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Article

Response of phytocenoses of the Sorokaozerki Area (Koibalskaya Steppe, Minusinsk Basin) to interannual changes in precipitation against the background of post-pasture demutation

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Abstract. Three model phytocenoses undergoing post-pasture demutation (ecological restoration) were observed from 2018 to 2023 on the restricted area of a coal mining enterprise (in order of decreasing soil moisture content): forb-cinquefoil-bluegrass meadow steppe (FC-1), caragana forb-onion-cinquefoil-cereal meadow steppe (FC-2), and caragana forb-feather-grass meadow steppe (FC-3). In 2019, the amount of precipitation was higher than the long-term average, while year 2022 was extremely dry. During the restoration succession, the proportion of species in phytocenoses and the total projective cover of the shrub and grass layers changed gradually. With this, the response of phytocenoses to pronounced interannual variations in the amount of precipitation was observed – fluctuations in the height of the grass (by 1.5–2 times) and aboveground phytomass (by 2.7–3.9 times). In the extremely dry year of 2022, a decrease or stagnation of the total projective cover of the grass layer was observed. The graphical model of polynomial regression showed that the grass stand height of FC-1 was directly associated with the amount of precipitation, with the relationship being close to linear. The grass stand height of FC-2 and FC-3, as well as the aboveground phytomass of all three model phytocenoses, changed curvilinearly with an increase in the amount of precipitation. Interpolation showed that the phytomass reaches its maximum values with a precipitation amount for April-August of 350–370 mm (for FC-1), 300-350 mm (for FC-2 and FC-3). With a greater amount of precipitation, the phytomass of FC-2 and FC-3 showed a tendency to decrease.

Keywords: climate change, climatogenic fluctuations of phytocenoses, total projective cover of phytocenosis, height of grass layer, phytomass

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Научная статья

Отклик фитоценозов урочища Сорокаозёрки (Койбальская степь, Минусинская котловина) на межгодовые изменения осадков на фоне постпастбищной демутации

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Аннотация. С 2018 по 2023 гг. на режимной территории угледобывающего предприятия наблюдали три модельных фитоценоза, проходящих постпастбищную демутацию (в порядке снижения увлажненности): разнотравно-лапчатково-мятликовую луговую степь (ФЦ-1), карагановую разнотравно-луково-лапчатково-злаковую луговую степь (ФЦ-2), карагановую разнотравно-ковыльную луговую степь (ФЦ-3). В 2019 г. количество осадков было выше среднего многолетнего значения, 2022 г. оказался экстремально засушливым. В ходе восстановительной сукцессии поступательно менялись доля участия видов в фитоценозах, общее проективное покрытие кустарникового и травяного ярусов. На этом фоне наблюдали отклик фитоценозов на ярко выраженные межгодовые колебания количества осадков – флуктуации высоты травостоя (в 1.5–2 раза) и надземной фитомассы (в 2.7–3.9 раза). В экстремально засушливый 2022 год наблюдали падение или стагнацию общего проективного покрытия травяного яруса. Графическая модель полиномиальной регрессии продемонстрировала, что высота травостоя ФЦ-1 имела прямую зависимость от количества осадков, близкую к линейной. Высота травостоя ФЦ-2 и ФЦ-3, а также надземная фитомасса всех трех модельных фитоценозов при повышении количества осадков менялись криволинейно. Интерполяция показала, что фитомасса достигает максимальных значений при сумме осадков за апрель–август 350–370 мм (для ФЦ-1), 300–350 мм (для ФЦ-2 и ФЦ-3). При большем количестве осадков фитомасса ФЦ-2 и ФЦ-3 демонстрировала тенденцию к снижению.

Ключевые слова: изменения климата, климатогенные флуктуации фитоценозов, общее проективное покрытие фитоценоза, высота травяного яруса, фитомасса

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Introduction

Currently, ecologists are very much concerned with global and regional climate trends and forecasting their impact on ecosystems (Chebakova and Parfenova, 2006; Häder and Barnes, 2019; Im, 2023; Kharlamova and Ostanin, 2012; Kharuk et al., 2021; Minin, 2011; Myers-Smith et al., 2020; Shi et al., 2021; Vincent, 2009). To create scenarios for the development of natural systems in the context of progressive changes in climate indicators, information is required on the state of these systems in the ranges of cyclic fluctuations in climatic parameters, as well as on the limits of system stability. This is important, in particular, for distinguishing between succession processes and climatogenic fluctuations of phytocenoses (Anenkhonov, 2010).

Fluctuations caused by year-to-year differences in the meteorology and hydrology of the ecotope belong to the ecotopic group, according to the classification of T.A. Rabotnov (1992). According to this author, such fluctuations are more typical of regions with a sharply continental climate and are more pronounced for herbaceous phytocenoses than for forest ones. It is also known that in herbaceous phytocenoses, crop yields and the structure of dominance strongly depend on moisture availability (Mirkin and Naumova, 2017). A direct dependence of phytomass on precipitation has been established for the desert steppes of the Northern Gobi (Kazantseva, 2004). In the mown and unmown steppe of the Central Black Earth Reserve, precipitation amounts for May–June of the current year demonstrated the highest values of the correlation coefficients with crop yields (Minin, 2011). Hydrothermal indicators were used to determine the productivity of meadow steppe phytocenoses in the Oka River basin (Zelenskaya et al., 2012) and in the steppes of Ukraine (Polevoy et al., 2019).

The climate of the Minusinsk Basin over the past 80 years showed the following trends: an increase in average annual temperatures (Nikolaeva, 2005; Pankova and Chernousenko, 2020), an increase in average annual precipitation (Chernousenko and Khitrov, 2019; Nikolaeva, 2005) and a decrease in aridization (Pankova and Chernousenko, 2020). Based on these data, a transformation of plant communities located in the most arid habitats should be expected. In the Minusinsk Basin, these include the center of its southern part, the interfluve of the Abakan and Yenisei Rivers – Koibalskaya steppe, within which the Sorokaozerki area is located.

The vegetation cover of the tract has been studied by florists, geobotanists and biologists of other profiles for many years. Meadow and steppe phytocenoses in connection with the environmental features and anthropogenic impacts are discussed in a series of studies (Cherepnin, 1956, 1961, 1963; Larionov, 2013; Larionov et al., 2015; Rastitelnyi pokrov..., 1976; Subbotin and Zorkina, 2004; Zhukova, 2015; Zhukova et al., 2011; Zorkina, 2016; Zorkina and Zhukova, 2006, 2009; Zorkina et al., 2013).

The area is currently known in the region due to the fact that local environmental activists actively oppose coal mining, and also as a key ornithological area of international significance[1], included in the Shadow List of the Ramsar Convention on the Conservation of Wetlands[2]. Here, the "Koibalskaya Steppe Lakes", a state nature reserve of regional significance, has been organized[3].

In 2016–2017, a detailed hydrogeological analysis of the territory was carried out, with the participation of the authors. The soils were studied, and catalogues of flora and avifauna were compiled (Otsenka vozdeistviya.., 2017). Since 2017, monitoring observations of the state of biological diversity in the territory of the "Koibalskaya Steppe Lakes Nature Reserve" and the licensed area of Kirbinsky Mine LLC, located in the area, have been carried out.

There are almost no intact ecosystems left in the Koibalskaya steppe. However, the preservation of elements of natural ecosystems and the sustainable existence of natural-anthropogenic systems enable the territory to function as an ecological framework of the Minusinsk Basin. Zonal and intrazonal phytocenoses, widely represented in the Sorokaozerki area – various types of steppes and meadows – are valuable in terms of biodiversity. Almost all of them are exposed to grazing. In the restricted area of the coal mining enterprise "Razrez Kirbinsky" since 2017 (the introduction of a closed regime), the grazing load has been removed, and demutation processes are observed outside industrial zones.

The purpose of this study is to identify the reactions of steppe phytocenoses undergoing post-pasture demutation to year-to-year variations in the amount of rainfall.

Material and methods

The studies were conducted in the Sorokaozerki area of the Koibalskaya steppe of the Minusinsk depression (Fig. 1). The area is an ancient valley of the Yenisei River. As a result of the shift of the Yenisei River channel, pebble ramparts were formed, and the transfer of sand formed dunes, as a result of which the relief acquired a gently undulating appearance (Voskresensky, 1962). At present, Sorokaozerki area is a plain with gentle hills (280–300 m) and small closed basins with oxbow lakes. The lakes are predominantly shallow, fresh and brackish, connected to each other by channels and canals of the Koibalskaya irrigation system. The irrigation system was built in the 1960s (Yavorsky, 1968) and is currently not used for its intended purpose.

The climate is continental. According to data for 1981–2000 (Nikolaeva, 2005), the average annual temperature in the Koibalskaya steppe was +2.2 °C, the average July temperature was +18.5 °C, the sum of active temperatures was 1900 °C, the amount of precipitation was 431 mm, 82% of which falls during the growing season. The climate aridity index of the Minusinsk Basin, according to data for 1955–2015, was 0.5, which corresponds to the "subarid territories" group (Pankova and Chernousenko, 2000).

