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SYSTEMATIC STUDY OF ARID TERRITORIES

Mechanisms of Primary Successions on the Caspian Sea Coast

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Abstract—Development patterns for vegetation on the Novo-Caspian plain are established on the basis of the study of spatiotemporal series. Three types of primary successions have been recognized, i.e., psammosere, halosere, and meadow sere, which differ in environmental conditions, regular features of temporal dynamics, and formation stages. The stages of the succession were identified on the basis of environmental and physiognomic properties of the dominants of vegetation communities.

Keywords: primary succession, spatiotemporal dynamics.

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INTRODUCTION

The purpose of this research was to identify the patterns of primary succession of the Caspian marine plain within Kazakhstan.

The modern history of the Caspian Sea region is associated with the Novo-Caspian stage starting in the Holocene (10 thousand years). The youngest generation of the marine plain is the Novo-Caspian. It lies at –22 m with respect to the horizontal up to the present coast line of the Caspian Sea (Akiyanova et al., 2006). Within the Novo-Caspian plain, two marine terraces are identified: the first marine terrace (late Novo-Caspian plain) is found at the absolute elevation from –27 m to –25 (25.5)m; the second one (early Novo-Caspian plain) is found on the absolute elevation from –25.5 m to –22 m (Doskach, 1956; Globally Significant ..., 2007). The terraces were formed at different times. The early Novo-Caspian plain came to the day surface in the 17th century. The formation of the late Novo-Caspian plain started after the sea regression at the turn of the 18th–19th centuries. The last regression of the sea level (by 3 m) was observed from 1929 to 1977. The studies of this period resulted in valuable material on the development of vegetation on the new dry land (Nikitin, 1954; Bykov, 1955; Katyshevtseva, 1957, 1960; Kirichenko, 1959; etc.). The authors noted the differences in plant colonization of sea-floor sediments and alluvial-delta plains. The transgressive stage in the sea's history began in 1978. By 2000, the level had stabilized at the mark of –27 abs. m (2 m above the 1977 level). Analysis of the basic stages of the plant colonization within the Novo-Caspian marine plain identified three types of primary succession: psammosere, halosere, and meadow sere.

MATERIALS AND METHODS

The studies were performed on the northeastern coast of the Caspian Sea within the Novo-Caspian marine terrace. The plants were studied using traditional methods of geobotanic field investigation (Field Geobotanics, 1959–1974; Bykov, 1978), including the geobotanic description of basic vegetation communities and landscape and environmental profiling. The character of the changes in vegetation was estimated by indirect indicators of the vegetation and soil cover (Aleksandrova, 1964) and publications in the period of the Caspian Sea regression. The succession status of the community was identified on the basis of the following: (1) temporal relations in spatial series, (2) ecological relicts and initial species (Beideman, 1962), (3) an account of the vitality of the community components, and (4) identification of the indicator species of the soil conditions.

RESULTS

Psammosere. As an example of a psammophytic succession, we consider the spatiotemporal series of the vegetation of the northern Caspian coast on the southern fringe of the Volga–Ural sands. The reconstruction of psammosere stages was also based on literary and cartographic sources (Katyshevtseva, 1957, 1960; Kirichenko, 1959; Faizov, 1970; Vegetation Map ..., 1995). The ecological stages of the succession (phases of the ecotope formation) were determined following the ideas of S.A. Nikitin (1954), i.e., littoral, solonchak, coastal salty and low salty sands, and zonal desert (Table 1). Shallow waters and the coast line of the Caspian Sea are almost everywhere overgrown with reed grass. In the band of the salt marshes, annual glasswort (*Suaeda prostrata*, *Salicornia europaea*) veg-

Table 1. Vegetation in ecological stages of the psammosere of the northern Caspian Sea coast

Ecological stage	Relief	Soil	Vegetation (succession stage)
Littoral	Slightly dipping plain	Coastal marshy solonchak	(1) Reed grass (*Phragmites australis*)
		Salt marshes	(2) Annual saltworts(*Suaeda acuminata*, *S. prostrata*, *S. salsa*, *Salicornia europaea*, *Petrosimonia oppositifolia*)
Solonchak	Slightly dipping plain	Coastal solonchak	(2) Annual saltwort aggregations with sarsazan (*Suaeda acuminata*, *Atriplex tatarica*, *Salicornia europaea*, *Halocnemum strobilaceum*)
		Coastal solonchakous	(3) Sarsazan (*Halocnemum strobilaceum*)
	Slightly dipping plain	Coastal solonchakous with blown sand cover	(4) Tamarisk and nitraria aggregations (*Tamarix laxa*, *Nitraria schoberi*)
Coastal salty and low salty sands	Heapy	Sandy saline	Combination (4) of nitraria, tamarisk hummocks (*Nitraria schoberi*, *Tamarix laxa*) and (3) sarsazan (*Halocnemum strobilaceum*) communities
			Combination (4) of nitraria, tamarisk (*Nitraria schoberi*, *Tamarix laxa*) communities by phytogenic hummocks and (6) wheat grass-sandy sage (*Artemisia arenaria*, *A. santonica*, *Agropyron fragile*), sandy sage, wheat grass–sandy sage with giant wild rye grass (*Artemisia arenaria*, *Agropyron fragile*, *Leymus racemosus*) communities on undulating interhummock surfaces
	Bumpy and ridge-bumpy	Sandy	(4) Sundy sage–nitraria (*Nitraria schoberi*, *Artemisia arenaria*, *A. santonica*)
			(4) Sandy sage–tamarisk (*Tamarix laxa*, *T. ramosissima*, *Artemisia arenaria*)
			(5) Sandy sage-calligonum (*Calligonum alatum*, *C. undulatum*, *C. aphyllum*, *Artemisia arenaria*)
			(6) Sundy sage with calligonum and tamarisk (*Artemisia arenaria*, *A. santonica*, *Calligonum alatum*, *C. aphyllum*, *C. undulatum*, *Tamarix laxa*)
Zonal desert preclimax and climax	Undulated	Brown sandy	(7) Sandy sage (*Artemisia arenaria*, *Achillea micrantha*, *Gipsophila paniculata*, *Agropyron fragile*)
	Pit-and-mount	Sandy	(6) Calligonum and sandy sage (*Artemisia arenaria*, *Calligonum alatum*, *C. undulatum*, *C. aphyllum*)
			(7) Sandy sage (*Artemisia arenaria*, *Agropyron fragile*, *Koeleria glauca*, *Leymus recemosus*)
	Hummocky and hummock-ridge	Sandy	(5) Psammophytic shrub (*Calligonum aphyllum*, *Atraphaxis spinosa*, *Anisantha tectorum*, *Poa bulbosa*)
			(7) Ephemeroid and wheat grass-white sagebrush (*Artemisia lerchiana*, *Poa bulbosa*, *Carex physodes*, *Agropyron fragile*)
	Undulated	Brown desert solonetzic sandy-loam	(7) Bluegrass-wheat grass-white sagebrush (*Artemisia lerchiana*, *Agropyron fragile*, *Poa bulbosa*)

