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Expansion of Tree Vegetation in the Forest–Mountain Steppe Ecotone on the Southern Urals in Relation to Changes in Climate and Habitat Moisture

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Abstract—As found by comparing historical topographic maps and present-day satellite images, steppificated areas in the southern part of the eastern macroslope of the Southern Urals have decreased in size by 17.6% between 1986 and 2015 due to forest expansion. Analysis of the age structure of tree stands in the forest–mountain steppe ecotone provided evidence for intense pine and larch regeneration in this region from 1915 to the 1960s, which has led to significant increase in stand density and upward shift of treelines along slopes and ravines by the end of the 20th century. Intense pine regeneration during the past 35–40 years has been observed at the boundary between closed and open forests and in sparse woodlands. Forest expansion to the mountain steppes throughout the ecotone proceeded against the background of increase in temperature and precipitation during the cold period of the year. The rate of forest expansion to particular areas varied depending on differences in moisture supply, which, in turn, depended on local microclimatic and edaphic conditions. This is confirmed by our measurements of snow depth and density and soil moisture and thickness, which show that forest has expanded at the highest rate in more snowy and moisture-abundant slope areas.

Keywords: forest–mountain steppe ecotone, tree stand dynamics, snow cover, soil moisture, climate change, Kraka massif, Southern Urals

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Climate warming and spatiotemporal changes in the distribution of precipitation in the 20th century have entailed transformations in the structure and properties of terrestrial ecosystems, the loss of many rare and endemic species, and reduction in the size of habitats in many regions of the earth [1, 2]. The effect of changes in the temperature regime is most distinct at high latitudes and high-mountain regions, while the dynamics of vegetation in arid and semiarid regions depend primarily on changes in moisture conditions [3, 4].

Against the background of current warming and redistribution of precipitation, the northern forest boundary shifts to the tundra zone, forests expand to treeless areas in forest–steppe regions, and the upper treeline advances to higher elevations [5–8]. At the same time, some specialists note that changes to a warmer and drier climate in certain regions of the world have resulted in decreasing forest productivity, deterioration and decline of forest stands, changes in their structure and species composition, reduction in area, and land desertification [9–12].

In the Southern Urals, where precipitation has increased in recent decades [6, 13], tree plants growing in the zone of contact with extrazonal mountain steppes can be used as an indicator of climate change. Their response to climate change will be most pronounced both at individual (growth) and population levels (regeneration and dispersal) due to their increased sensitivity to these changes under extreme growing conditions (insufficient moisture).

Petrophyte mountain steppes are practically not exposed to anthropogenic impact due to their location on steep slopes with stony soils and remoteness from industrial centers. In the mountain regions of the Republic of Bashkortostan and Chelyabinsk oblast, such steppes occupy a considerable part (10–15%) of southern slopes [14]. Farther north (to the Middle Urals), on the eastern macro-slope of the Southern Urals, they “penetrate” into the boreal zone, occurring there as small areas surrounded by forests [15]. Severe microclimatic and edaphic conditions in the mountain steppes [16] prevent the growth of woody plants. Nevertheless, comparison of recent and past descriptions of vegetation, aerial and satellite images, topographic maps, and forestry management data has shown that mountain steppes are being overgrown by woody vegetation in those areas of the Baikal region and the Urals where precipitation has increased in the past few decades [6, 7, 17–19].

Observations on the spatial dynamics of vegetation in one of the areas where mountain steppes are widespread in the Southern Urals, on the Southern Kraka massif, which began in the 1970s [20], failed to give unambiguous answers at the quantitative level about the direction and extent of changes in communities at the forest–mountain steppe boundary and their determining factors, since the methods of monitoring have not been sufficiently developed by that time. Therefore, our purposes at the current stage of research were as follows: (1) to adapt well-proven methods of studies on the climatogenic dynamics of tree vegetation at the upper limit of its growth in high-mountain regions of the Southern Urals [5, 13] to the conditions of the forest–mountain steppe ecotone; (2) to quantify changes in the position of the boundaries of closed forests and the extent of reduction in the size of steppificated areas not only on the slopes of the Southern Kraka massif but also in the more northern areas of the Southern Urals; and (3) to study the morphometric, spatial and age structure and dynamics of tree stands in the forest–mountain steppe ecotone on the slopes of the Kraka massif and assess the impact of changes in climatic factors and soil conditions on these stands.

OBJECTS AND METHODS

Studies were performed in the gabbro–hyperbasite Kraka mountain range consisting of four individual massifs (north to south): Northern, Central, Uzyansky, and Southern Kraka (53°15′–53°50′ N, 57°36′–58°12′ E). They form a partially segregated mountain plexus lying west of the central mountains of the Southern Urals (Fig. 1). The Kraka range is unique in its origin and orography, as well as in vegetation and soils [21]. Its distinctive orographic feature is that there are complex plexus systems of ridges formed of ultrabasic igneous rocks and dissected by erosion. They have steep ridge-and-runnel slopes that often form a sharp crest at the top. The topography and climate of the Kraka range have created prerequisites for the development of the forest–steppe landscape where light conifer forests dominated by Scots pine (*Pinus sylvestris* L.) and Siberian larch (*Larix sibirica* Ledeb.) are combined with mountain steppes. Steppe communities typically occur on slopes of southern aspects at elevations of 550 to 1045 m a.s.l., depending on the degree of slope. The flora of the Kraka mountain steppes includes species belonging to the Pleistocene floristic complex of the Urals, which may be evidence for the relict origin of some steppe formations dating from the Holocene xerothermic period [22]. The study region has a cold continental climate. The annual average air temperature is 1.2°C, with the maximum and minimum temperatures being 31.0 and –41.5°C; the annual average precipitation is 532 mm [23].

Eight series of test areas forming altitudinal transects were established in the forest–mountain steppe ecotonal zone on the south- and southeast-facing slopes of the Southern and Northern Kraka in the summer of 2015 and 2017 (Fig. 1). Within each transect, three altitudinal levels were distinguished: (1) the upper level at the upper boundary of sparse stands (groups of trees with a crown closure of 5–10%); (2) the middle level at the upper boundary of open forests (20–30% crown closure); and (3) the lower level at the upper boundary of closed forests (40–50% crown closure). Three 20 × 20-m plots were established at the lower and middle levels in areas with relatively smooth mesotopography and conditions typical for a given slope (in terms of soil moisture, steepness, and edaphic features) in order to evaluate factors having an effect on tree vegetation throughout the slope. Test areas at the upper level had a size if 1–3 ha and were shaped as rectangles. The transect on Mt. Bashart (360 × 220 m) was not divided into levels because of extremely uneven distribution of trees over the altitudinal profile (in clusters) and the absence of gradual transition from closed forests to mountain steppes. Below, it is referred to as transect test area. Each tree in the test areas and plots was examined to record the following parameters: height, trunk diameter at the base and at 1.3 m above the soil surface, crown diameter in two directions, and life state. To estimate the time when trees appeared in a given area, core samples from each tree with a trunk diameter of more than 3 cm were collected using an increment borer. However, since such samples are taken at a certain height above the root collar, they not allow accurate estimation of the relationship between tree age and height. Therefore, we took cross-cut samples of wood at the root collar from every third young tree more than 0.1 m tall but less than 2 cm in diameter. Using the data on the age (A) and height (H) of such trees, we calculated a regression equation for the dependence between these parameters ($A = 25.3 \times H^{0.5307}$) and used it to estimate the time when each of older trees reached the height at which the core sample was taken. All wood samples were dated by standard dendrochronological methods [24].

