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Primary Successions of Vegetation on the Young Moraines in the Severo-Chuiskiy Center of Glaciation (Central Altai)

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Abstract—The primary successions of vegetation have been investigated in the continental conditions of the Severo-Chuiskiy center of present-day glaciation (Central Altai) from the colonization of deglaciated terrains by the first plants to the formation of simple plant groups to the primary plant communities. The observations were carried out for 15 years on the young moraines of the valley glaciers of Malyi Aktru (2200–2250 m a.s.l.) and Bolshoi–Levyi Aktru (2370–2500 m a.s.l.) in chrono-sequences from the ends of glaciers to the moraines of the mid-19th century. Three stages and four sub-stages of the primary succession of vegetation are identified. The species composition of vascular plants, mosses, and ground lichens is identified; the dominant species and the peculiarities of primary vegetation are characterized. Ideas about the course of successions and their peculiarities at different altitudes in the upper part of the forest and subchalet altitudinal zones are obtained. It has been found that, in the 150 year period, a young forest community has been formed on new moraines in the upper part of the forest altitudinal zone, and a combination of microcenoses similar to tundra communities have been formed in the alpine altitudinal zone. The primary succession of vegetation on both glacier forelands has some similarities, especially in early stages of ecosystem development (pioneer species composition and three-stage structure of successions). Strong differences appear during the late stages of succession. The primary succession of vegetation on the foreland of the Malyi Aktru glacier involves 146 species of vascular plants, 44 species of mosses, and 6 species of lichens. On the foreland of Bolshoi Levyi Aktru, 128 species of vascular plants, 26 species of mosses, and 8 ground lichens have been recorded.

Keywords: young moraines, vascular plants, mosses, lichens, primary successions, dynamics, Severo-Chuiskiy center of glaciation, Central Altai

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INTRODUCTION

In the modern period of global climate change, glaciers are retreating in all the mountain systems of the world (Barry, 2006). A study of the successions of vegetation in the deglaciated territories were carried out in areas with a milder and more humid climate than in Siberia: in the mountains of Western Europe, the Alps (Lüdi, 1945; Zollitsch, 1969; Richard, 1973; Schubiger, 1988; Burga et al., 2010; Andreis et al., 2001), in Scandinavia (Stork, 1963; Elven and Ryywarden, 1975; Elven, 1978; Matthews and Whittacker, 1987), and in the mountains of North America (Cooper, 1939; Lawrence, 1958; Reiners et al., 1971; Birks, 1980; Spence, 1985; Jones and del Moral, 2005).

Studies of successions on young moraines of Asian mountain systems are scarse; they were carried out only in the Himalayas (Tishkov, 2007) and in Kamchatka (Vyatkina et al., 2007). We have started the investigaitons of the primary sucessions of vegetaion in the continental conditions of the Altai in the 2000; the young moraines of the Severo-Chuiskiy, Yuzhno-Chuisky and Katusky ranges were examined (Timoshok et al., 2003, 2008, 2012; Timoshok et al., 2016). The studies were carried out in more detail in the Severo-Chuisky glaciation center in the Aktru mountain glacier basin. We separately studied the composition and distribution of one of the groups of vascular spore plants, ferns, in the periglacial zone of the glaciers of Central Altai, including moraines (Gureyeva and Timoshok, 2016).

The purpose of this study was investigation the primary successions and their features at different absolute heights and in different environmental conditions on the young moraines of the Malyi Aktru and Bolshoy Levyi Aktru valley glaciers, starting from the glacier tongues to the terminal moraine rims of the mid-19th century.

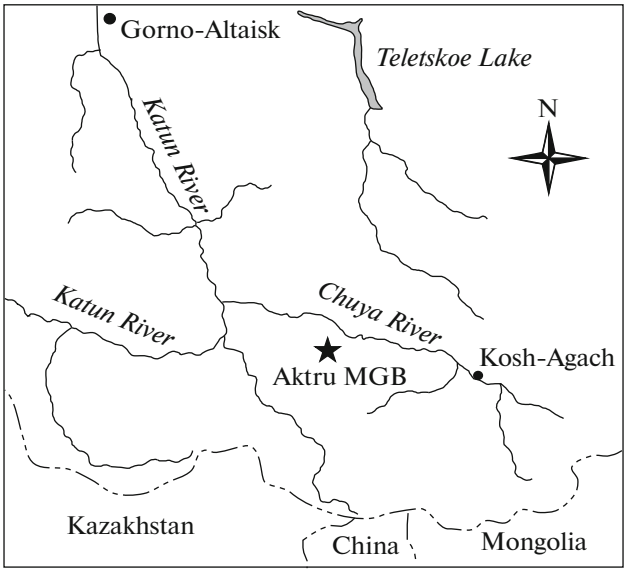

Fig. 1. Map of Russian Altai. The asterisk indicates the location of the Aktru mountain–glacial basin (Aktru MGB).

MATERIALS AND METHODS

Central Altai is the highest part of Altai Mountains, where more than 80% of all glaciers of the Russian Altai are concentrated. The average height of the rims in the Severo-Chuisky, Yuzhno-Chuisky, and Katunsky glaciation centers reaches 3100–3300 m above sea level. The continental climate of Altai and these glaciation centers is determined by the occurrence of this highland in the center of the Asian continent and a significant distance from the seas and oceans (Tronov, 1966).

In the Severo-Chuisky center, glaciation reaches its greatest development in the Bish-Iirdu mountain node, in the eastern part of which the Aktru mountain-glacial basin (50°05′ N, 87°45′ E) is located (Fig. 1). By the data of the Aktru weather station (2150 m a.s.l.), the average annual temperature in the basin is –5.2°C, the average annual rainfall is 520 mm, and the relative humidity is on average 67%. In the summer months, even in July, at night the temperature often drops to 0 to +4°C; during the day it rises to +15 to +17°C. In the basin, south and southwest winds prevail throughout the year. In the summer, the diurnal and mountain winds change is clearly distinguishable in the diurnal course: the valley winds arise in the afternoon and are directed from the valley to the axial part of the rim, and at night the opposite winds blow in the mountains (*Ledniki Aktru*, 1987; Sevast'yanov, 1998).

We studied vegetation successions on young moraines of the valley glaciers Malyi Aktru (2200–2250 m) and Bolshoi Levyi Aktru (2370–2500 m a.s.l.) for 15 years.

The maximum advance of the Malyi Aktru glacier has occurred in the middle of the 19th century (Dushkin, 1965), when it reached the altitude of 2200 m, where a high terminal moraine rim was formed. This glacier is the glaciological reference point of Altai and is best provided with glaciological data: in 1911, the position of its edge location was marked by Professor V. V. Sapozhnikov and, in 1936, by M.V. Tronov. Since 1952, the glacier recession was measured annually by glaciologists at Tomsk University. From 1850 to 2008, the glacier receded by 810 m: from 1850 to 1911 by 260 m, from 1911 to 1936 by 90 m, from 1936 to 1952 by 59 m, from 1952 to 1999 by 256 m, and from 1999 to 2008 by 146 m (Tronov, 1939, Narozhniy, Okishev, 1999, Narozhnyi and Zemtsov, 2011).

Young moraines of the Small Aktru glacier are descending to the upper part of the forest altitudinal zone. Vegetation succession here takes place at an average summer temperature of +8.7°C, with average temperatures of +8.4°C in June, +9.7°C in July, and +7.9°C in August. The relief are represented by flattened areas, mesicosities, and slopes of different steepness.

In the middle of the 19th century, the Bolshoi Aktru glacier formed a well-distinguished terminal moraine rim at an altitude of 2370 m a.s.l. (Dushkin, 1965). From 1850 to 1936, the glacier retreated 288 m from the terminal moraine rim, to 1962 another 172 m, and in general 460 m. In the 1960s, the Bolshoi Aktru glacier was divided into two independent glaciers in the course of further recession: Bolshoi Levyi and Bolshoi Pravyi Aktru. From 1962 to 2008, Levyi Aktru receded 500 m. Bolshoi Pravyi Aktru, whose tongue is armored with a powerful moraine cover, retreated 200 m (Narozhniy and Zemtsov, 2011).

