stands growing at different elevations on Mount Dal'nii Taganai were compared with respect to age structure (Fig. 1). The results showed that spruce

generations in the lower part of the transect (950–1005 m a.s.l.) consisted mainly of trees that emerged between 1810 and 1860 (61%). The age of trees in the stand did not exceed 320 years, and one of the previous periods favorable for tree growth was between 1710 and 1750. In the middle of the transect (1050–1065 m a.s.l.), most trees in the stands emerged between 1850 and 1936 (85%), although the age of some trees reached 300 years. In the upper part (1080–1095 m a.s.l.), 94% of trees emerged after 1915 (64.5%, after 1970), and the oldest trees were no more than 150 years old. These data showed that forest communities at elevations higher than 1050 m a.s.l. had not been formed earlier than in the mid-19th century.

In the plots located on the southwestern slope of Mount Malyi Iremel', the average values of morphological parameters of trees increased by a factor of 2–3 as the elevation decreased by 100 m (Table 2). We also revealed an increase in the number of living spruce trees higher than 20 cm (from 179 to 1450), the total area of projections of their crowns (from 238 to 6083 m²/ha), and the proportion of dead and damaged trees in the sample. The undergrowth lower than 20 cm was virtually absent. The trunks of multitemmed trees accounted for 45% of the sample.

The proportion of birch trunks was greater in the plots located in the upper part of the transect (67%), varying from 10 to 48% in other plots. In addition to spruce and birch, the stands included Siberian larch, Scotch pine, and Siberian fir. Their proportion was slightly greater at the timberline but, nevertheless, did not exceed 1%.

Comparing the age structure of spruce stands at three elevations on Mount Malyi Iremel' (Fig. 2), we

Table 1. Parameters of tree stands in test plots established on the northwestern slope of Mount Dal'nii Taganai

Parameter	Test plot								
	A	B	1	2	C	3	5	E	7
Test plot, elevation a.s.l. (m)	1095	1085	1080	1065	1050	1050	1005	990	950
Trunk diameter at the base, cm									
mean	10.6±0.7	9.3±0.6	7.3±0.4	13.4±0.4	19.6±1.1	18.5±0.9	22.9±0.8	34.7±3.8	37.6±4.6
maximum	30.0	23.0	14.5	34.0	39.0	40.5	37.0	80.0	76.0
Breast-high diameter, cm									
mean	6.4±0.5	5.4±0.5	6.5±0.5	11.3±0.3	15.4±0.8	15.1±0.8	19.5±0.6	28.8±3.3	27.5±3.0
maximum	19.0	18.0	19.5	29.0	29.0	38.0	30.0	70.0	59.0
Trunk height, m									
mean	2.8±0.1	2.7±0.1	2.2±0.1	4.6±0.1	6.8±0.3	6.6±0.3	9.1±0.4	8.4±0.7	10.6±0.9
maximum	4.7	5.5	5.1	8.9	9.0	12.0	13.8	11	16.0
Tree age, years									
mean	50±4	27±2	42±3	106±3	74±3	127±9	158±4	198±21	144±11
maximum	143	152	124	177	186	329	206	306	196
Crown diameter, m									
mean	1.3	1.8	1.6	1.9	2.5	2.6	2.7	4.0	5.0
maximum	3.2	4.2	5.0	5.0	4.0	5.0	5.0	6.4	8.0
Number per hectare									
living spruce trunks	3950	3650	3900	3620	2400	1740	1120	400	360
living birch trunks	2150	250	2120	160	0	400	140	75	80
young spruce plants (>20 cm)	2500	1600	700	0	0	100	460	0	2420
Proportion of spruce trunks, %									
dead	15.9	3.3	1.9	15.8	35.6	20.2	30.0	11.1	5.3
damaged	13.4	8.2	30.3	19.1	18.6	31.2	18.8	38.9	10.5
intact	70.7	88.5	67.7	65.1	45.8	48.6	51.3	50.0	84.2
Total area of crown projections, m ² /ha									
spruce	5420	8515	7318	11670	11085	9904	6626	5725	7490
birch	3765	270	1008	434	0	3936	2756	978	758

