ISSN 0096-7807

Vol. 9, No. 3, May-June, 1978

January, 1979

SJECAH 9(3) 203-302 (1978)

THE SOVIET JOURNAL OF

ECOLOGY

ЭКОЛОГИЯ/ÉKOLOGIYA

TRANSLATED FROM RUSSIAN

CONSULTANTS BUREAU, NEW YORK

PRIMARY SUCCESSIONS OF VEGETATION ON CHALK OUTCROPS IN WESTERN KAZAKHSTAN

P. L. Gorchakovskii and G. V. Matyashenko UDC 581.555;581.526.54

The main stages in succession of plant communities on chalk outcrops were traced in proportion to their weathering in the semiarid steppe subzone of the Western Kazakhstan steppe zone on the Sub-Ural Plateau. Changes in the floristic composition, the ratio of ecological groups of plants, and the stocks of overground and underground phytomass in the course of successions are characterized.

Clarification of regularities governing the formation and development of plant communities is an important biological problem that attracts the attention of many investigators. Early stages in the formation of plant communities are most conveniently studied on recently exposed substrates such as the congealed lava flows of volcanoes (Poli, 1964; Eggler, 1966); rocky detritus and waste in high mountains (Hartmann, 1968; Gorchakovskii, 1975); moraines of receding glaciers (Person, 1964; Vilreck, 1966; Tisdale et al., 1966); exposed bottoms of seas and lakes (Beideman, 1957; Karapetyan, 1966); wind-shifted sands (Gordienko, 1964; Burgess, 1965); and young river alluviums (Firsova, 1952; Gorchakovskii and Peshkova, 1970, 1976). Also of great interest in this regard are chalk outcrops on the summits and slopes of hills, where washout of eluvium (melkozem and detritus) occurs due to erosion, and indigenous chalk untouched or nearly untouched by weathering emerges on the surface.

The plant world of chalk outcrops has already become the subject of interesting floristic (Litvinov, 1891, 1902; Taliev, 1904, 1905; Dubyanskii, 1905; Kozo-Polyanskii, 1931; Smirnov, 1934; Vinogradov and Golitsyn, 1963; etc.) and phytocenological (Adamova, 1973; etc.) investigations conducted in a number of regions of the European part of the USSR, viz., the Central Russian upland, the Don River basin, and the Trans-Volga region. Successions of vegetation on chalk substrates have been studied in England (Hope-Simpson, 1940; Tansley, 1920; Tansley and Adamson, 1925; Lloyd and Pigott, 1967), France (Duvigneaud and Mouze, 1966), and in the European part of the USSR (Blagoveshchenskii, 1952; Semenova-Tyan-Shanskaya, 1954).

However, chalk hills with their unique plant world are also dispersed in Western Kazakhstan (within the boundaries of the Ural'sk, Gur'ev, and Aktyubinsk Oblasts), where chalk outcrops occupy a far greater area than in the mentioned regions of the European part of the USSR. Until recently, the plant world of chalk outcrops in Western Kazakhstan has been studied almost exclusively from the floristic point of view (Yanishevskii, 1905; Savich, 1908; Kol'chenko, 1964, 1965, 1967, 1968, 1969; Kol'chenko and Makarova, 1966; Cherkasova, 1970, 1971; Gorchakovskii and Matyashenko, 1975). A general botanicogeographic sketch of the chalk hill region in the Aktyubinsk Oblast was given only in the study of I. N. Safronova (1974).

The authors of the present paper set out to establish the basic stages of primary successions on chalk outcrops in Western Kazakhstan; and to trace how the floristic composition, structure, ratio of ecological groups of species, and productivity of plant communities change in the course of successions.

REGIONS AND OBJECTS OF INVESTIGATION

Chalk outcrops in Western Kazakhstan (Ural'sk, Gur'ev, and Aktyubinsk Oblasts) are concentrated within the boundaries of the so-called Sub-Ural plateau (or Pre-Ural upland). This plateau is situated between the Caspian Plain and the Mugodzhary Range, touching the Obshchii Syrt upland in the north). The plateau consists of a hilly-residual mountain-ridgy upland plain, which drops steeply to the north, west, and south, and is cut up by the valleys of

---

Institute of Plant and Animal Ecology, Ural Scientific Center, Academy of Sciences of the USSR. Translated from Ékologiya, No. 3, pp. 11-23, May-June, 1978. Original article submitted February 17, 1978.

 0096-7807/78/0903-0208$07.50

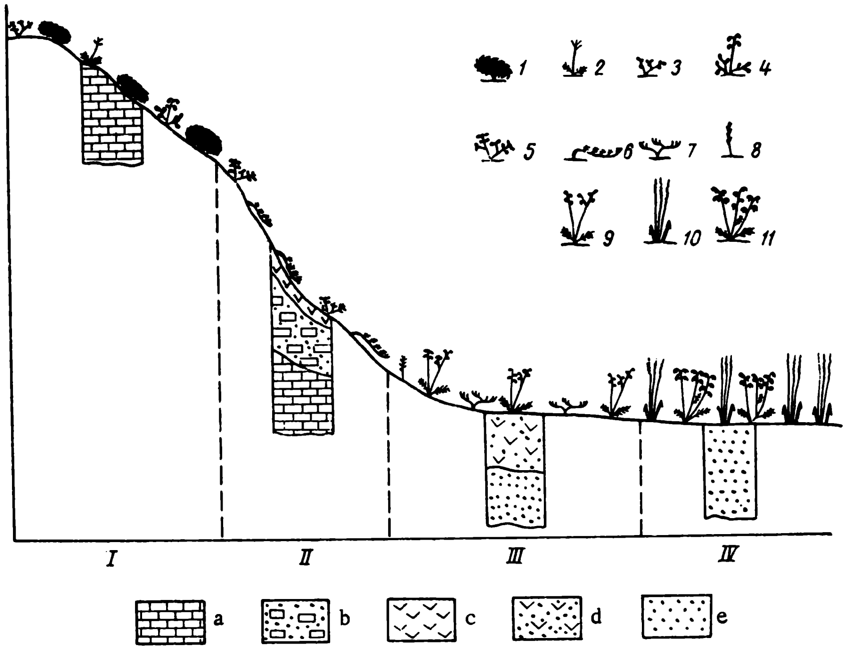

Fig. 1. Stages of successions (I-IV) and their connection with relief elements and substrate types on the southern slope of Mount Akshatau. a) Indigenous chalk; b) blocks and plates of weathered chalk containing melkozem in its cracks; c) fine detritus containing gravel; d) melkozem containing detritus and gravel; e) melkozem (loam). 1) *Anabasis cretacea*; 2) *Pimpinella titanophila*; 3) *Linaria cretacea*; 4) *Atraphaxis frutescens;* 5) *Zygophyllum macropterum*; 6) *Nanophyton erinaceum*; 7) *Anabasis salsa*; 8) *Climacoptera brachiata*; 9) *Artemisia lercheana*; 10) *Agropyrum desertorum*; 11) *Artemisia pauciflora*.