Analysis of morphometric parameters of trees provided a general idea of tree stands growing in the test areas (Table 1). The numbers of dead-standing and live trees and undergrowth were calculated, and the average values of parameters such as basal trunk diameter, height, and crown diameter were calculated for all live trees. Trees up to 1.5 m high were classified as undergrowth. To evaluate specific features in the formation of tree stands in the forest–mountain steppe ecotone, the series of the distribution of trees by the calendar years of their appearance were compiled for each altitudinal level. It is known [25] that light conifer species abundantly bear fruit every 3–5 years, with

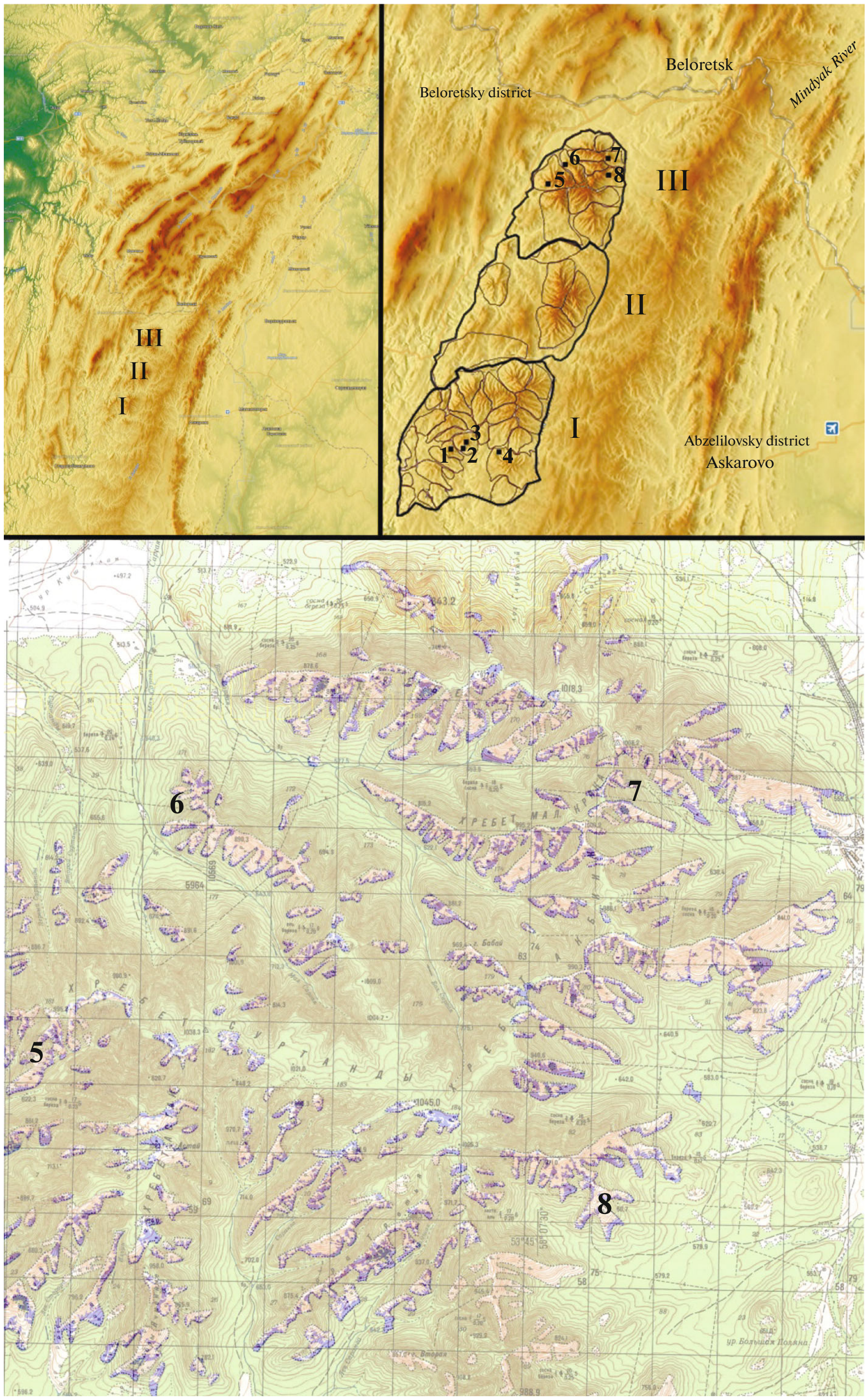

Fig. 1. Top panel: the southern part of the eastern macroslope of the Southern Urals. Roman numerals indicate (I) Southern Kraka, (II) Central Kraka, and (III) Northern Kraka massifs; (1–8) altitudinal transects: (1) Bolshoi Bashart, (2) Bashart, (3) Bashart test area, (4) Avdekte, (5) Surtandy, (6) Maly Sargaya, (7) Shigay, (8) Akbiik. Bottom panel: part of Northern Kraka massif with areas of closed forests shown on the 1990 map (light gray (green) shading) and steppificated areas occupied by closed tree stands between 1990 and 2015 (dark gray (blue) shading).

very few trees appearing in the intervals between mast years. Therefore, trees of annual calendar groups were pooled into 5-year age groups.

