Reproduction of the Siberian Spruce in the Timberline Ecotone of the Iremel' Massif

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Abstract—Quantitative and qualitative characteristics of cones and seeds and the emergence and survival of seedlings in the Siberian spruce (*Picea obovata* Ledeb.) were studied in different parts of the timberline ecotone on the Iremel' Massif, the Southern Urals, from 2003 to 2006. In the productive year 2003, a decrease in the number of cones (from 110000 to 3000 per hectare), the yield of seeds (from 13×10^6 to 0.09×10^6 per hectare), and their laboratory germination rate (from 34 to 14%) with an increase in elevation above sea level was recorded. In 2004, significant differences in the number of seedlings per hectare were revealed between the lower, middle, and upper parts of the ecotone (85 200, 19 800, and 0–400 ind., respectively). It has been shown that the greater part of seedlings (76–96%) perish during the first cold period. New generations of spruce trees are formed only after productive years. Seed production and seedling mortality in spruce apparently depend not only on air temperature and soil moistening but also on snow depth and soil temperature, which change more abruptly along the altitudinal gradient.

In the last decades of the 20th century, increasing interest in problems related to global warming stimulated a number of studies on high-mountain forest–tundra ecosystems, which are especially sensitive to climatic changes. An analysis of relevant publications (for review, see Holtmeier, 2003) has shown that most researchers concentrated on the influence of climatic factors on the growth and survival of mature trees, paying little attention to the effect of climatic changes on processes related to natural regeneration of tree stands.

The number of trees per unit area rapidly decreases as the upper limit of their growth is approached, which is usually attributed to sharp deterioration of conditions for the growth and regeneration of tree stands above a certain altitudinal level. As shown in studies on the growth and survival of older tree generations on the Iremel' Massif (Babenko et al., 2008), the growth of young trees throughout the mountain forest–tundra ecotone has improved in recent decades, with tree mortality being lower than 4% (Moiseev et al., 2004). On this basis, we hypothesized that the limited distribution of the Siberian spruce in the upper part of this ecotone may be explained by deterioration of conditions for tree stand regeneration in areas approaching the upper limit of tree growth.

To check this hypothesis, we performed studies in the forest–tundra ecotone of the Iremel' Massif, along the altitudinal gradient, to estimate elevation-dependent changes in soil and air temperatures; the maximum snow depth; the structure of spruce stands; the number, size, and weight of spruce cones; the number and quality of spruce seeds; the quality and state of seedlings; and the survival of spruce undergrowth in the first years of life. On the basis of these data and the results of soil studies in the same area (Kammer et al., 2007), we made an attempt to find out what factors have an effect on the processes of spruce stand regeneration at the upper limit of their growth on the Iremel' Massif.

OBJECTS AND METHODS

The Iremel' Massif (1582.3 m a.s.l.), which belongs to the chain of the highest central summits of the Southern Urals (54°30′–34′N, 58°49′–54′E), is part of the Iremel'sko-Avalyakskii natural region characterized by considerable elevations (1200–1600 m a.s.l.) and elevation differences (up to 1100 m), a complex geological structure, a humid climate (with annual precipitation exceeding 800 mm), the prevalence of dark taiga forests, and distinct altitudinal zonality. Tree stands at the upper forest boundary (in the timberline ecotone) lying at elevations of 1250–1365 m a.s.l. are formed by the Siberian spruce (*Picea obovata* Ledeb.) and mountain birch (*Betula tortuosa* Ledeb.) (Moiseev et al., 2004).
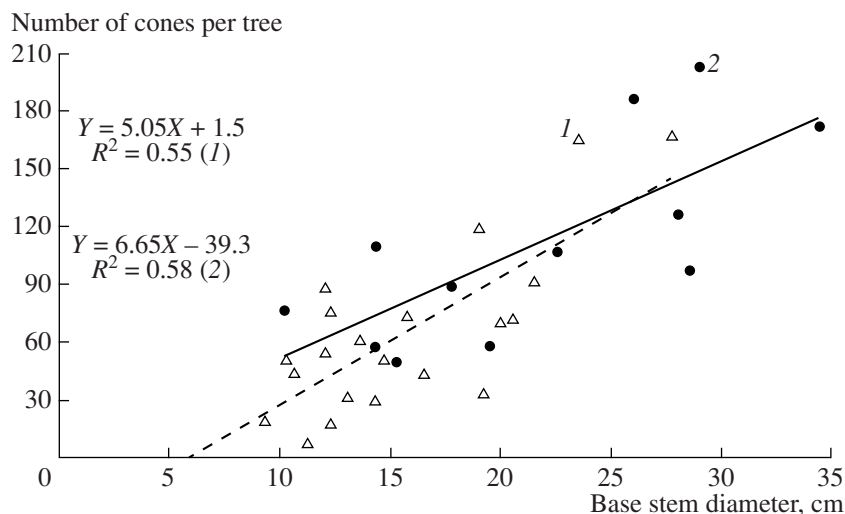
Number of cones per tree