The development of soils in the area was affected by the pebble layer of the ancient valley, arid climate and specific hydrogeological conditions. The tract is characterized by small slopes in the relief, a high groundwater level (1.25–1.40 m), and a relatively large catchment area. The combination of these factors predetermined the manifestation of such processes as swamping and salinization. The soil cover is represented by a complex of sandy and sandy loam soils of the chestnut type, saline to varying degrees. Solonchaks, strongly saline and bog-saline soils are widespread in lake depressions. Anthropogenically transformed soils are represented – structural-metamorphic abrazems. The soils have a thin organic horizon, are characterized as very low- and low-humus, with a low level of fertility (Otsenka vozdeistviya..., 2017).

As a result of melioration works in the mid-20th century, it became possible to engage in agriculture in the Koibalskaya steppe, and almost all flat areas were plowed (Yavorsky, 1968). At present, most agricultural land is fallow, agricultural production has generally decreased and remaining agriculture has developed towards livestock[4].

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[1] Key ornithological territories of Russia. Web page. URL: https://котр.рф (accessed: 10.02.2024).

[2] Wetlands of Russia. Web page. URL: https://fesk.ru/wetlands/195.html (accessed: 10.02.2024).

[3] Resolution of the Government of the Republic of Khakassia dated 10.23.2020 no. 570 "On the establishment of a specially protected natural area of regional significance – the state nature reserve "Lakes of the Koibalskaya Steppe".

[4] Resolution of the Government of the Republic of Khakassia dated 14.11.2011 no. 763 "On approval of the territorial planning scheme of the Republic of Khakassia".

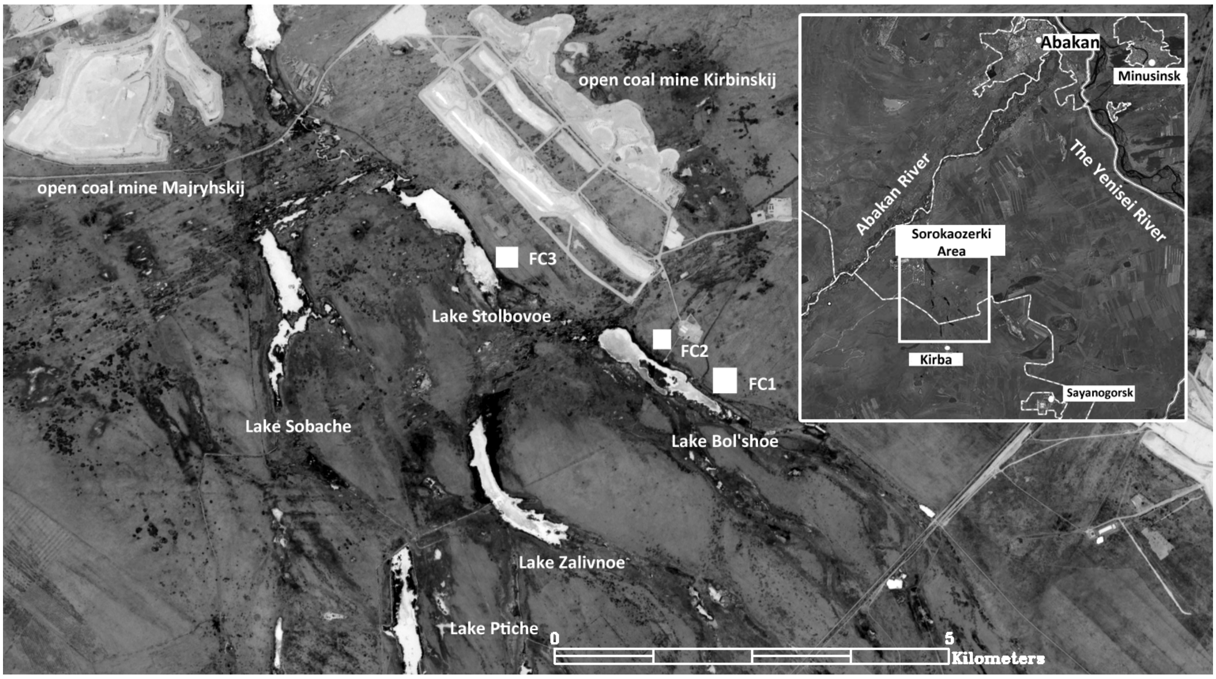

Fig. 1. Map of the study area. FC-1–3 – model phytocenoses.

The area of the tract is subject to powerful anthropogenic impact: there are three open-pit coal mines, locals graze their cattle, collect sea buckthorn berries, and the lakes are popular with local fishermen. The soils are contaminated with fluorine, exceeding the MAC in some areas (most likely due to the proximity of the Sayan Aluminum Plant).

Field work was carried out over five years: 2018, 2019, 2021–2023. Phytocenotic diversity was studied using the route geobotanical research method. The fieldwork study covered all types of habitats in the tract.

The sites for geobotanical monitoring were laid out on the restricted territory of the coal mining enterprise in order to exclude the impact of pastoral and recreational activities. Since 2017, only the employees of the enterprise who move along the roads outside the industrial zones are here. Within the boundaries of the license area, sites were selected that were as far away as possible from mining facilities (quarries, dumps) and, accordingly, from aerotechnogenic impacts.

Phytocenoses were described at 15 sites three times during the vegetation season for five years, with 256 complete geobotanical descriptions obtained according to standard methods (Polevaya geobotanika..., 1964, 1972). The plant nomenclature follows S.K. Cherepanov (1995). The classification of vegetation is adopted according to A.V. Kuminova (Rastitelnyi pokrov..., 1976).

To achieve the set goal, phytocenoses with a wide representation in the area and a low contribution of groundwater to the moisture supply of plants were selected. The following associations met these criteria most comprehensively (in order of decreasing moisture): forb-cinquefoil-bluegrass meadow steppe (FC-1), caragana forb-onion-cinquefoil-cereal meadow steppe (FC-2), caragana forb-feather-grass meadow steppe (FC-3). They are located on flat relief areas at a small distance from lakeside depressions (Fig. 1).

Within the model phytocenoses, geobotanical descriptions were carried out on fixed sites of 100 m^2 and the aboveground phytomass was determined for August 20–25. The phytomass was determined by mowing in three replicates on 1 m^2 plots. Each plot, in turn, was divided into four more parts of 0.25 m^2. Thus, the average values were determined for 12 variants. The plants were cut at the soil level and weighed in an air-dried state. OHAUS PX2202 scales (China) were used with an accuracy of hundredths of a gram, the results were then rounded to the nearest integer.

Data on temperature and precipitation are taken from the archive of the weather station "Beya" (N 53.05° E 90.92°, 468 m above sea level)[5]. Variation and regression analyses were performed using MS Office Excel 2010.

Results and discussion

The Sorokaozerki tract contains a significant portion of the species and ecological diversity of the steppes of the basin and the entire Republic of Khakassia. During monitoring studies, only in the territory of the Koibalskaya Steppe Lakes Nature Reserve and the licensed area of the coal mine, about 200 species of plants found in steppe communities were identified, which is more than 40% of the number of species in the steppe communities of Khakassia (Rastritelnyi mir..., 2015).

The vegetation cover of the territory consists of meadow and steppe types of vegetation. True steppe plants are represented by large-bunch (feather grass), small-bunch (polydominant cereal, wormwood) and solonetzic large-bunch-rhizome (pikulnik solonetzic) steppes.

Forb-grass meadow steppes (fescue-grass, bluegrass-grass, sedge-grass) are characterized by a high species diversity; of the grasses, the following are constant: *Festuca valesiaca* Gaudin, *Koeleria cristata* (L.) Pers., *Phleum phleoides* (L.) H. Karst., *Helictotrichon desertorum* (Less.) Nevski, *Leymus chinensis* (Trin.) Tzvel.; of the sedges, *Carex pediformis* C.A. Mey.

The forb-cereal-feather-grass steppes smoothly transition into wormwood-feather-grass and iris-feather-grass steppes with the participation of *Artemisia frigida* Willd., *Achnatherum splendens* (Trin.) Nevski*, Iris biglumis* Vahl. Solonetzic steppe is formed in areas with shallow saline groundwater under conditions of periodic moisture. *Achnatherum splendens*, growing in small clusters of 3 to 8sods, is found with small-bunch grasses (*Festuca pseudovina* Hack. ex Wiesb., *Cleistogenes squarrosa* (Trin.) Keng, *Puccinellia tenuissima* Litv. ex V.I. Krecz, etc.). In solonetzic large-bunch-rhizome steppes, *Iris biglumis* dominates; less often, the species is a codominant, occurring with steppe xerophytic grasses and forbs.

Meadow vegetation is represented by halophytic floodplain and valley meadows (mesohalophytic (*Galeopsis*-salt-valley) and hygrohalophytic (*Halerpestes*-*Blysmus*)) and glycophytic floodplain (steppe valley, floodplain valley).

The steppe-salt marsh meadows are in contact with steppe vegetation on one side and with marsh-salt marsh vegetation on the other side.

Forb glycophytic meadows occupy low-lying areas in steppe plant communities. Along the shorelines of lakes or in small fragments on swampy meadows, dense thickets of *Phragmites australis* (Cav.) Trin. ex Steud. and forb-tuberous reed-cereal damp meadows are formed. *Suaeda corniculata* (C.A. Mey) Bunge, *Puccinellia dolicholepis* (V.I. Krecz.) Pavlov, *Puccinellia subspicata* (V.I. Krecz.) V.I. Krecz. ex Ovcz. & Czukav, *Plantago salsa* Pall., *Agrostis gigantea* Roth. grow in patches on damp sandy salt marshes.