etation forms. In the surging zone, along with the annual saltworts, sarsazan (*Halocnemum strobilaceum*) communities are widespread. Sarsazan often occurs together with communities of halophilic grasses (*Puccinellia dolicholepis*, *P. gigantea*) on the meadow solonchaks. Halophytic meadow vegetation occupies certain positions in space and suggests a mosaic of soil conditions but is not a stage of psammosere succession. The settlement of nitraria (*Nitraria schoberi*) and tamarisk (*Tamarix ramosissima*, *T. laxa*) leads to the formation of a phytogenic relief. The ideally smooth relief gradually becomes undulated, turning into cumulose sands. In parallel with the changed relief, the vegetation changes from halophytic vegetation to psammophytic. As they recede from the sea, solonchak species are retained in salty interhummock depressions as relicts from the previous stages. As the sand deposits are blown and desalinized, combinations of the tamarisk and nitraria communities are formed on phytogenic hummocks with *Artemisia* species, with wheat grass and giant wild ray grass (*Artemisia arenaria*, *A. santonica*, *Agropyron fragile*, *Leymus racemosus*) communities on low wave interhummock surfaces.

The succession development of sand vegetation leaving the zone of the sea's influence is closely connected with the relief conditions, the character of moisture, and the processes of soil formation. The native vegetation communities of the Naryn sands consist of two species of sage, i.e., *Aremisia arenaria* and *A. lerchiana*. The climax and preclimax vegetation are confined to absolute heights within the late-Khvalyn plain. The phytocenotic diversity and spatial patterns (Vegetation Map ..., 1995) of late-succession and climax stages make it possible for them to be considered the final links of the psammosere.

The psammophyte succession (psammosere) on the northern coast of the Caspian Sea is a primary succession on sand sediments including the temporal series from the initial annual hyperhalophylous saltwort communities to dwarf subshrub sagebrush vegetation at the concluding stages of the formation. In the spatial relationship, the vegetation communities of different stages of succession can be found close to each other, forming combinations with the communities of the previous stages. Seven stages of succession have been found (Dimeyeva, 2010):

(1) stage of halomesohygrophylous herbs (*Phragmites australis*) on marine marshy solonchak soils;

(2) stage of annual halomesophytes and haloxeromesophytes (*Salicornia europaea*, *Suaeda acuminata*, *S. prostrata*, *S. salsa*) on solonchaks on marshy and coastal solonchaks;

(3) stage of halomesoxerophilic dwarf subshrubs (*Halocnemum strobilaceum*) on coastal solonchaks and coastal solonchakous soils;

(4) stage of halomesoxerophilic shrubs (*Tamarix laxa*, *Nitraria schoberi*) on coastal solonchakous soils with blown soil cover and salty hummocky sands;

(5) stage of psammomesoxerophilic shrubs (*Calligonum* spp., maybe *Eremosparton aphyllum*) on nonsalty hummocky sands;

(6) psammophytic sage stage (*Artemisia arenaria* with participation of *A. scoparia*, *A. santonica*) on nonsalty hummocky sands;

(7) dwarf subshrub–sage stage (formation of preclimax and climax communities *Artemisia arenaria*, *A. lerchiana*) on brown sandy and brown desert solonetzic soils.

Halosere. Salty sediments of heavy soil texture prevail on the northeastern coast of the Caspian Sea. Soils associated with excessive salinization prevail here. The desalinization process of the primary marine grounds of heavy texture is hampered by the nearby occurrence of mineralized ground waters and their increased level under the current transgression. From the littoral belt in the amphibian range of the sea and land, the ecological stages of halophytic succession begin (Table 2). Annual glasswort aggregations prevail on solonchak marsh at the littoral stage. The solonchak stage begins on sections periodically flooded during "moryans," periods of a strong wind where annual saltwort and reed grass communities are formed. In the vegetation cover on the first marine terrace, annual wheatgrass (eremopyrum), annual wheatgrass–climacoptera, climacoptera–annual wheatgrass, and wheatgrass–sarsazan are widespread.

In the limits of the second marine terrace, outside the zone of surging, the moss-, ephemeral-, ephemeral–climacoptera–sarsazan, and ephemeral–perennial saltwort communities are formed. The lowering of ground water table and development of solotnetzic processes cause the transition to the solonetz stage. In the semi-hydromorphic water regime, the sarsazan maintains its dominant position, but its biotic state deteriorates. In the vegetative cover, a notable significance is acquired by white-earth sage (*Artemisia terrae-albae*), santonian sage (*A. santonica*), and anabasis (*Anabasis salsa*): they transit to the subdominant position. In the species composition, a solid position is taken by herb perennials (*Rheum tataticum*, *Ferula caspica*, *Tanacetum millefolium*, *T. achilleifolium*).