Table 2. Parameters of tree stands in test plots established on the southwestern slope of Mount Malyi Iremel'

Parameter	Altitudinal level				
	I	II	III	IV	V
Test plot, elevation a.s.l. (m)	1355	1325	1300	1275	1250
Trunk diameter at the base, cm					
mean	6.5 ± 1	5.9 ± 0.6	10.6 ± 0.7	12.9 ± 0.9	13.5 ± 0.7
maximum	24.8	25.8	44.9	40.1	50.3
Breast-high diameter, cm					
mean	3.1 ± 0.6	3.3 ± 0.4	7.5 ± 0.5	9.4 ± 0.7	10.4 ± 0.6
maximum	11.8	19.7	27.4	32.5	36.6
Trunk height, m					
mean	1.7 ± 0.2	2.1 ± 0.1	3.3 ± 0.2	4.4 ± 0.2	5.3 ± 0.2
maximum	4.1	7.0	9.2	9.5	13.0
Tree age, years					
mean	38 ± 4	31 ± 3	48 ± 3	52 ± 5	74 ± 3
maximum	72	88	105	112	124
Crown diameter, m					
mean	1.25	1.0	1.7	2.3	2.75
maximum	4.6	6.2	7.2	7.5	7.2
Number per hectare					
living spruce trunks	179	1025	1417	1100	1450
living birch trunks	367	375	633	1033	158
Proportion of spruce trunks, %					
dead	0.0	3.9	8.6	2.9	11.2
damaged	9.3	16.4	29.6	22.8	19.4
intact	90.7	79.7	61.8	74.3	69.4
Total area of crown projections, m ² /ha					
spruce	238	1092	4467	3875	6083
birch	442	638	1725	3242	725

found that the stands in the lower part of the transect (1250–1275 m a.s.l.) consisted of trees with single or multitemmed stems whose age did not exceed 127 years. In the middle and upper parts of the transect (1300 and 1325–1355 m a.s.l.), the oldest trees in the stand were 112 and 92 years of age, respectively. Therefore, forest communities at elevations above 1250 m a.s.l. had not been formed until the last quarter of the 19th century, and spruce had appeared there as low or dwarfed trees dating from the same century. The greater part (96%) of single-stemmed trees emerged between 1915 and 1990, and the peak of seed reproduction (about 60%) occurred in the period from 1973 to 1990.

The zone of transition from separate clumps of trees to the stand with a crown density of more than 50% was

only 10–30 m (by elevation) on Mount Dal'nii Taganai and 100 m on Mount Malyi Iremel'. Hence, it was correct to compare forest communities of the entire Iremel' transect with those in the upper part of the Taganai transect. Although the corresponding stands markedly differed in their density because of differences in site conditions (wind load, slope angle and exposure, etc.), they were closely similar in the temporal pattern of formation of spruce generations (Figs. 1, 2). On both mountains, approximately 60–65% of the trees appeared due to active seed reproduction during the past 30 years: in 1975–1989 in the Iremel' transect and in 1980–1996 in the upper part of the Taganai transect. In both areas, seed reproduction ceased after 1995. The previous three generations of spruce trees in the present-day forest–tundra ecotone appeared in 1915–