The vegetation cover of the tract is mosaic, which is explained by the presence of soils of light mechanical composition, the presence of channels and depressions, as well as pasture digression. The main characteristics of the model phytocenoses are shown below.

FC-1 – forb-cinquefoil-bluegrass meadow steppe (*Artemisia frigida* + *Heteropappus altaicus* + *Vicia cracca* + *Potentilla longifolia* + *Stipa capillata* + *Poa botryoides*). The community is located 300–350 m from the north-eastern shore of Lake Bolshoe, N 53°19′56.4″ E 91°16′6.9″, altitude 291 m a.s.l.

The shrub layer is formed by *Caragana pygmaea* (L.) DC., the projective cover of the species decreased during the study period from 5–7 to 1–2%. The total projective cover (TPC) of the grass layer has doubled since 2018 and was 60–65% in 2023. The grass layer is formed by two sub-layers. The first sub-layer (height 40–60 cm, single specimens reach 80 cm) is dominated by *Poa botryoides* (Trin. ex Griseb.) Kom., in addition, the cereal base is made up of *Stipa capillata* L., less often *Bromopsis inermis* (Leyss.) Holub. Of the forbs, *Potentilla longifolia* Willd. ex Schltdl. and *Medicago sativa* L. The second sub-layer (height 8–35 cm) is formed by *Festuca valesiaca brunnescens* (Tzvelev) E. Aleks., *Poa angustifolia* L., *Heteropappus altaicus* (Willd.) Novopokr., *Vicia cracca* L., *Potentilla bifurca* L.,

[5] Weather and climate. Internet resource. URL: http://www.pogodaiklimat.ru/weather.php?id=29962 (accessed February 10, 2024).

Artemisia frigida Willd., *Galium verum* L. *Convolvulus arvensis* L., *Artemisia scoparia* Waldst.et Kit., *Artemisia commutata* Bess. are recorded from single occurrences.

FC-2 – Caragana forb-onion-cinquefoil-cereal meadow steppe (*Caragana pygmaea* + *Astragalus danicus* + *Galium verum* + *Allium ramosum* + *Allium anisopodium* + *Potentilla multifida* f. *ornithopodia* + *Potentilla bifurca* + *Festuca valesiaca* + *Koeleria cristata* + *Stipa capillata*). The community is located 300–350 m from the northern shore of Lake Bolshoe, N 53°20′13.7″ E 91°15′16.866″, altitude 292 m a.s.l.

The shrub layer, represented by *Caragana pygmaea*, is sparse – the TPC is no more than 3%. The average height of dwarf caragana is 0.50–0.60 m, young shoots up to 0.15 m high are found. The TPC of the herbaceous layer has increased since the beginning of observations and in 2023 was 50–55%. The grass layer is represented by three sub-layers. The first sub-layer (height 50–75 cm, in some plants up to 90–95 cm) is dominated by cereals: *Stipa capillata, Poa botryoides*, *Poa angustifolia, Helictotrichon desertorum altaicum* (Tzvelev) Holub., from the forbs in the upper layer, *Potentilla longifolia* is described. The second sub-layer (height 15–40 cm) is formed by *Festuca valesiaca, Koeleria cristata* (L.) Pers., *Phleum phleoides* (L.) H. Karst., *Heteropappus altaicus, Galium verum, Astragalus danicus* Rets., *Hedysarum gmelinii* Ledeb., *Kitagawia baicalensis* (I. Redowsky ex Willd.) Pimenov, *Potentilla sericea* L., *Potentilla bifurca* L., *Potentilla multifida* L., *Artemisia frigida, Allium ramosum* L., *Allium anisopodium* Ledeb., *Polygala tenuifolia* Willd., *Iris biglumis, Iris humilis* Georgi, *Carex duriuscula* C.A. Mey. The third sub-layer (height 4–7 cm) is formed by *Veronica incana* L.

FC-3 – Caragana forb-feather grass meadow steppe (*Caragana pygmaea* + *Artemisia frigida* + *Potentilla bifurca* + *Stipa capillata*). The community is located 300–350 m away from the north-eastern shore of Lake Stolbovoe, N 53°20′37.9″ E 91°13′58.6″, altitude 290 m above sea level.

The projective cover of *Caragana pygmaea* increased during the years of research and in 2023 amounted to 5–7%. The height of the shrub layer reaches 0.7–0.8 m. Two sub-layers are distinguished in the grass layer. In the upper one, the absolute dominant is *Stipa capillata* (projective cover 20–30%). The maximum height (80–85 cm) is determined by the generative shoots of this species. All other species are in the second sublayer (height 10–40 cm): *Festuca valesiaca, Poa botryoides*, *Poa angustifolia*, *Elytrigia repens* (L.) Nevski., *Potentilla longifolia*, *Galium verum* L., *Artemisia frigida, Potentilla bifurca, Allium ramosum* L., *Allium tenuissimum* L., *Heteropappus altaicus, Veronica incana* L., *Carex duriuscula* C.A. Mey., *Androsace septentrionalis* L., *Dianthus versicolor* Fisch. ex Link. The TPC of the grass layer has also increased since the beginning of observations and in 2023 amounted to 50–55%. Single growing plants of *Carduus crispus* L., *Chenopodium album* L., *Artemisia commutata* Bess., and *Artemisia scoparia* Waldst.et Kit were observed.

Over the six years (from 2018 to 2023), the species richness of plant communities did not change significantly, but the share of individual species varied. In 2018 and 2019, species of the genus *Artemisia* made a greater contribution to the steppes, the projective cover of which was 2–4 times higher (*Artemisia frigida* (3–5%), *Artemisia scoparia* (7–11%), *Artemisia commutata* (1–3%)) than in 2023. In the first years of the study, all plant communities were characterized by a higher projective cover of *Elytrigia repens* (L.) Nevski (3–7%) and ruderal plant species: *Cynanchum sibiricum* (L.) R. Br. (3–7%), *Urtica dioica* L. (3–5%), *Carduus crispus* L. (1–2%), *Chenopodium album* L. (1–2%). Later, by 2023, the role of species of the family Fabaceae increased: *Astragalus danicus, Vicia cracca, Medicago sativa, Hedysarum gmelinii*, as well as species of forbs – *Dianthus versicolor, Veronica incana, Potentilla sericea, Potentilla bifurca, Potentilla multifida*, cereals – *Stipa capillata, Poa botryoides, Poa angustifolia, Festuca valesiaca, Koeleria macrantha*, sedge – *Carex duriuscula*.

Analysis of the structure of the studied phytocenoses showed that signs of demutation appeared as early as in the first years after the removal of the grazing load. Changes in the ratio of species, life forms of plants, and economic and botanical groups were observed. Complex quantitative characteristics of phytocenoses also changed – the total projective cover, the height of layers, and phytomass. Quantitative characteristics of the vertical structure of the model phytocenoses are shown in Table 1, and phytomass indicators are shown in Table 2.

Table 1. Vertical structure of plant communities.

Phytocenosis	Year	TPC of the shrub layer, %	TPC of the grass layer, %	Height of the grass layer, cm	
				max	mean
Forb-cinquefoil-bluegrass meadow steppe (FC-1)	2018	5–7	25–30	85–90	45–50
	2019	5–7	40–45	90–120	55–60
	2021	2–3	50–55	90–95	45–55
	2022	2–3	45–50	50–55	35–40
	2023	1–2	60–65	70–80	45–55
Caragana forb-onion-cinquefoil-cereal meadow steppe (FC-2)	2018	1–2	17–20	80–85	40–50
	2019	1–3	20–25	85–90	55–60
	2021	1–2	40–45	80–90	50–55
	2022	2–3	40–45	50	20–25
	2023	2–3	50–55	90–95	45–50
Caragana forb-feather grass meadow steppe (FC-3)	2018	1–3	10–15	90–95	25–30
	2019	1–3	20–30	95–110	40–50
	2021	3–5	45–50	90–95	40–50
	2022	3–5	40–45	65	25–27
	2023	5–7	50–55	80–85	45–50

Table 2. Air-dried phytomass at the end of August, g/m^2.

Phytocenosis	Year of study				
	2018	2019	2021	2022	2023
Forb-cinquefoil-bluegrass meadow steppe (FC-1)	209 ± 23	426 ± 67	425 ± 37	151 ± 14	418 ± 40
Caragana forb-onion-cinquefoil-cereal meadow steppe (FC-2)	411 ± 68	342 ± 49	345 ± 52	150 ± 37	294 ± 29
Caragana forb-feather grass meadow steppe (FC-3)	219 ± 27	337 ± 44	480 ± 123	124 ± 8	355 ± 38

Quantitative indicators of plant communities in the study period demonstrate both progressive (successional) and oscillatory (fluctuation) changes. The TPC of the shrub and grass layers changes progressively (Table 1). From 2018 to 2023, a decrease in the bushiness of the forb-cinquefoil-bluegrass meadow steppe and an increase in the bushiness of the caragana forb-onion-cinquefoil-cereal and caragana forb-feather-grass meadow steppes are observed. The TPC of the grass layer gradually increases during the same period. The exception is 2022, when the TPC of the grass layer in two communities (FC-1 and FC-3) slightly decreased compared to the previous year, and in one community (FC-2) remained at the same level. Moreover, the following year, a tendency towards growth of the projective cover of the grass layer was again observed in all phytocenoses.