$Y = 5.05X + 1.5$
$R^2 = 0.55$ (*1*)

$Y = 6.65X - 39.3$
$R^2 = 0.58$ (*2*)

Base stem diameter, cm

Fig. 1. Number of cones per tree in 2003 as a function of stem diameter in Siberian spruce in (*1*) the middle and (*2*) lower parts of the forest–tundra ecotone on Mount Malyi Iremel'.

Studies were performed from 2002 to 2004. To characterize tree stands, we established 34 test plots (20 × 20 m) on the southwestern slope of Mount Malyi Iremel' and the northern slope of Mount Bol'shoi Iremel', with four to eight plots in the lower (1255–1290 m a.s.l.), middle (1310–1330 m), and upper (1345–1365 m) parts of the forest–tundra ecotone. The values of crown closure in the respective stands were 40–60, 20–40, and 5–20%. In each plot, we made geobotanical descriptions including characterization of the composition and structure of the tree layer.

In the autumn of 2003, on the southwestern slope of Malyi Iremel', we collected 762 cones from 23 trees 3.5–4 m high (the average tree height for the entire timberline ecotone) growing in the lower (8 ind.), middle (9 ind.), and upper (6 ind.) parts of the ecotone. In the laboratory, the cones were dried and examined to determine the length, width, and weight of each cone and the number and weight of seeds. Thereafter, the average values of these parameters were calculated, and the results were processed statistically. The seed germination rate was determined according to GOST (State Standard) 13056.6–97.

Using data on the total weight of generative organs in 33 model trees (cut in 2003 to study phytomass accumulation in Siberian spruce trees in the lower and middle parts of the ecotone) and the calculated average weight of one cone, we estimated the number of such average cones in each model tree. This number proved to correlate strongly with the taxonometric parameters of model trees, such as age, crown projection diameter, height, and stem diameter at the base. As the coefficients of correlation with the stem diameter had the highest values, the corresponding regression equations (Fig. 1) were used to calculate the numbers of average cones per tree in all test plots (equations for the middle part of the ecotone were also used for its upper part) and

to estimate cone yield per unit area. Knowing the total number of cones and the average number of seeds per cone characteristic of each part of the ecotone, we calculated the average number of seeds per unit area.

To estimate the number of tree seedlings in test plots, we divided each plot into four parts (10 × 10 m) and established 16 microplots (1 × 1 m) along two perpendicular diagonal lines, each passing through the centers of two these parts (four microplots per line segment extending from the plot center). The microplots were further divided into 20 × 20-cm squares, and each square was examined to record the number and species of tree seedlings, their age and state, and the type of substrate and nanorelief. The microplots were surveyed in August 2004, early June and August 2005, and early June and early September 2006.

In September 2003, one test plot in each part of the timberline ecotone on Mount Malyi Iremel' was equipped with two StowAway TidbiT TBI32-20+50 temperature data loggers (Onset Computer Corp., Bourne, MA), one installed in the tree crown near the stem, 2 m above ground, and the other dug 10 cm deep into the soil beyond the crown. Measurements were made every hour until mid-September 2005. On the basis of these data, we calculated monthly average air and soil temperatures in the lower, middle, and upper parts of the ecotone. In March 2006, snow depth was measured in all test plots.

RESULTS

Tree stand structure. By comparing characteristics of tree stands in our test plots (Table 1), it can be seen that the average values of morphometric parameters of trees decrease by a factor of two to three as elevation increases by 70–100 m. This is accompanied by a decrease in the number of living spruce stems exceed-

Table 1. Characteristics of tree stands in different parts of the forest–tundra ecotone on the Iremel' Massif