Approaching the upper boundary of the Novo-Caspian Sea, the flat relief of the sea bottom becomes slightly undulated; on the late Khvalyn plain, it is undulated-ridgy. On knap peaks, anabasis communities are formed on the automorphous desert solonetz, and in depressions the sarsazan are form communities on the solonchak. The vegetation of the knap slopes (white-earth sagebrush–sarsazan–anabasis, sagebrush–sarsazan) is in the intermediate position. Formation of the zonal white-earth sage vegetation is limited to the plains with brown desert soils. On the slightly undulated plain, the zonal vegetation commu-

Table 2. Vegetation in ecological stages of the halosere of the northeastern Caspian Sea coast

Ecological stage	Relief	Soil	Vegetation (succession stage)
Littoral	Shallow-slope plain	Marine marsh solonchak	Reed grass (*Phragmites australis*)
		Salt marshy	(1) Annual saltwort aggregations (*Suaeda acuminata*, *S. prostrata*, *Salicornia europaea*)
Solonchak	Shallow-slope plain	Coastal solonchak	(1) Annual saltwort (*Salicornia europaea*, *Suaeda prostrata*)
			(1) Annual saltwort (*Atriplex aucheri*, *Climacoptera brachiata*, *Climacoptera crassa*, *Suaeda confusa*)
			(2) Annual wheatgrass-, annual wheatgrass-and-climacoptera, climacoptera–annual wheatgrass–ephemeral–sarsazan (*Halocnemum strobilaceum*, *Eremopyrum orientale*, *E. triticeum*, *Climacoptera crassa*, *C. brachiata*, *Lepidium perfoliatum*)
			(2) Glasswort-sarsazan with halophilic grasses (*Halocnemum strobilaceum*, *Salicornia europaea*, *Puccinellia distans*, *Aeluropus littoralis*)
		Coastal solonchak residual	(2) Ephemeral-sarsazan (*Halocnemum strobilaceum*, *Eremopyrum triticeum*, *E. orientale*, *Lepidium perfoliatum*, *Senecio noeanus*)
			(2) Moss and sarsazan (*Halocnemum strobilaceum*, *Tortula desertorum*)
			(2) Ephemeral–climacoptera–sarsazan (*Halocnemum strobilaceum*, *Climacoptera crassa*, *Eremopyrum triticeum*, *E. orientale*, *Lepidium perfoliatum*)
			(2) Ephemeral–perennial saltwort (*Kalidium foliatum*, *Eremopyrum orientale*, *E. triticeum*, *Lepidium perfoliatum*)
	Slightly dipping plain	Coastal solonchakous	(2) Annual saltwort with sarsazan (*Halocnemum strobilaceum*, *Climacoptera brachiata*, *C. lanata*, *C. crassa*, *Atriplex aucherii*, *Ceratocarpus arenarius*, *Bassia hyssopifolia*)
			(2) Sagebrush– perennial saltwort–sarsazan (*Halocnemum strobilaceum*, *Kalidium capsicum*, *Artemisia schrenkiana*)
			(2) Annual wheatgrass–sarsazan (*Halocnemum strobilaceum*, *Eremopyrum triticeum*, *E. orientale*)
		Coastal solonetzic-solonchakous	(2) Annual wheatgrass–white-earth sagebrush–sarsazan (*Halocnemum strobilaceum*, *Artemisia terrae-albae*, *Eremopyrum triticeum*)
Solonetzic	Slightly dipping plain	Brown solonetzic-solonchakous	(2) Ephemeral–white-earth sagebrush-sarsazan (*Halocnemum strobilaceum*, *Artemisia terrae-albae*, *Eremopyrum triticeum*, *Rheum tataricum*, *Ferula caspica*)
			(3) Annual saltwort–atraphaxis–white-earth sagebrush (*Artemisia terrae-albae*, *Atraphaxis replicata*, *Climacoptera crassa*, *C. brachiata*)
			(2) White-earth sagebrush–sarsazan with anabasis (*Halocnemum strobilaceum*, *Artemisia terrae-albae*, *Anabasis salsa*)
			(2) Sarsazan–santonian sage (*Artemisia santonica*, *Halocnemum strobilaceum*)
			(3) Ephemeral–anabasis (*Anabasis salsa*, *Eremopyrum triticeum*)
Solonetz	Undulated-knap plain with sor declines	Automorphic solonetz	(3) Anabasis (*Anabasis salsa*)
	knap top		(3) White-earth sagebrush–sarsazan–anabasis (*Anabasis salsa*, *Halocnemum strobilaceum*, *Artemisia terrae-albae*)
	knap slope	Solonetz solonchakous	(2) Sagebrush–sarsazan (*Halocnemum strobilaceum*, *A. santonica*, *A. schrenkiana*)
	depression	Solonchak	(2) Sarsazan (*Halocnemum strobilaceum*)
Zonal desert	Slightly undulated	Brown desert solonetzic	(3) White-earth sagebrush–anabasis (*Anabasis salsa*, *Artemisia terrae-albae*)
			(3) Anabasis–white-earth sage (*Artemisia terrae-albae*, *Anabasis salsa*)
	Plain	Brown desert	(3) White-earth sagebrush (*Artemisia terrae-albae*)

nities include white-earth sagebrush–anabasis and anabasis–white-earth ones on brown solonetzic soils.