brooks and "sais" into small water-separated massifs (Fedorovich and Nazarevskii, 1969). Absolute elevations are equal to 250-400 min the northeastern part of the plateau and 150-200 m in the southwestern part.

Deposits of Cretaceous age more or less covered by Tertiary and Quaternary deposits are widely disseminated within the boundaries of the plateau. Chalk outcrops are encountered in the vicinity of the town of Ural'sk (the Chalk Hills); in the region of Lake Chelkar (the Sasai and Santas uplands); and in the basins of the Utva River (Mount Aktau, hills near the settlements of Akbulak and Mirgorodka), the Bol'shaya Khobda River (a tributary of the Ilek) (Mount Ishkekargantau), the Uil River (Mounts Akshatau and Terektytau), and the Émba River (Mounts Aktolagau and Imankara). Chalk emerges on the surface on the summits and southern slopes of the hills. In places (especially in the basin of the Émba River), chalk outcrops have been greatly exposed to water and wind erosion, are perforated by deep canyons, and have the appearance of almost perpendicular walls, cupolas, and towers.

All of the mentioned chalk hills were inspected preliminarily by us, and Mount Akshatau (Akchatau) in the Uil Region of the Aktyubinsk Oblast' was selected for study of successions, the indicated hill being located on the right bank of the Uil River and its tributary the Kiil. The northern part of the hill is situated in the arid steppe subzone, in its southern belt of arid sod grassy steppes on chestnut soils to be more precise, while its southern part is situated in the semiarid steppe subzone on light chestnut soils (Safronova, 1974). Successions of vegetation were studied in the semiarid steppe subzone of the southern part of Mount Akshatau near the settlement of the same name, where chalk outcrops are well expressed on slopes facing the Uil River.

As the objects of investigation, we selected plant communities formed in the semiarid steppe subzone on a chalk substrate in proportion to its weathering: from outcrops of indigenous chalk with a small amount of eluvium to sectors where indigenous greatly weathered chalk is covered by a thick layer of deluvium.

TABLE 1. Floristic Composition of Plant Communities on Chalk Outcrops at Different Stages (I-IV) of Successions