The height of the grass layer (Table 1) and phytomass (Table 2) were subject to fluctuating changes. The average height of the grass layer in all phytocenoses reached its minimum value in 2022, and its maximum in 2019. Phytomass in all phytocenoses was also the lowest in 2022; the highest value of this indicator in different phytocenoses was observed in different years. At the same time, significant fluctuations in phytomass were recorded – by 2.7–3.9 times between years.

The analyzed complex characteristics of phytocenoses are the result of the multidirectional action of many direct and indirect factors. The biological production of communities depends on the amount of moisture, heat, the provision of soil with mineral nutrients and other indicators; their contribution varies in different communities, and the phenomenon of limiting factors is manifested (Mirkin and Naumova, 2017). It appears that post-pasture demutation processes and weather conditions were decisive for the model territories during the observation period. Productivity, or phytomass formed during the growing season, is the most integral indicator reflecting the functioning of the plant community. The height and projective cover of the grass stand can be considered as indicators contributing to productivity.

Restoration of grass communities after reduction or cessation of grazing leads to changes in productivity, manifested in the form of long-term trends. The dynamics of vegetation during pasture restoration in the Koibalskaya steppe was studied by G.T. Kandalova and G.I. Lysanova (2010). They showed that an increase with subsequent stagnation is observed in the 8th–9th year, and a decrease in the phytomass of steppe pastures was recorded in the 20th year.

According to classical concepts (Mirkin and Naumova, 2017), productivity is determined primarily by the species composition of the phytocenosis, but yields can vary by 10 or more times as a result of interannual differences in the moisture supply of plants.

In the Koibalskaya Steppe, the mean temperature in April–August in the period 2018–2023 fluctuated from 12.8 to 14.4 °C. These values are within the range of Xcp ± σ calculated based on recorded temperature records for the past 20 years (13.63 ± 0.76), so they are not considered extreme. On the contrary, the amount of precipitation in April–August varied dramatically from year to year (Fig. 2). For precipitation, the most favorable year was 2019: the maximum amount for the year as a whole (561 mm), in April–August (441 mm), and in the hottest month of the year (138 mm). The driest year was 2022: in the summer months, the amount of precipitation was 2.9 times less than in 2019 (151 mm). The maximum and minimum values of precipitation for April–August, recorded during our observation period (441 and 151 mm), go far beyond the limits of Xcp ± σ (323.4 ± 88.9), also calculated based on archival data for the past 20 years. Moreover, in this area from 1966 to 2023, only five years had precipitation equal to or greater than in 2019 (1967, 1970, 2001, 2002, 2003), and only two years had precipitation equal to or less than in 2022 (1973 and 1977). Thus, 2022 can be considered an extremely dry year, and 2019 – a year with precipitation significantly above average.

In the year with the highest amount of precipitation (2019), the maximum (FC-1, FC-2) or close to the maximum (FC-3) grass height was observed (Table 1). In the dry year of 2022, on the contrary, the grass height and phytomass were minimal (Tables 1, 2). Thus, fluctuations in one of the partial indicators (grass height) and the integral indicator (phytomass) can be caused by fluctuations in the amount of precipitation. A graphical analysis was carried out to identify the nature of the relationships between phytocenotic and climatic indicators. This relationship is the best shown by a polynomial regression model (Figs. 3, 4).

For the phytocenosis with the highest moisture content (FC-1), a linear positive relationship between the amount of precipitation and the height of the grass layer is evident with high approximation accuracy

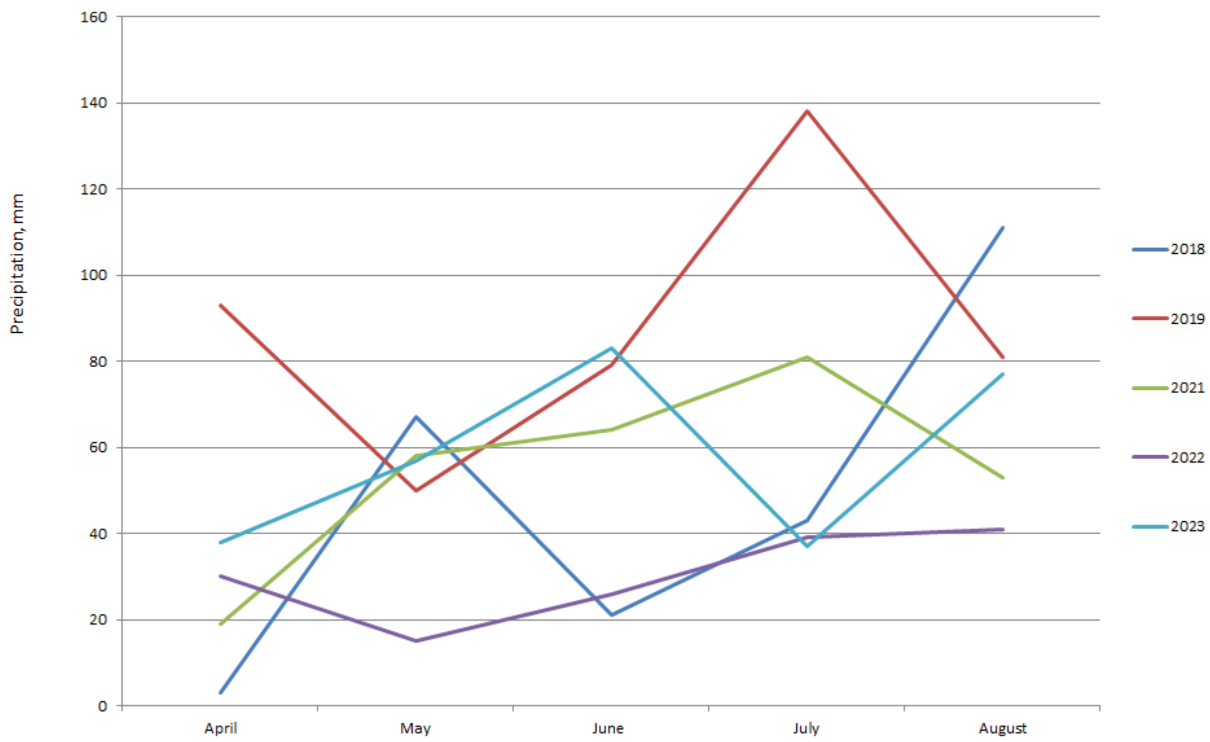

Fig. 2. Dynamics of precipitation during the growing season (according to data from the Beya weather station).

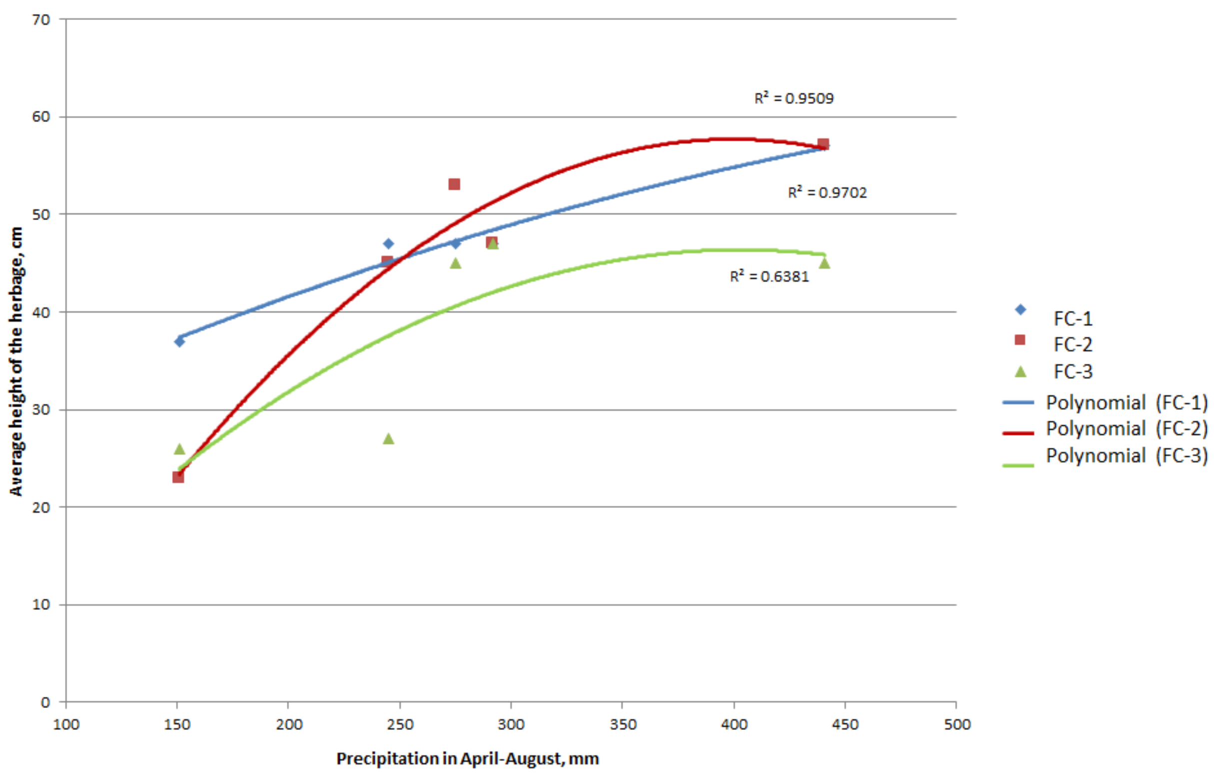

Fig. 3. Dependence of the height of the grass layer on the amount of precipitation during the growing season. Names of phytocenoses as in Table 1.