Young moraines of the Bolshoi Levyi Aktru glacier are located at altitudes of 2370–2500 m a.s.l. in the subalpine altitudinal zone, 200–300 m above the moraines of the Malyi Aktru. Vegetation successions occurs here at lower summer temperatures (on average, 1.5–2°C lower): average temperatures are +7.1°C in summer, +6.7°C in June, +7.8°C in July, and +6.6°C in August.

High hills (up to 10–20 m high), composed almost exclusively of bouldery and crushed stones substrate; the steep slopes of the hills are unstable, dominate in the moraine relief of Bolshoi Aktru. The areas with melkozem cover small areas, mainly in cup-shaped lowerings between the hills. The moraines of the Levyi Aktru are represented by gentle and steep (up to 40°) areas composed mainly of macrofragmental material.

The moraine deposits of the Malyi Aktru and Bolshoi Levyi Aktru glaciers are represented by the products of physical weathering and redeposition of bedrock: sericite–chlorite slates, phyllites, and quartzites (*Ledniki Aktru*, 1987). They contain mainly macrofragmental material: boulders; crushed stone; and a small amount of melkozem, which includes carbonates. They are absent in macrofragmental material (Davydov and Timoshok, 2010). Primary successions

Table 1. Number of plants of different life forms at the stages and substages of the primary succession of vegetation on the moraines of the Malyi Aktru and Bolshoi Levyi Aktru glaciers

Stages and substages of succession	Malyi Aktru					Bolshoi Levyi Aktru				
	T	Tsh+DSh	H	M	L	T	Tsh+DSh	H	M	L
I.1	–	13	22	4	–	–	4	11	3	–
I.2	–	13	25	4	–	–	17	24	5	3
I (total)	–	13	25	5	–	–	17	24	6	3
II.1	2	15	35	10	–	–	20	29	8	3
II.2	2	18	39	12	–	–	22	35	8	3
II (total)	2	19	39	14	–	–	22	35	9	3
III	2	18	35	14	–	–	22	35	9	3

T, trees; TSh, tall shrubs; DSh, dwarf shrubs; H, herbs; M, mosses; and L, lichens.

of vegetation on young moraines of both glaciers occur on a calcareous substrate.

The collection of materials on young moraines of the both glaciers was carried out in chronological sequences from the glacier tongues to the terminal moraine rims of the mid-19th century on moraines deposited 0–5, 5–20, 20–40 (50), 40–70, 70–100, and 100–150 years ago which dating is based upon the long-term instrumental glaciological data (Tronov, 1939, 1949; Narozhnyi and Okishev, 1999; Narozhniy and Zemtsov, 2011). We are througly registered the distribution, cover and abundance for all vascular plant, moss and ground lichen species found for each chronosequence fragment. The abundance of each species was registered in marks of Braun-Blanquet scale (1932): +, single; 1, multiple individuals with a coverage of 1–5%; 2, abundant, 5–15%; 3, coverage of 15–25%; 4, 25–50%; and 5, coverage of more than 50% of the area. Pregenerative and generative individuals of vascular plants were noted separately. Forty-one sampling plots were laid in the selected chronological sequences on the moraines of the Malyi Aktru and 38 sampling plots (10 × 10 m^2) were on the moraines of the Bolshoi Levyi Aktru; more than 90 microsite groupings were described.

All species found in the relevés are divided into two groups: the primary participants in the succession, which are noted in the majority of geobotanical descriptions, and the secondary species, noted in some ones. The same species in different environmental conditions on moraines of different glaciers may be the primary participants or accidental species.

The peculiarities of the formation of primary vegetation—from single individuals, single-species aggregations, and simple and complex groups in the early stages of succession to primary communities or microcenoses at the late stage—were recorded on the studied moraines. The stages and substages of primary succession were identified on the basis of changes in the groups of dominant species, life forms, and the complexity of the structure of primary vegetation. Only large divisions of life forms were considered (Table 1).

RESULTS

Malyi Aktru glacier. The primary succession on the moraines of the Malyi Aktru glacier goes through three stages: the first (pioneer), second, and third (Fig. 2). The pioneer and second stages of succession are divided into two substages each.

The pioneer succession stage (I) (50–230 m from the glacier on moraines deposited 5–40 years ago) begins in flat areas composed mainly of macrofragmental material with small spots of sandy loam melkozem. The first plants are single individuals of the herbs *Saxifraga oppositifolia* L., *Chamaenerion latifolium* (L). Sweet, and *Crepis karelinii* Popov et Schischk. ex Czerep. which occur 50 m from the tongue of the glacier on microsites with melkozem.

In the first substage of succession (I.1) (50–150 m from the glacier, moraines deposited 5–20 years ago), 68 species of vascular plants were recorded. Fifty-three species of herbs and 16 species of tall shrubs were recorded in microsites favorable for settlement with moist melkozem earth between stones; the primary participants here are 35 species of herbs, tall shrubs, and dwarf shrubs (Tables 1, 2); there was also 33 accidental species. Herbaceous plants reach the generative period of ontogenesis, begin to bloom and bear fruit, and tall shrubs are still in the pregenerative period of ontogenesis. In the same microsites, extremely rare patches of seven species of acrocarpous mosses were recorded. Four of these species are the primary participants (Table 2). All plants occur as singular individuals, randomly distributed over the area. The total cover of plants at the end of the substage is about 5%.

In the second substage of this stage (I.2) (150–230 m from the glacier, moraines deposited 20–40 years ago), 60 species of vascular plants (42 herbs and 18 tall shrubs and dwarf shrubs) were recorded. The primary participants here are 38 species are herbs, tall shrubs,

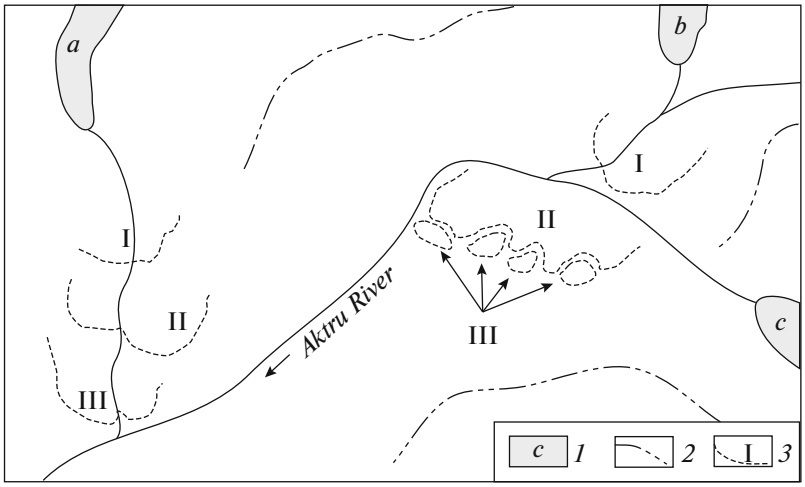

Fig. 2. Map of the stages of primary succession of vegetation in young moraines of the Malyi Aktru and Bolshoi Levyi Aktru glaciers. Legend: (*1*) glaciers: (*a*) Malyi Aktru, (*b*) Bolshoi Pravyi Aktru, (*c*) Bolshoi Levyi Aktru, (*2*) watershed lines, (*3*) boundaries of the stages of primary vegetation successions on young moraines of Malyi Aktru and Bolshoi Levyi Aktru glaciers, (I) pioneer stage, (II) second stage, and (III) third stage.

and dwarf shrubs (Tables 1, 2). There are six species of acrocarpous mosses, four of which are the primary participants (Table 2). Main peculiarity of this substage is the formation of single-species aggregations of herbs, multi-species groupings which include a little number of herb and tall shrub species in a pregenerative state, and the growth of separately growing pregenerative willows and dryads. Small single-species aggregations of individuals of different ages and the simple groupings of herbs form on moist melkozem; they most often include *Draba cana* Rydb., *Braya aenea* Bunge, *Saxifraga oppositifolia*, *Poa glauca* Vahl., and *Trisetum mongolicum* (Hultén) Peschkova. The abundance of plants is low, with the exception of three species: Draco*cephalum imberbe*, *Chamaenerion latifolium*, and *Crepis karelini*i (Table 2). Less commonly, mainly in fine-grained areas, there are simple groupings of tall shrubs and perennial herbs:: *Salix saposhnikovii* A.K. Skvortsov + *Dracocephalum imberbe* Bunge + *Saxifraga oppositifolia* + *Crepis karelinii*; *Salix vestita* Pursh. + *Draba cana* Rydb. + *Poa glauca*; *Myricaria dahurica* DC. + *Saxifraga oppositifolia* + *Crepis karelinii* + *Braya aenea*. Mosses (Table 2) form very small (about 2 cm diam.) isolated patches. The total projective cover of plants at the end of the substage is about 10%.