Parameter	Mount Malyi Iremel', southwestern slope					Mount Bol'shoi Iremel' northern slope		
Elevation a.s.l., m	1255	1280	1310	1345	1360	1290	1330	1365
Stem diameter at breast height, cm:								
average	10.4 ± 0.6	9.4 ± 0.7	7.5 ± 0.5	3.3 ± 0.4	3.1 ± 0.6	12.3 ± 0.6	5.3 ± 0.4	5.6 ± 0.5
maximum	36.6	32.5	27.4	19.7	11.8	32.0	31.0	11.0
Stem height, m:								
average	5.3 ± 0.2	4.4 ± 0.2	3.3 ± 0.2	2.1 ± 0.1	1.7 ± 0.2	5.2 ± 0.2	2.4 ± 0.1	2.5 ± 0.2
maximum	13.0	9.5	9.2	7.0	4.1	11.0	7.5	4.3
Tree age, years:								
average	74 ± 3	52 ± 5	48 ± 3	31 ± 3	38 ± 4	80 ± 3	70 ± 4	72 ± 8
maximum	124	112	105	88	72	211	290	116
Crown diameter, m:								
average	2.75	2.3	1.7	1.0	1.25	2.0	1.4	1.7
maximum	7.2	7.5	7.2	6.2	4.6	7.5	6.6	5.1
Number of stems per hectare:								
spruce	1440	700	1250	817	150	1445	2051	167
birch	158	1033	633	375	367	0	108	8
Total crown projection area, m²/ha	6808	7117	6192	1729	679	5670	4316	459

ing 20 cm in height (from 1450 to 150 ind.), the total crown projection area of all tree species (from 5700–7100 to 450–700 m²/ha), and the proportion of damaged and dead stems in the whole sample. Multistemmed trees accounted for approximately 45% of the total number of stems in the sample. Plots with a large proportion of birch (up to 67%) concentrate in the middle part of the ecotone; in other plots, this proportion varies from 10 to 48%. In addition to spruce and birch, tree stands include Siberian larch, Scots pine, and Siberian fir, but the proportion of these species does not exceed 1%.

Cone yield. It is well known that fruiting in representatives of the genus *Picea* has a certain periodicity, with intervals between productive (high-yield) years varying from three to six years. The abundance of fruiting trees and the total amount of cones before the productive year 2003 (1999–2002) and after it (2004–2006), which were estimated in the course of visual observations and examination of trees cut in order to study trends in the accumulation and distribution of phytomass, proved to be very low. According to regional forestry agencies, high yields in spruce forests of the Southern Urals were recorded in 1997, 1993, 1987, 1982, 1978, 1973, 1969, and 1966, which confirms the periodicity of abundant fruiting in this tree species.

As noted by Mamaev and Popov (1989), the numbers of cones on different Siberian spruce trees mark-

edly differ even in productive years, being dependent on the size of the tree, its location within the stand, conditions in the year of formation of generative organs and their rudiments, specific features of mineral nutrition, and local climate. However, there is also a direct dependence of the number of cones on the age and morphometric parameters of a tree, which is common to all conifers. In the study area, the coefficients of correlation between the number of cones and tree age, crown projection diameter, tree height, and stem diameter in the productive year 2003 were 0.62, 0.68, 0.72, and 0.76, respectively.

As follows from data shown in Table 2, an increase in elevation leads to a rapid decrease both in the number of cone-bearing trees (from 330–370 to 39–64 ind./ha) and in the total cone yield (from 97300–111400 to 3600 cones per hectare). This decrease is most distinct upon transition from the middle to the upper part of the forest–tundra ecotone (by a factor of 5–7 for the number of cone-bearing trees and by a factor of 10–17 for the total cone yield). Upon transition from the lower to the middle part of the ecotone, these parameters decrease by a factor of only 1.5–2.

Cone size and number of seeds per cone. The average length of Siberian spruce cones in different parts of the ecotone varies from 37 to 54 mm (Table 3), with the total variation range being markedly wider (from 20 to 70 mm). On the whole, both the size and weight of cones decrease by 29–33% along the altitudinal gradient, with this decrease being nonlinear: 12–

Table 2. Average numbers of Siberian spruce cones, seeds, and seedlings in different parts of the forest–tundra ecotone on the Iremel' Massif in 2003 and 2004

Parameter	Summit							
	Malyi Iremel'					Bol'shoi Iremel'		
Elevation a.s.l., m	1255	1280	1310	1345	1360	1290	1330	1365
Number of trees with cones, ind./ha	330	237	259	139	39	352	370	64
Number of cones, 1×10^3/ha	97.30	60.25	60.23	17.03	3.59	111.36	62.90	6.43
Number of seeds per cone	136	126*	116	66*	14	136*	116*	14*
Seed yield, 1×10^6 seeds/ha	13.23	7.59	6.99	1.12	0.05	15.15	7.30	0.09
Laboratory seed germination rate, %	34	31*	27	20*	14	34*	27*	14*
Number of viable seeds, 1×10^6/ha	4.50	2.35	1.89	0.22	0.007	5.15	1.97	0.013

* Tentative (extrapolated) values.