As found in studies on Mt. Konzhakovsky Kamen (the Northern Urals) [26], the upper boundary of low forests (crown closure about 20%) described by

Table 1. Characteristics of tree stands at different altitudinal levels of transects on the slopes of Kraka massifs, the Southern Urals

Transect	Level	Elevation a.s.l., m	Slope (degrees)	Number of trees, ind./ha			Average parameters of live trees			
				live	young	dead	basal diameter, cm	height, m	age, years	crown diameter, m
		Southern Kraka massif								
I	1–2	730–810	30–35	29.0	8.6	5.2	32.1	9.5	152.2	5.2
I	3	690–700	25–30	933.0	950.0	283.0	16.4	8.7	73.7	2.8
II	1	715–750	25–30	20.0	2.4	–	24.8	8.0	138.2	4.3
II	2	705–715	20–25	537.5	137.5	50.0	20.8	7.9	99.1	3.2
II	3	680	20–25	1125.0	875.0	112.5	14.7	7.5	80.0	2.9
III	1	610–650	25–30	39.0	11.0	1.0	29.3	10.4	130.7	5.3
III	2	580–595	20–25	850.0	1533.3	58.3	11.2	5.2	45.6	2.4
III	3	575	20	616.7	433.3	91.7	24.7	13.8	92.8	4.4
IV	1–2	700–800	25–30	33.9	5.7	2.8	28.0	9.7	136.0	4.5
		Northern Kraka massif								
I	1	730–760	20	9.9	33.8	0	7.2	2.8	29.5	1.7
I	2	720–680	20–30	708.3	1033.3	150.0	9.9	4.9	39.2	2.1
I	3	650–680	20–25	1025.0	708.3	216.7	12.1	6.9	51.0	2.3
I	4	620–650	20	891.7	66.7	41.7	17.9	12.6	70.1	3.0
II	1	650–700	25	13.8	11.0	2.6	17.8	6.5	45.6	3.6
II	2	630–650	25	358.3	250.0	8.3	15.3	8.7	48.4	3.1
II	3	620–630	20	933.3	366.7	83.3	16.5	10.1	58.4	3.0
III	1	780–900	30	43.5	38.2	1.2	12.8	3.4	47.2	1.9
III	2	750–770	30–25	308.3	600.0	275	13.9	3.8	40.5	1.8
III	3	700–730	20	1066.7	325.0	491.7	20.2	9.9	87.2	3.2
IV	1	710–750	10–15	17.1	27.6	4.0	12.1	3.7	28.7	2.1
IV	2	690–700	20	433.3	566.7	16.7	8.9	4.3	30.7	1.7
IV	3	650–690	20	958.3	133.3	25.0	16.2	9.6	60.1	3.3

S.G. Shiyatov in 1956 was located, on average, 18 m higher than the forest boundary shown in the 1957 topographic map (1 : 25000). We compared the contours of forest boundaries in historical and modern topographic maps (1 : 25000) and tree vegetation maps that we constructed for certain summits of the Urals based on aerial photographs of the 1960–1980s and on recent (2010–2013) aerial and satellite images with a resolution of <1 m^2 per pixel taken from Google Satellite or Yandex Satellite layers using SAS. Planet 131111 software. The results showed that the boundaries of forest communities shown in topographic maps coincided most closely with the boundaries of stands with 35–40% crown closure. Therefore, we consider it possible to use the contours of forest boundaries in the large-scale topographic maps made in 1950–1960 and 1980–1990 for reconstructing the boundaries of tree stands with the above crown closure.

The magnitude of changes in the size of treeless areas on the slopes of Southern, Central, and Northern Kraka massifs was quantitatively evaluated with SAS. Planet 160707 software. Using "tools" in the tab "Placemarks," all areas with a tree crown closure of less than 30–40% were delimited in modern satellite images of submeter resolution (2015) and in 1 : 25000 maps (~1986) obtained from the State GIS Center (Gosgistsentr). The size of each area as of 1986 and 2016 was estimated based on data from the tab "Placemark information."

To evaluate the pattern of snow cover and the amount of moisture contained in it, snow surveys on the transects were carried out in late February to early March. Snow depth was measured with a snow ruler in 1-cm increments. To determine the distribution of snow over the transect, the survey involved three to four passages across and one passage along the slope. Measurement was performed at intervals of 2–4 m: along the slope, from the level 10–20 m below the boundary of closed forests up to the top; across the slope, one passage throughout the transect width at each altitudinal level (about 100 samples). The survey at the upper level was performed in the middle of the transect; at the middle and lower levels, in the test plots. Snow density was measured with a VS-43 snow gauge at three points: in the beginning, middle and end of the snow depth measurement line at the upper levels and in the centers of the test plots at the middle and lower levels.

Soil moisture was determined at the beginning of the growing season, when tree plants growing in conditions of moisture deficiency develop most actively. Measurements at each altitudinal level were made in three 20 × 20-m square plots using a Delta-T HH2 Moisture Meter with an ML3 ThetaProbe. These squares at the middle and lower levels coincided with the test plots, and at the upper level they were evenly distributed over the slope along the transect midline. Soil moisture was measured at the surface and at 10-cm depth along the central lines, from left to right and from bottom to top (10 samples per line). To assess moisture distribution over the soil profile, soil pits down to the bedrock were dug in each square plot at four points (the centers of 10 × 10-m squares), where eight measurements were made in each soil layer: 0–5, 5–10, 10–20, and 20–30 cm (where available). In parallel, descriptions of the soil profile were made and the depth of soil horizons was determined.

RESULTS

Changes in the Size of Steppificated Areas over the Past 30–40 Years

The identified steppificated plots (943 in total) were grouped into 31 subregions on the Southern Kraka, seven subregions on the Central Kraka (326 plots), and nine subregions on the Northern Kraka (202 plots) with total areas of 6559.8, 1923.6 and 3176.6 ha, respectively. Comparisons of the area they occupied in 1986 with that in 2016 showed that it decreased by a total of 17.6% over the Kraka range (see Fig. 1). The size of low-forested areas decreased in all subregions, slightly increasing only in a few places affected by fires and in zones of anthropogenic impact near populated areas. The most significant changes occurred on the Northern Kraka slopes where the total size of steppificated areas decreased by 28.1%, compared to 14.1% in the Southern Kraka and 12.1% in the Central Kraka. Areas that have been almost completely overgrown by forest were found in many parts of the Kraka range. These were mainly the areas that had a small area (a few hectares) in the initial period or those located in the lower parts of the slopes.

Characteristics of Tree Stands in the Forest–Mountain Steppe Ecotone

The average diameter, height, and age of trees on the Southern Kraka increase from the lower to the upper level of the ecotone (Table 1). Most common at the upper level are single old-age pine and larch trees whose morphometric parameters are characteristic of trees growing in severe conditions, i.e., a small height at considerable trunk diameter and age. The number of undergrowth is only 2.4–11.0 ind./ha. It is obvious that young trees in this area manage to survive only in places where microclimatic growing conditions are less severe, such as microdepressions shaded in the daytime. Microclimatic conditions improve down the slope, and the number of young trees increases 15-fold at the middle and 56-fold at the lower level. At the same time, the average age and diameter of trees are decreasing and the height is increasing (Table 1). The abundance of viable undergrowth also increases down the slope.