In general, 78 species of vascular plants participate in the pioneer stage of succession, of which 38 are the primary participants—herbs, tall shrubs and dwarf shrubs (Tables 1, 2)—and 40 are accidental species. Herbal plants (*Braya rosea* Bunge, *Chorispora bungeana* Fisch., *Crepis nana* Richardson, *Draba sapozhnikovii* Ebel, *Erigeron politus* Fr., *Mesostemma martjanovii* (Krylov) Ikonn., *Minuartia verna* (L.) Hiern., and *Oxyria digyna* (L.) Hill., etc.) dominate among accidental species. Tall shrubs (*Grossularia acicularis* Spach, *Ribes graveolens* Bunge, *Salix viminalis* L., etc.) are rare; trees (*Populus laurifolia* Ledeb. and *P. tremula* L.) are singular. During the observation period, ten species of mosses were recorded at the pioneer stage, of which five are the primary participants in succession (Table 2) and five are accidental species (*Bryum argenteum* Hedw., *B. creberrimum* Taylor, *Dicranella subulata* (Hedw) Schimp, etc.). The core of the pioneer stage is composed of short (5–15 cm tall) perennial herbs that bloom, bear fruit, and propagate steadily by seeds, as evidenced by single-species clusters of individuals of different ages. The distribution of plants by area is random, mosaic for some individuals, their aggregations, and multi-species groups. The total projective cover of plants by the end of the stage reaches 10%.

The second stage of succession (II) (230–600 m from the glacier, on moraines deposited 40–100 years ago) is distinguished in leveled areas with small elevated areas (rocky rims) and depressions (channels of temporary streams).

In the first substage (II.1) (230–340 m from the glacier, moraines deposited 40–60 years ago), 83 species of vascular plants were found, including 54 species of herbs and 26 species of tall shrubs and dwarf shrubs (Tables 1, 2). The primary participants were of 52 species: 35 herbs, 15 tall shrubs, and 2 trees. Seventeen species of mosses were recorded here, of which ten are the primary participants (Table 2). The highest occurrence was noted for eight species of herbs (*Castilleja pallida* (L.) Spreng., *Crepis karelinii*, *Chamaenerion latifolium*, *Draba cana*, *Dracocephalum imberbe*, *Poa glauca*, *Saxifraga oppositifolia*, and *Trisetum mongolicum*), four species of tall shrubs (*Juniperus sibirica* Burgsd., *Myricaria dahurica*, *Salix tuvinensis* Gudoschn., *S. saposhnikovii*), and three species of dwarf shrubs

Table 2. Primary participants in primary successions on young moraines of the Malyi Aktru and Bolshoi Levyi Aktru glaciers

Young moraines	Malyi Aktru glacier					Bolshoi Levyi Aktru glacier				
Stages of succession	I		II		III	I		II		III
Substages of succession	I.1	I.2	II.1	II.2		I.1	I.2	II.1	II.2	
Herbs										
Antennaria dioica	–	–	+	+	+	–	–	–	–	+
Aquilegia sibirica	–	–	+	+	+	–	–	–	–	–
Aster alpinus	–	–	+	+	+	–	–	–	–	–
A. sibiricus	–	–	+	+	+	–	–	–	–	–
Astragalus frigidus	–	–	+	+	1	–	–	–	–	–
Bergenia crassifolia	–	–	+	+	+	–	–	–	–	–
Bistorta vivipara	–	–	–	–	–	–	+	+	+	+
Braya aenea	+	+	+	+	+	+	+	+	+	+
Campanula rotundifolia	+	+	+	+	+	–	+	+	+	+
Carex macroura	–	–	–	+	+	–	–	–	+	+
C. tristis	–	–	–	+	+	–	+	+	+	1
Castilleja pallida	+	+	1	1	+	–	+	+	1	1
Chamaenerion latifolium	+	1	1	1	+	+	+	1	1	+
Crepis karelinii	+	1	1	+	+	+	+	+	+	+
C. polytricha	–	–	–	–	–	+	+	+	+	+
Draba cana	+	+	+	+	+	+	+	+	–	–
Dracocephalum imberbe	+	1	1	1	+	+	+	1	1	+
Elymus sajanensis	+	+	+	+	+	–	+	+	+	+
Erigeron altaicus	+	+	+	+	+	–	–	–	+	+
E. eriocalyx	+	+	+	+	–	+	+	+	+	+
Festuca altaica	–	–	+	+	+	–	–	–	–	+
F. kryloviana	–	–	–	–	–	–	–	–	+	+
F. lenensis	+	+	+	+	+	–	–	–	+	+
Galium ruthenicum	–	–	–	–	–	–	–	–	+	+
Gentiana macrophylla	–	–	–	+	+	–	–	–	–	–
Gypsophila cephalotes	–	–	+	+	+	–	–	+	+	+
Hedysarum neglectum	–	+	+	+	1	–	–	+	+	+
Leontopodium ochroleucum	+	+	+	+	+	–	+	+	+	+
Lupinaster eximius	–	–	–	–	–	–	+	+	+	1
Minuartia kryloviana	+	+	+	–	–	–	+	+	+	+
Orthilia obtusata	–	–	–	+	+	–	–	–	–	–
Oxytropis alpestris	–	–	–	–	–	–	–	+	+	+
O. alpina	–	–	–	–	–	–	–	+	+	+
O. ambigua	+	+	+	+	1	–	–	–	–	–
O. oligantha	+	+	+	+	+	–	–	–	–	–
O. pauciflora	+	+	+	+	+	–	–	–	–	–
Pachypleurum alpinum	–	–	+	+	+	+	+	+	+	+
Patrinia sibirica	–	–	–	–	–	–	+	+	+	+
Poa alpina	–	–	+	+	+	–	–	+	+	+
P. altaica	+	+	+	+	+	–	+	+	+	+
P. attenuata	+	+	+	+	–	–	–	–	–	–
P. glauca	+	+	+	+	–	+	+	+	+	+
Pyrola rotundifolia	–	–	–	+	+	–	–	–	–	–
Rhodiola coccinea	+	+	+	+	–	–	–	–	–	–
Saxifraga oppositifolia	+	+	+	+	+	+	+	+	+	+
S. sibirica	–	–	–	–	–	+	+	+	+	+
Silene chamarensis	–	+	+	+	+	–	+	+	+	+
S. turgida	–	+	+	+	+	–	+	+	+	+
Trisetum mongolicum	+	+	+	+	+	+	+	+	+	+
Dwarf shrubs										
Dryas oxyodonta	+	+	1	2	1	+	+	1	1	3
Empetrum nigrum	–	–	–	–	–	–	+	+	+	+
Salix arctica	–	–	–	–	–	–	+	+	+	+
S. berberifolia	+	+	1	1	1	+	+	1	1	+
S. rectijulis	–	–	–	+	+	–	+	+	+	+
S. reticulate	–	–	–	+	+	–	–	–	+	+

Table 2. (Contd.)