Table 3. Length and weight of Siberian spruce cones in different parts of the forest–tundra ecotone on Mount Malyi Iremel'

Elevation a.s.l., m	Number of cones per sample	Proportions of cones (%) of different length classes, mm											Average	
		20–24	25–29	30–34	35–39	40–44	45–49	50–54	55–59	60–64	65–69	70–74	cone length, mm	cone weight, g
1255	257	–	–	–	2.7	4.7	20.6	24.9	24.9	15.6	6.2	0.4	54 ± 0.4	3.4 ± 0.1
1310	352	–	0.6	3.1	8.2	20.7	28.1	25.0	12.5	1.1	0.6	–	47 ± 0.4	3.0 ± 0.1
1360	153	2.6	6.5	26.8	25.5	20.9	11.8	5.2	0.7	–	–	–	37 ± 0.6	2.4 ± 0.1

13% upon transition from the lower to the middle part and 20–22% upon transition from the middle to the upper part of the ecotone.

The number of seeds per cone in Siberian spruce, as in other conifers, may vary markedly depending on differences in cone size (Mamaev and Popov, 1989). We calculated coefficients of correlation between this parameter and the diameter, length, and weight of cones produced in 2003, and these coefficients proved to be fairly high: 0.83, 0.82, and 0.63, respectively. As noted above, the average cone dimensions decrease at higher elevations (see Table 2), and it could be expected that the average number of seeds per cone would decrease likewise. This was confirmed in the course of our study (Table 3).

Seed productivity of tree stands. As in other species, individual Siberian spruce trees differ markedly from each other in the numbers of cones and seeds they produce. Calculations made for Mount Malyi Iremel' showed that the average number of full seeds produced by one tree may vary from 40100 in the lower part of the ecotone to 1300 in its upper part, with seed production decreasing drastically (by a factor of almost 21) upon transition from the middle to the upper part of the ecotone. However, the greatest differences were revealed when the average values of seed production in different parts of the ecotone were compared (Table 3). Thus, the number of seeds per hectare in the productive year 2003 averaged $(13.2–15.1) \times 10^6$ in the lower part, $(7.0–7.3) \times$

10^6 in the middle part, and $(0.05–0.09) \times 10^6$ in the upper part of the ecotone. Therefore, this parameter decreased by a factor of only 1.9–2.1 upon transition from the lower to the middle part of the ecotone and by a factor of 70–140 upon transition from its middle to upper part.

Seed quality. The sowing quality of seeds is usually estimated from their absolute weight, germination rate, and vigor. In 2003, the absolute weight of 1000 Siberian spruce seeds varied from 6.4 to 3.7 g, averaging 5.4 g in the lower, 4.5 g in the middle, and 4.2 g in the upper part of the ecotone. The germination rate usually characterizes the degree of seed maturation, with insufficient maturation resulting primarily from a shortage of assimilates. This is why the highest seed germination rate (34%) and seed vigor (10%) were recorded in the lower part of the ecotone (where growing conditions are more favorable), compared to 27 and 6% in its middle part and 14 and 2% in its upper part.

On the basis of data on seed production and laboratory germination rate, we calculated how many seeds (out of their actual numbers) could potentially germinate under optimal conditions and in the absence of damage or consumption by insects, rodents, or birds. The results showed that no more than $(4.5–5.1) \times 10^6$ seedlings per hectare could appear in the lower part of the ecotone. The potential numbers of seedlings in other areas were markedly smaller, ranging from (1.9–

Table 4. Numbers and survival of Siberian spruce seedlings in different parts of the forest–tundra ecotone on the Iremel' Massif, 2004–2006

Parameter				Summit							
				Malyi Iremel'					Bol'shoi Iremel'		
Elevation a.s.l., m				1255	1280	1310	1345	1360	1290	1330	1365
Seedlings of 2004, 1000 ind./ha				85.2	45.4	19.8	0.4	0	20.2	31.5	0
Seedlings of 2004, proportion of seed yield (%)				0.64	0.60	0.29	0.04	0	0.14	0.43	0
Survived seedlings of 2004	2005	by June 1	1000 ind./ha	5.4	1.9	1.3	0	0	1.7	7.5	0
			%	6.4	4.1	6.3	0	0	8.2	23.8	0
		by September 1	1000 ind./ha	4.6	1.5	1.0	0	0	1.0	5.6	0
			%	5.4	3.2	5.3	0	0	5.2	17.9	0
	2006	by June 1	1000 ind./ha	3.1	0.8	0.6	0	0	0.4	3.8	0
			%	3.7	1.8	3.2	0	0	2.1	11.9	0
		by September 1	1000 ind./ha	3.1	0.6	0.6	0	0	0.4	3.5	0
			%	3.7	1.4	3.2	0	0	2.1	11.3	0
Seedlings of 2005, 1000 ind./ha				0.8	1.0	0.4	0	0	3.8	0	0
Survived seedlings of 2005	2006	by June 1	1000 ind./ha	0	0.2	0	0	0	0.8	0	0
			%	0	20.0	0	0	0	21.1	0	0
		by September 1	1000 ind./ha	0	0	0	0	0	0.6	0	0
			%	0	0	0	0	0	16.7	0	0
Seedlings of 2006, 1000 ind./ha				0	0	0.2	0	0	0	0	0