Unlike on the Southern Kraka, the average tree diameter, height, and age on the Northern Kraka decrease from the lower to the upper level of the ecotone (Table 1). The number and average age of trees are significantly lower than on the Southern Kraka, especially at the upper levels. This is evidence that forest expansion to mountain steppes on the Northern Kraka started slightly later and conditions for the survival of tree undergrowth were less favorable.

The number of trees in the Northern Kraka forest–mountain steppe ecotone changes more abruptly than on the Southern Kraka, especially upon transition from the middle to the upper level (Table 1). The number of undergrowth reaches a peak at the middle level. This fact suggests that conditions under the relatively thin canopy of maternal trees at this level are most favorable for seed germination and seedling survival, while at lower levels, in more dense stands, the mortality of undergrowth is markedly higher because of increased competition for light from the maternal canopy.

Specific Features of Site Conditions and Snow Distribution over the Transects

The transects are located on the southern slopes, at elevations of 575 to 900 m a.s.l. In general, slope steepness increases only slightly from the lower to the upper level, varying between 20 and 30 degrees (Table 1), but in places it may reach 45 degrees. The treeless areas lie mostly above 700 m a.s.l. and, depending on slope degree and exposure, may extend down the slope to 600 m.

The pattern of snow accumulation in the Kraka range is characterized by significant spatial heterogeneity and variability conditioned by geomorphological features of the mountains. As follows from Table 2, the overall average parameters of snow depth in the Southern and Northern Kraka differ by only 2–10 cm. However, snow depth in some transects was 20–30 cm greater than in others. Differences in this parameters depend on slope exposure, steepness, and prevailing wind direction.

The depth of snow cover regularly decreases from the lower to the upper altitudinal level. Its minimum

Table 2. Average snow depth, water content, and snow density at different altitudinal levels (1–3) in the forest–mountain steppe ecotone of Kraka massifs, the Southern Urals

Year	Massif	Transect	Snow depth, cm			Water content, L/m^2			Snow density, kg/cm		
			1	2	3	1	2	3	1	2	3
2017	Southern Kraka	I	85.9	88.1	90.4	195.3	223.4	229.1	0.23	0.25	
		II	67.8	82.4	80.5	143.3	162.6	158.8	0.21	0.20	
		III	42.8	62.7	69.4	88.5	126.3	139.8	0.21	0.20	
		Average	**67.9**	**79.6**	**80.1**	**143.8**	**173.1**	**175.9**	**0.215**	**0.217**	
	Northern Kraka	III	27.8	50.1	80.4	68.5	109.4	175.8	0.25	0.22	
2018	Southern Kraka	I	29.9	49.0	42.2	70.8	103.0	78.5	0.234	0.208	0.186
		II	25.6	28.8	36.4	55.5	57.7	67.6	0.217	0.207	0.186
		III	20.4	27.0	34.9	50.6	47.7	70.3	0.246	0.176	0.201
		VI	26.9	27.6	41.4	48.8	49.2	77.3			
		Average	**25.7**	**33.1**	**38.7**	**56.4**	**64.4**	**73.4**	**0.232**	**0.197**	**0.191**
	Northern Kraka	I	37.1	43.9	45.0	70.9	81.3	88.2	0.194	0.185	0.196
		II	33.3	38.3	38.2	63.7	67.3	82.8	0.193	0.175	0.218
		III	31.3	38.2	39.9	66.0	92.0	74.8	0.209	0.239	0.188
		VI	61.4	58.2	58.0	110.6	99.9	122.3	0.182	0.174	0.210
		Average	**37.5**	**43.7**	**43.7**	**73.1**	**84.1**	**89.8**	**0.200**	**0.195**	**0.206**
2019	Southern Kraka	I	33.6	72.7	62.7	64.4	127.4	115.3	0.192	0.175	0.184
		II	37.2	58.4	60.5	62.9	97.4	101.8	0.169	0.167	0.168
		III	42.3	48.7	51.7	113.4	111.8	110.3	0.268	0.239	0.213
		VI	40.0	47.4	63.7	72.6	84.4	119.1	0.182	0.178	0.187
		Average	**38.3**	**56.8**	**59.7**	**78.4**	**105.3**	**111.6**	**0.203**	**0.190**	**0.188**
	Northern Kraka	I	50.2	52.7	51.5	101.2	95.3	94.2	0.202	0.181	0.183
		II	29.0	46.9	52.5	48.1	80.9	84.6	0.166	0.172	0.161
		III	34.5	63.3	61.1	75.0	123.1	94.9	0.217	0.194	0.155
		VI	32.2	48.7	54.2	64.3	85.2	91.6	0.200	0.175	0.169
		Average	**36.4**	**52.9**	**54.8**	**72.2**	**96.1**	**91.3**	**0.196**	**0.181**	**0.167**

and maximum values vary very strongly even within the same level. This parameter is most variable at the boundary of open forests (middle level) and somewhat less variable in sparse forests (upper level), whereas snow distribution at the boundary of closed forests (lower layer) is relatively uniform. Such variation pattern may be due to the most active redistribution of snow by wind from the upper to lower parts of the slope and from mesorelief elevations ("ribs" of the slope) to depressions, where its depth may by two to three times greater than average, while snow transfer by wind at the boundary of closed forests and in these forests is reduced by tree stand. Variation in snow depth is the highest on transects III (Shigay) and II (Maly Sargaya) on the Northern Kraka and transect III (Avdekte) on the Southern Kraka. The wind blows the snow away from the top to the lower parts of the slope, and snow depth at the summits of ridges is no more than 5–7 cm.

Snow water content directly depends on snow depth and therefore has similar dynamics (Table 2). The average snow density is higher at the upper and middle levels; in general, it is higher on the Southern Kraka than on the Northern Kraka.

Characteristics of Soils and Soil Moisture on the Transects

In all the areas surveyed, the soil is a relatively thin humous layer that usually contains a large amount of rock fragments and is sodded by interweaving plant roots. On the Southern Kraka, the average soil thickness at the upper transect level varies from 7.3 cm on Mt. Bolshoy Bashart to 14.3 cm on Mt. Avdekte (Table 3). On the Northern Kraka, the soil layer at the upper level is only 5–7 cm thick, there are numerous bedrock outcrops, and fine earth accumulates on ledges (benches) of the slope. Soil thickness gradually increases at the middle and lower levels. At the middle

Table 3. Average depth of the lower boundary of soil horizon, soil moisture, and soil water content in 2018 at different altitudinal levels of transects on the slopes of Kraka massifs, the Southern Urals