Plot No.	Plant names	Abundance I	Abundance II	Abundance III	Abundance IV
1	*Agropyron desertorum* (Fisch.) Schult. et Schult. f.	—	—	—	cop.2
2	*A. cristatum* (L.) Gaertn.	—	—	—	sol.
3	*Allium decipiens* Fisch. ex Loem.	—	—	—	sol.
4	*A. delicatulum* Siev. ex Roem. et Schult.	—	—	sol.	sol.
5	*A. globosum* M. B. ex Redouté	—	—	sol.	sol.
6	*A. inderiense* Fisch. ex Bge	—	—	sol.	sol.
7	*A. lineare* L.	—	—	sol.	sol.
8	*Alyssum desertorum* Stapf.	—	sol.	—	—
9	*A. tortuosum* Waldst. et Kit.	—	sol.	sol.	sol.
10	*Anabasis cretacea* Pall.	cop.1	—	—	—
11	*A. salsa* (C. A. Mey) Benth.	—	sol.	cop.1	—
12	*Anthemis trotzkiana* Claus. ex Bge	sol.—sp.	sol.—sp.	—	—
13	*Artemisia austriaca* Jacq.	—	—	sol.	sol.
14	*A. lercheana* Web. ex Stechm.	—	sol.	cop.2	sol.
15	*A. monogyna* Waldst. et Kit.	—	—	—	sol.
16	*A. pauciflora* Web.	—	—	—	cop.1
17	*A. salsoloides* Willd.	sol.	sol.—sp.	—	—
18	*A. terrae-albae* ssp. semiarida Krasch. et Lavr.	—	—	—	sol.
19	*Asparagus inderiensis* Blume	—	—	sol.	—
20	*Astragalus arcuatus* Kar. et Kir.	sol.	sol.	—	—
21	*A. medius* Schrenk	—	—	sol.	—
22	*A. rupifragus* Pall.	—	sol.	sol.	—
23	*A. tauricus* Pall	—	—	sol.	—
24	*A. testiculatus* Pall.	—	—	—	sol.—sp.
25	*A. varius* G. S. Gmel.	—	—	—	sol.
26	*Atraphaxis frutescens* (L.) Ewersm.	sol.	—	—	sol.
27	*A. spinosa* L.	sol.	—	—	—
28	*Atriplex cana* C. A Mey.	—	—	sol.	sol.—sp.
29	*Brassica elongata* Ehrh.	sol.	sol.	—	—
30	*Camphorosma monspeliaca* L.	—	sol.	sol.—sp.	sol.
31	*Capparis spinosa* L.	sol.	—	—	—
32	*Caragana balchaschensis* (Kom.) Pojark.	—	—	—	sol.
33	*Centaurea kasakorum* Iljin	—	sol.—sp.	—	—
34	*Ceratocarpus arenarius* L.	—	—	—	sol.
35	*Ceratocephala testiculata* (Crantz) Roth	—	—	—	sol.
36	*Climacoptera brachiata* (Pall.) Botsch.	—	—	sol.	sp.
37	*C. lanata* (Pall.) Botsch.	—	—	—	sol.
38	*Convolvulus fruticosus* Pall.	sol.	—	—	—
39	*Crambe tatarica* Sebeók	sol.	sp.	—	—
40	*Echinops meyeri* (DC.) Iljin	sol.	sol.—sp.	—	—
41	*Ephedra distachya* L.	sol.	—	sol.	sol.
42	*Eremopyrum orientale* (L.) Jaub. et Spach.	—	—	—	sol.
43	*E. triticeum* (Gaertn.) Nevski	—	—	—	sol.
44	*Euphorbia seguieriana* Neck.	—	—	—	sol.
45	*E. uralensis* Fisch. ex Link	—	—	—	sol.
46	*E. subcordata* C. A. Mey. ex Ledeb.	—	—	—	sol.
47	*Eurotia ceratoides* (L.) C. A. Mey.	—	—	sol.	sol.
48	*Ferula caspica* M. B.	—	—	sol.	sol.
49	*F. tatarica* Fisch. ex Spreng.	—	—	sol.	sol.
50	*Gagea bulbifera* (Pall.) Roem. et Schult.	—	—	sol.	sol.
51	*G. pusilla* Roem. et Schult.	—	—	—	sol.
52	*Glaucium corniculatum* (L.) Curt.	un.	—	—	—
53	*Hedysarum razoumovianum* Fisch. et Helm.	sol.	—	—	—
54	*Iris pumila* L.	—	—	—	sp.
55	*Jurinea kirghisorum* Janisch.	sol.—sp.	sol.—sp.	—	—
56	*Kochia prostrata* (L.) Schrad.	—	—	sol —sp.	sol.—sp.
57	*Lagochilus acutilobus* (Ledeb.) Fisch. et C. A. Mey.	sol.	—	—	—
58	*Lappula echinata* Gilib.	—	—	—	sol.
59	*L. myosotis* Moench.	—	sol.	—	—
60	*Lepidium meyeri* Claus.	sol.—sp.	sol.	—	—
61	*Limonium cretaceum* Tscherkasova	sol.—sp	—	—	—
62	*L. gmelinii* (Willd.) O. Kuntze	—	—	sol.	sol.
63	*L. suffruticosum* (L.) O. Kuntze	—	sol.	sp.	—
64	*Linaria cretacea* Fisch.	sol.—sp.	—	—	—
65	*Linosyris tatarica* (Less.) C. A. Mey.	—	—	sol.—sp.	sol.—sp.
66	*L. villosa* (L.) DC.	—	—	sol.—sp.	sp.
67	*Matthiola fragrans* Bge	sol.—sp.	—	—	—
68	*Nanophyton erinaceum* (Pall.) Bge	sol.	cop.2	—	—
69	*Nepeta pannonica* L.	—	—	—	sol.
70	*Onosma simplicissimum* L.	—	sp.	—	—
71	*Pimpinella titanophila* Woron.	sol.	—	—	—
72	*Poa bulbosa* L.	—	—	sol.	sol.
73	*Pseudosedum lievenii* (Ledeb.) Berger	—	—	sol.	—
74	*Rhammatophyllum pachyrhizum* (Kar. et Kir.) O. F. Schulz	—	sol.	—	—
75	*Rheum tataricum* L.	—	sol.—sp.	—	—
76	*Rhinopetalum karelinii* Fisch.	—	—	sol.	—
77	*Rindera tetraspis* Pall.	—	—	—	sol.
78	*Salsola laricina* Pall.	—	—	sol.	sp.
79	*S. tamariscina* Pall.	—	—	sol.	sol.—sp.
80	*Scabiosa isetensis* L.	sol.	sol.—sp.	—	—
81	*Scorzonera pusilla* Pall.	—	sol.	—	—
82	*S. pubescens* DC.	—	sol.	—	—
83	*Senecio jacobaea* L.	—	sol.	—	—
84	*Seseli eriocephalum* (Pall.) Schischk	sol.	sol.	—	—
85	*S. glabratum* Willd.	sol.	sol.	—	—
86	*Silene suffrutescens* M. B.	sol.	sol.—sp.	—	—
87	*Stipa capillata* L.	—	—	—	sol
88	*S. lessingiana* Frin.	—	—	—	sol
89	*Tauscheria lasiocarpa* Fisch. ex DC.	—	—	—	sol
90	*Thesium multicaule* Ledeb.	—	—	sol.	—
91	*Tulipa biebersteiniana* Schult.	—	—	sol.	sol.—sp.
92	*T. schrenkii* Rgl.	—	—	—	sol.
93	*Verbascum phoeniceum* L.	—	—	—	sol.
94	*Zygophyllum macropterum* C. A. Mey	—	sp.—cop.	sol.	—
	Total species	26	29	33	51

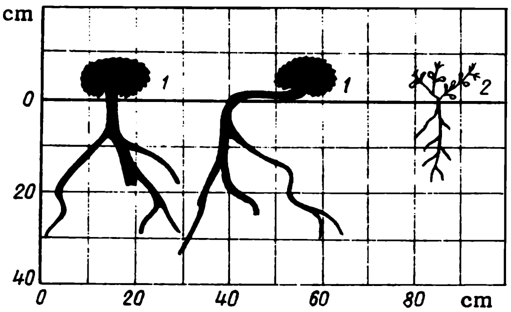

Fig. 2

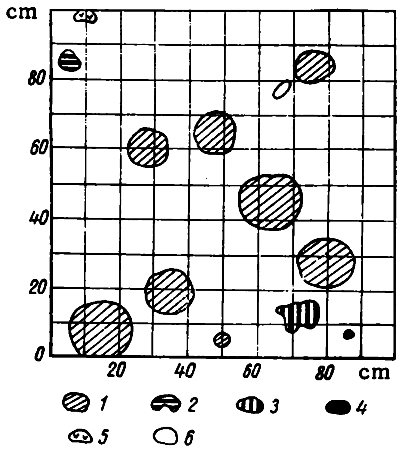

Fig. 3

Fig. 2. Vertical projection of the overground and underground parts of plants at stage I of successions. 1) *Anabasis cretacea*; 2) *Linaria cretacea*.