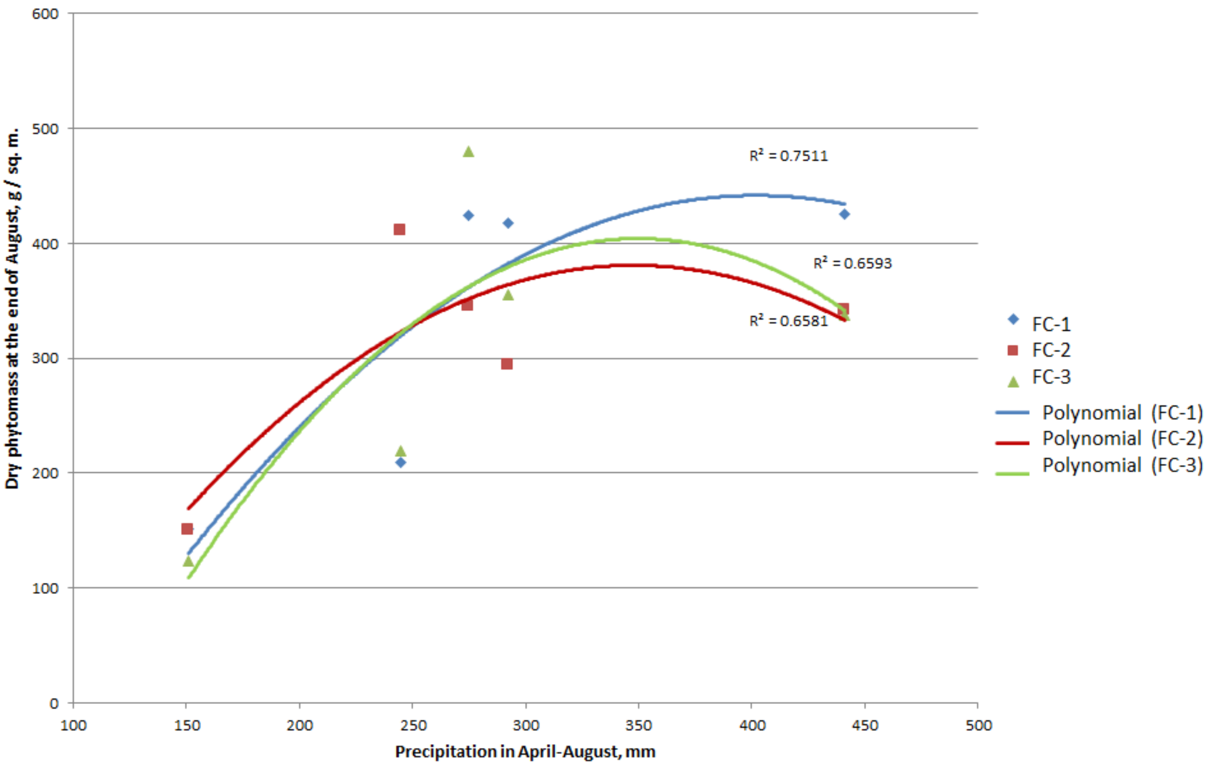

Fig. 4. Dependence of phytomass on the amount of precipitation during the growing season. Names of phytocenoses as in Table 1.

(R^2 = 0.97). For the remaining phytocenoses (FC-2 and FC-3), a curvilinear relationship is evident between these parameters with medium and high approximation accuracy (R^2 = 0.64 and 0.95): at a precipitation amount of 370 mm, the curves reach a plateau (Fig. 3).

The graphical model of the phytomass response to precipitation is less accurate (R^2 = 0.66–0.75), probably due to the complexity of the character analyzed. Nevertheless, the phytomass of all three communities shows a nonlinear dependence on moisture supply. Interpolation shows that the phytomass curves for FC-2 and FC-3 reach a plateau in the range of 300–350 mm of precipitation, a further increase in the amount of precipitation leads to a decrease in phytomass (Fig. 4). The phytomass curve of FC-1 reaches a plateau at 350–370 mm of precipitation and does not change its course further. Thus, the minimum precipitation amount observed in 2022 for April–August is pessimal for the formation of aboveground phytomass of meadow steppes. The maximum precipitation for the same months (2019) is in the optimum zone for forb-cinquefoil-bluegrass and suboptimal for forb-bulb-cinquefoil-cereal and forb-feather-grass meadow steppes. The optimum precipitation for the last two phytocenoses is probably in the range of 310–360 mm.

With different moisture supply, the aboveground phytomass of FC-1 varied in the range of 151–426 g/m^2, FC-2 – 150–411 g/m^2, and FC-3 – 124–480 g/m^2 (Table 2). Studies of the productivity dynamics of steppe phytocenoses of the Koibalskaya steppe, conducted in 2000–2017 at the transect site, also showed differences in phytomass between years with favorable and unfavorable hydrothermal conditions: in the small-bunch grass-feather grass steppe with caragana, the phytomass fluctuated from 96 to 309 g/m^2 (Dubynina, 2018). A 3–4-fold increase in productivity indicates a high potential and a wide range of variability of the steppe ecosystems of the Koibalskaya steppe.

The main contribution to the productivity of our model phytocenoses was made by steppe grasses and forbs (up to 60% of the total phytomass). It is these components of the grass layer that have the closest connection with precipitation (Minin, 2011) and react very quickly to changes in moisture conditions (Bobrovskaya and Sveshnikova, 1988; Lavrenko et al., 1991; Sveshnikova and Bobrovskaya, 1980).

The projective cover of communities did not respond to precipitation fluctuations and changed gradually, except for an extremely dry year (Table 1). The extremely low amount of precipitation in 2022 suspended the gradual growth of the grass layer projective cover for one season. Fluctuations in moisture supply in other years were probably leveled by other factors affecting the projective cover. The increase in this indicator is most likely a manifestation of a change in the dominant and spatial structure of communities during restoration processes. In areas with different moisture supply, these processes occur at different rates and may have opposite trends.

The shrub layer of three model phytocenoses is formed by the perennial plant *Caragana pygmaea*. The aboveground part of the plant is formed over several years and cannot change its characteristics in opposite directions every year. The shallow occurrence of groundwater (1.25–1.40 m) provides this plant with deeply penetrating roots with a lower dependence on atmospheric moisture, due to which the TPC of the species changed progressively. Differences in the dynamics of TPC were observed in phytocenoses with different degrees of moisture. An increase in the contribution of this shrub to the projective cover of more xerophytic steppe communities (FC-2 and FC-3), for which *Caragana* is one of the edificator species, may be a consequence of the cessation of grazing. In pastures, farm animals break off and consume young shoots even of thorny bushes; while in the model phytocenosis, there is no reduction of shoots by cattle or sheep. The reason for the gradual decrease in the proportion of caragana in the more mesophytic community (FC-1) is probably the post-pasture decrease in xerophytization, resulting in pessimal conditions for the species.

The results obtained by the study demonstrate a complex and ambiguous relationship between the process of formation of climax communities during post-pasture succession and fluctuations in the amount of precipitation. As successional changes occur, the proportions of species in the communities and bushiness gradually change, and an increase in the TPC of the grass layer is observed. Against the background of demutation of steppe vegetation, sharp interannual fluctuations in the amount of precipitation lead to fluctuations in the height of herbaceous plants, which affects the total phytomass.

Conclusions

The post-pasture succession of the meadow steppes observed in 2018–2023 was manifested in an increase in the total projective cover of the grass layer, a decrease in the participation of some species of the genus *Artemisia* and a number of ruderal species, and an increase in the role of the family Fabaceae, forbs and cereals. The shrub density of phytocenoses also changed progressively: the participation of *Caragana pygmaea* decreased in the forb-cinquefoil-bluegrass meadow steppe and increased in the caragana forb-onion-cinquefoil-cereal and caragana forb-feather-grass meadow steppes.

From 2018 to 2023, precipitation fluctuations were clearly evident in the Koibalskaya steppe: the amount of precipitation for April–August in the wettest year (2019) was 2.9 times greater than in the driest year (2022).

Using the example of forb-cinquefoil-bluegrass, caragana forb-onion-cinquefoil-cereal and caragana forb-feather grass meadow steppes, phytocenoses demonstrating a response to the amount of precipitation were characterized. Fluctuations were observed for the grass stand height (by 1.5–2 times) and aboveground phytomass (by 2.7–3.9 times). In the extremely dry year of 2022, a drop or stagnation of the TPC of the grass layer, minimum values of the height of the grass layer and phytomass were observed.

The polynomial regression model showed that the grass stand height in the most humid phytocenosis is directly dependent on the amount of precipitation, with relationship close to linear. The grass stand height of less humid phytocenoses and the phytomass of all model phytocenoses changed curvilinearly with an increase in the amount of precipitation. The phytomass of the forb-cinquefoil-bluegrass meadow steppe increases with increasing humidity and reaches its maximum values with a precipitation amount for April–August of 350–370 mm. The course of changes in phytomass in the environments with greater precipitation was not revealed. In drier caragana meadow steppes, with increasing humidity, the aboveground phytomass also grows and reaches its maximum values with a precipitation amount for April–August of 300–350 mm; with a greater amount of precipitation, the phytomass, on the contrary, shows a tendency to decrease.