Transect	Level	Date	Depth of the lower boundary of soil horizon, cm				Soil moisture (%) at depth of				Water content, L/m^2
			A0	A1	AB	B	5 cm	10 cm	20 cm	30 cm	
Southern Kraka massif											
I	1	June 19	0.5	3.7	_	7.3	9.6				9.6
I	3	June 19	1.9	7.2	11.9	26.5	11.3	13.7	10.5	7.6	33.7
II	1	June 24	0.5	3.5	_	7.5	7.0				7.0
II	2	June 24	1.3	10.4	13.1	22.5	5.8	9.4	8.1		20.4
II	3	June 24	2.2	9.9	11.9	24.5	6.2	9.8	8.3	6.0	24.3
III	1	June 25	0.7	6.7	_	14.3	4.9	9.7			6.4
III	2	June 25	1.2	6.7	9.3	18.6	5.9	8.7	8.7		21.0
III	3	June 25	1.4	5.3	7.2	20.1	7.4	11.0	10.6	7.7	29.2
Northern Kraka massif											
I	1	July 12	0.5	3.4	5.1		6.0				3.6
I	2	July 12	1.1	8.3	10.3	28.9	23.7	28.3	26.3	25.6	79.2
I	3	July 12	0.8	9.0	11.5	30.3	24.4	30.7	27.8	30.2	85.8
II	1	July 22	0.7	3.8	5.5	11.7	29.1				29.1
II	2	July 22	0.9	8.4	10.1	27.3	23.7	28.3	26.3	27.1	80.0
II	3	July 22	1.3	5.6	7.1	25.7	18.5	21.9	21.0	22.0	63.1
III	1	June 16	0.5	3.7	5.3		12.3				7.4
III	2	June 16	1.4	11.1	14.7	29.8	14.6	17.2	17.4	22.0	52.9
III	3	June 16	1.9	6.3	11.8	29.9	11.5	14.1	15.9	12.2	41.8
IV	1	June 15	0.5	3.5	5.0		23.7				14.2
IV	2	June 15	1.6	8.2	12.2	23.8	19.9	23.0	23.5	23.8	68.3
IV	3	June 15	2.7	8.6	11.3	27.5	19.0	24.1	24.5	22.5	69.4

level, it varies between 18.6 ± 7.2 cm on Mt. Avdekte to 29.8 ± 9.1 cm on the Shigay transect. The situation at the lower level is generally similar, but the depth of the soil profile is greater (on average, 30 cm), soil horizons are better differentiated, and the content of bedrock fragments is lower. High values of standard deviation indicate that soil thickness strongly varies even within the same transect level. Bedrock outcrops occur even at the boundary of closed forests, and the depth of the soil profile exceeds 40 cm only in rare cases (in runoff gullies).

The spatial distribution of moisture in the soil directly depends on the depth of soil profile and position within the ecotone, increasing from the upper to the lower level. It has also been noted that soil moisture decreases with an increase in the amount of rubble in the soil. Its content proved to be greater in those places where studies were conducted at an earlier time of the growing season (Table 3), when the soils were still saturated with meltwater (Shigai and Akbiik transects), or within 2–3 days after rainfall (Surtany and Maly Sargaya transects).

The distribution of moisture by soil horizons is similar for all the areas under study. Its amount in the 0–5 cm layer is minimum (Table 3), but it increases in areas where the ground vegetation layer is well developed and a litter layer has formed. The moisture content reaches a peak at a depth of about 10 cm, in the humus horizon (which has the highest water-holding capacity and the lowest content of rubble), and gradually decreases at depths of 20 and 30 cm.

Analysis of Climate Change in the Study Region

Long-term average data on climatic parameters over the periods of 1935 to 1970 and 1971 to 2004 were obtained from weather station of the Bashkir State Nature Reserve located at 3–4 km from transects on the Southern Kraka. Their comparative analysis showed that monthly average air temperatures became 0.2–0.6ºC higher in May, June, and July but 0.1°C lower in August; as a result, the average temperature over the growing season increased by 0.3°C. In the cold season (October–March), monthly average temperatures increased by 0.4–1.2°C, with the increase