The halophytic succession (halosere) of the northeastern coast of the Caspian Sea is the primary succession on salty sediments of the heavy texture, which has passed a number of stages from annual saltwort hyperhalophytic communities to the haloxerephytic and xerophytic dwarf subshrub communities. If one accepts the thesis of edaphic climax, the vegetation communities of automorphic habitats (white-earth sage, anabasis) can be taken as zonal. The sarsazan phytocenoses under hydromorphic conditions of solonchak depressions are ecological relicts of the previous stages. Three stages of the halophytic succession have been identified:

(1) stage of annual halomesophytes and haloxeromesophytes (*Salicornia europaea*, *Suaeda acuminata*, *S. prostrata*) on marshy and coastal solonchaks;

(2) stage of halomesoxerophilic dwarf subshrubs (*Halocnemum strobilaceum*) on coastal solonchaks and coastal solonchakous soils;

(3) stage of haloxerophilic and xerophilic dwarf subshrubs: (a) anabasis (*Anabasis salsa*) on desert solonetz, (b) white-earth sagebrush–anabasis (*Artemisia terrae-albae*, *Anabasis salsa*) and anabasis–white-earth sagebrush (*Artemisia terrae-albae*) on brown desert solonetzic soils, and (c) white-earth sagebrush (*Artemisia terrae-albae*) on brown desert soils.

Meadow sere is a plant succession on fresher marine sediments formed under the stream of the Volga, Ural, and Emba rivers independent of texture of marine sediments. These processes are most visible on the northern coast of the Caspian Sea. To detect the temporal regularities, the changes of vegetation communities are considered in ecological-dynamic ranges of the present Ural river delta. The major source was studies on wetlands of the Ural delta (Globally Important ..., 2007), specifically, maps of soils, vegetation, and ecosystems, as well as the works by V.G. Katyshevtseva (1960) and N.P. Ogar' (2003). On the meadow series, three ecological stages (Table 3) have been identified.

Within the marine accumulative plain, the distribution of vegetation is of a clear belt character. In shallow waters, it is reed grass thickets alternating with annual saltwort communities in combination with reeds. On the plain subject to surging phenomena, annual and perennial saltwort communities form in combination with halophytic meadows, and with tamarisk (*Puccinellia distans*, *Aeluropus littoralis*, *Tamarix ramosissima*). On the first marine terrace, communities of tamarisk–weeping alkali grass, sagebrush-tamarisk-grass, forb-grass (*Puccinellia distans*, *Tamarix* spp., *Elytrigia repens*, *Artemisia santonica*, *A. nitrosa*, *Leymus ramosus*, *Calamagrostis epigeios*, *Aeluropus littoralis*, *Glycyrrhiza glabra*) communities, are abundant. The ecological range ends at the second marine terrace, where zonal vegetation communities are observed, i.e., anabasis and white-earth sagebrush.

On the alluvial-delta plain of the Ural, the formation of vegetation occurs under conditions of surface flooding and surge from the sea (Globally Important ..., 2007). In the lower marine part of the delta, reed thickets dominate. With the drying of intradelta water ponds, the reed thickets alternate at first with tuber bulrush (*Bolboschoenus maritimus*, *B. popovii*) and then with licorice–reedgrass meadow (*Calamagrostis epigeios–Glycyrrhiza glabra*). Communities with dominance of tamarisk and nitraria are limited to terraces above the floodplain.

The present-day delta of the Ural was formed a relatively short time ago. The recession of the Khvalyn Sea alternated with long pauses when the coast line remained in the same position. In these periods, the formation of ancient deltas took place. M.M. Zhukov (1945) identifies three stages of the ancient Ural delta: (1) Kushum, (2) Bagyrdai, and (3) Novobogatin.

The studies were carried out on the Novo-Caspian plain within the Novobogatin and left-bank ancient deltas of the Ural (up to –22 m). The investigation of the vegetation of the ancient Ural deltas allows one to estimate possible changes in the vegetation under conditions of reduction of the surface drain and aridization. The soil-forming rocks are old alluvial heavy loamy and clay salty sediments. Graund waters are heavily mineralized and occur at a depth of 2.5–4.5 m (Faizov, 1970). The vegetation cover of ancient delta plains is developing according to the residually meadow-solonchak type, where the hydromorphic and semihydromorphic water regime of ecosystems is maintained. In transition to the automorphic regime, the development of ecosystems proceeds according to the solonetz type.

Along the flow paths, the vegetation is distributed by ecological ranges of plant communities: reed grass (*Phragmites australis*) ⟶ forb weeds (*Polygonum maritimum*, *Persicaria hydropiper*, *Xanthium strumarium*) ⟶ forb herbs–common cocklebur (*Xanthium strumarium*, *Argusia sibirica*, *Butomus umbellatus*, *Cirsium arvense*, *Erygeron canadensis*) ⟶ forb (*Phragmites australis*, *Leymus ramosus*, *Polygonum maritimum*, *Xanthium strumarium*, *Atriplex sagittata*, *Artemisia nitrosa*, *Crypsis schoenoides*, *Suaeda acuminata*, *S. altissima*).

Dried flow paths overgrow with saltwort, tamarisk, halostachys with ephemerals, annual saltworts, and halophilic herbs. In pits and in some dried flow paths, strong salinization conditions cause the development of only annual saltwort and sarsazan aggregations, and along the slopes sea spear grass, orach, and santonian sage (*Puccinellia dolicholepis*, *Atriplex sagittata*) locate themselves. On relief rises, anabasis occur on automorphic sodic soils, often in combination with halocnemum on solonchak or on solonetz solonchakous.