References

Anenkhonov, O.A., 2010. Klimatogennye izmeneniya rastitel'nykh soobshchestv: fluktuatsii ili suktsessii? [Climatogenic changes in plant communities: fluctuations or successions?]. *Rastitel'nyi mir Aziatskoi Rossii [Vegetation of the world of Asian Russia]* **2** (6), 1–6. (In Russian).

Bobrovskaya, N.I., Sveshnikova, V.M., 1988. Ekologo-fiziologicheskie osobennosti rastenii sukhikh stepei: Vodnyi rezhim [Ecological and physiological features of plants of dry steppes: Water regime]. In: Lavrenko, E.M. (ed.), *Sukhie stepi MNR. Ch 2. Statsionarnye issledovaniya (somon Undzhul) [Dry steppes of the Mongolian People's Republic. Part 2. Stationary studies (somon Undzhul)].* Nauka, Leningrad, USSR, 31–52. (In Russian).

Chebakova, N.M., Parfyonova, E.I., 2006. Prognoz prodvizheniya granits lesa pri izmenenii klimata k kontsu 20 veka v Srednei Sibiri [Forecast of forest boundary advancement under climate change by the end of the 20th century in Central Siberia]. *Vychislitel'nye tekhnologii [Computing Technologies]* **11** (3), 77–86. (In Russian).

Cherepanov, S.K., 1995. Sosudistye rasteniya Rossii i sopredel'nykh gosudarstv (v predelakh byvshego SSSR). 2-e izdanie [Vascular plants of Russia and neighboring countries (within the former USSR). 2nd edition]. Mir i sem'ya-95, Sankt-Peterburg, USSR, 990 p. (In Russian).

Cherepnin, L.M., 1956. Rastitel'nyi pokrov yuzhnoi chasti Krasnoyarskogo kraya i zadachi ego izucheniya [Vegetation cover of the southern part of the Krasnoyarsk Territory and the tasks of its study]. *Uchyonye zapiski Krasnoyarskogo pedagogicheskogo instituta [Scientific Notes of the Krasnoyarsk Pedagogical Institute]* **5**, 3–43. (In Russian).

Cherepnin, L.M., 1961. Rastitel'nost' Krasnoyarskogo kraya [Vegetation of the Krasnoyarsk Territory]. In: Gromov, L.V. (ed.), *Prirodnye usloviya Krasnoyarskogo kraya [Natural conditions of the Krasnoyarsk Territory]*. Publishing House of the USSR Academy of Sciences, Moscow, USSR, 160–187. (In Russian).

Cherepnin, L.M., 1963. Flora yuzhnoi chasti Krasnoyarskogo kraya [Flora of the southern part of the Krasnoyarsk Territory] *Uchyonye zapiski Krasnoyarskogo pedagogicheskogo instituta [Scientific Notes of the Krasnoyarsk Pedagogical Institute]* **24** (4), 1–325. (In Russian).

Chernousenko, G.I., Khitrov, N.B., 2019. Izmenenie klimata v zone rasprostraneniya zasolennykh pochv krioaridnykh regionov na yuge Vostochnoi Sibiri [Climate change in the saline soil distribution zone of cryoarid regions in the South of Eastern Siberia]. *Ekosistemy: ekologiya i dinamika [Ecosystems: Ecology and Dynamics]* **3**, 5–57. (In Russian).

Dubynina, S.S., 2018. Sezonnaya i pogodichnaya dinamika zapasov zelyonoi massy Koibal'skoi stepi v usloviyakh izmeneniya klimata [Seasonal and weather dynamics of green mass reserves of the Koibal steppe in the context of climate change]. *Uspekhi sovremennogo estestvoznaniya [The Successes of Modern Natural Science]* **6**, 65–70. (In Russian).

Häder, D.P., Barnes, P.W., 2019. Comparing the impacts of climate change on the responses and linkages between terrestrial and aquatic ecosystems. *Science of Total Environment* **682**, 239–246. https://doi.org/10.1016/j.scitotenv.2019.05.024

Im, S.T., 2023. Otsenka vliyaniya klimaticheskikh faktorov na dinamiku rastitel'nogo pokrova Khakasii [Assessment of the influence of climatic factors on the dynamics of vegetation cover in Khakassia]. *Materialy X Mezhdunarodnoi nauchnoi konferentsii "Regional'nye problemy distancionnogo zondirovaniya Zemli"* [*Materials of the X International Scientific Conference "Regional problems of remote sensing of the Earth"*]. Krasnoyarsk, Russia, 93–96. (In Russian).

Kandalova G.T., Lysanova G.I., 2010. Vosstanovlenie stepnykh pastbishch Khakasii [Restoration of steppe pastures of Khakassia]. *Geografiya i prirodnye resursy [Geography and Natural Resources]* **4**, 79–85. (In Russian).

Kazantseva, T.I., 2004. Dinamika i produktivnost' rastitel'nykh soobshchestv somona Bulgan [Dynamics and productivity of plant communities of somon Bulgan]. *Aridnye ekosistemy [Arid ecosystems]* **10** (24–25), 13–148. (In Russian).

Kharlamova, N.F., Ostanin, O.V., 2012. Obzor sovremennogo termicheskogo rezhima Altae-Sayanskogo ekoregiona i vozmozhnye prognozy [Overview of the current thermal regime of the Altai-Sayan ecoregion and possible forecasts]. *Izvestiya Altajskogo gosudarstvennogo universiteta [Proceedings of the Altai State University]* **3–1** (75), 145–142. (In Russian).

Kharuk, V.I., Im, S.T., Petrov, I.A., 2021. Alpine ecotone in the Siberian Mountains: vegetation response to warming. *Journal of Mountain Sciences* **18**, 3099–3108. https://doi.org/10.1007/s11629-021-6876-2

Larionov, A.V., 2013. Sintaksony nastoyashchikh i sukhikh stepei *Cleistogenetea squarrosae* iz Khakasii [Syntaxons of the real and dry steppes *Cleistogenetea squarrosae* from Khakassia]. *Vestnik Novosibirskogo gosudarstvennogo universiteta. Seriya: Biologiya, klinicheskaya medicina [Bulletin of Novosibirsk State University. Series: Biology, Clinical Medicine]* **11**(1), 61–67. (In Russian).

Larionov, A.V., Ermakov, N.B., Polyakova, M.A., Ankipovich, E.S., 2015. Stepnaya rastitel'nost' Khakasii: raznoobrazie i ekologiya [Steppe vegetation of Khakassia: diversity and ecology]. Publishing House of Khakassian State University named after N.F. Katanov, Abakan, Russia, 196 p. (In Russian).

Lavrenko, E.M., Karamysheva, Z.V., Nikulina, R.I., 1991. Stepi Evrazii [Steppes of Eurasia]. Nauka, Leningrad, USSR, 146 p. (In Russian).

Minin, A.A., 2011. Nekotorye aspekty vzaimosvyazei nazemnykh ekosistem s izmenyayushchimsya klimatom [Some aspects of the interrelationships of terrestrial ecosystems with a changing climate]. *Uspekhi sovremennoi biologii [The Successes of Modern Biology]* **131** (4), 407–415. (In Russian).

Mirkin, B.M., Naumova, L.G., 2017. Vvedenie v sovremennuyu nauku o rastitel'nosti [Introduction to modern vegetation science]. GEOS, Moscow, Russia, 280 p. (In Russian).

Myers-Smith, I.H., Kerby, J.T., Phoenix, G.K. et al., 2020. Complexity revealed in the greening of the Arctic. *Nature Climate Change* **10**, 106–117. https://doi.org/10.1038/s41558-019-0688-1

Nikolaeva, Z.N., 2005. Agroklimaticheskii monitoring Yuzhno-Minusinskoi kotloviny [Agro-climatic monitoring of the South Minusinsk basin]. *PhD in Agricultural Sciences thesis abstract*. Krasnoyarsk, Russia, 19 p. (In Russian).

Otsenka vozdeistviya na bioraznoobrazie proektiruemykh ugol'nykh predpriyatii OOO “KVSU-Khakasiya” i OOO “Khakasskaya ugol'naya kompaniya” v raione Beiskogo kamennougol'nogo mestorozhdeniya (Altaiskii raion Respubliki Khakasiya) i razrabotka kompensatsionnykh meropriyatii, 2017. Otchyot o NIR (zaklyuchitel'nyi po 3 etapu) [Assessment of the impact on biodiversity of the projected coal enterprises of LLC "KVSU-Khakassia" and LLC "Khakass Coal Company" in the area of the Bey coal deposit (Altai region of the Republic of Khakassia) and development of compensation measures: research report (final stage 3)] Khakassian State University; head Zlotnikova T.V. Deposited in the EGISU R&D on May 29, 2017. Registration number АААА-Б17-217052950040-9. Abakan, Russia, 171 p. (In Russian).