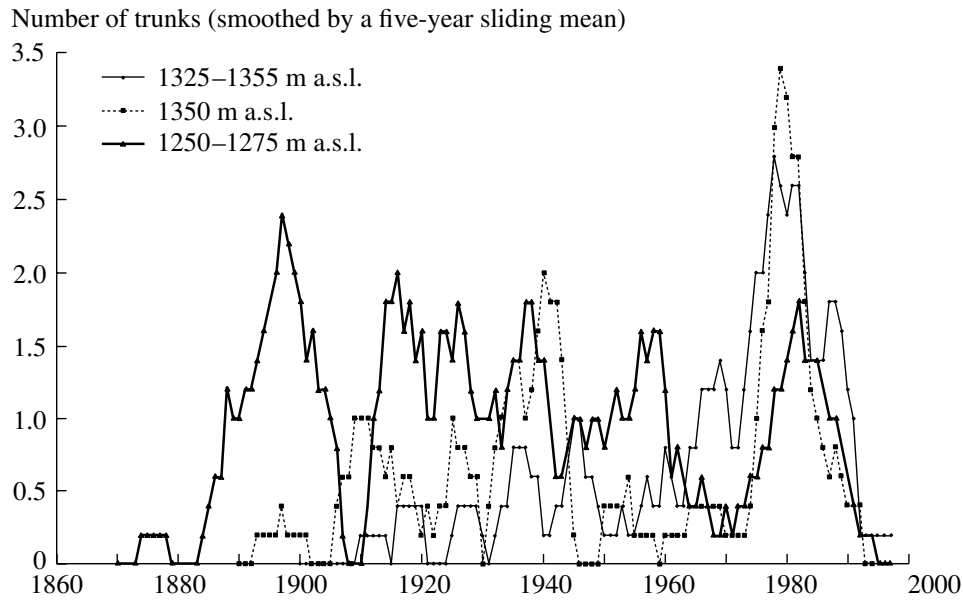


Fig. 2. Age structure of tree stands at different altitudinal levels on the southwestern slope of Mount Malyi Iremel'.

1932 (8.3–9.3%), 1944–1952 (4.8–8.8%), and 1958–1966 (8.0–8.4%).

In the middle part of the Taganai transect, where the boundary of open forests passed in the early 20th century (55.5% of them appeared after 1900), the formation of spruce generations occurred in 1854–1867 (7.7%), 1875–1887 (14.2%), 1891–1896 (5.2%), 1900–1904 (3%), 1910–1917 (9.5%), and 1921–1936 (33.3%). The last three periods largely coincided with the first periods of tree stand formation in the upper parts of both transects, i.e., at the present-day boundary of open forests and krummholz. Identification of such periods before 1850 was difficult, because the proportion of trees belonging to older age groups was very small (9.1%).

Forest renewal virtually ceased after 1936 (9%). This was probably explained by crown thickening and consequent shading of the soil surface, which inhibited the development of new seedlings.

In the lower part of the transect on Mount Dal'nii Taganai, where the boundary of closed forests passed in the early 20th century (9.3% of them appeared after 1900), the formation of spruce generations occurred in 1809–1816 (9.1%), 1821–1827 (7.7%), 1839–1845 (11.2%), 1850–1855 (16.5%), and 1873–1886 (5.6%). The last period coincided with the initial stage of tree stand formation in the middle part of the transect. The proportion of trees that appeared before 1809 was 20%.

Using regression analysis, we revealed significant correlations between the numbers of single-stemmed trees in spruce generations (Fig. 3e) and the sums of above-zero temperatures recorded five years before their appearance (Fig. 3c). For the trees that appeared

in the middle part of the Taganai transect in 1880–1930, the coefficient of correlation was +0.46; for the trees that appeared in the upper part of this transect and the entire Iremel' transect in 1890–1930 and 1947–1990, the respective coefficients were +0.47 and +0.65. In other periods, no significant correlations with this temperature factor were revealed. This could be accounted for by other factors with stronger effects on the emergence and survival of seedlings and young plants. These factors eventually provided for differences in the loss of plants in spruce generations and, thus, impaired the above correlation. The sum of above-zero temperatures in the fifth year before the emergence of trees has an effect on the formation of spruce generations because the number of viable seeds depends on thermal conditions in the period of flower bud formation and seed maturation in the cones (Kearney, 1982; Mamaev and Popov, 1989). The five-year shift probably occurs because the seeds accumulate in the upper soil horizon and germinate en masse in one of the nearest favorable summer periods. Note that, under laboratory conditions, the germination rate of Siberian spruce seeds decreases by only 7–25% in the first five years and drastically decreases later (Mamaev and Popov, 1989).