Table 3. Vegetation in ecological stages of the meadow sere in alluvial-deltaic plains of the Caspian Sea

Ecological stage	Relief	Soil	Vegetation (succession stage)
Delta of the Ural River			
Littoral	Slightly inclined plain	Marine marsh solonchak	(1) Reed grass (*Phragmites australis*)
		Marshy solonchak	(2) Annual saltwort aggregenions (*Salicornia europaea*, *Suaeda acuminata*) in combination with reed grass (*Phragmites australis*)
Meadow solonchakous		Coastal meadow solonchak	(3) Alkali grass, annual saltwort–alkali grass (*Aeluropus littoralis*, *Petrosimonia sibirica*, *Climacoptera crassa*); aeluropus-weeping alkali grass with tamarisk (*Puccinellia distans*, *P. gigantea*, *P. dolicholepis*, *Aeluropus littoralis*, *Tamarix ramosissima*)
	Shallow sloping plain, with coastal bars	Meadow coastal solonchakous	(4) Weeping alkali grass, tamarisk-weeping alkali grass (*Puccinellia distans*, *Tamarix ramosissima*, *T. laxa*)
	Coarse plain dismembered	Meadow coastal solonchakous desertifying	(5) Forb–grass (*Leymus ramosus*, *Calamagrostis epigeios*, *Alhagi pseudalhagi*, *Karelinia caspia*), sagebrush–tamarisk–grass; (*Elytrigia repens*, *Tamarix ramosissima*, *Artemisia santonica*, *A. nitrosa*), tamarisk–santonian sage (*Artemisia santonica*, *Tamarix ramosissima*)
Zonal desert	Shallow sloping plain	Complex of desert solonetz with brown desert solonetzic soils	(6) Complexes of anabasis (*Anabasis salsa*) and white-earth sagebrush (*Artemisia terrae-albae*) communities
Old delta plains of the Ural River			
	Plain with active and intermittent flows, dry beds and hollows	Meadow solonchak	Ephemeral–climacoptera–sarsazan (*Halocnemum strobilaceum*, *Climacoptera crassa*, *Eremopyrum triticeum*, *E. orientale*)
			Sea spear grass–orach–perennial saltwort (*Kalidium foliatum*, *Atriplex tatarica*, *Puccinellia dolicholepis*)
		Meadow solonchakous	Ephemeral–saltwort (*Salsola laricina*, *Climacoptera brachiata*, *C. lanata*, *Bassia hyssopifolia*, *Atriplex aucheri*, *Descurainia sophia*, *Eremopirum triticeum*, *E. orientale*)
			Orach-climacoptera– perennial saltwort (*Halostachys belangeriana*, *Kalidium caspicum*, *Climacoptera crassa*, *Atriplex sagittata*)
		Meadow solonchakous desertifying	Swamp timothy (*Crypsis schoenoides*, *Juncus gerardii*, *Chenopodium rubrum*, *Lactuca tatarica*)
Residual meadow-solonchakous	Plain with acting and intermittent flows, dry beds and hollows	Meadow desertifying	Forb- halophytic grass–ephemeral with tamarisk and annual saltworts (*Eremopirum triticeum*, *Descurainia sophia*, *Lepidium perfoliatum*, *Senecio noeanus*, *Aeluropus littoralis*, *Puccinellia dolicholepis*, *Leymus ramosus*, *Inula salicina*, *Polygonum patulum*, *Rumex marschallianus*, *Tamarix ramosissima*, *Suaeda prostrata*, *Petrosimonia triandra*)
		Meadow-brown solonchakous	Halophytic grass–ephemeroid–annual saltwort (*Climacoptera brachiata*, *Climacoptera lanata*, *Bassia hyssopifolia*, *Aeluropus littoralis*, *Puccinellia dolicholepis*, *Leymus ramosus*, *Ferula caspica*, *Prangos odontalgica*, *Rheum tataricum*, *Megacarpea megalocarpa*)
		Meadow-brown solonchakous	Sagebrush with tamarisk and halophytic grasses (*Artemisia terrae-albae*, *A. santonica*, *Tamarix ramosissima*, *Aeluropus littoralis*, *Leymus ramosus*, *Puccinellia dolicholepis*)
			Ephemeral–saltwort with tamarisk (*Suaeda physophora*, *Atriplex calotheca*, *Senecio noeanus*, *Lepidium perfoliatum*, *Eremopyrum orientale*, *Tamarix hispida*)
		Meadow light-solonetzic soil	Climacoptera–weeping alkali grass–santonian sage (*Artemisia santonica*, *Aeluropus littoralis*, *Climacoptera crassa*)
			Halophytic herb-lyme grass (*Leymus ramosus*, *Zygophyllum fabago*, *Climacoptera crassa*)

Table 3. (Contd.)

Ecological stage	Relief	Soil	Vegetation (succession stage)
Solonetz		Solonetz meadow-desert solonchakous	(6) Annual wheatgrass-climacoptera-anabasis (*Anabasis salsa*, *Climacoptera brachiata*, *C. crassa*, *Eremopyrum triticeum*, *E. orientale*).
		Automorphic solonetz	(6) Annual saltwort–anabasis (*Anabasis salsa*, *Climacoptera brachiata*)
			(6) Ephemeral-anabasis (*Anabasis salsa*, *Eremopyrum orientale*, *E. triticeum*, *Lepidium perfoliatum*)
		Brown desert solonetzic	(6) Annual saltwort–anabasis (*Anabasis salsa*, *Climacoptera brachiata*, *Salsola foliosa*), anabasis-black sage (*Artemisia pauciflora*, *Anabasis salsa*)
Delta of the Emba River			
Littoral	Slightly dipping	Marine marshy solonchak	(1) Reed grass (*Phragmites australis*)
Meadow solonchakous		Coastal meadow solonchak	(3) Sea spear grass–sarsazan (*Halocnemum strobilaceum*, *Puccinellia dolicholepis*)
			(3) Ephemeral–sarsazan (*Halocnemum strobilaceum*, *Eremopyrum triticeum*, *Lepidium perfoliatum*, *Senecio noeanus*).
		Meadow coastal solonchakous	(4) Sarsazan–reed grass–shrub (*Tamarix ramosissima*, *Atraphaxis spinosa*, *Phragmites australis*, *Halocnemum strobilaceum*)
			(4) Sea lavender–sarsazan– weeping alkali grass (*Puccinellia distans*, *Halocnemum strobilaceum*, *Limonium caspium*)
			(4) Reed grass–sarsazan (*Halocnemum strobilaceum*, *Phragmites australis*)
	Slightly dipping horizontal, with solonchak depressions and shallow flows	Coastal meadow-marsh solonchakous	(1–3) Ecological range of communities: reed grass (*Phragmites australis*) → annual saltwort (*Salicornia europaea*, *Salsola soda*, *Suaeda confusa*, *S. acuminata*) → tuber bulrush (*Bolboshoenus maritimus*) → aeluropus–tamarisk (*Tamarix laxa*, *Aeluropus littoralis*)
		Meadow-brown solonchakous	(4) Annual wheatgrass-aeluropus-spear grass (*Puccinellia dolicholepis*, *Aeluropus littoralis*, *Eremopyrum triticeum*, *E. orientale*)