Pankova, E.I., Chernousenko, G.I., 2020. Problema aktivizatsii zasoleniya v pochvakh yuga Vostochnoi Sibiri i Mongolii v svyazi s aridizaciei klimata [The problem of activation of salinization in the soils of the South of Eastern Siberia and Mongolia in connection with climate aridization]. *Byulleten' Pochvennogo instituta im. V.V. Dokuchaeva [Bulletin of the V.V. Dokuchaev Soil Institute]* **101**, 19–45. (In Russian). https://doi.org/10.19047/0136-1694-2020-101-19-46

Polevaya geobotanika. Tom 3 [Field geobotany. Vol. 3], 1964. Lavrenko, E.M., Korchagin, A.A. (eds.). USSR Academy of Sciences, Leningrad Department, Moscow – Leningrad, USSR, 530 p. (In Russian).

Polevaya geobotanika. Tom 4 [Field geobotany. Vol. 4], 1972. Lavrenko, E.M., Korchagin, A.A. (eds.). Nauka, Leningrad, USSR, 336 p. (In Russian).

Polevoi, A.N., Bozhko, L.E, Barsukova, E.A., 2019. Formirovanie produktivnosti lugovoi i stepnoi rastitel'nosti v usloviyakh izmeneniya klimata [Formation of productivity of meadow and steppe vegetation in conditions of climate change]. *Fundamental'naya i prikladnaya klimatologiya [Fundamental and Applied Climatology]* **3**, 102–126. (In Russian). https://doi.org/10.21513/2410-8758-2019-3-102-126

Rabotnov, T.A., 1992. Fitotsenologiya [Phytocenology]. Publishing House of Moscow State Univbersity, Moscow, Russia, 352 p. (In Russian).

Rastitel'nyi mir Respubliki Khakasiya: uchebno-metodicheskii kompleks po distsipline: laboratornyi praktikum [Flora of the Republic of Khakassia: educational and methodological complex for the discipline: laboratory workshop], 2015. Ankipovich, E.S., Lagunova, E.G. (eds.). Publishing House of Khakassian State University named after N.F. Katanov, Abakan, Russia, 124 p. (In Russian).

Rastitel'nyi pokrov HKhakasii [Vegetation cover of Khakassia], 1976. Kuminova, A.V. (ed.). USSR Academy of Sciences, Siberian Department, Central Siberian Botanical Garden, Nauka, Siberian Branch, Novosibirsk, USSR, 423 p. (In Russian).

Shi, S., Wang, P., Zhang, Y., Yu, J., 2021. Cumulative and time-lag effects of the main climate factors on natural vegetation across Siberia. *Ecological Indicators* **133**, 108446. https://doi.org/10.1016/j.ecolind.2021.108446

Subbotin, M.A., Zorkina, T.M., 2004. Osobennosti pasteral'noi digressii stepei Beiskogo rajona [Features of the pasteur digression of the steppes of the Baysky district]. *Materialy Mezhdunarodnoi nauchno-prakticheskoi konferentsii “Ekologiya Yuzhnoi Sibiri i sopredel'nykh territorii”. Ch. 1 [Materials of the International Scientific and Practical Conference "Ecology of Southern Siberia and adjacent territories". Part 1].* Abakan, Russia, 140. (In Russian).

Sveshnikova, V.M., Bobrovskaya, N.I., 1980. Vodnyi rezhim [The water regime]. In: Lavrenko, E.M. (ed.), *Pustynnye stepi i severnye pustyni MNR. Ch. 1. Prirodnye usloviya (Bulgan somon) [Desert steppes and northern deserts of the Mongolian People's Republic. Part 1. Natural conditions (Bulgan somon)*]. Nauka, Leningrad, USSR, 127–136. (In Russian).

Vincent, W.F., 2009. Effects of climate change on lakes. In: Likens, G.E. (ed.), *Encyclopedia of Inland Waters*. Elsevier, Amsterdam, Netherlands, 55–60. https://doi.org/10.1016/B978-012370626-3.00233-7

Voskresenskii, S.S., 1962. Geomorfologiya Sibiri [Geomorphology of Siberia]. Publishing House of the Moscow University, Moscow, USSR, 352 p. (In Russian).

Yavorskii, O.V., 1968. Melioratsii v Khakasii [Land reclamation in Khakassia]. Book Publishing House, Krasnoyarsk, USSR, 80 p. (In Russian).

Zelenskaya, N.N., Kerzhentsev, A.S., Ableeva, V.A., Tereshonok, N.A., 2012. Dinamika produktivnosti lugovykh stepei na severo-zapadnom predele ikh areala (basseina Oki) [Dynamics of productivity of meadow steppes in the northwestern limit of their range (Oka basin)]. *Izvestiya RAN. Seriya Geograficheskaya [News of the Russian Academy of Sciences. Series Geographical]* **6**, 47–54. (In Russian).

Zhukova, E.Yu., 2015. Primenenie spektral'nykh indeksov Landsat 8 dlya otsenki fitotsenozov priozernoi kotloviny ozera Turlan'e (Respublika Khakasiya) [Application of Landsat 8 spectral indices for the assessment of phytocenoses of the Lake Turlanye Lake basin (Republic of Khakassia)]. *Materialy Mezhdunarodnoi nauchno-prakticheskoi konferentsii “Ekologiya Yuzhnoi Sibiri i sopredel'nykh territorii”. Ch. 1 [Materials of the International Scientific and Practical Conference "Ecology of Southern Siberia and adjacent territories". Part 1].* Abakan, Russia, 19. (In Russian).

Zhukova, V.M., Kut'kina, N.V., Zorkina, T.M., 2011. Kharakteristika lugovoi rastitel'nosti i ee sostoyaniya Sorokaozernoi ravninno-solonchakovoi peschanoi stepi [Characteristics of meadow vegetation and its condition of the Sorokaozernoj plain-salt-marsh sandy steppe.]. *Materialy Mezhdunarodnoi nauchno-prakticheskoi konferentsii “Ekologiya Yuzhnoi Sibiri i sopredel'nykh territorii”. Ch. 1 [Materials of the International Scientific and Practical Conference "Ecology of Southern Siberia and adjacent territories". Part 1].* Abakan, Russia, 3–4. (In Russian).

Zorkina, T.M., 2016. Ekologicheskaya otsenka lugovoi rastitel'nosti sorokaozernoi peschanoi stepi (Khakasiya) [Ecological assessment of meadow vegetation of the sorokaozernoj sandy steppe (Khakassia).]. *Materialy shestoi Vserossijskoi konferentsii s mezhdunarodnym uchastiem “Flora i rastitel'nost' Sibiri i Dal'nego Vostoka” [Materials of the sixth All-Russian conference with international participation "Flora and Vegetation of Siberia and the Far East"].* Krasnoyarsk, Russia. 211–219. (In Russian).

Zorkina, T.M., Zhukova, V.M., 2006. Monitoring antropogennogo vozdeistviya na strukturno-funktsional'nye osobennosti rastitel'nogo kompleksa Sorokaozernogo peschanogo stepnogo raiona Khakasii [Monitoring of anthropogenic impact on the structural and functional features of the vegetation complex of the Sorokaozerny sandy steppe region of Khakassia]. *Materialy Mezhdunarodnoi nauchno-prakticheskoi konferentsii “Ekologiya Yuzhnoi Sibiri i sopredel'nykh territorii”. Ch. 1 [Materials of the International Scientific and Practical Conference "Ecology of Southern Siberia and adjacent territories". Part 1].* Abakan, Russia, 114. (In Russian).

Zorkina, T.M., Zhukova, V.M., 2009. Rastitel'nye stepnye soobshchestva Khakasii: ikh struktura i funktsional'noe sostoyanie [Plant steppe communities of Khakassia: their structure and functional state]. *Materialy Mezhdunarodnoi nauchno-prakticheskoi konferentsii “Ekologiya Yuzhnoi Sibiri i sopredel'nykh territorii”. Ch. 1 [Materials of the International Scientific and Practical Conference "Ecology of Southern Siberia and adjacent territories". Part 1].* Abakan, Russia, 3–5. (In Russian).

Zorkina, T.M., Zhukova V.M., Kut'kina, N.V., 2013. Monitoring rastitel'nosti zasolyonnykh lugov na osnove nazemnykh i sputnikovykh metodov v usloviyakh Koibal'skoi stepi (Khakasiya) [Vegetation monitoring of saline meadows based on terrestrial and satellite methods in the conditions of the Koibal steppe (Khakassia)]. *Vestnik KGPU im. V. P. Astaf'eva [Bulletin of the Kransoyarsk State Pedagogical University named after V.P. Astafiev]* **3** (25), 229–234. (In Russian).

Список литературы

Аненхонов, О.А., 2010. Климатогенные изменения растительных сообществ: флуктуации или сукцессии? *Растительный мир Азиатской России* **2** (6), 1–6.

Бобровская, Н.И., Свешникова, В.М., 1988. Эколого-физиологические особенности растений сухих степей: Водный режим. В: Лавренко, Е.М. (ред.), *Сухие степи МНР. Ч. 2. Стационарные исследования (сомон Унджул).* Наука, Ленинград, СССР, 31–52.

Воскресенский, С.С., 1962. Геоморфология Сибири. Издательство Московского университета, Москва, СССР, 352 с.

Дубынина, С.С., 2018. Сезонная и погодичная динамика запасов зеленой массы Койбальской степи в условиях изменения климата. *Успехи современного естествознания* **6**, 65–70.