Fig. 3. Horizontal projection of the overground parts of plants at stage I of successions. 1) *Anabasis cretacea*; 2) *Linaria cretacea*; 3) *Artemisia salsoloides*; 4) *Pimpinella titanophila*; 5) *Lagochilus acutilobus*; 6) *Astragalus arcuatus*.

METHODS

Both direct and indirect methods can be used to study successions of vegetation. The latter possess a number of undoubted advantages and in many cases present the unique possibility of tracing the course of successions completed over long intervals of time (Clements, 1928; Aleksandrova, 1964). The method of ecologo-genetic series comprised the basis of our investigation. This method essentially consists of clarifying the nature of spatial ecological series of plant communities that are at the same time genetic, i.e., temporal. In this case, communities arranged in a spatial series and reflecting changes of vegetation in proportion to changes in the regime of some leading ecological factor (and the series of factors linked with it) correspond to stages of successions. Reliability of the obtained results depends upon how correctly we uncover the mechanisms of successions and clarify the leading ecological factors determining changes in the composition and structure of plant communities in both space and time.

At the first stage of our work, we studied regularities governing the distribution of plant communities on chalk outcrops using numerous transects and reference plots to clarify the connection between the composition and structure of plant communities on the one hand and the regime of basic environmental factors (steepness, slope orientation, degree of rock weathering, soil, etc.) on the other. Here it was clarified that mechanical composition of the substrate behaves as the leading ecological factor in the course of successions of vegetation on chalk outcrops. Indigenous chalk undergoes pulverization in proportion to weathering (large blocks → small blocks → detritus → gravel → melkozem). The relief undergoes leveling in the process, the intensity of erosion declines, mobility of the products of weathering decreases, alluvium and deluvium accumulate, soil of greater development is formed, and the content of humus in its upper horizons increases. In places where the plant cover is undisturbed by antropogenic influences, it is possible to clarify links of communities in a unified ecological series passing from the brow of the hill with exposed indigenous chalk to the foot with developed melkozen soil. These links correspond to the stages of primary successions.

In the course of preliminary study of the ecologo-genetic series, we isolated four links corresponding to four stages of successions. Reference plots each measuring 4 m^2 in area were laid out to study the composition and structure of vegetation at all stages of successions. The species composition and share of participation of separate species according to the Drude scale were recorded on each plot. The number of reference plots needed for full clarification of the floristic composition of separate stages varied from 20 to 40. The affiliation of plots with one or another stage of successions was verified statistically by means of paired comparisons and determination of the coefficient of floristic generality

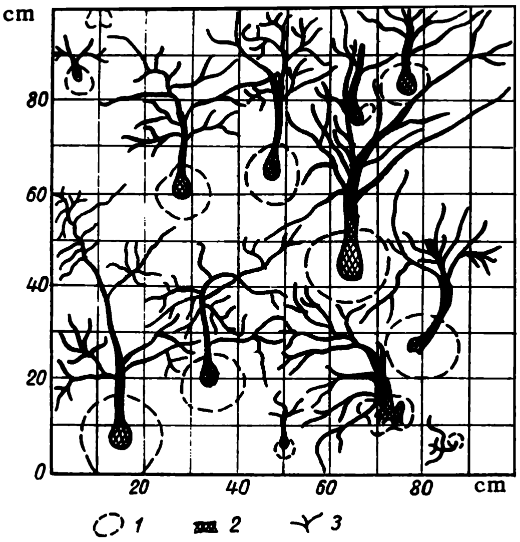

Fig. 4

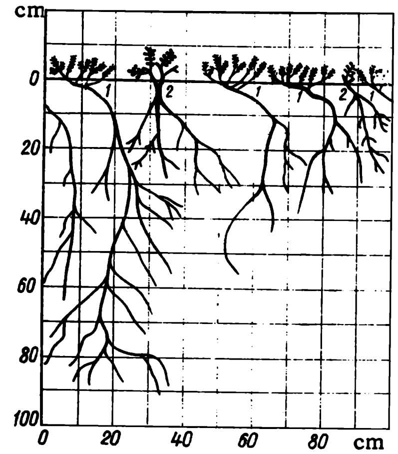

Fig. 5

Fig. 4. Disposal of underground parts in relation to overground parts of plants at stage I of successions (horizontal projection on the same plot as in Fig. 3). 1) Projection of overground parts of plants; 2) stem and exposed part of roots; 3) underground part of plants (roots).

Fig. 5. Vertical projection of the overground and underground parts of plants at stage II of successions. 1) *Nanophyton erinaceum*; 2) *Zygophyllum macropterum*.

according to the Jacquard formula. All in all, 120 reference plots were laid out for four stages of successions. Drawing of the horizontal and vertical structure of vegetation was carried out on some of them.

From 10 to 15 plots each measuring 1 m^2 in area were laid out to determine the stock of overground phytomass in each stage. This made it possible to obtain results with a statistical error not exceeding 15-20%. The overground parts of all plants were cut (separately for each species, with subsequent separation into structural elements) during the period of flowering of dominant species on the plots.

Calculation of underground phytomass was conducted by taking monoliths of soil and dirt in the layer housing the bulk of the roots. The monoliths were taken on the same plots where overground phytomass was calculated. The was done in threefold replication, one of the monoliths measuring 50 × 50 cm, the other two 20 × 125 cm (Rodin et al., 1968). Twelve monoliths were taken in all for the four stages. The bulk of the roots was removed from the monoliths. The remainder (consisting of small roots) was washed out of average substrate samples on fine screens, conversion to total substrate mass being performed subsequently. All specimens of both overground and underground plant parts were dried to an air-dry state and weighed.

RESULTS AND DISCUSSION

Four stages of successions are isolated during the process of development of plant communities on chalk outcrops in proportion to weathering of the indigenous rock, leveling of the surface, and formation of developed soil. They are as follows: the *Anabasis cretacea* stage (I); the *Zygophyllum macropterum—Nanophyton erinaceum* stage (II); the *Anabasis salsa—Artemisia lercheana* stage (III); and the *Artemisia pauciflora—Agropyrum desertorum* stage (IV). Figure 1 shows the distribution of plant communities forming the succession series throughout relief elements.