2.3) $\times 10^6$ ind./ha in the middle part to $(0.007–0.013) \times 10^6$ ind./ha in the upper part of the ecotone.

Emergence of seedlings. In August 2004, no seedlings were found in the upper part of the timberline ecotone on mounts Malyi and Bol'shoi Iremel' (Table 4). Their number in the zone of transition from the upper to the middle part of the ecotone was very small (400 ind./ha) but sharply increased to $(19.8–31.5) \times 10^3$ ind./ha in its middle part. The greatest number of seedlings was recorded in the lower part of the ecotone on Mount Malyi Iremel', reaching 85.2×10^3 ind./ha. On Mount Bol'shoi Iremel', their number in the lower part of the ecotone at the end of the growing season was only 20.2×10^3 ind./ha, being 1.5 times smaller than in the middle part of the ecotone on this summit and 4 times smaller than on Mount Malyi Iremel'. It is known that the numbers of sprouts and seedlings reach a peak in the middle of the growing season and decrease by a factor of two to four by its end (*Faktory* …, 1983). As our observations were made in August, their results concern the numbers of seedlings at the end of the growing season.

Survival of seedlings in subsequent years. According to our observations, the proportion of seedlings surviving for one year varies from 0 to 17.6% of their initial number (Table 4); one year later, it decreases to 1.4–11.3%. It should be noted that the conditions in the period between two growing seasons appear to be crucial for spruce seedlings in the first

years of life, as their mortality in this period reaches the highest values. Thus, mortality among seedlings in the cold period of 2004/2005 reached 76–96% of their total number recorded in August 2004, and that in the cold period of 2005/2006 was 30–60% of their total number in August 2005. The proportion of seedlings that perished during the growing season varied from 15 to 40% in 2005 and from 0 to 25% in 2006. Thus, the mortality rate over the growing season was three to four times lower than in the cold period (Table 4).

The number of seedlings that emerged in the middle and lower parts of the ecotone in the summer period of 2005 was only 0.9–3.8% of that recorded in 2004; in 2006, this proportion was even smaller, no more than 0.5%. According to previous studies on the age structure of tree stands in the Southern Urals (Moiseev et al., 2004), no more than 50–80 trees per hectare survive to an age of 30–50 years. This is equivalent to approximately 0.1% of the number of seedlings recorded in 2004. We calculated the probable numbers of plants that would live to such an age after the low-yield years 2004 and 2005 (i.e., among seedlings recorded in 2005 and 2006). In most cases, the result was less than 1 ind./ha. This fact shows that new generations of the Siberian spruce at the upper limit of its growth appear only after the most productive years, whereas individuals emerging in unproductive years do not participate in the formation of the upper tree layer, since they perish before reaching maturity.

Table 5. Monthly average air and soil temperatures in different parts of the forest–tundra ecotone on Mount Malyi Iremel',
2003–2005