Young moraines	Malyi Aktru glacier					Bolshoi Levyi Aktru glacier				
Stages of succession	I		II		III	I		II		III
Substages of succession	I.1	I.2	II.1	II.2		I.1	I.2	II.1	II.2	
S. turczaninowii	–	–	–	–	–	–	+	+	+	+
S. vestita	+	+	+	1	+	+	+	+	1	1
Tall shrubs										
Juniperus pseudosabina	+	+	+	+	+	–	+	+	+	+
Juniperus sibirica	+	+	+	1	1	–	+	1	1	1
Betula rotundifolia	–	–	+	1	4	–	–	+	+	+
Lonicera hispida	+	+	+	+	+	–	–	+	+	+
Myricaria dahurica	+	+	1	1	+	+	+	+	+	+
Pentaphylloides fruticosa	–	–	–	–	–	–	+	+	+	+
Salix coesia	+	+	+	1	+	–	+	+	1	1
S. divaricata	+	+	+	+	+	–	+	+	+	+
S. glauca	+	+	+	+	1	–	+	+	1	1
S. hastata	+	+	+	+	+	–	+	+	+	+
S. pyrolifolia	–	–	+	+	+	–	–	+	+	+
S. recurvigemmis	–	–	–	+	+	–	–	–	+	+
S. sajanensis	+	+	+	+	+	–	+	+	+	+
S. saposhnikovii	+	+	1	2	1	–	+	1	1	2
Trees										
Larix sibirica	–	–	+	+	2	–	–	–	–	–
Pinus sibirica	–	–	+	+	+	–	–	–	–	–
Mosses										
Abietinella abietina	–	–	–	–	1	–	–	–	–	+
Ceratodon purpureus	+	+	+	–	+	+	+	+	+	
Brachythecium salebrosum	–	–	–	+	1	–	–	–	–	–
Bryum caespiticium	+	+	+	+	–	–	–	–	–	–
B. elegans	+	–	+	–	+	+	–	+	–	+
B. lonchocaulon	–	–	–	–	–	+	+	+	+	+
Hypnum cupressiforme	–	–	+	+	+	–	–	–	–	–
Didymodon rigidulus	–	–	–	+	+	–	–	–	–	–
Ditrichum flexicaule	+	+	+	1	1	–	+	+	+	1
Distichium capillaceum	–	+	+	1	+	–	+	+	+	+
Pseudoleskeella rupestris	–	–	–	+	+	–	–	–	–	–
Pylaisia polyantha	–	–	+	+	+	–	–	–	–	–
Sanionia uncinata	–	–	–	+	1	–	–	–	+	1
Syntrichia ruralis	–	–	+	1	1	–	–	+	+	+
Stereodon revolutus	–	–	+	1	2	–	–	–	–	
Tortella fragilis	–	–	–	–	–	+	+	+	+	+
T. inclinata	–	–	–	–	–	–	–	+	+	1
T. tortuosa	–	–	+	1	+	–	–	–	–	–
Ground lichens										
Cladonia pyxidata	–	–	–	–	–	–	+	+	+	+
Stereocaulon alpinum	–	–	–	–T	–	–	+	2	1	+
Vulpicida tilesii	–	–	–	–	–	–	+	+	+	+

The columns show the projective cover—the abundance of species in points on the Braun-Blanquet scale (1932): (+) single; (1) multiple individuals with a cover of 1–5%; (2) abundant, cover of 5–15%; (3) cover of 15–25%; (4) cover of 25–50%; and (5) cover of more than 50% of the area.

(*Dryas oxyodonta*, *Salix berberifolia* Pall., and *S. vestita*). The first substage is characterized by the appearance of complex multispecies groups in the relief lowerings. They are usually formed by tall shrubs and mosses and are small in area (up to 1 m in diameter.). They include generative individuals of *Myricaria dahurica*, *Salix saposhnikovii*, *S. vestita*, *S. tuvinensis*, *S. hastata* L., *S. glauca* L., and *S. sajanensis* Nasarov. Under the tall shrubs, a moss cover is formed from isolated patches (10 × 15 cm) of *Bryum caespiticum*, *Distichium capillaceum*, *Ditrichum flexicaule*, *Ceratodon purpureus*, *Syntrichia ruralis* (Hedw.) F. Weber et D. Mohr, *Stereodon revolutus* Mitt., and *Hypnum cup. Tortella tortuosa* (Hedw.) Limpr. The groups include single individuals of herbs, most often *Erigeron altaicus* Popov, *Dracocephalum imberbe*, and *Castilleja pal-*

lida. All herbs and tall shrubs are in the generative period of ontogenesis; they bloom, bear fruit, and form full-fledged seeds; trees are in the pregenerative period of ontogenesis. The abundance of most species is very low; only eight species reach 1 mark abundance (Table 2). The distribution of primary vegetation is mosaic. Isolated complex groups occur only at depressions, and simple groups of pioneer herbs occur at elevated areas. At the end of the substage, the total projective cover of plants reaches 15%.

In the second substage (II.2) (470–600 m from the glacier, moraines deposited 60–100 years ago), 100 species of vascular plants were found: 62 herbs and 32 tall shrubs and dwarf shrubs. The primary participants are 59 species, of which 39 are herbs, 18 are tall shrubs and dwarf shrubs, and 2 are trees (Tables 1 and 2). Twenty-two species of mosses grow here, including 12 primary participants (Table 2), and 6 species of lichens, all of them are accidental (*Cladonia pocillum* (Ach.) Grognot, *C. pyxidata* (L.) Hoffm., *Flavocetraria nivalis* (L.) Karnefelt, *Peltigera scabrosa* Th. Fr., *Stereocaulon alpinum* Laur., *Vulpicida tilesii* (Ach.) Mattsson). Eight species of tall shrubs, three types of herbs, and five species of mosses reach mark 1 or greater on this substage (Table 2). The most important dominants are species of the genus *Salix*: S. *berberifolia*, *S. saposhnikovii*, *S. vestita*, and *S. tuvinensis* (Table 2), which form a well-developed shrub storey, above which a few young trees of *Larix sibirica* and *Pinus sibirica* rise. Under the canopy of tall shrubs, an almost continuous cover of acrocarpous (*Distichium capillaceum* (Hedw.) Bruch., *Ditrichum flexicaule* (Schw.) Hampe, *Syntrichia ruralis*, and *Tortella tortuosa*) and pleurocarpous (*Stereodon revolutus* (Hedw.) Loeske) mosses grows. During this substage, the mass death of individuals of *Myricaria dahurica* occurs, as a result of which *Myricaria*-dominated groups are replaced by Drias-dominated ones; these groups are including *Salix saposhnikovii*, *S. hastata*, *S. vestita*, *Chamerion latifolium*, *Erigeron altaica* Trin., etc.; the size of the groups is gradually increasing. Simple groups of herbs *Castilleja pallida*, *Dracocephalum imberbe*, *Campanula rotundifolia*, *Antennaria dioica* (L.) Gaerth, *Aster alpinus* L., etc. are common at elevated areas. However, herbs lose their leading role in the formation of primary vegetation. The total cover of plants at the end of the second substage reaches 50%.

In general, at the second stage of succession, the largest number of vascular plant species was recorded (111), of which the primary participants were 60 species of trees, tall shrubs, dwarf shrubs, and herbs (Tables 1, 2). Here, the highest participation of accidental species was found (51), among which the herbaceous flowering *Bistorta vivipara* (L.) Gray, *Erigeron flaccidus* (Bunge) Botsch., *Geranium albiflo*rum Ledeb., *Kobresia myosuroides* (Vill.) Flori, *Po sibirica* Roshev., *Hylotelephium ewersii* (Ledeb.) Ohba, *Valeriana martjanovii* Krylov et al., ferns *Cystopteris fragilis* (L.) Bernh., *Woodsia glabella* Br., dwarf shrubs *Salix arctica* Pall., *S. viminalis* L., *S. turczaninowii* Laksch. et al., *Betula pendula* Roth, *Picea obovata* Ledeb., and trees of *Populus tremula*. At this stage, 29 species of mosses were noted, 14 of which are the primary participants (Table 2) and 15 are accidental species *Atrichum tenellum* (Roehl.) Bruch, *Bryum bimum* (Schreb.) Turner, *B. capillare* Hedw., *Rhytidium rugosum* (Hedw.) Kindb., and others. All lichens encountered at this stage are accidental species. The core of the second stage is dominated by tall shrubs *Juniperus sibirica* and *Myricaria dahurica*; tall and dwarf willow shrubs: *Dryas oxyodonta*; and acrocarpous mosses *Distichium capillaceum*, *Ditrichum flexicaule*, *Sintrichia ruralis*, and *Tortella tortuosa* (Table 2). This stage is characterized by the change in the dominant life form: herbs are replaced by tall shrubs and dwarf shrubs. The distribution of primary vegetation is combination of mosaic and thickets: tall shrubs occurred only at low areas and patches of *Dryas oxyodonta*, *Betula rotundifolia*, and simple groups of herbs at elevated areas.