The *Anabasis cretacea* Stage (Stage I). This stage is characteristic of the summits and "brows" of chalk hills, where chalk in the initial stages of its weathering (blocks and plates with a small amount of melkozem eluvium in cracks in the surface layer) emerges on the surface. Open (with a projective cover of 10-15%) pioneer groupings are formed here (Figs. 2, 3, and 4), with dominance of the calciphilo-petrophilous pillow-like caudex-forming shrublet *Anabasis cretacea*. In addition to this species, the pioneer stage is characterized by a

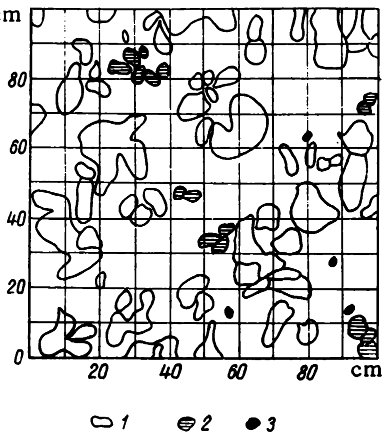

Fig. 6

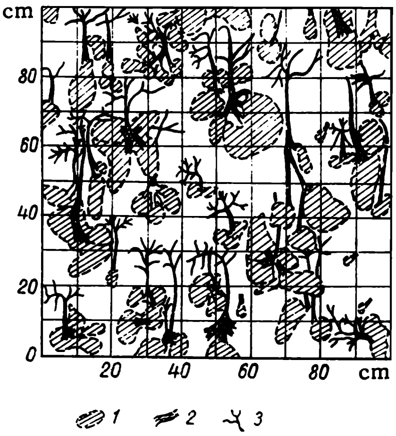

Fig. 7

Fig. 6. Horizontal projection of the overground parts of plants at stage II of successions. 1) *Nanophyton erinaceum*; 2) *Zygophyllum macropterum;* 3) *Scorzonera pubescens.*

Fig. 7. Disposal of underground parts in relation to overground parts of plants at stage II of successions (horizontal projection on the same plot as in Fig. 6). 1) Projection of overground parts of plants; 2) stem and exposed part of roots; 3) underground part of plants (roots).

number of other typically small calciphilo-petrophilous plants: *Linaria cretacea, Anthemis trotzkiana, Matthiola fragrans, Jurinea kirghisorum, Lepidium meyeri*, and *Limonium cretaceum.* Petrophytes (*Atraphaxis spinosa, A. frutescens*, etc.) are also encountered. Twenty-six species in all are registered in this stage (Table 1). Differentiation of overground parts of the plants into substories is lacking.

The *Zygophyllum macropterum–Nanophyton erinaceum* Stage (Stage II). Communities of the second stage (Figs. 5, 6, and 7) occupy upper and middle parts (with a steepness of 20-30°) of the southern slopes of chalk hills. Here the indigenous chalk passes over into weathered chalk closer to the surface, the indicated weathered chalk containing melkozem in its cracks. The indigenous chalk is covered with a loose layer of melkozem containing detritus and gravel (at a depth of 6-20 cm) and with a thin layer of fine detritus containing a small amount of gravel on the surface. The soil is of a detritic, primitive carbonate type. The superficial detritic layer is weakly secured by plants and is mobile. The dominant role is played by the calciphilo-halopetrophilous pillow-like caudex-forming shrublet *Nanophyton erinaceum*, which performs the function of the main securer of the detritic substrate, and *Zygophyllum macropterum* stands out by virtue of its increased abundance. This stage is also characterized by the typically cretaceous calciphilo-petrophilous semishrublets *Artemisia salsoloides, Anthemis trotzkiana, Jurinea kirghisorum*, and *Silene suffrutescens*; and by the petrophilous semishrublets and grasses *Scorzonera pubescens, Echinops meyeri, Centaurea kasakorum, Scabiosa isetensis, Rheum tataricum, Crambe tatarica*, and *Onosma simplicissimum*. Twenty-nine species are recorded in all. The projective cover fluctuates from 20 to 30%, being equal to 25% on the average. Subdivision into substories is indistinct.

The *Anabasis salsa–Artemisia lercheana* Stage (Stage III). This stage is expressed in the lower parts of southern slopes with a steepness ranging from 5 to 15°. The indigenous chalk here lies at a considerable depth (about 1.5 m) and is covered on the surface by a thick layer of the products of its weathering (melkozem containing detritus). The soil is of a light chestnut, incompletely developed detrito-loamy type. The arid steppe calciphilo-halopetrophilous semishrublet *Artemisia lercheana* and the halopetrophilous shrublet *Anabasis salsa* are dominant in the plant cover (Fig. 8). In addition to this, we encountered the petrophilous and halopetrophilous shrublets and semishrublets *Camphorosma monspeliaca, Atriplex cana, Kochia prostrata, Limonium suffruticosum, Salsola laricina, Astragalus tauricus*, and *A. medius*; the grass *Poa bulbosa*; the xerophilous representatives of mixed grass *Linosyris tatarica, L. villosa*, and *Thesium multicaule*; and the ephemeroid geophytes *Tulipa bibersteiniana* and *Gagea bulbifera*. The total number of species comprises 33. The projective cover ranges from 40 to 45%. The overground parts are weakly differentiated into two substories in the vertical direction, with *Artemisia lercheana* in the first (up to 40 cm);