Year	Elevation a.s.l., m	Air temperature near tree stem 2 m above ground			Soil temperature at a depth of 10 cm		
		1255	1310	1360	1255	1310	1360
	Month						
2003	October	–2.6	–2.8	–3.3	1.6	1.5	1.2
	November	–7.6	–7.7	–8.2	0.6	0.5	–0.2
	December	–19.7	–19.4	–19.7	0.2	0	–2.5
2004	January	–13.6	–13.4	–13.7	0	–0.5	–4
	February	–16.6	–16.4	–16.8	0	–0.5	–4.7
	March	–10.1	–10	–10	0	–0.5	–5.2
	April	–1.8	–1.8	–2.4	0	–0.2	–1.6
	May	5.1	5.3	4.8	2.1	2.8	0.5
	June	7.6	7.6	6.8	6.9	7.4	4.1
	July	12.1	12.3	11.6	9.5	11.1	8.5
	August	13.6	14	13.7	10.3	11.4	9.6
	September	–	–	–	6.1	6.8	4.7
	October	–	–	–	3.1	3.3	0.9
	November	–8.3	–8.2	–8.7	1.3	1.3	–0.1
	December	–12.0	–11.9	–12.0	1.0	0.9	–1.4
2005	January	–12.7	–12.6	–12.5	0.6	0.4	–3.0
	February	–14.9	–14.8	–15.1	0.2	0.0	–5.8
	March	–11.5	–11.4	–12.2	0	–0.3	–4.9
	April	–0.7	–0.6	–1.6	0	–0.3	–1.9
	May	7.9	8.1	8.1	4.0	4.4	2.4
	June	10.0	10.1	9.6	7.7	8.7	6.3
	July	12.2	12.3	12.0	8.9	10.0	9.2
	August	9.7	9.8	9.8	9.0	10.1	9.3

Altitudinal gradient of air and soil temperatures. An analysis of records made by temperature data loggers between 2003 and 2005 showed that monthly average temperatures recorded in different parts of the ecotone over the year differ by only 0.3–0.5°C, and only the April temperatures are noticeably (0.6–1°C) higher in the lower part than in the middle part (Table 5). However, soil temperatures at a depth of 10 cm in the upper part of the ecotone differ from those in its middle and lower parts by a few degrees in both summer (by 1.5–3°C) and winter months (by 3–5°C).

Altitudinal gradient of snow depth. The results of measurements made in March 2006 show that the average snow depth abruptly decreases from 75–90 to 10–25 cm upon transition from the middle to the upper part of the ecotone in the elevation range of 1330–1370 m (Fig. 2). At higher elevations, this parameter varies only slightly, although snow accumulating in micro- and mesodepressions and behind sparse trees in the tundra may be 80–110 cm deep. Snow depth at lower elevations becomes slightly smaller (55–75 cm), as the crown closure of spruce stands gradually increases from 20–30 to 80–90%, and, therefore, a large part of snow is retained on tree crowns. The aforementioned drastic decrease in snow depth (by a factor of three to eight) could also be attributed to changes in crown closure, which decreases from 20–30% (providing for a considerable snow-trapping effect) in the middle part to only 5% in the upper part of the ecotone. An analysis of correlations between the total crown projection area and snow depth confirmed this conclusion ($R^2 = 0.75$).

DISCUSSION

Seed production and environmental factors. Studies on seed production in the timberline ecotone of the Iremel' Massif in the productive year 2003 showed that, upon a 100-m increase in elevation, the number of spruce cones and full seeds per hectare decreased from 100–110 to $(3–6) \times 10^3$ and from 13–15 to $(0.05–0.09) \times 10^6$, respectively, with the number of seeds per cone decreasing from 136 to 14. These changes were most
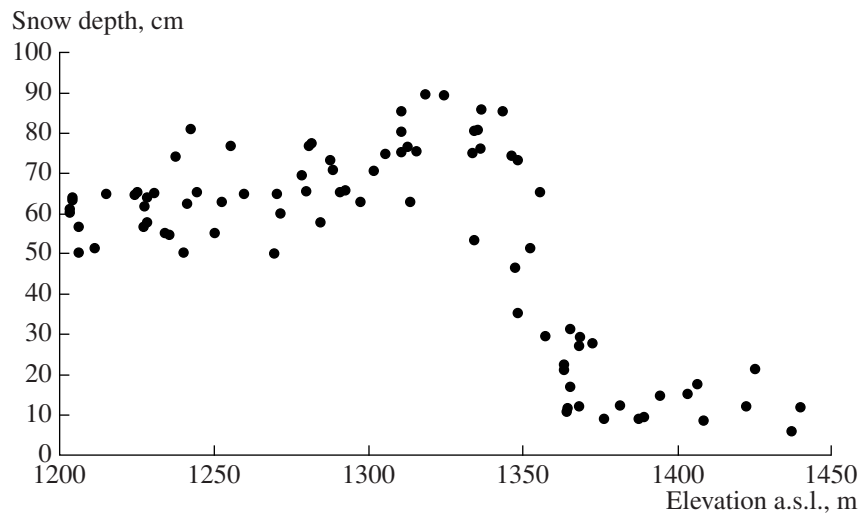
Snow depth, cm

Fig. 2. Average snow depth in different parts of the forest–tundra ecotone on the Iremel' Massif in 2006.

distinct upon transition from the middle to the upper part of the ecotone. In our opinion, differences between the average values of morphometric parameters and the age of trees (by a factor of 1.5–2) and between monthly average air temperatures (by 0.3–0.5°C) in these areas cannot fully account for such a distinct tendency toward seed yield reduction (see Table 3).