The third stage of succession (III) (600–810 m from the glacier, on moraines deposited 100–150 years ago) is identifies on moraines composed of boulders, large stones, rubbles, and melkozem. The number of vascular plants at this stage decreases to 84 and the primary participants are 55 species: 2 trees, 18 tall shrubs and dwarf shrubs, and 35 herbs (Tables 1, 2). The number of accidental species decreases to 29; these are herbs (*Astragalus alpinus* A. Gray, *Dianthus superbus* L., *Hieracium korshinskyi* Zahn., *Parnassia palustris* L., *Saussurea controversa* DC, *Scorzonera radiata* Fisch., etc.), ferns (*Woodsia glabella* and *Cystopteris dickieana* Sim), tall shrubs (*Betula fruticosa* Pall., *Rosa oxyacantha* Bieb., and others), and trees (*Picea obovate* and *Populus laurifolia*). Twenty-four species of mosses were recorded here: 14 are the primary participants (Table 2) and 10 are accidental (*Bryum capillare* Hedw., *Brachythecium turgidum* (Hart.) Kindb., *Drepanocladus aduncus*, etc.); in addition, there were the same six accidental lichen species as in the previous stage.

This stage has significant differences of composition, abundance of the primary participants, and structure of vegetation from the first two ones. A young four-storey forest community formed here. Young trees of *Larix sibirica* 4–6 m high prevail in a sparse (crown density of 0.2) tree storey; the participation of *Pinus sibirica* is negligible. *Betula rotundifolia* of 100–120 cm high dominates in the shrub storey, which is accompanied by the same *Salix* species as in the second stage. A continuous moss cover composed mainly of pleurocarpous mosses *Stereodon revolutus*, *Abietinella abietina* (Hedw.) Fleisch., *Brachythecium salebrosum* (Weber) Bruchet., and *Sanionia uncinata* Hedw forms under the tall shrubs. A grass storey is dominated by *Astragalus frigidus* Gray, *Oxytropis ambigua* DC, *Hedysarum neglectum* Ledeb. is formed in open areas between dense tall shrubs. In rocky areas

with a unstable substrate outside the tall shrubs, groups of herbs and young *Betula rotundifolia* individuals predominate. It allows us to predict the further growth of its thickets into open moraine sections. The core of the third stage is *Larix sibirica*, *Betula rotundifolia*, and pleurocarpous mosses. Here, a sparse tree storey is formed from Siberian larch. In the shrub storey, the dominance changes from willows to *Betula rotundifolia*; in the moss storey, acrocarp mosses are replaced by pleurocarp mosses. The distribution of primary vegetation is combination of mosaic one and large thickets. By the end of the stage, the total cover of mature plant communities reaches 80%.

Bolshoi Levyi Aktru glacier. The primary succession on the moraines of the Bolshoi Levyi Aktru glacier (Fig. 2) includes three stages and four substages.

The pioneer stage of succession (I) takes place on the moraines of the glacier (50–500 m from the glacier, moraines deposited 5–50 years ago) composed of macro-fragmental material.

In the first substage (I.1) (50–250 m from the Levyi Aktru glacier, moraines deposited 5–20 years ago), 37 species of vascular plants were recorded, the herbs (30 species) are dominant life form, though they occur only as isonalted individuals. The primary participants are 15 species (Tables 1, 2). Young plants of *Crepis karelinii*, *Chamaenerion latifolium*, *Dracocephalum imberbe*, *Saxifraga oppositifolia*, and *Bryum lonchocaulon* moss are the first to appear on moist melkozem in the niches between the boulders; they were found 50 m from the edge of the glacier. Further from the glacier, *Braya aenea*, *Poa glauca*, and *Trisetum mongolicum* are added to them. Almost all herbaceous plants are short perennials that bloom and bear fruit. Generative individuals of tall shrub species are rarely occur in during the substage (Tables 1, 2). Five species of acrocarpous mosses were registered on wet melkozem in the niches between the stones, including three primary participants (Table 2); they form very small (0.5 cm in diameter) isolated patches. The abundance of all plant species is very low. All plants are found singly, randomly distributed over the area; the total cover at the end of the substage does not exceed 1%.

The number of species of vascular plants increases to 49 in the second substage (I.2) (250–500 m from the glacier, moraines deposited 20–50 years ago). The primary participants is 41 species of herbs, tall shrubs, and dwarf shrubs (Tables 1, 2). Eight species of acrocarpous mosses were found here, five of which are the primary participants (Table 2) and three species are accidental. The ecological conditions of moraines of the Levyi Aktru (subalpine altitudinal zone) is more severe than on the moraines of the Malyi Aktru (forest altitudinal zone). Majority of tall shrubs from the genus *Salix* and *Juniperus* exist only on this substage because of harsher ecological conditions. Their pregenerative individuals are found singly at a great distance from each other. In microsites, single aggregations of the same-aged individuals of the same species and small 2–3 species groups of herbs *Poa glauca*, *Trisetum mongolicum*, and *Crepis karelinii* are formed on melkozem, and rarely on gravel. Small groups of herbs and mosses *Draba cana* + *Bryum lonchocaulon*; *Erigeron eriocalix* + *Campanula rotundifolia* + *Silene chamarensis* + *Bryum lonchocaulon* + *Tortella fragilis* + *Ditrichum flexicaule*; and groupings of willow shrubs (*Salix saposhnikovii* and *S. tuvinensis*) and herbs (*Chamaenerion latifolium*, *Erigeron eriocalix*, *Campanula rotundifolia*, and *Silene chamarensis*) are formed but they are less common than aggregations. Acrocarpous mosses grow under tall shrubs or form small isolated spots from individual patches; some of them include lichens *Cladonia pyxidata: Bryum lonchocaulon* + *Tortella fragilis* + *Cladonia pyxidata*; *Bryum pallescens* + *Tortella inclinata* + *Cladonia pyxidata*. Separate patches of pioneer lichens *Stereocaulon alpinum* and *Vulpicida tilesii* on the crushed stones substrate are occurring extremely rare. The abundance of plants is very low (Table 2). All recorded plant species and their simple groups on small spots of melkozem are scattered; they are isolated, and randomly distributed over the area. The total cover by the end of the substage barely reaches 5%.

In total, 60 species of vascular plants (43 species of herbs and 17 species of tall shrubs and dwarf shrubs) participate in the pioneer stage of succession. Among them 41 species are the primary participants and 19 species are accidental ones, represented by herbs (Braya *rosea*, *Chorispora bungeana*, *Crepis nana*, *Draba alpina* L., *Festuca brachiphylla* Shult., *Oxytropis pauciflora* Bunge, *Saussurea glacialis* Herder, *Waldheimia tridactylites* Kar. et Kir., etc.). During the pioneer stage, eight species of mosses (six primary participants and two accidental species *Bryum dichotomum* Hedw. and *B. pallescens* Sw.) and three species of ground lichens appear; all of them are primary participants. The abundance of all plants is very low. Under these environmental conditions, the core of the pioneer stage cannot be fetched out. All herbs are low perennials; they bloom and bear fruit; tall shrubs are in the pregenerative period of ontogenesis. The distribution of plants in this area is random; patched; and composed of isolated individuals, their aggregations, and multi-species groups with low number of species. The total cover of plants during the pioneer stage increases from 1 to 5%.

The second stage of succession (II) (500–750 m from the Levyi Aktru glacier, moraines deposited more than 70 years ago) were fetched out on the high moraine hills of Bolshoi Aktru, composed of bouldery and crushed stones substrate.