Significant correlations between the number of single-stemmed trees and the average temperature of the cold period (November–March) were revealed for spruce generations of 1865–1927 in the middle part of the Taganai transect ($r = +0.68$) and generations of 1940–1995 in the upper part of this transect and in the transect on Mount Malyi Iremel' ($r = +0.74$) (Fig. 3c). The effect of this temperature factor on the formation of spruce generations could be explained by both the

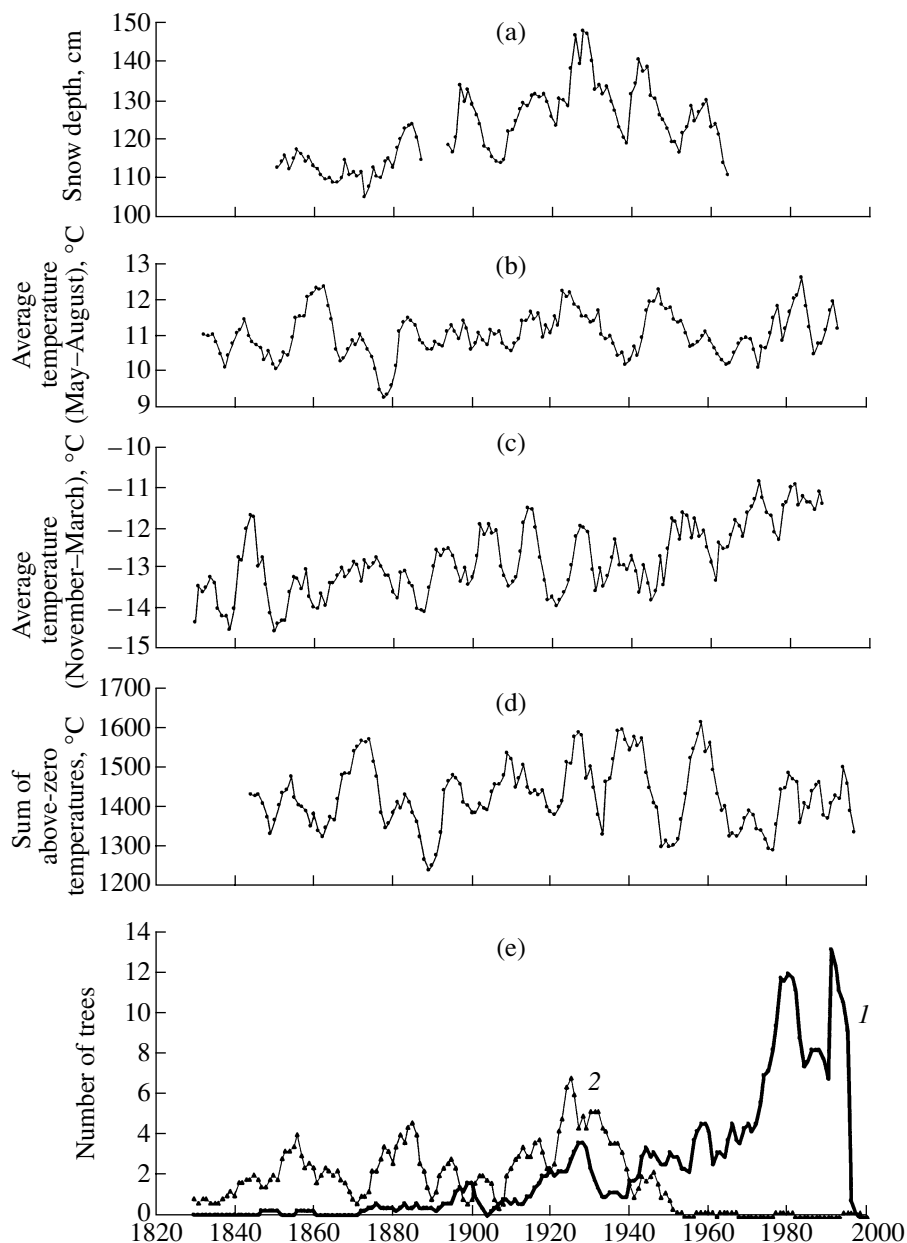


Fig. 3. Dynamics of five-years sliding means for (a) the amount of precipitation over the period from October to April in the 29th year after the emergence of trees; (b) the average temperature of the warm season (May–August) in the seventh year after the emergence of trees; (c) the average temperature of the cold season (November–March) in the year of emergence of trees; (d) the sum of above-zero daily temperatures in the fifth year before the emergence of trees; and (e) the number of single-stemmed trees in spruce generations growing (1) at elevations of 1080–1095 m a.s.l. on Mount Dal'nii Taganai and the entire transect on Mount Malyi Iremel' and (2) at elevations of 950–1065 m a.s.l. on Mount Dal'nii Taganai.