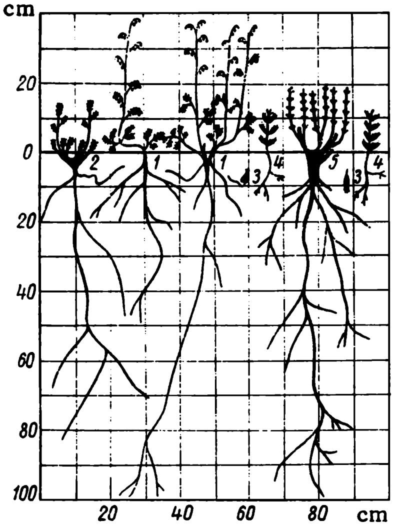

Fig. 8

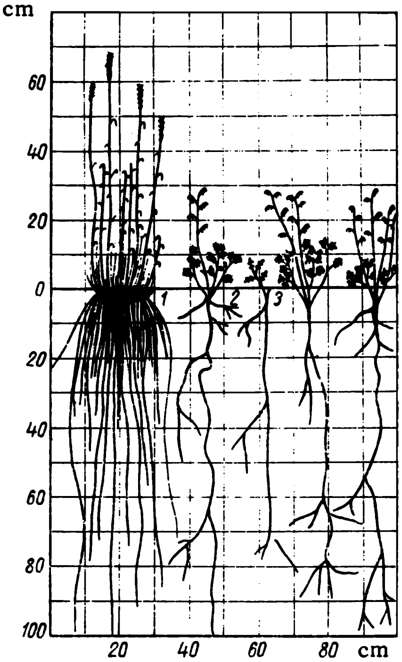

Fig. 9

Fig. 8. Vertical Projection of the overground and underground parts of plants at stage III of successions. 1) *Artemisia lercheana*; 2) *Camphorosma monspeliaca*; 3) *Tulipa schrenkii*; 4) *Climacoptera branchiata*; 5) *Limonium suffruticosum*.

Fig. 9. Vertical projection of the overground and underground parts of plants at stage IV of successions. 1) *Agropyrum desertorum*; 2) *Artemisia pauciflora;* 3) *Astragalus testiculatus*.

and *Anabasis salsa*, *Camphorosma monspeliaca*, *Climacoptera branchiata*, *Limonium suffruticosum*, etc. in the second (up to 20 cm). The root systems of the plants enter the soil to a depth of up to 1 m.

The *Artemisia pauciflora–Agropyrum desertorum* Stage (Stage IV). This stage is found at the foot (tail) of chalk hills on level or slightly sloping sites with a thick layer of deluvium. The euxerophilous sod grass *Agropyrum desertorum* is dominant, with the euxerophilous semishrublet *Artemisia pauciflora* in the role of a codominant. Encountered in lesser abundance are the euxerophilous sod grasses *Stipa pillata* and *S. lessingiana*; and the haloxerophilous and euxerophilous shrublets and semishrublets *Salsola laricina*, *Astragalus testiculatus*, *Eurotia ceratoides*, and *Linosyris tatarica*; and the ephemeroid geophytes *Iris pumila*, *Gagea bulbifera*, *G. pusilla*, *Tulipa bieberste iniana*, and *T. schrenkii*. The total number of species comprises 51. The projective cover ranges from 40 to 50%, and vertical differentiation is rather clearly expressed: *Agropyrum desertorum* (height of vegetative parts, 30-35 cm; height of generative parts, 60–70 cm) forms the first substory; *Artemisia pauciflora*, *Salsola laricina*, and other species form the second; and *Linosyris tatarica*, *L. villosa*, species of the genus *Astragalus*, and other species form the third. The depth of root penetration comprises more than 1 m.

Under conditions of the dry climate of semiarid steppes of Western Kazakhstan, the colonization of outcrops of indigenous chalk, which lends itself readily to weathering, starts directly with higher plants, bypassing the stages of lichens and mosses characteristic of more humid regions (high mountains, rock outcrops in the boreal zone). Unclosed or slightly closed groupings of calciphilo-petrophilous semishrublets are formed at the first stages of successions (Stages I and II). They have a mosaic horizontal structure, vertical differentiation of the overground parts is poorly expressed, and floristic composition is impoverished. The composition of such communities includes plants characteristic of chalk outcrops, viz., *Anabasis cretacea*, *Anthemis trotzkiana*, *Lepidium meyeri*, *Linaria cretacea*, *Silene suffrutescens*, *Matthiola fragrans*, *Jurinea kirghisorum*, and *Limonium cretaceum* (the last species is endemic to Western Kazakhstan, while the next to last is endemic to Western Kazakhstan and

TABLE 2. Phytomass Stocks in Communities of Chalk Outcrops (air-dry weight, g/m²)

Phytomass	Stages of successions			
	I	II	III	IV
Overground	548	492	414	636
Underground	2216	4183	3314	4506
Overall stock	2764	4675	3728	5142
Ratio of overground to underground	1 4	1 8	1 : 8	1 7

TABLE 3. Structure of Overground Phytomass in Communities of Chalk Outcrops

Stages of successions	Main components of communities	Phytomass, g/m²		
		Annual (green)	Perennial	total
I	*Anabasis cretacea*	32	420	452
	Atraphaxis spinosa	5	56	61
	Other species	11	24	35
	Total	48	500	548
II	*Nanophyton erinaceum*	57	365	422
	Zygophyllum macropterum	10	30	40
	Other species	16	14	30
	Total	83	409	492
III	*Artemisia lerchiana*	102	73	175
	Anabasis salsa	72	69	141
	Kochia prostrata	32	23	55
	Other species	23	20	43
	Total	229	185	414
IV	*Agropyron desertorum*	300	—	300
	Artemisia pauciflora	40	85	125
	Salsola laricina	21	90	111
	Other species	64	36	100
	Total	425	211	636

the Trans-Volga region). In addition to this, these groupings include the semishrublets *Nanophyton erinaceum* and *Anabasis salsa*, which possess a fairly broad ecological amplitude, but are encountered only on chalks on the Sub-Ural plateau, where the western boundary of their ranges runs. *Anabasis cretacea* is dominant at the initial (first) stage of successions: Its powerful root system deeply penetrates cracks in the primary chalk substrate. At the second stage, however, where mobility of the substrate increases, dominance passes over to *Nanophyton erinaceum*, which is capable of settling on rocky wastes and quickly securing them, withstanding pressure exerted by the downward sliding detritus and mechanical injuries to the overground parts caused by it.

Floristic richness gradually increases in the course of successions, density of the overground parts increases, their vertical differentiation becomes more distinct, and their horizontal structure becomes more homogeneous. At the third stage, all of the species most characteristic of chalk outcrops drop out of the composition of plant communities, dominance passes over to the arid steppe semishrublet *Artemisia lercheana*, and other (predominantly halopetrophilous) shrublets and semishrublets appear along with ephemeroid geophytes.