In the first substage of the second stage (II.1), 68 species of vascular plants were identified and registered on the flat tops of moraine hills (46 herbs and 22 tall shrubs and dwarf shrubs). The primary participants include 49 species of herbs, tall shrubs, and

dwarf shrubs (Tables 1, 2). There are 13 species of acrocarpous mosses, 8 of which are the primary participants (Table 2), and 5 species of ground lichens, 3 of which are the primary participants, among which *Stereocaulon alpinum* is most abundant (Table 2). The substage is characterized by the formation of the first complex plant groupings, occurring exclusively in the mesodepressions on the flat tops of moraine hills. Groupings are very fragmented and have small sizes (up to 1–2 m in diameter). Their composition is dominated by willow shrubs *Salix berberifolia* and *S. vestita* and tall shrubs *Juniperus sibirica* and *Salix saposhnikovii*, which survive under these environmental conditions (low temperatures and strong winds) only in creeping form (up to 20 cm high). Herbs and willows bloom, bear fruit, and form seeds. The patches of acrocarpous mosses—*Distichium capillaceum*, *Ditrichum flexicaule*, *Sintrichia ruralis*, *Tortella inclinata*, and others—grow only in depressions under tall shrubs. Perennial herbs with insignificant abundance are part of complex groups with tall shrubs or form isolated simple groups on a rocky substrate. Lichens grow in elevated areas. Their patches, in which *Stereocaulon alpinum* and *Vulpicida tilesii* dominate, occupy about 10% of the moraine surface. The abundance of 1 mark or more was noted only for four species of tall shrubs, two species of herbs, and *Stereocaulon alpinum* (Table 2). The distribution of primary vegetation is mosaic: separate complex groups of tall shrubs occur only in mesodepressions on hilltops; simple groupings of pioneer herbs and lichen spots are associated with elevated areas. At the end of the substage, the total cover is 15%.

The second substage of the second stage (II.2) was fetched out on the slopes of moraine hills, composed of unstable, bouldery, and crushed stones substrate. Seventy-teo species of vascular plants: 43 herbs, 24 tall shrubs and dwarf shrubs, and 5 species of trees were registered on this substage. The primary participants are 57 species of herbs, tall shrubs, and dwarf shrubs (Tables 1, 2), and 15 species are accidental. Eighteen species of mosses (8 primary species and 10 accidental species) and 5 species of lichens, 3 of which are primary and 2 are accidental, were recorded here (Table 2). On this substage, complex groups are occur only in mesodepressions on hillsides. Their sizes increase insignificantly and groups do not merge in areas with a coarse-grained substrate. An important role in the formation of groups belongs to 7 species of tall shrubs and dwarf shrubs. Herbs, small perennials, do not play any significant role in the development of vegetation of this substage. In addition to these species, *Erigeron eriocalix*, *Campanula rotundifolia*, *Silene chamarensis*, etc., are found in complex and simple groups with a low abundance. Two species of lichens, *Stereocaulon alpinum* and *Vulpicida tilesii*, play a significant role in succession in the second stage. The abundance of most plant species is very low, only 11 species reach mark 1 (Table 2). The distribution of primary vegetation is mosaic. Separate complex groups of tall shrubs are associated with depressions on the slopes of moraine hills; simple groups of pioneer herbs and lichen patches are associated with elevated areas. By the end of the substage, the total cover is 15–20%.

In total, 82 species of vascular plants are involved in the second stage of succession on moraines of the Bolshoi Aktru; 57 of them are the primary ones (Tables 1, 2) and 25 are accidental species, among which are the herbaceous flowering *Draba sapozhnikovii*, *D. fladnizensis*, *Elymus transbaicalensis*, *Erigeron politus*, *Minuartia verna*, *Myosotis imitata* Serg., and *Papaver pseudocanescens* Popov, etc.; fern *Cystopteris dickieana*; tall shrubs *Salix bebbiana* Sarg. and *S. ledebouriana* Trautv. et al.; and trees *Larix sibirica*, *Pinus sibirica*, *Picea obovata*, *Populus laurifolia*, and *Betula pendula*. Mosses are represented by 19 species, of which 9 are primary and 10 are accidental species (*Brachythecium turgidum*, *B. cirrosum* (Schwagr.) Schimp., *Pohlia cruda* (Hedw.) Lindb., *Stereodon vaucheri*, etc.). There are six species of ground lichens: three primary and three accidental species (*Cladonia pocillum*, *Flavocetraria nivalis*, and *Stereocaulon paschale* (L.) Hoffm.). The core of this stage in the conditions of the subalpine altitudinal zone is formed by tall shrubs *Juniperus sibirica* and *Salix* species; dwarf shrub *Dryas oxyodonta*; lichen *Stereocaulon alpinum*; and herbs *Castilleja pallida*, *Dracocephalum imberbe*, and *Chamaenerion latifolium*. At the second stage of succession, a change in the dominant life form of primary vegetation occurs: the herbs are replaced by dwarf shrubs *Dryas oxydonta* and *Salix berberifolia* and tall shrubs from the genera *Salix* and *Juniperus* in a creeping form; the role of soil lichens is increasing. The distribution of primary vegetation is mosaic: separate complex groups of tall shrubs occur only in the lowered areas of the relief both on the tops and on the slopes of the moraine hills. Complex *Dryas*-dominated and simple groups of pioneer herbs and lichen patches are associated with the elevated areas. The total cover of plants at the end of the stage is about 20%.

The third stage of succession (III) (750–960 m from the tongue of the glacier, moraines deposited more than 100 years ago) also takes place on the moraines of Bolshoi Aktru in the most moistened, cup-shaped depressions protected from winter winds by surrounding moraine hills with melkozem and fine crushed stone substrate. At this stage, 90 species of vascular plants were registered: 57 species are primary participants: 35 herbs and 22 tall and dwarf shrubs (Tables 1 and 2); 33 species are accidental, including herbs (*Aster alpinus*, *Astragalus austrosibiricus Schischk*, *Bupleurum multinerve* DC., *Dracocephalum nutans* L., *Orostachys spinosa*, *Pedicularis anthemifolia* Fisch., *Pyrethrum abrotanifolium* Bunge, etc.), tall shrubs (*Cotoneaster uniflorus* Bunge, *Spiraea flexuosa* Fisch., etc.), and trees (*Larix sibirica*, *Pinus sibirica*, and *Populus laurifolia)*. Mosses are represented by 19 species, 9 of which are primary participants (Table 2)

and 10 are accidental (*Brachythecium turgidum*, *Encalypta procera Bruch.*, *Stereodon vaucheri*, etc.). Lichens are the same as in the second stage.

In the third stage of the succession, three primary variants of microcenoses are formed: in lower areas they are dominated by *Salix saposhnikovii*, *S. glauca*, and *Carex tristis* (willow sedge tundra); on elevated stony areas they are formed by *Dryas oxyodonta* (dryad tundra). These micoenoses are similar to the tundra ones. The core of the third stage consists mainly of the same (as in the second stage of succession) tall (*Juniperus sibirica*, *Salix saposhnikovii*, *S. coesia*, and *S. glauca*) and dwarf shrubs (*Salix vestita* and *Dryas oxyodonta*), to which herbs *Carex tristis*, *Lupinaster eximius*, and *Castilleja pallida* join (Table 2). The distribution of primary vegetation is mosaic-thicket; the projective cover averages about 60%.

DISCUSSION

The studies of primary successions on young moraines of two valley glaciers located in close proximity to each other indicated that the species composition of plants forming the vegetation cover on the deglaciated terrain has both similarities and significant differences.