Жукова, Е.Ю., 2015. Применение спектральных индексов Landsat 8 для оценки фитоценозов приозерной котловины озера Турланье (Республика Хакасия). *Материалы Международной научно-практической конференции «Экология Южной Сибири и сопредельных территорий». Ч. 1*. Абакан, Россия, 19.

Жукова, В.М., Кутькина, Н.В., Зоркина, Т.М., 2011. Характеристика луговой растительности и ее состояния Сорокаозерной равнинно-солончаковой песчаной степи. *Материалы Международной научно-практической конференции «Экология Южной Сибири и сопредельных территорий». Ч. 1*. Абакан, Россия, 3–4.

Зеленская, Н.Н., Керженцев, А.С., Аблеева, В.А., Терешонок, Н.А., 2012. Динамика продуктивности луговых степей на северо-западном пределе их ареала (бассейна Оки). *Известия РАН. Серия Географическая* **6**, 47–54.

Зоркина, Т.М., 2016. Экологическая оценка луговой растительности сорокаозерной песчаной степи (Хакасия). *Материалы шестой Всероссийской конференции с международным участием «Флора и растительность Сибири и Дальнего Востока».* Красноярск, Россия, 211–219.

Зоркина, Т.М., Жукова, В.М., 2006. Мониторинг антропогенного воздействия на структурно-функциональные особенности растительного комплекса Сорокаозерного песчаного степного района Хакасии. *Материалы Международной научно-практической конференции «Экология Южной Сибири и сопредельных территорий». Ч. 1*. Абакан, Россия, 114.

Зоркина, Т.М., Жукова, В.М., 2009. Растительные степные сообщества Хакасии: их структура и функциональное состояние. *Материалы Международной научно-практической конференции «Экология Южной Сибири и сопредельных территорий». Ч. 1*. Абакан, Россия, 3–5.

Зоркина, Т.М., Жукова В.М., Кутькина, Н.В., 2013. Мониторинг растительности засоленных лугов на основе наземных и спутниковых методов в условиях Койбальской степи (Хакасия). *Вестник КГПУ им. В.П. Астафьева* **3** (25), 229–234.

Им, С.Т., 2023. Оценка влияния климатических факторов на динамику растительного покрова Хакасии. *Материалы X Международной научной конференции «Региональные проблемы дистанционного зондирования Земли»*. Красноярск, Россия, 93–96.

Казанцева, Т.И., 2004. Динамика и продуктивность растительных сообществ сомона Булган. *Аридные экосистемы* **10** (24–25), 13–148.

Кандалова, Г.Т., Лысанова, Г.И., 2010. Восстановление степных пастбищ Хакасии. *География и природные ресурсы* **4,** 79–85.

Лавренко, Е.М., Карамышева, З.В., Никулина, Р.И., 1991. Степи Евразии. Наука, Ленинград, СССР, 146 с.

Ларионов, А.В., 2013. Синтаксоны настоящих и сухих степей *Cleistogenetea squarrosae* из Хакасии. *Вестник Новосибирского государственного университета. Серия: Биология, клиническая медицина* **11**(1), 61–67.

Ларионов, А.В., Ермаков, Н.Б., Полякова, М.А., Анкипович, Е.С., 2015. Степная растительность Хакасии: разнообразие и экология. Издательство Хакасского государственного университета им. Н.Ф. Катанова, Абакан, Россия, 196 с.

Минин, А.А., 2011. Некоторые аспекты взаимосвязей наземных экосистем с изменяющимся климатом. *Успехи современной биологии* **131** (4), 407–415.

Миркин, Б.М., Наумова, Л.Г., 2017. Введение в современную науку о растительности. ГЕОС, Москва, Россия, 280 с.

Николаева, З.Н., 2005. Агроклиматический мониторинг Южно-Минусинской котловины. *Автореферат диссертации на соискание ученой степени кандидата сельскохозяйственных наук*. Красноярск, Россия, 19 с.

Оценка воздействия на биоразнообразие проектируемых угольных предприятий ООО «КВСУ-Хакасия» и ООО «Хакасская угольная компания» в районе Бейского каменноугольного месторождения (Алтайский район Республики Хакасия) и разработка компенсационных мероприятий, 2017. Отчет о НИР (заключительный по 3 этапу). Хакасский государственный университет; рук. Злотникова Т.В. Деп. в ЕГИСУ НИОКТР 29 мая 2017 г. Рег. номер АААА-Б17-217052950040-9. Абакан, Россия, 171 с.

Панкова, Е.И., Черноусенко, Г.И., 2020. Проблема активизации засоления в почвах юга Восточной Сибири и Монголии в связи с аридизацией климата. *Бюллетень Почвенного института им. В.В. Докучаева* **101**, 19–45. https://doi.org/10.19047/0136-1694-2020-101-19-46

Полевая геоботаника. Т. 3, 1964. Е.М. Лавренко, А.А. Корчагин (ред.). Академия наук СССР, Ленинградское отделение, Москва – Ленинград, СССР, 530 с.

Полевая геоботаника. Т. 4, 1972. Е.М. Лавренко, А.А. Корчагин (ред.). Наука, Ленинград, СССР, 336 с.

Полевой, А.Н., Божко, Л.Е, Барсукова, Е.А., 2019. Формирование продуктивности луговой и степной растительности в условиях изменения климата. *Фундаментальная и прикладная климатология* **3**, 102–126. https://doi.org/10.21513/2410-8758-2019-3-102-126

Работнов, Т.А., 1992. Фитоценология. МГУ, Москва, Россия, 352 с.

Растительный мир Республики Хакасия: учебно-методический комплекс по дисциплине: лабораторный практикум, 2015. Анкипович, Е.С., Лагунова, Е.Г. (ред). Издательство ХГУ им. Н.Ф. Катанова, Абакан, Россия, 124 с.

Растительный покров Хакасии, 1976. Куминова, А.В. (ред.). АН СССР, Сибирское отделение, Центральный сибирский ботанический сад, Наука, Сибирское отделение, Новосибирск, СССР, 423 с.

Свешникова, В.М., Бобровская, Н.И., 1980. Водный режим. В: Лавренко, Е.М. (ред.), *Пустынные степи и северные пустыни МНР. Ч. 1. Природные условия (Булган сомон)*. Наука, Ленинград,СССР, 127–136.

Субботин, М.А., Зоркина, Т.М., 2004. Особенности пастеральной дигрессии степей Бейского района. *Материалы Международной научно-практической конференции «Экология Южной Сибири и сопредельных территорий». Ч. 1*. Абакан, Россия, 140.

Харламова, Н.Ф., Останин, О.В., 2012. Обзор современного термического режима Алтае-Саянского экорегиона и возможные прогнозы. *Известия Алтайского государственного университета* **3–1** (75), 145–142.

Чебакова, Н.М., Парфёнова, Е.И., 2006. Прогноз продвижения границ леса при изменении климата к концу 20 века в Средней Сибири. *Вычислительные технологии* **11** (3), 77–86.

Черепанов, С.К., 1995. Сосудистые растения России и сопредельных государств (в пределах бывшего СССР). 2-е издание. Мир и семья-95, Санкт-Петербург, СССР, 990с.

Черепнин, Л.М., 1956. Растительный покров южной части Красноярского края и задачи его изучения. *Ученые записки Красноярского педагогического института* **5**, 3–43.

Черепнин, Л.М., 1961. Растительность Красноярского края. В: Громов, Л.В. (ред.), *Природные условия Красноярского края*. Издательство АН СССР, Москва, СССР, 160–187.

Черепнин, Л.М., 1963. Флора южной части Красноярского края. *Ученые записки Красноярского педагогического института* **24** (4), 1–325.

Черноусенко, Г.И., Хитров, Н.Б., 2019. Изменение климата в зоне распространения засоленных почв криоаридных регионов на юге Восточной Сибири. *Экосистемы: экология и динамика* **3**, 5–57.

Яворский, О.В., 1968. Мелиорации в Хакасии. Книжное издательство, Красноярск, СССР, 80 с.

Häder, D.P., Barnes, P.W., 2019. Comparing the impacts of climate change on the responses and linkages between terrestrial and aquatic ecosystems. *Science of Total Environment* **682**, 239–246. https://doi.org/10.1016/j.scitotenv.2019.05.024

Kharuk, V.I., Im, S.T., Petrov, I.A., 2021. Alpine ecotone in the Siberian Mountains: vegetation response to warming. *Journal of Mountain Sciences* **18**, 3099–3108. https://doi.org/10.1007/s11629-021-6876-2

Myers-Smith, I.H., Kerby, J.T., Phoenix, G.K. et al., 2020. Complexity revealed in the greening of the Arctic. *Nature Climate Change* **10**, 106–117. https://doi.org/10.1038/s41558-019-0688-1

Shi, S., Wang, P., Zhang, Y., Yu, J., 2021. Cumulative and time-lag effects of the main climate factors on natural vegetation across Siberia. *Ecological Indicators* **133**, 108446. https://doi.org/10.1016/j.ecolind.2021.108446

Vincent, W.F., 2009. Effects of climate change on lakes. In: Likens, G.E. (ed.), *Encyclopedia of Inland Waters*. Elsevier, Amsterdam, Netherlands, 55–60. https://doi.org/10.1016/B978-012370626-3.00233-7