dependence of plant survival in the undergrowth on the degree of soil freezing (Kullman and Engelmark, 1997) and the adverse influence of low winter temperatures on seed germination rate.

Moreover, we revealed positive correlations between the number of single-stemmed trees and the average temperature in May–August in the seventh year after their emergence for spruce generations of

1882–1938 in the middle part of the Taganai transect ($r = +0.66$) and generations of 1910–1954 and 1955–1990 in the upper part of the Taganai transect and in the Iremel' transect ($r = +0.57$ and $r = +0.74$, respectively). This correlation is explained by the dependence of plant survival in the undergrowth on thermal conditions in the period when the undergrowth rises above the average level of the herb-dwarf shrub layer (Shiyatov, 1965).

In the case of correlations between the number of single-stemmed spruce trees and the amount of precipitation in the period from October to April for spruce generations of 1860–1938 in the middle part of the Taganai transect and of 1910–1960 in the upper part of the Taganai transect and in the Iremel' transect, the correlation coefficients had higher values in the 27th to 32nd years after the emergence of trees (with a peak in the 29th year: +0.68 and +0.42, respectively). The influence of this climatic parameter on the age structure of spruce stands can be explained by the dependence of plant survival in the undergrowth on snow depth in the period when the height of the undergrowth approaches or exceeds the long-term average snow depth (Shiyatov, 1965). When the snow in this period is deeper, it covers the tops of young trees and helps them survive the severe winter period. If snow depth in the following years decreases, the apical plant parts rise above the critical interval (50 cm above the snow surface) in which the speed of snow transfer by wind and, hence, the abrasive action of snow crystals reach the highest levels.

According to the results of multiple regression analysis, the coefficient of correlation between the numbers of trees in 1-year age groups of all the stands studied and the aforementioned four climatic factors is +0.64. This is evidence that the processes involved in the formation of spruce generations in subgoltsy stands can be predicted with a high degree of probability, and their dynamics depend on these climatic factors.

The corresponding multiple regression equation is as follows:

$$\begin{aligned} \text{Log}(N) = & 10.8 - 1.19\text{Log}(\text{Sum}T_w^{-5}) - 2.93\text{Log}(-T_c) \\ & + 0.16T_w^{+7} + 0.038\text{Pr}_c^{+29}, \end{aligned}$$

where N is the number of trees in 1-year age groups, $\text{Sum}T_w^{-5}$ is the sum of above-zero temperatures in the fifth year before the emergence of trees, T_c is the average temperature of the cold period (November–March), T_w^{+7} is the average temperature of the warm period (May–August) in the seventh year after the emergence of trees, and Pr_c^{+29} is the total amount of precipitation in the period from October to April in the 29th year after the emergence of trees.

Comparing the dynamics of the four climatic factors with the curves of change in the number of trees, it can be seen that the values of all these factors were optimal for the emergence and survival of young plants in the periods of increased numbers of trees in spruce generations; in the periods of decrease in the number of trees, the values of at least two factors were close to the pessimum.

The results of this study confirm our hypothesis that the formation of spruce generations in the subgoltsy tree stands of the Southern Urals is under the combined

influence of both summer and winter climatic factors, namely, thermal conditions of the warm season during the five to seven years before and after the emergence of trees, conditions of the cold season in the year of their emergence, and snow depth in late April in the years 27–32 of tree growth. These results may be useful for assessing the responses of such communities to changes in climatic conditions and predicting the future dynamics of age structure in tree stands of the forest-tundra ecotone.