On the Malyi Aktru moraines located in the upper part of the forest altitudinal zone, 146 species of vascular plants are involved in succession. As the age of moraines increases, their number increases from 78 at the pioneer stage to 111 species in the second stage, and it decreases to 84 species in the third stage. On the Bolshoi Levyi Aktru moraines located in the subalpine altitudinal zone, 128 species of vascular plants are involved in succession. Their number increases from 60 at the pioneer stage to 89 at the second stage and remains the same at the third stage (90 species). However, the number of the primary participants of both successions is almost the same: 59 (40%) of species on the moraines of the Malyi Aktru and 62 (48%) on the moraines of the Bolshoi Levyi Aktru. Although the participation of accidental species is high, 60 and 52%, respectively, their role in the succession of vegetation is negligible. On the Malyi Aktru moraines, 44 species of mosses participate in succession: their number increases from 10 species at the pioneer stage to 27 in the second stage and slightly decreases in the third stage (24 species). Twenty-six species of mosses were found on the moraines of the Bolshoi Levyi Aktru. Their number increases from 8 at the pioneer stage to 19 at the second stage and 21 at the third stage. The number of the primary participants in the succession at the Bolshoy Leviy Aktru is 1.5 times smaller than on the moraines of the Malyi Aktru: 15 and 10 species, respectively. In the conditions of the subalpine altitudinal zone near the Bolshoi Levyi Aktru glacier, the role of pleurocarpous mosses is especially remarkable. On the moraines of Malyi Aktru, all ground lichens are accidental; on the moraines of the Bolshoi Levyi Aktru, three species of lichens are the primary participants in the succession.

On the moraines of the Malyi Aktru glacier at the pioneer stage of succession, single herbs and mosses appear in microsites favorable for settlement, then they are replaced by simple groups of pioneer herbs and tall shrubs that have not yet reached adulthood. The distribution of plants in the area is random, mosaic, weakly associated with the topography, and significantly associated with the substrate. At the second, willow–moss stage of primary succession, in small areas with melkozem, small complex groups of *Myricaria dahurica*, willow shrubs, and mosses appear, other areas are covered by extensive thickets of willow shrubs moss cover are forming under them, willow and dryad groups. The spatial distribution of vegetation is still controlled by relief. The third, larch–birch–moss stage, is the stage of a young forest with a sparse tree storey of *Larix sibirica*, a dense shrub storey with domination of *Betula rotundifolia*, and a developed moss storey with a predominance of pleurocarpous mosses. The spatial distribution of vegetation is isolated thickets, slightly dependent on the substrate and topography, with the gradual invasion of tall shrubs to the adjacent open rocky areas.

On young moraines of the Bolshoi Levyi Aktru glacier, the pioneer, mixed-grass stage begins in microsites with melkozem, where single herbs and mosses appear; species diversity is very poor. Then, simple groups, formed by pioneer herbs, herbs and mosses, and mosses and lichens appear. The spatial distribution of plants has a random mosaic character and depends on the substrate. The second, moss–lichen–willow stage develops on the tops and slopes of moraine hills. Complex groups of willow shrubs with patches of moss under them are forming only in the depressions. The tops of moraine hills are confined to fairly extensive lichen spots. The distribution of vegetation is mosaic, largely controlled by the relief. The third, willow–dryad stage is characterized by a patchy-thicket distribution of microcenoses with a domination of willow, dryad, and sedge, depending on the moisture content and rockiness of the substrate. All microcenoses form only in depressions between moraine hills; that is, the relief still determines the spatial distribution of vegetation.

In the examined young moraines of both glaciers, the largest role in the succession is played by relatively few dominant species. At the beginning of the observed succession, these are herbaceous plants *Chamaenerion latifolium*, *Crepis karelinii*, and *Dracocephalum imberbe*. At the second stage, tall shrubs *Juniperus sibirica* and *Salix sapozhnikovii* and dwarf shrubs S*alix berberifolia*, *S. vestita*, and *Dryas oxyodonta*. The primary vegetation differences between the moraines are especially significant at the third stage of succession: on the Malyi Aktru moraines it is *Betula rotundifolia*, *Larix sibirica*, *Oxitropis ambigua*, *Astragalus frigi-*

dus, and *Hedysarum neglectum*; on the Bolshoi Aktru moraines, *Dryas oxyodonta*, *Salix sapozhnikovii*, *S. glauca*, *Carex tristis*, and *Lupinaster eximius Castilleja pallida*. In addition, at the second and third stages of succession, there are significant differences in the composition of the dominant species of mosses and lichens (Table 2). Mosses play an important role on the moraines of Malyi Aktru; lichens play an important role on the moraines of Bolshoi Aktru. It should be noted that a significant role of lichens on the macrofragmental moraine substrate was also noted for moraines of the Great Aletsch Glacier in the Swiss Alps (Lüdi, 1945; Richard, 1973).

Our studies have shown that the total cover of vegetation over 150 years of succession in the moraines of Malyi Aktru varies from 5% at the beginning of the pioneer stage to 50% at the second and reaches 80% by the end of the third stage. On the moraines of the Bolshoi Levyi Aktru, the total projective cover is very low, it barely reaches 1% at the beginning and increases to 5% at the end of the pioneer stage. It increases to 20% at the second and reaches an average of 60% in microcenoses of the third stage of primary succession. The lower cover on moraines of the Bolshoi Levyi Aktru is apparently due to the fact that they are composed of a less structured, rough rocky substrate and located in more severe environmental conditions of the subalpine altitudinal zone.

Stork (1963) and Zollitsch (1969) noted the S-shaped dynamics of the cover increase with a phase of a relatively rapid growth at the middle stage of succession. A rapid increase in this indicator was noted at the middle stage of succession at the moraine of Malyi Aktru glacier; at the moraine of the Bolshoy Levyi Aktru the rapid grow phase occurs at the final third stage. It, apparently, is associated with more severe environmental conditions latter moraine. The key role in the increase of the cover is played by tall and dwarf shrubs starting from the first substage of the second stage of succession. In young moraines of Malyi Aktru, their cover significantly increases: from 8–10% at the end of the pioneer stage to 40% by the end of the second stage and to 70% by the end of the third stage. On the moraines of the Bolshoi Levyi Aktru, the phase of rapid growth of the total cover is also associated with tall and dwarf shrubs: this indicator increases from 5% at the end of the pioneer stage to 20% by the end of the second stage and on average to 60% in the third stage of succession.

It should be noted that the growth rate of the total cover of plants on the studied moraines is significantly lower than in the mountains with a more humid and less continental climate of Western Europe and North America. Thus, the cover on the moraines of the Pasterce Glacier (Alps) reaches 100% in less than 100 years (Zollitsch, 1969), on the moraines of Sweden's glaciers in less than 60 years (Stork, 1963), and on the moraines of the Alaskan glaciers in less than in 40 years (Reiners et al., 1971). In the continental climate of the Severo-Chuisky glaciation center, the total cover on the studied moraines reached 80% in 150 years of primary succession in the most favorable ecological conditions of the upper part of the forest altitudinal zone on the Malyi Aktru moraines and only 60% on the Bolshoi Levyi Aktru moraines.

CONCLUSIONS

In the continental climatic conditions of the Severo-Chuisky glaciation center under the environmental conditions of the upper part of the forest altitudinal zone (2220–2240 m a.s.l.) on young moraines of the Malyi Aktru glacier and in the conditions of the subalpine altitudinal zone (2370–2500 m a.s.l.) on the moraines of the Bolshoi Levyi Aktru glacier, three stages and four substages of the primary succession of vegetation are distinguished. During succession, the deglaciated territories are populated by vascular plants, mosses, and ground lichens.

On moraines of the Malyi Aktru glacier, 146 species of vascular plants, 44 species of mosses, and 6 species of lichens are involved in primary succession. On moraines of the Bolshoi Levyi Aktru glacier, 128 species of vascular plants, 26 species of mosses, and 8 species of lichens are involved.

Significant differences in environmental conditions within the same mountain-glacial basin allow us to observe two variants of primary succession of vegetation. During the succession on the Malyi Aktru moraines, the herbal stage is replaced by willow–moss one and by a young forest community is formed in 150 years. On the moraines of the Bolshoi Levyi Aktru, the herbal stage is replaced by lichen–willow; separate microcenoses, similar to tundra communities, have been formed over 150 years.

Tall and dwarf shrubs play the most significant role in the growth rate of cover on the moraines of both Malyi Aktru and Bolshoi Levyi Aktru. The growth rate of the total vegetation cover on the examined young moraines is much lower than in areas with a wetter and milder Western European and North American climate.