As shown by Cairns (2001), strong winds in the mountains (over 10–15 m/s), which usually grow stronger as elevation increases, cause frost desiccation and snow abrasion of needles, buds, and shoots located above the snow surface. As a result, trees annually lose 4–10% of their assimilatory apparatus. Moreover, the winds redistribute snow, causing considerable variation in its depth across the timberline ecotone (Holtmeier, 2003). Thus, the average snow depth in its upper part on the Iremel' Massif is two to four times smaller than in the middle part (10–25 vs. 75–90 cm), which accounts for freezing (to –5 or –6°C), 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°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 fungi, which markedly impairs the capacity of plants for absorbing soil nitrogen and phosphorus. 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 the soil temperature in summer is lower (the difference between soil temperatures in the upper and middle parts of the timberline ecotone is 1.5–3°C), with a consequent decrease in the activity of soil bacteria and retarded turnover of mineral substances (Kammer et al., 2007). Therefore, not

only differences in the structure of tree stands and air temperature but also higher losses of assimilatory structures and fine roots in winter and inferior conditions of mineral nutrition produce a significant effect on net photosynthesis, assimilation of nutrients, the number and size of reproductive organs, and, finally, the amount and quality of seeds produced in the upper part of the timberline ecotone.

The laboratory germination rate of spruce seeds from the forest–tundra ecotone of the Iremel' Massif proved to decrease from 34 to 14% with an increase in elevation, but the magnitude of this change (by a factor of 2–2.5) was markedly smaller than in the case of seed production. According to Almqvist et al. (1998), *Picea abies* requires a sum of no less 700 degree–days with air temperature above 5°C to reach 50% seed maturation and a sum of 875 degree–days to reach 95% seed maturation. The sums calculated from the records made by temperature data loggers in the lower, middle, and upper parts of the ecotone (1125, 1150, and 1085 degree–days, respectively) were higher than published values and did not differ significantly from each other. Hence, we concluded that this factor could not account for differences in the quality of seeds collected in these parts of the ecotone. Apparently, both seed quality and seed productivity depended on the processes considered in the previous section.

Emergence of seedlings and environmental factors. Censuses taken after the productive year 2003 showed that the number of seedlings in the zone of transition from the middle to the upper part of the ecotone decreased from 20–30 × 10^3 ind./ha to zero. In our opinion, this cannot be attributed solely to the aforementioned sharp decrease in the amount of seeds per unit area but is largely explained by a significant effect of local habitat conditions on seed germination and seedling survival in the first months of life. It is known

that the main limitations on the processes of seed germination are imposed by an unfavorable water regime and physicochemical properties of the litter, low air temperature and humidity, insufficient aeration, and high abundance and activity of animals and pathogenic organisms consuming or damaging spruce seeds in the soil (Gortinskii, 1964; *Faktory…*, 1983). Conditions of illumination and mineral nutrition during seed germination and at the earliest stages of seedling development do not play any significant role, as seedlings in this period are highly shade-tolerant and grow mainly on account of nutrients stored in the seed.

On the basis of his own experiments and analysis of published data, Gortinskii (1964) concluded that 9–11°C is the lower limit of substrate temperatures at which seeds of the genus *Picea* can germinate within an ecologically acceptable period (no more than 40 days). When this temperature rises to 18°C, the germination period decreases to five days. Temperature fluctuations within the range of 18–25°C have little effect on its duration. A further temperature rise leads to increased water losses from the litter and deterioration of conditions for seed germination. Gortinskii emphasized that the period of germination at low temperatures was impossible to determine accurately because of severe seed infection by mold fungi, suggesting that this factor may play a major role not only under experimental conditions but also in nature. His experiments on spruce seed germination under different conditions of moisture supply showed that litter moistening below 30% of its full water capacity did not ensure seed germination. As moistening increased to 70%, the seed germination rate at the optimum temperature reached the maximum possible value. Still higher moistening at average temperatures below 13°C led to a decrease in the number of germinated seeds. The author attributed this fact to the inhibitory effect of biologically active substances contained in the litter.