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REFERENCES

- Cui, M. and Smith, W.K., Photosynthesis, Water Relations and Mortality in *Abies lasiocarpa* Seedling during Natural Establishment, *Tree Physiol.*, 1991, no. 8, pp. 37–46.
- Denton, G.H. and Karlen, W., Holocene Glacial and Tree-Line Variation in the White River Valley and Skolai Pass, Alaska and Yukon Territory, *Quant. Res.*, 1977, no. 7, pp. 63–111.
- Jakubos, B. and Romme, W.H., Invasion of Subalpine Meadows by Lodgepole Pine in Yellowstone National Park, Wyoming, USA, *Arct. Alp. Res.*, 1993, no. 25, pp. 382–390.
- Kearney, M.S., Recent Seedling Establishment at Timberline in Jasper National Park, Alberta, *Can. J. Bot.*, 1982, no. 60, pp. 2282–2287.
- Kullman, L., Recent Tree-Limit History of *Picea abies* in the Southern Swedish Scandes, *Can. J. For. Res.*, 1986, no. 16, pp. 761–771.
- Kullman, L. and Engelmark, O., Neoglacial Climate Control of Subarctic *Picea abies* Stand Dynamics and Range Limit in Northern Sweden, *Arc. Alp. Res.*, 1997, vol. 29, no. 3, pp. 315–326.
- Lavoie, C. and Payette, S., Black Spruce Growth Forms as Records of a Changing Winter Environment at Treeline, Quebec, Canada, *Arc. Alp. Res.*, 1992, vol. 24, no. 1, pp. 315–326.
- Lloyd, A.H. and Graumlich, L.J., Holocene Dynamic of Treeline Forests in the Sierra Nevada, *Ecology*, 1997, no. 78, pp. 1199–1210.
- Shiyatov, S.G., The Linear Growth of Larch at the Timberline during the Growing Season in the Polar Ural Mountains, *Tr. Inst. Biol. Ural. Fil. Akad. Nauk SSSR*, Sverdlovsk, 1965, vol. 43, pp. 249–253.
- Shiyatov, S.G., Climate Fluctuations and Age Structure of Tree Stands in Open Larch Forests in the Polar Ural Mountains, in *Rastitel'nost' tundr i puti ee osvoeniya* (Tundra Vegetation and Approaches to Its Exploitation), Leningrad: Nauka, 1967, pp. 271–278.
- Shiyatov, S.G., Experience in Using Old Photographs in Studies on Successions in Forest Vegetation at the Upper Limit of Its Growth, in *Floristicheskie i geobotanicheskie issledovaniya na Urale* (Floristic and Geobotanical Research in the Urals), Sverdlovsk, 1983, pp. 76–109.

Shiyatov, S.G., The Upper Timberline Dynamics during the Last 1100 Years in the Polar Ural Mountains, in *Oscillation of the Alpine and Polar Tree Limits in the Holocene*, Stuttgart: Gustav Fischer, 1993, pp. 195–203.

Soll, J.A., Seed Number, Germination and First Year Survival of Subalpine Fir (*Abies lasiocarpa*) In Subalpine Meadows of the Northeastern Olympic Mountains, *M.S. Thesis*, University of Washington, 1994.

Taylor, A.H., Forest Expansion and Climate Change in the Mountain Hemlock (*Tsuga mertensiana*) Zone, Lassen Volcanic National Park, California, USA, *Arc. Alp. Res.*, 1995, vol. 27, pp. 207–216.

Wardle, P. and Coleman, M.C., Evidence for Rising Upper Limits of Four Native New Zealand Forest Trees, *N. Zeal. J. Bot.*, 1992, no. 30, pp. 303–314.

Weisberg, P.J. and Baker, W.L., Spatial Variation in Tree Seedling and Krummholz Growth in the Forest–Tundra Ecotone of Rocky Mountain National Park, Colorado, *Arc. Alp. Res.*, 1995, vol. 27, no. 2, pp. 40–49.

Woodward, A., Schreiner, E.G., and Silsbee, D.G., Climate, Geography, and Tree Establishment in Subalpine Meadows of the Olympic Mountains, Washington, USA, *Arc. Alp. Res.*, 1995, vol. 27, pp. 217–225.