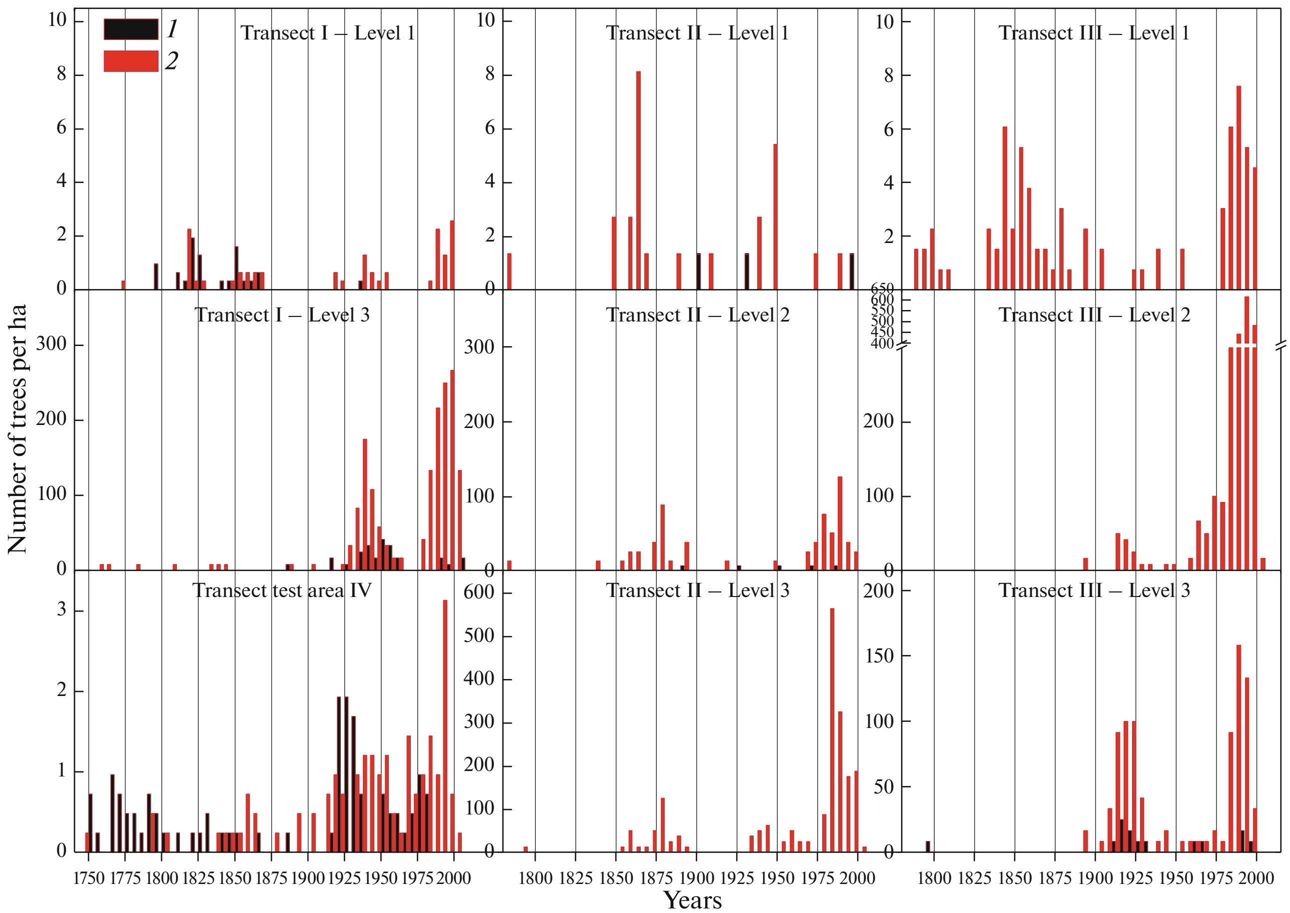

Fig. 2. Age structure of tree stands at different levels of altitudinal transects in the Southern Kraka massif. Here and in Fig. 3, bars show the numbers of (*1*) larch and (*2*) pine tree trunks that appeared during 5-year intervals.

over the season reaching 1.0°C. Similar trends were observed in the neighboring regions. For example, seasonal average air temperatures at the Verkhneuralsk weather station (111 km northwest of the study region) became 0.3°C higher in May to August and 0.9°C higher in October to May.

Comparing the data on precipitation in 1935–1970 and 1971–2004, it was noted that its monthly amount increased by 4–7 mm in May and August but decreased by 1–6 mm in June, July and September, with increase in precipitation over the warm period of the year amounting to 3 mm (1%). In In the cold period (October to April), an increase in precipitation by 3–11 mm was observed in all months, reaching 41 mm (16.5%) over the entire period.

Tree Stand Dynamics in the Forest–Mountain Steppe Ecotone

As a result of analysis of the age structure of tree stands, we found that the first trees that have survived to date on the Southern Kraka massif appeared in the 1750s in transect test area IV (Fig. 2). In other transects, the first single trees began to appear in the period from the 1770s to 1805, and their number did not differ significantly between altitudinal levels. Until the 1850–1870s, regeneration of pine and larch on the steppificated slopes of the Southern Kraka was relatively uniform on all the transects. In the 20th century, active development of a new generation of trees on the slope of Mt. Bolshoy Bashart (transect I) occurred in the 1930a to 1955 and then in the 1980–2000s, and the peak of regeneration was noted in 1990, when 250 trees per hectare appeared and survived to date at the lower transect level.

Active development of a new tree generation on Mt. Bashart (transect II) took place in the period of 1850–1870 at the upper level and 1860–1880 at the middle and lower levels. The second regeneration wave at the middle and lower layers was noted between 1930 and 1955, as on transect I (see Fig. 2).

The formation of pine stands at the middle and lower levels of transect III on Mt. Avdekte was most active in the periods from 1910 to 1930 and from 1980 to 2005, with the numbers of trees that appeared and survived to date reaching a maximum of 100 and 160 ind./ha

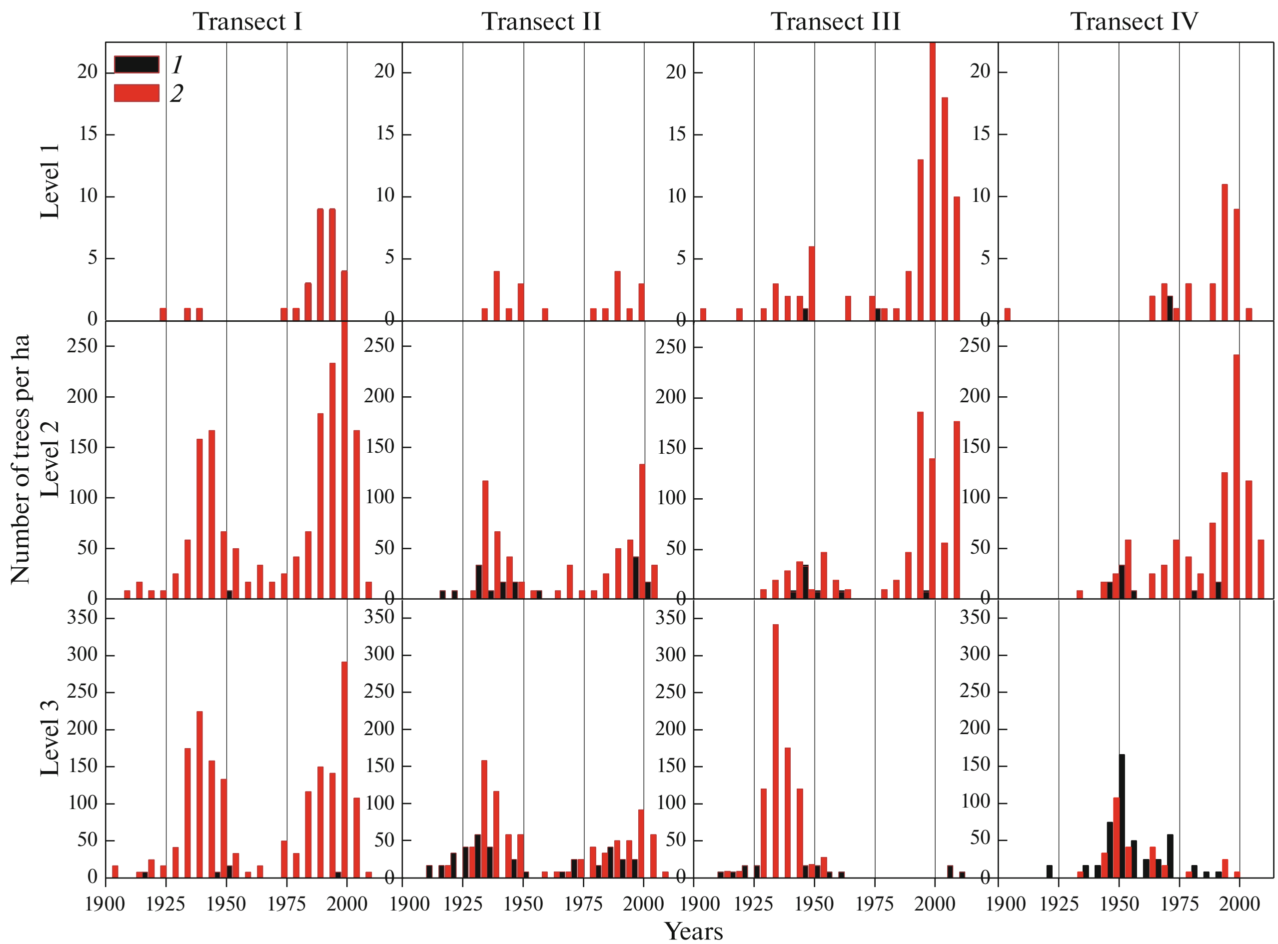

Fig. 3. Age structure of tree stands at different levels of altitudinal transects in the Northern Kraka massif.

over 5 years, respectively (Fig. 3). At the upper level of this transect, one generation was formed in the period from 1790 to 1810 and the next regeneration wave occurred between 1930 and 1950, unlike at the middle and lower layers.