These data show that the combined limiting effect of insufficient or excessive moisture and heat supply may reduce the period favorable for seed germination to only a few days. In our opinion, this factor (along with the small amount of viable seeds) accounted for the small number of spruce seedlings in the upper part of the timberline ecotone (0–400 ind./ha). Seed germination at the beginning of the growing season (in June) was impossible because of low temperatures of the upper soil layer (4.1°C at a depth of 10 cm and 6.8°C on the surface), although substrate moistening after snow melt was optimal. Later, when the soil temperature reached the level suitable for seed germination, soil moisture decreased because of water drainage down the slope (creeks at an elevation of 1250 m dried out in late June) and insufficient precipitation in August. A similar situation is also observed in zonal spruce forests, where conditions of soil moistening are favorable for spruce seed germination only in the first half of May, but this process is retarded because of a low soil temperature at the surface (Abrazhko and Abrazhko, 1995).

Survival of seedlings in the first months of life and environmental factors. As seedlings take root and become autotrophic, their survival and life state become increasingly dependent on conditions of illumination, mineral nutrition, and the phytoenvironment (*Faktory…*, 1983). Of primary significance are different forms of competition with edificator trees and plant species of the lower vegetation layer, which eventually determine the fate of new spruce generations. Thus, in communities of all spruce forest types in the southern taiga subzone, the roots of seedlings rarely penetrate the soil by more than 3–4 cm (Abrazhko and Abrazhko, 1995), but the absorbing roots of trees, dwarf shrubs, and herbaceous plants also concentrate in the surface soil layer, which often creates problems in moisture and mineral nutrient supply to self-sown spruce. In primary spruce forest communities, the physical evaporation of water and its intensive uptake by the roots of trees and plants of lower vegetation layers in the periods of insufficient water supply from the atmosphere may result in the critical depletion of soil moisture in the surface layer. Such depletion is often the main factor accounting for mass death of spruce seedlings and juvenile trees (Karpov, 1969; Abrazhko and Abrazhko, 1995).

Beginning from the age of 15–20 days, the survival of spruce seedlings is also dependent on conditions of illumination (Karpov, 1969). For example, the illumination level in dense herb–dwarf shrub synusiae of wood sorrel spruce forests decreases to only 0.4–1.1% of that in open areas, whereas the compensation threshold for spruce is 1.7–2.0% (Tranquillini, 1960; cited from Karpov, 1969). The lower part of the timberline ecotone on Mount Bol'shoi Iremel' is mainly occupied by dense tall-herb (*Polygonum alpinum*) meadows, where the level of illumination at the soil surface is low. This may account for the fact that the number of spruce seedlings recorded in this area is smaller than in the middle part of the ecotone, where low and sparse herb–dwarf shrub communities prevail.

Seedling survival in subsequent years and environmental factors. As follows from some publications (*Faktory…*, 1983; Abrazhko and Abrazhko, 1995), a late emergence of seedlings (because of unfavorable germination conditions) reduces the growing period and, therefore, the seedlings cannot complete their developmental cycle, their stems fail to lignify, and roots barely penetrate the soil. As a result, most of them (in mineralized soils, up to 80–95%) perish from frost heaving during the first cold season. Frost heaving takes place in spring or, more rarely, in autumn, in the period of soil subsidence after thawing or upon the formation of ice lenses at the soil surface after autumn or spring frosts (several-days-long temperature drops to −6 to −15°C), when deeper soil layers have not yet frozen or have already thawed out. The maximum rise of the soil surface upon spring or autumn frosts or in winter reaches 50–70 mm, which is greater than the length of tap roots in the majority of spruce seedlings (the range of variation in root length is 40–150 mm) (Sover-

shaev, 1961). It is also probable that herbaceous plant debris (in our case, large stems and leaves of dead *Polygonum alpinum* plants) plays a role in the elimination of spruce seedlings (Abrazhko and Abrazhko, 1995): being buried under a layer of debris in autumn and pressed down by snow in winter, the seedlings often suffer damage and die.

We cannot specify which of these factors accounted for mass mortality (76–96%) of spruce seedlings in the study area during the first cold period. However, frost heaving of two- to three-year old spruce seedlings takes place only in strongly mineralized soils (Sovershaev, 1961), which have not been found in our test plots. Therefore, 30–60% mortality of seedlings in the second cold period (2005/2006) can be attributed to the impact of tall-herb debris.

Thus, the results of this study provide evidence that snow depth; soil temperature; and the numbers and quality of Siberian spruce cones, seeds, and seedlings in the timberline ecotone of the Iremel' Massif change significantly with an increase in elevation. The majority of seedlings die during the first cold period, and only 1.4–11.7% of them reach the age of two years. Seed production and seedling mortality apparently depend not only on air temperature and soil moisture but also on snow depth and soil temperature, which change more abruptly along the altitudinal gradient.

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