Artemisia pauciflora–Agropyrum desertorum communities are formed at the fourth stage of successions, these communities being characterized by dominance of the arid steppe sod grass *Agropyrum desertorum* and participation of halo- and euxerophilous shrublets and semishrublets, perennial grasses, and ephemeroid geophytes. The grass *Agropyrum desertorum* is widely disseminated in the steppe zone of Kazakhstan, often appearing as a dominant, while the communities formed by it in combination with wormwoods are very characteristic of the semiarid steppe subzone (Lavrenko, 1956). The communities of stage IV successions that are formed at the foot of chalk hills in their composition and structure approach the zonal wormwood—sod grass communities of semiarid steppes.

The overall stock of phytomass (overground and underground) tends to increase in the course of successions, a certain decrease of it occurring at stage III (Table 2). The stock of underground phytomass is four times greater than that of overground phytomass at stage I of successions. In the next stage, this difference attains a seven- to eightfold value.

Two to three dominant species produce the bulk of the overground phytomass at all stages of successions (Table 3). In communities of the initial links of the succession series, the bulk of the overground phytomass is produced by long-lived shrublets (*Anabasis cretacea*, *Nanophyton erinaceum*) whose age numbers several tens of years. The stock of perennial parts of plants is therefore 10 times greater than the stock of annual parts (leaves and young annual shoots) at stage I in the succession series and five times greater at stage II. In connection with change in the composition of dominants, the stock of annual parts is already insignificantly greater than the stock of perennial parts at stage III. At stage IV, where dominance passes over to grasses with overground parts that die out completely over winter, the annual (green) phytomass is already twice as great as the stock of perennial phytomass.

CONCLUSIONS

1. Primary successions of plant communities on chalk outcrops are closely connected with the process of weathering of indigenous chalk, which is accompanied by redeposition of the products of weathering (detritus, melkozem) and gradual leveling of the relief. The stages of succession correspond to the main stages in evolution of the relief of chalk hills, in the course of which they are broken down under the influence of weathering, wind erosion, and water erosion, in the final analysis merging with the surrounding plain.

2. In the semiarid steppe subzone of the Western Kazakhstan steppe zone, the recently exposed chalk substrate is directly colonized by higher plants, bypassing the stages of lichens and mosses. The following stages of successions are discernible here: the *Anabasis salsa* stage (stage I); the *Zygophyllum macropterum—Nanophyton erinaceum* stage (stage II); the *Anabasis salsa—Artemisia lercheana* stage (stage III); and the *Artemisia pauciflora—agropyrum desertorum* stage (stage IV).

3. The early stages of successions on chalk outcrops are characterized by floristically rather impoverished weakly closed communities having a mosaic horizontal structure with dominance of calciphilo-petrophilous shrublets and participation of a number of typically cretaceous species, including several endemic to Western Kazakhstan and the Trans-Volga region. In the course of successions, such communities are gradually replaced by *Artemisia pauciflora—Agropyrum desertorum* communities that are richer in composition, more compact, differentiated in the vertical direction, and homogeneous, with participation of halo- and euxerophilous shrublets and semishrublets along with ephemeroid geophytes. With respect to their composition and structure, these communities already approach zonal semiarid wormwood—sod grassy steppes of the Europeo-Kazakhstan type.

4. The overall stock of phytomass in communities of chalk outcrops increases in proportion to successions, and the relative share of underground phytomass also increases in the process. Significant (10-fold) predominance of perennial overground plant parts over annual parts is replaced by twofold predominance of annual parts.

LITERATURE CITED

Abramova, T. I., "Vegetation of chalk outcrops in the steppe part of the Don River basin in the Rostov and Volgograd Oblasts," Botan. Zh., 58, No. 4 (1973).

Aleksandrova, V. D., "Study of changes of the plant cover," in: Field Geobotany [in Russian], Vol. 3, Nauka, Moscow—Leningrad (1964).

Beideman, I. N., "Observations on changes of shore vegetation and colonization of the sea bottom after recession of the Caspian Sea," Tr. Botan. Inst. Akad. Nauk SSSR, Ser. 3 (Geobotan.), No. 11 (1957).

Blagoveshchenskii, V. V., "Dynamics of vegetation on chalk outcrops in the middle part of the Volga basin," Botan. Zh., 37, No. 4 (1953).

Burgess, R. L., "A study of plant succession in the sandhills of southeastern North Dakota," Proc. N. Dakota Acad. Sci., 19 (1965).

Cherkasova, G. I., "A new species of sea lavender from chalk outcrops of Western Kazakhstan," Byull. Mosk. Obshchestva Ispytatelei Prirody, Otd. Biol., No. 4 (1970).