The data obtained under the continental conditions of the Severo-Chuisky glaciation center allow us to expand our understanding of the course, duration, and characteristics of the primary successions of vegetation on young moraines of Asian mountain systems.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. This article does not contain any studies involving animals performed by any of the authors.

REFERENCES

Andreis, C. Caccianiga, M., and Cerabolini, B., Vegetation and environmental factors during primary succession on glacier forelands: some outlines from the Italian Alps, *Plant Biosyst.*, 2001, vol. 35, pp. 295–310.

Barry, R.G., The status of research on glaciers and global glacier recession: a review, *Prog. Phys. Geogr.*, 2006, vol. 30, no. 3, pp. 285–306

Birks, H.J.B., The present flora and vegetation of the moraines of the Klutlan glacier, Yukon territory, Canada: A study in plant succession, *Quat. Res.*, 1980, vol. 14, pp. 60–86.

Braun-Blanquet, J., *Plant Sociology*, New York: McGraw-Hill, 1932.

Burga, C.A., Krüsi, B., Egli, M., et al., Plant succession and soil development on the foreland of the Morteratsch glacier (Switzerland): straight forward or chaotic? *Flora*, 2010, vol. 205, pp. 561–576.

Cooper, W.S., A fourth expedition to Glacier Bay, Alaska, *Ecology*, 1939, vol. 20, pp. 59–130.

Davydov, V.V. and Timoshok, E.E., Forming of soils of the young moraines of the Aktru basin (Central Altai, Severo-Chuyskiy Range), *Contemp. Probl. Ecol.*, 2010, vol. 3, no. 3, pp. 505–514. https://doi.org/10.1114/S1995425510030161

Dushkin, M.A., Long-term fluctuations of Aktru glaciers and conditions for the development of young moraines, in *Glyatsiologiya Altaya* (Glaciology of the Altai), Tomsk: Tomsk. Gos. Univ., 1965, no. 4, pp. 83–101.

Elven, R., Association analysis of moraine vegetation at the glacier Hardangerjokulen, Finse, South Norway, *Norw. J. Bot.*, 1978, vol. 25, pp. 171–191.

Elven, R. and Ryywarden, L., Dispersal and primary establishment of vegetation, in *Fennoscandian Tundra Ecosystems*, Part 1: *Plants and Microorganisms*, Berlin: Springer-Verlag, 1975, pp. 82–85.

Gureyeva, I.I. and Timoshok, E.E., Ferns in the present-day periglacial zone of the Central Altai, *Contemp. Probl. Ecol.*, 2016, vol. 9, no. 1, pp. 18–28. https://doi.org/10.1134/S1995425516010054

Jones, C.C. and del Moral, R., Patterns of primary succession on the foreland of Coleman Glacier, Washington, USA, *Plant Ecol.*, 2005, vol. 180, pp. 105–116. . https://doi.org/10.1007/s11258-005-2843-1

Lawrence, D.B., Glaciers and vegetation in southeastern Alaska, *Am. Sci.*, 1958, vol. 46, pp. 89–122.

Ledniki Aktru (Altai) (Aktru Galciers (Altai)), Leningrad: Gidrometeoizdat, 1987.

Lüdi, W., *Besiedlung und Vegetationsentwicklung auf den Jungen Seitenmoränen des Großen Aletschgletschers—mit Einem Vergleich der Besiedlung im Vorfeld des Rhonegletschers und des Oberen Grindelwaldgletschers, Bericht über das Geobotanische Forschungsinstitut Rübel in Zürich für das Jahr 1945*, Zurich: Rübel und Lüdi Verlag, 1945, pp. 35–112.

Matthews, J.A. and Whittaker, R.J., Vegetation succession on the Storbreen glacier foreland, Jotunheimen, Norway: a review, *Arct. Alp. Res.*, 1987, vol. 19, pp. 385–395.

Narozhnyi, Yu.K. and Okishev, P.A., Dynamics of Altai glaciers into regressive phase of Low Ice Period, *Mater. Glyatsiol. Issled.*, 1999, no. 87, pp. 119–123.

Narozhniy, Yu. and Zemtsov, V., Current state of the Altai glaciers (Russia) and trends over the period of instrumental observations 1952–2008, *Ambio*, 2011, vol. 40, pp. 575–588.

Reiners, W., Worley, I., and Lowrence, D., Plant diversity in a chronosequence at Glacier Bay, Alaska, *Ecology*, 1971, no. 52, pp. 55–69.

Richard, J.L., Dynamique de la ve'ge'tation au bord du grand glacier d'Aletsch (*Alpes suisses*), *Ber. Schweiz. Bot. Ges.*, 1973, vol. 83, pp. 159–174.

Schubiger, C., Die Vegetation des Rhonegletscher Vorfeldes, ihre Sukzession und naturräumliche Gliederung, *Beitr. Geobot. Landesaufnahme Schweiz*, 1988, vol. 64, pp. 1–190.

Sevast'yanov, V.V., *Klimat vysokogornykh raionov Altaya i Sayan* (Climate of High-Altitude Regions of Altai and Sayan Mountains), Tomsk: Tomsk. Gos. Univ., 1998.

Spence, J.R., A floristic analysis of neoglacial deposits in the Teton Range, Wyoming, U.S.A., *Arct. Alp. Res.*, 1985, vol. 17, pp. 19–30.

Stork A., Plant immigration in front of retreating glaciers with examples from Kebnekajse area, northern Sweden, *Geogr. Ann.*, 1963, vol. 45, pp. 1–22.

Timoshok, E.E., Narozhnyi, Yu.K., Dirks, M.N., and Berezov, A.A., Experience in combined glaciological and botanical studies on the primary plant successions on young moraines in the Central Altai, *Russ. J. Ecol.*, 2003, vol. 34, no. 2, pp. 91–97.

Timoshok, E.E., Narozhnyi, Yu.K., Dirks, M.N., Skorokhodov, S.N., and Berezov, A.A., *Dinamika lednikov i formirovanie rastitel'nosti na molodykh morenakh Tsentral'nogo Altaya* (Dynamics of Glaciers and Formation of Vegetation on Young Moraines of Central Altai), Tomsk: Izd. Nauchno-Tekh. Lit., 2008.

Timoshok, E.E., Timoshok, E.N., and Davydov, V.V., Relationship of ecosystem and climate processes on moraines of mountain-glacial Aktru basin, *Opt. Atmos. Okeana*, 2012, vol. 25, no. 2, pp. 144–151.

Timoshok, E.E., Timoshok, E.N., Nikolaeva, S.A., Savchuk, D.A., Filimonova, E.O., Skorokhodov, S.N., and Bocharov, A.Yu., Monitoring of high-altitude terrestrial ecosystems in the Altai Mountains, *IOP Conf. Ser.: Earth Environ. Sci.*, 2016, vol. 48, no. 1, pp. 1–9. https://doi.org/10.1088/1755-1315/48/1/012008

Tishkov, A.A., Primary successions of vegetation on moraines of the Rongbuk Glacier (Everest Mountain, China), *Izv. Ross. Akad. Nauk, Ser. Geogr.*, 2007, no. 1, pp. 28–34.

Tronov, M.V., Glaciers of the Bish-Yirdu massif, *Tr. Tomsk. Gos. Univ.*, 1939, vol. 95, pp. 10–27.

Tronov, M.V., *Ocherki oledeneniya Altaya* (Descriptions of Glaciation of Altai), Moscow: Geografgiz, 1949.

Tronov, M.V., *Ledniki i klimat* (Glaciers and Climate), Leningrad: Gidrometeoizdat, 1966.

Vyatkina, M.P., Kazakov, N.V., and Murav'ev, Ya.D., Dynamics of vegetation and soils in the valley of Bil'chenok glacier after deglaciation, *Mater. Glyatsiol. Issled.*, 2007, no. 102, pp. 178–186.

Zollitsch, B., Die Vegetationsentwicklung im Pasterzenvorfeld, *Wissenschaftliche Alpenvereinsheft*, 1969, vol. 21, pp. 267–290.

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