Along the dry beds with shallow ground water table on meadow salt marshes, ephemeral–climacoptera–sarsazan communities are observed. The communities include sea spear grass, aeluropus, and santonian sage (*Puccinellia dolicholepis*, *Aeluropus littotalis*, *Artemisia santonica*). As a result of stronger salinization, halophilic meadow species drop out of the communities and annual saltwort and halocnemum communities form on the sides of along solonchaks. In semi-hydromorphic conditions on meadow salty soils, communities of sage with tamarisk and halophilic grasses, ephemeral–saltwort with tamarisk, and climacoptera (orach)–perennial saltwort develop (*Halostachys belangeriana*, *Kalidium caspicum*, *Climacoptera crassa*, *Atriplex sagittata*). Within the territory, flat depressions are common, that is, estuaries in which halophytic meadows and halophytic grass–saltwort communities occur. Succulent saltwort vegetation prevails. Lyme grass (*Leymus ramosus*) often wedges in as microphytocenoses. Deepened soil waters promote the development of the solonetz processes. In the vegetation cover, *Anabasis salsa* dominates on meadow-desert and desert sodic soils. The zonal vegetation communities are formed largely by two species: *Anabasis salsa* and black sage (*Artemisia pauciflora*).

For the Emba river delta, a great number of flow paths, salt lakes, estuaries, and solonchaks (sors) is characteristic. The soil-forming rocks are layered alluvial sediments, mostly of light texture. At the littoral stage, reed vegetation occurs. In the zone of "moryans," halocnemum—alkali grass salt meadow, halocnemum–sea lavender–alkali grass salt meadow, ephemeral–halocnemum, halocnemum–aeluropus–weeping alkali grass salt meadow communities are formed. Outside the zone of surges, halocnemum–reed–shrub, sea lavender-halocnemum–alkali grass salt meadow, reed–halocnemum communities are widespread. On the flow paths of the Emba, the vegetation is distributed by their ecological ranges (Table 3). In the composition of communities, *Alysma plantago-aquatica*, *Lactuca tatarica*, and *Limonium caspium* occur. In the drying beds, the mesohygrophytic vegetation (*Phragmites australis*, *Scirpus tabernaemontani*) remains, but the halophytic vegetation (*Salicornia europaea*, *Salsola soda*, *S. nitraria*, *Suaeda confusa*, *S. acuminata*, *Tamarix laxa*, *Rumex marschallianus*) is

most represented. Between the flow paths in semihydromorphic conditions, the annual wheatgrass–halocnemum, annual wheatgrass–aeluropus–weeping alkali grass salt meadow communities occur. In the absence of river or sea water, the flow paths turn into solonchaks (sors) with annual saltwort and halocnemum microbelt series of communities in the periphery.

In the analysis of the succession of stages of the meadow sere of the present-day Ural and Emba deltas and the ancient delta plains of the Ural, along with the general features, some features inherent in each of the regions are identified. For the marine accumulative plain of the Ural delta, the spatial belts of vegetation correspond to the succession stages. In the Emba delta, the mosaic quality of the soil–ground conditions causes the fragmentation of passages developing by the meadow sere. In the present-day and ancient Ural deltas, it is possible to detect late succession and zonal vegetation communities. In the Emba delta within the Novo-Caspian plain, they are absent. The vegetation cover within the late Khvalyn plain is informative of the vegetation development in automorphic conditions. In the late Khvalyn plain adjoining the Emba delta, ephemeral –white sage with wheatgrass (*Artemisia lerchiana*, *Eremopyrum orientale*, *Trigonella orthoceras*, *Poa bulbosa*, *Peganum harmala*, *Agropyron fragile*) communities are found on brown soils; wheatgrass–white-earth sage (with prostrate summer cypress and barnyard grass) (*Artemisia terrae-albae*, *Eremopyrum orientale*, *E. tririceum*, *Kochia prostrata*, *Anabasis aphylla*) is found on brown desert solonetzic soils, and anabasis and black sagebrush communities are found on desert sodic soils.

The analysis of spatial regularities of the vegetation of the present-day Ural and Emba deltas and reconstruction of the stages of meadow sere of the old Ural delta plains have detected common features and determined the sequence of the stages. The meadow sere is the primary succession on salty sediments of various texture with the periodically flushing type of water regime and formation of long-existing halophytic grass seral communities and haloxerophytic dwarf subshrub vegetation on late succession stages. For the meadow succession, six stages have been detected:

(1) stage of halomesohygrophilic grass (*Phragmites australis*) on marine marshy solonchak soils;

(2) stage of annual halomesophytes and haloxeromesophytes in combination with halomesohygrophilic grass (*Salicornia europaea*, *Suaeda acuminata*, *Phragmites australis*) on salt marshes;

(3) stage of haloxeromesophilic and halomesoxerophilic grasses (*Aeluropus littoralis*, *Puccinellia distans*, *P. gigantea*, *P. dolicholepis*) on coastal meadow solonchak in the zone of run-surge phenomena;