Transect test area IV is characterized by extremely uneven, mosaic distribution of trees over the steppificated slope. The proportion of larch in tree stands is higher, and several tree generations can be distinguished in their age structure: the generations of larch were formed in the periods of 1750 to 1805, 1820 to 1855, 1915 to 1940, and 1950 to 1985; the generations of pine, in 1840 to 1870, 1915 to 1930, 1935 to 1960, and 1970 to 2005 (Fig. 2).

On the Northern Kraka, trees began to appear only after 1800, except for a few trees that appeared slightly earlier on transect III (Shigay), and the greater part of stands were formed in the 20th century, i.e., significantly later than on the Southern Kraka (see Fig. 3). Two peaks of emergence of trees in the test areas can be noted, which are synchronous on all the transects. Thus, the first generation of trees on the Northern Kraka was formed in 1925 to 1950, and the second, in 1975 to 2005, which coincides with the second regeneration wave on the Southern Kraka. At the lower level of transect III (Shigay), a new generation formed after 1960 is absent, which is probably due to a ground fire that destroyed the undergrowth in this area, On transect IV (Mt. Central Akbiik), the age structure of stands is different in that the bulk of trees at the upper and middle levels appeared after 1960, with a peak of regeneration in 2000; at the lower level, active regeneration began in 1935, with its activity gradually increasing by 1950 and then decreasing by 1990 (Fig. 3).

Effect of Local Conditions and Climatic Factors on the Structure and Dynamics of Tree Stands

As shown above, the most active formation of closed tree stands has occurred in recent decades in the lower parts of the steppificated slopes, where soil moisture contents are higher than in the upper parts (Table 3) and forest regeneration is therefore more successful (Table 1). This is confirmed by the results of analysis of the relationships between the number of undergrowth counted in the plots (Table 1) and moisture contents in the snow (Table 2) and the soil (Table 3): as these contents increase down the slope, the density

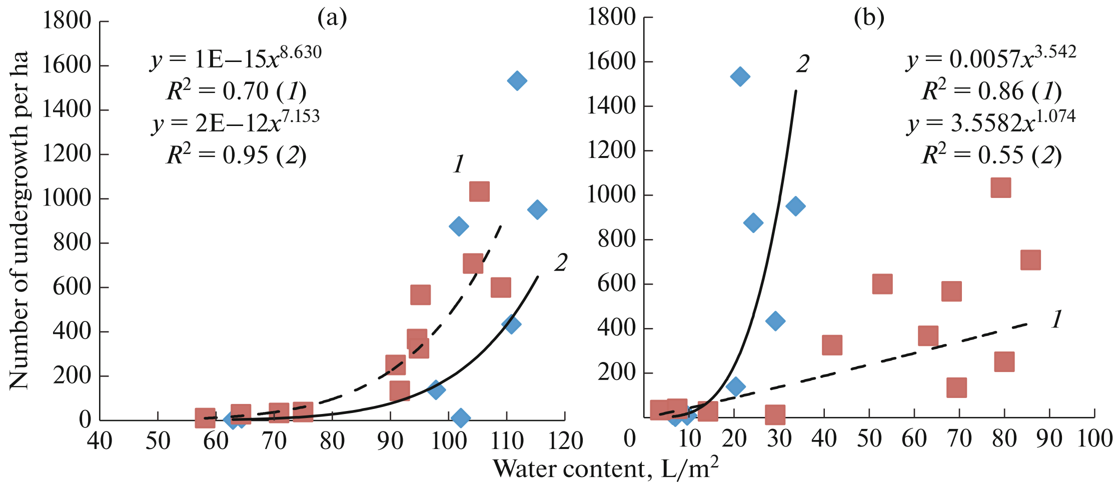

Fig. 4. The number of undergrowth as a function of (a) snow water content in 2019 and (b) soil water content in 2018 in plots surveyed in the forest–mountain steppe ecotone on (*1*) Southern Kraka and (*2*) Northern Kraka massifs.

and seed productivity of stands also increase two- to threefold, and the abundance of live undergrowth becomes tens of time greater against this background (Fig. 4).

Although the growth of tree plants in arid areas is largely limited by the conditions of the summer months (negative correlations with air temperatures and positive with precipitation) [3, 28], we revealed close positive correlations between the numbers of trees in age groups and the amount of precipitation in May–August ($R^2 = 0.65$) only for the period between 1930 and 1950. and only for the tree stands growing in the lower parts of the forest–mountain steppe ecotone. Such correlations for other periods and other parts of the ecotone were absent or insignificant.

As follows from Figs. 2 and 3, a surge of regeneration in the period after 1975 occurred on all transects, both at the recent boundary between closed and open forests and in areas bordering on mountain steppes. At the same time, the proportion of pine relative to larch in tree stands showed a tendency to increase in all parts of the slopes. Analysis of the dependence between the number of trees averaged over eight transects in 5-year age groups and the amount of precipitation in the previous cold period (October–April) showed that winter precipitation had no significant effect on the formation of tree stands (the appearance and subsequent survival of trees) until 1970, but a clear correlation between the numbers of trees in age groups and the amount of precipitation in the winter months ($R^2 = 0.61–0.74$) was revealed in the period from 1975 and 2005 at all altitudinal levels in the transition zone from the closed forest to the mountain steppes (Fig. 5).

DISCUSSION

During the past few decades, tree vegetation in the study region has been actively regenerating throughout the altitudinal gradient in the forest–mountain steppe transition zone. The expansion of tree vegetation on the slopes of different aspects (southwestern, southern, and southeastern), steepness (15–35 degrees), and stoniness in the absence of signs of fires and intensive livestock grazing indicates that the widespread improvement of conditions for the emergence and survival of tree undergrowth is due to the influence of certain factors that are common to the entire study region, i.e., no other factors but climatic. The analysis of weather data over the past 80 years (see above) provides evidence that climate in this region has become warmer and more humid, especially in the winter months, as in other regions of the Southern Urals [13].