Cherkasova, G. I., "Groupings of *Artemisia salsoloides* on chalk hills of Western Kazakhstan," Vestn. Mosk. Gos. Univ., Biol., Pochvoved., No. 7 (1971).
Clements, F. E., Plant Succession and Indicators, New York (1928).
Dubyanskii, V. A., "The nature of vegetation of chalk outcrops in the Khoper River basin," Izv. St. Peterb. Botan. Sada, 5, No. 3 (1905).
Duvigneaud, J. and Mouze, L., "La vêgêtation de la partie septentrionale de la Champagne crayeuse. La colonization des eboulis crayeux," Bull. Soc. Botan. Nord France, 19, No. 4 (1966).
Eggler, W. A., "Plant succession on the recent volcano Sunset Crater," Plateau Q. Mus. North. Ariz., 38, No. 4 (1966).
Fedorovich, B. A., and Nazarevskii, O. V., Kazakhstan [in Russian], Nauka, Moscow (1969).
Firsova, M. I., "The overgrowing of sand alluviums of the Volga River," Uch. Zap. Kazansk. Univ., Ser. 7 (Biol.), 112 (1972).
Gorchakovskii, P. L., The Plant World of the Ural Highlands [in Russian], Nauka, Moscow (1975).
Gorchakovskii, P. L., and Matyashenko, G. V., "The flora of chalk hills of Western Kazakhstan," in: Abstracts of Papers Presented at the 12th International Botanical Congress [in Russian], Vol. 1, Leningrad (1975).
Gorchakovskii, P. L., and Peshkova, N. V., "Early stages in successions of vegetation on a recent alluvium in the middle course of the Ural River," Ékologiya, No. 5 (1970).
Gorchakovskii, P. L., and Peshkova, N. V., "Changes in the productivity of plant communities in the course of successions on a river alluvium," Ékologiya, No. 5 (1977).
Gordienko, I. I., "On the question of natural overgrowing and fixing of barren sands," Botan. Zh., 49, No. 12 (1964).
Hartmann, H., Über der Vegetation des Karakorum. I. Teil: Gesteinsfluren, subalpine Strauchbestände und Steppengesellschaften im Zentralkarakorum," Vegetatio, 15, Nos. 5-6 (1968).
Hope-Simpson, J. F., "Studies of the vegetation of the English chalk. VI. Late stages in succession leading to chalk grassland," J. Ecol., 28 (1940).
Karapetyan, R. A. "Regularities governing the colonization of Lake Sevan with vegetation in connection with sinking of the lake," Botan. Zh., 51, No. 9 (1966).
Kol'chenko, O. T., "On the flora of Mount Bol'shaya Ichka," in: Materials on the Flora and Vegetation of the Northern Part of the Caspian Basin [in Russian], Leningrad (1964).
Kol'chenko, O. T., "On the flora of Mount Santas," in: Abstracts of Papers Presented at the 29th Scientific Conference of the Ural'sk Pedagogical Institute [in Russian], Ural'sk (1965).
Kol'chenko, O. T., "On the flora of Akcha-Tau," in: Abstracts of Papers Presented at the 31st Scientific Conference of the Ural'sk Pedagogical Institute [in Russian], Ural'sk (1967).
Kol'chenko, O. T., "On the flora of Iman-Kara and Koi-Kara," in: Abstracts of Papers Presented at the 32nd Scientific Conference of the Ural'sk Pedagogical Institute [in Russian], Ural'sk (1968).
Kol'chenko, O. T., "On the flora of Aktolagai," in: Abstracts of Papers Presented at the 33rd Scientific Conference of the Ural'sk Pedagogical Institute, Ural'sk (1969).
Kol'chenko, O. T., and Makarova, L. I., "On the study of the flora of chalk outcrops on the Sub-Ural chalk plateau," in: Materials on the Flora and Vegetation of the Northern Part of the Caspian Basin [in Russian], Vol. 2, Article 3, Leningrad (1966).
Kozo-Polyanskii, B. M., In the Land of Living Fossils: Essay on the History of Upland Millet Grasses on the Steppe Plain of the Central Chernozem Region [in Russian], Gos. Uch.-Ped. Izd., Moscow (1931).
Lavrenko, E. M., "Steppes and agricultural lands on steppe sites," in: The Plant Cover of the USSR (Geobotanical Map of the USSR, Explanatory Text) [in Russian], Vol. 2, Izd. Akad. Nauk SSSR, Moscow—Leningrad (1956).
Litvinov, D. I., "Geobotanical notes on the flora of European Russia," Byull. Mosk. O. Ispyt. Prior., No. 3 (1891).
Litvinov, D. I., "On the relict nature of the flora of rocky slopes in European Russian," Tr. Botan. Muzeya Akad. Nauk, No. 1 (1902).
Lloyd, P. S., and Pigott, C. D., "The influence of soil conditions on the course of succession on the chalk of Southern England," J. Ecol., 55, No. 1 (1967).
Persson, A., "The vegetation at the margin of the receding glacier Scaftafellsjökull, Southeastern Iceland," Botan. Notiser, 117, No. 4 (1964).
Poli, E., "L'Etna e il Fujiyama. Cenni geobotanici comparativi," Ann. Botan., 28, No. 1 (1964).

Rodin, L. E., Remezov, N. P. and Bazilevich, N. I., Procedural Instructions for Studying Dynamics and Biological Circulation in Phytocenoses [in Russian], Nauka, Leningrad (1968).
Savich, V. M., "Botanico-geographical investigations conducted on steppes of the Caspian basin and deserts of Trans-Uralia," Tr. Imperatorsk. Botan. Sada, 28, No. 2 (1908).
Safronova, I. N., "On the vegetation of chalk hills in the western steppe part of the Aktyubinsk Oblast'," Botan. Zh., 59, No. 11 (1974).
Semenova–Tyan-Shanskaya, A. M., "Biology of the plants and dynamics of the vegetation of chalk outcrops along the Derkul River," Tr. Botan. Inst. Akad. Nauk SSSR, Ser. 3 (Geobotan.), No. 9 (1954).
Smirnov, L. A., "On the flora of chalk outcrops in the Trans-Volga region," Byull. Mosk. O. Ispyt. Prir. Otd. Biol., 43, No. 1 (1934).
Taliev, V. I., "The vegetation of chalk outcrops of Southern Russia," Tr. Obshchestva Ispytatelie Prirody pri Khar'kovsk. Univ., 39, No. 1 (1904).
Taliev, V. I., "The vegetation of chalk outcrops of Southern Russia," Tr. Obshchestva Ispytatelei Prirody pri Khar'kovsk. Univ., 40, No. 2 (1905).
Tansley, A. G., "Studies of the vegetation of the English chalk. I. Early stages of development of woody vegetation on chalk grassland," J. Ecol., 10 (1920).
Tansley, A. G., and Adamson, R. S., "Studies of the vegetation of the English chalk. III. The chalk grasslands of the Hampshire–Sussex border," J. Ecol., 13, No. 2 (1925).
Tisdale, E. W., Fosberg, M. A., and Poulton, C. E., "Vegetation and soil development on a recently glaciated area near Mount Robson, British Columbia," Ecology, 47, No. 4 (1966).
Viereck, L. A., "Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska," Ecol. Monographs, 36, No. 3 (1966).
Vinogradov, N. P., and Golitsyn, S. V. "History of the flora of depressed alps of the Central Russian uplands," in: Materials on History of the Flora and Vegetation of the USSR [in Russian], Vol. 4, Izd. Akad. Nauk SSSR, Moscow–Leningrad (1963).

 0096-7807/78/0903-0218$07.50