(4) stage of halomesoxerophilic grasses (*Puccinellia distans*) with participation of halomesoxerophilic shrubs (*Tamarix ramosissima*, *T. laxa*) and dwarf subshrubs (*Halocnemum strobilaceum*) on coastal meadow solonchakous soils outside the zone of run-surge phenomena;

(5) stage of mesophilic and haloxeromesophilic grasses (*Elytrigia repens*, *Calamagrostis epigeios*, *Leymus ramosus*) with participation of halomesoxerophilic shrubs (*Tamarix ramosissima*) and dwarf subshrubs (*Artemisia nitrosa*, *A. santonica*) on coastal meadow solonchakous desertifying soils (the Ural);

(6) stage of haloxerophilic and xerophilic dwarf subshrubs: (a) anabasis (*Anabasis salsa*), black sagebrush (*Artemisia pauciflora*) on desert solonetz, (b) white-earth sage (*Artemisia terrae-albae*), white sagebrush (*Artemisia lerchiana*) on brown desert solonetzic soils.

RESULTS

The comparison of the data obtained by the author with the features of the vegetation formation within the Novo-Caspian plain of the northwestern Caspian Sea region has detected both common features and differences. On sand sediments (Petrov, 2005), the spatial change of vegetation communities on the first marine terrace begins with reed thickets. At the medium level, sea lavender – sea spear grass (*Puccinellia gigantea*, *Limonium caspium*, *L. gmelinii*) vegetation is found, while higher up along the profile there are communities of santonian sage (*Artemisia santonica*) and annual saltsworts (*Salsola australis*, *Horaninovia minor*, *Climacoptera brachiata*) with participation of tamarisk and sarsazan (*Tamarix ramosissima*, *Halocnemum strobilaceum*). The sand sediments of the second marine terrace are weakly supported by tickseed, pastil, and melilot (*Corispermum nitidum*, *Isatis sabulosa*, *Melilotus polonicus*). On the salty sands, communities of santonian sage and tamarisk are also found.

The meadow sere of the Caspian coast of Kalmykia (Lazareva, 2003) is distinguished by the composition of dominant species. On the littoral stage, cattail thickets (*Typha angustifolia*, *T. latiflia*) are widespread. At the stage of halomesophilic and haloxeromesophilic annuals in the vegetation cover, species of rush and orach (*Juncus gerardii*, *J. bufonius*, *Atriplex tatarica*) may dominate. The common feature is that, within the Novo-Caspian plain, the hydromorphic and semihydromorphic regime is preserved, which supports the development of long-existing halophytic grass and shrub communities of the intermediate stages of the primary succession.

In the period of lowering of the Caspian Sea level (Katyshevtseva, 1960), a number of special features were detected. In the Volga and Ural interstream area, at the first stages of plant colonization in the sea and land ecotonic band, herb marshes of cattail and bulrush (*Typha laxmannii*, *Scirpus tabernaemontani*) occurred widely, alternating with reed and spike rush (*Phragmites australis*, *Eleocharis acicularis*). These were followed by a band of sea aster (*Tripolium vul-*

gare) and glasswort alternating with sea-blite (*Suaeda salsa*). The farther from the desalinating influence of river waters, the more halophilic the image acquired by the first stages of plant colonization. The general patterns of plant colonization are as follows: the thickets of cattail and spike rush on the sea coast ⟶ reed band ⟶ seepweed (petrosimonian) ⟶ sea spear grass, aeluropus (tamarisk–sea spear grass, aeluropus–sea spear grass). In the Ural–Emba interfluve, the vegetation cover is of a more halophytic type: spike rush (reed) ⟶ glasswort–reed band (reed–sea spear grass–glasswort) ⟶ annual saltwort (glasswort–sea blite, sea spear grass–petrosimonian) ⟶ aeluropus–knotgrass (sea spear grass, sea spear grass–aeluropus, sea spear grass–orach). It was noted that the formation of the zonal dwarf subshrub vegetation communities (*Anabasis-salsa*) has occurred over the 30-year period of the terrestrial development of the territory.

The present transgression of the Caspian Sea has an ambiguous effect on the established coastal ecosystems. On the northwestern coast (Estimate of the Effect ..., 2005; Lazareva, 2003), the hydrophytization and halophytization of vegetation is taking place. At the level of vegetation types no change is occurring, but the phytocenotic and species diversity has increased. The spatiotemporal seres suggest the return to earlier stages of succession. On the northeastern coast, where the sea slope is very small, the rising sea level has led to flooding of vast territories with halocnemum, reed-halocnemum, and sea spear grass vegetation. The underflooding of the territory and the higher groundwater level are leading to halophytization of the vegetation cover.

CONCLUSIONS

Three types of primary succession (psammosere, halosere, and meadow sere) were identified on the basis of the study of spatiotemporal pattern of vegetation distribution within Novo-Caspian plain in the norteastern coast of the Caspian sea. Ecological phases (stages) of succession for each types of succession were determined on soil-ground conditions indicating primary character of exogenic factors. Ecological-physiognomic features of dominant plants were taken into account during defining of succession stages.

The development of psammo- and haloseres of vegetation is caused by edaphic conditions and the gradual transition to an automorphic water regime. The similar stages are typical of littoral and solonchak ecological stages. With a decrease in the influence of the sea and desalination of sand soils in the vegetation cover, the psammomesoxerophytic communities begin to dominate, but with the occurrence of fragments of halophytic communities typical of the previous stages in them. The psammosere is completed by dwarf subshrub–sage communities (*Artemisia arenaria*, *A. lerchiana*) at the subclimax and climax stages, respectively. In the halosere, the salinization of the primary sea soils of heavy texture persists. The lower depth of the ground waters leads to development of solonetz processes and formation of communities of haloxerophilic and xerophilic dwarf subshrubs (*Anabasis salsa*, *Artemisia pauciflora*). In the meadow sere, the specificity is seen at early-succession stages with predominance in the vegetation cover of haloxeromesophilic and halomesoxerophilic grasses (*Aeluropus littoralis*, *Puccinellia distans*, *P. gigantea*, *P. dolicholepis*). The periodically flushing type of water regime determines the development of long-existing seral communities of halophytic grasses, and herbs. The meadow sere is completed with haloxerophytic dwarf subshrub (*Anabasis salsa*, *Artemisia pauciflora*) and xerophytic dwarf subshrub (*Artemisia terrae-albae*, *A. lerchiana*) communities at the late succession stages.