It should be noted that the processes of forest expansion to certain steppe and forest–steppe areas are characteristic of some parts of the Baikal region, where conditions are closely similar to those in the study region [28], and also of some regions of Mongolia. The expansion of forest areas and improvement of forest productivity observed under conditions of moisture deficiency (in semiarid and arid regions) are attributed to increase in the availability of soil moisture, especially at the beginning of the growing season [30]. If not enough moisture is available for trees, their growth in inhibited because of water stress, and forests die off [4, 31].

The period of active synchronous regeneration and rapid growth of trees in 1975 to 2005 was also noted in other regions of the world [32]. Pine regeneration in the mountain steppes during the past 20 years has been described in the foothills of the Ilmen Range (the Southern Urals) [33]. Tree vegetation in the Middle Urals has also expanded during the past 4–5 decades,

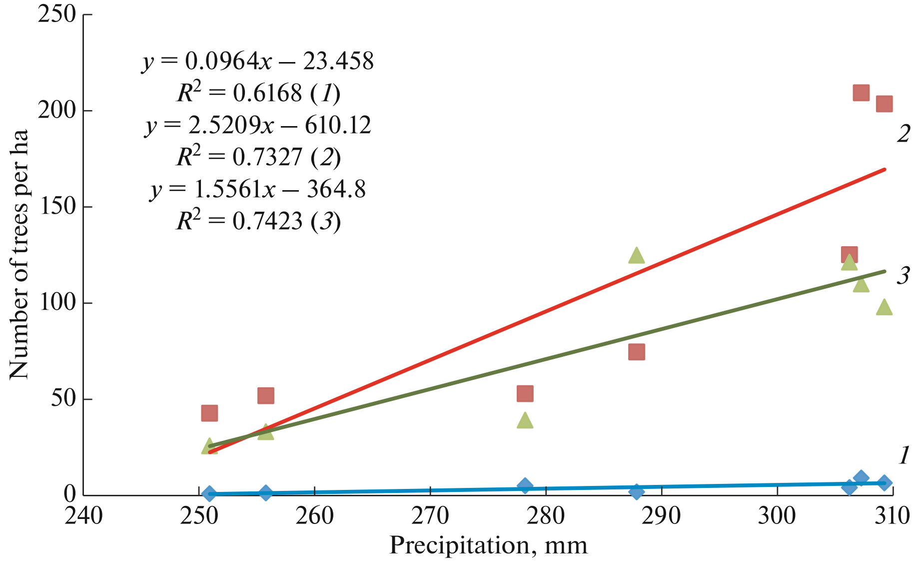

Fig. 5. The number of trees in 5-year age groups (averaged over all transects) as a function of total precipitation of the previous cold period (October–April) averaged over 5-year periods (1975–2005): (*1*) upper level, (*2*) middle level, (*3*) lower level.

with consequent reduction of the area occupied by extrazonal steppe vegetation. A survey of steppificated areas previously described in the vicinity of Yekaterinburg showed that three of them had virtually disappeared as a result of overgrowing by pine [17]. At the moment, conditions for the development of tree vegetation are favorable even in areas where steppe vegetation has been preserved for thousands of years [15].

The decrease in areas occupied by steppe communities in recent decades has been explained by climatic changes such as rising winter temperatures and precipitation and decreasing anthropogenic impact [7]. It was during the period of increase in precipitation that the large-scale appearance of pine trees was revealed on the steppe slope of the Bolshaya Hill in the Krasnoufimskaya forest–steppe in 1952–1954, and in the steppe section of Elizavetinsky Log in 1967–1988. Kazantseva et al. [34] also consider that the active development of trees plants in the Kamennaya steppe (Voronezh oblast) since 1972 coincides with an increase in annual average air temperature, precipitation, and water table rise. Active pine establishment in steppe communities bordering on forests in southwestern Transbaikalia in 1988–1993 is also attributed to the effect of moisture cycles against the background of reduced anthropogenic loads [35].

It is known that soil moisture in dry areas at the beginning of the growing season primarily depends on the amount of precipitation in the previous period (October–April). Rainfall in autumn and spring immediately penetrates the soil, while the degree of replenishment of soil moisture reserves due to snow melt largely depends on the depth of soil freezing, soil thickness, and water-holding capacity. In the mountains, the “loss” of snow moisture to surface runoff and evaporation in spring is significant. In our opinion, the sharp difference in the sensitivity of tree stand regeneration to the amount of winter precipitation between the periods before and after 1970 is due to a decrease in the depth of freezing of the surface soil layer due to rising air temperatures and precipitation in winter and more rapid soil thawing in spring. This circumstance has contributed to an increase in the proportion of snowmelt moisture penetrating the soil and decrease in the relative amount of surface runoff.

As follows from Table 2, the depth of the snow cover and moisture reserves accumulated in it during winter in the upper parts of the slopes are, on average, two to three times smaller than in the lower parts and high insolation results in more rapid snow melting in spring and drying of the thin soil layer in summer. As a result, tree seedlings regularly appearing in these areas die off within a few years, since soil moisture is the leading factor of their survival in the initial period of growth [37]. On the other hand, areas in topographic depressions (hollows, ravines, terraces) and near the boundary of closed forests retain snow cover for a longer time and receive additional moisture supply due to subsurface snowmelt runoff from higher elevations. In addition, they are shaded by tree crowns in summer, which protects from excessive warming and loss of soil moisture. Similar results have been obtained in studies on the effect of topographic features and slope exposure on soil moisture and snow depth [31]. On the whole, this explains more active forest regeneration in such areas during the past decades against the background of general increase in winter precipitation. According to [10], soil moisture in the mountains primarily depends on altitudinal location of a given area, slope steepness, and also on the properties and thickness of soils, while regeneration intensity and the state of trees depend on slope exposure and soil properties.

Zolotareva and Zolotarev [7] consider that the rate of forest expansion to steppificated areas depends on their size and proximity to forest massifs. In the case of extrazonal steppes (especially represented by small sites), any climatic and microclimatic changes providing favorable conditions for the development of trees lead to the complete loss of steppe vegetation. This is apparently due to a higher level of seed flow per unit area of small steppe sites adjoining the forest edge and more abundant moisture supply provided by greater amounts of snow accumulated during winter.

CONCLUSIONS

The total size of steppificated areas on the slopes of the Kraka range in the southeastern part of the Southern Urals has decreased by 17.6% between 1986 and 2015 as a result of their overgrowing by closed forests. This is due to active forest regeneration that occurred in the lower parts of steppificated slopes during the periods of higher summer precipitation between 1915 and the 1960s, which subsequently provided for an increase in the density of tree stands and displacement of the boundaries of closed forests up the slopes. Active regeneration of pine and larch both at the boundary of closed forests and above it has also been observed in the past 35-40 years marked by relatively high winter precipitation. In the future, an increase in the amount of precipitation in the absence of fires may lead to further reduction of steppificated areas in this region of the Urals.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest

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