REFERENCES

Akiyanova, F.Zh, Medeu, A.R., Nurmambetov, E.I., Potapova, G.M., and Sarsenova, A.S., Geomorphology, in *Respublika Kazakhstan* (Republic of Kazakhstan), Alma-Ata: Orint-S, 2006, vol .1, pp. 171–214.

Aleksandrova, V.D., Study of Change of Plant Cover, in *Polevaya geobotanika* (Field Geobotany), Moscow, Leningrad: Nauka, 1964, vol. 3, pp. 300–447.

Beideman, I.N., Alteration of Plants and Soil Salinity Affected by Drainage (Case Study: Mugansk Land-Reclamation Experimental Station "Dzhafarkhan" in Trans-Caucasia), in *Ekologo-geobotanicheskie i agromeliorativnye issledovaniya v Kura-Araksinskoi nizmennosti Zakavkaz'ya* (Ecological-Geobotanical and Agroreclamation Studies in the Kura-Araksinsk Depression in Trans-Caucasia), Moscow, Leningrad: Izd. AN SSSR, pp. 4–222.

Bykov, B.A., *Rastitel'nost' i kormovye resursy Zapadnogo Kazakhstana* (Flora and Fodder Resources of Western Kazakhstan), Alma-Ata: Izd. AN KazSSR, 1955, p. 136.

Bykov, B.A., *Geobotanika* (Geobotany), Alma-Ata: Nauka, 1978, p. 288.

Dimeyeva, L.A., Psammophyte Succession of Northern Coast of the Caspian Sea, *Izv. NAN RK, Ser.: Biologiya i Meditsina*, 2010, no. 3, pp. 11–15.

Doskach, A.G., Genesis of Volga-Ural Interfluve Relief, in *Trudy Instituta Geografii* (Transactions of the Institute of Geography), Moscow: Izd. AN SSSR, 1956, vol. 96, issue 16, pp. 16–123.

Faizov, K.Sh., *Pochvy Gur'evskoi oblasti* (Soils of Gur'ev Region), Alma-Ata: Nauka, issue 13, p. 352.

Global'no znachimye vodno-bolotnye ugod'ya Kazakhstana (Global Significant Wetlands of Kazakhstan), Astana: Tipografiya Kompleks, 2007, vol. 1, p. 264.

Karta rastitel'nosti Kazakhstana i Sredei Azii (v perdelakh pustynnoi oblasti). Masshtab: 1:2500000 (A Map of Flora of Kazakhstan and Central Asia (Steppe Zone), Scale: 1:2500000), St.-Petersburg, 1995.

Katyshevtseva, V.G., Geobotanical Study of Northern Coast of the Caspian Sea, in *Tr. In-ta botaniki AN KazSSR* (Transactions of the Institute of Botany, Acad-

emy of Sciences, KazSSR), Alma-Ata: Izd. AN KazSSR, 1957, issue 5, pp. 30–88.

Katyshevtseva, V.G., Change of Flora on the Northern Coast of the Caspian Sea, in *Tr. In-ta botaniki AN KazSSR* (Transactions of the Institute of Botany, Academy of Sciences, KazSSR), Alma-Ata: Izd. AN KazSSR, 1960, issue 8, pp. 43–85.

Kirichenko, N.G., Flora and Fodder Resources of Volga-Ural Sands of the Northern Part of the Caspian Sea, in *Tr. In-ta botaniki AN KazSSR* (Transactions of the Institute of Botany, Academy of Sciences, KazSSR), Alma-Ata: Izd. AN KazSSR, vol. 6, pp. 3–73.

Lazareva, B.G., *Botanicheskoe rsznoobrazie ekosistem Severo-Zapadnogo Prikaspiya v usloviyakh kolebaniya urovnya Kaspiiskogo morya* (Botanical Diversity of Ecosystems of North-Western Part of the Caspian Sea at Fluctuation of the Level of the Caspian Sea), Elista: APP Dzhangar, 2003, p. 206.

Nikitin, S.A., Flora of Eastern Part of the Caspian Depression, in *Pustyni SSSR i ikh osvoenie* (Deserts of USSR and Their Exploration), Moscow, Leningrad: Izd. AN SSSR, vol. 2, pp. 216–263.

Ogar', N.P., Flora of the River Valleys, *Botanicheskaya geografiya Kazakhstana i Srednei Azii (v predelakh pustynnoi oblasti)* (Botanical Geography of Kazakhstan and Central Asia (Desert Region), St.-Petersburg: Boston-Spektr, pp. 119–144.

Otsenka vliyaniya izmeneniya vod sushi na nazemnye ekosistemy (Evaluation of the Influence of the Change of the Land Waters on the Land Ecosystems), Novikova, N.M., Ed., Moscow: Nauka, 2005, p. 365.

Petrov, K.M., *Biogeografiya, 2-e izd.* (Biogeography, Second Edition), St.-Petersburg: Sanktpereburgskogo Univ., 2005, p. 294.

Polevaya geobotanika (Field Geobotany), Moscow, Leningrad: Nauka, 1959–1976, vols. 1–5.

Zhukov, M.M., Pliocene and Quaternary History of the North of Caspian Depression, in *Problemy Zapadnogo Kazakhstana* (Problems of Western Kazakhstan), Moscow, Leningrad: Izd. AN SSSR, 1945, vol. 2, p. 240.