RESEARCH ARTICLES

INVASION OF *OPUNTIA HUMIFUSA* AND *O. PHAEACANTHA* (CACTACEAE) INTO PLANT COMMUNITIES OF THE KARADAG NATURE RESERVE

Valentina V. Fateryga[1], Nataliya A. Bagrikova[2]

[1]*T.I. Vyazemsky Karadag Scientific Station – Nature Reserve of RAS, Russia*
e-mail: valentina_vt@mail.ru
[2]*The Order of the Red Banner of Labour Nikitsky Botanical Gardens – National Scientific Centre of RAS, Russia*
e-mail: nbagrik@mail.ru

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The results of a study of *Opuntia humifusa* and *O. phaeacantha* naturalised in the Karadag Nature Reserve (southeastern part of the Crimean Peninsula) are presented. There, the largest coenopopulations of *Opuntia* plants are confined to the «biostation» territory (bordering with the park, administrative buildings and housing estate). Twelve localities were described in the Karadag Reserve. These differ by phytocoenotic characteristics, area and floristic composition. Seven localities include only *O. humifusa* plants; four ones include only *O. phaeacantha* individuals; and both the species are present on the twelfth locality. The total number of individuals of each species and ontogenetic structure of the population were studied in each locality. The total number of *O. humifusa* individuals in the Karadag Reserve is more than 600 plants within the «biostation» territory, while the total number of *O. phaeacantha* plants is about 400 individuals. Studying of the plant communities has been carried out according to the Braun-Blanquet method. *Opuntia* plants form derivate communities within degraded steppes, phryganoid-steppes, and semi-desert badland phytocoenoses almost at all studied localities. A significant number of synanthropic species (including alien plants) was found within these communities. *Opuntia* plants are able to self-reproduce predominantly vegetatively. Self-seeding reproduction occurs less frequently. Both species can be considered as invasive plants because they have a high adaptive capacity.

Key words: alien plants, Crimea, Karadag Nature Reserve, *Opuntia*, phytoinvasion, plant communities

Introduction

Recently, the invasion of alien species has become one of the most significant problems and is considered as a threat to biodiversity of natural ecosystems (Vinogradova et al., 2010). Such invasions are also known in biodiversity hotspots – Protected Areas. One of them is the Karadag Nature Reserve. It is located on the Black Sea coast on the southeastern part of the Crimean Peninsula. The Reserve was founded in 1979. Besides natural landscapes it houses the area of the Karadag biological station (founded in 1914). It includes administrative-economic buildings, a park and housing stock. The Karadag Nature Reserve was ascribed to the highest priority category on Crimean biodiversity conserving (Biodiversity Support Program, 1999).

The change of climatic epochs, mountain-building processes and physical-geographical features of the Karadag Nature Reserve have contributed to the forming of both its phytocoenotical and floristic diversity. The vegetation of the Karadag Reserve is diverse. It forms two indistinctly expressed belts: 1) the lower belt presented by pubescent oak (*Quercus pubescens* Willd.) forests and steppes; and 2) the upper belt presented by durmast oak (*Quercus petraea* (Matt.) Liebl.) forests, hornbeam (*Carpinus orientalis* Mill.) forests and ash (*Fraxinus excelsior* L.) forests. In general, forests cover about 50% of the Karadag Reserve's area, while steppes cover about 25% of it. Phryganas (7.5% of the total area) and savannoid communities (about 2% of the total area) occur on separate spots amongst the massifs of forests and steppes. In addition, halophytic communities are distributed along the sea coast (Didukh & Shelyag-Sosonko, 1982). Within the area of the Karadag Reserve, 1165 vascular plant species, including 31 endemics, are known (Mironova & Fateryga, 2015) from the in total 2536 species of the Crimean flora (Yena, 2012), including 106 endemics.

Despite the obvious conservation value of the Karadag Nature Reserve, intensive economic activity has been carried out at almost all its area until 1979. This fact, in turn, has contributed to the penetration of alien plant species there, as well as to their spread along the natural landscapes of other parts of the Karadag Reserve. According to recent data, about 50 alien plant species are registered within the Karadag Nature Reserve (Kamenskikh & Potapenko, 2012; Mironova & Fateryga, 2015), or

more than 90 alien plant species including archeophytes (Bagrikova, 2013a). Many of the aliens are capable to self-reproduction under the conditions of the Karadag Nature Reserve. Some of these plants have accidentally been penetrated into the Reserve. Others have been cultured purposefully. Species of the genus *Opuntia* Mill. are classified within the second group. They form the object of our present study.

Opuntia Mill. is one of the richest genera in the family Cactaceae, with 200 to 250 species in consistent with different authors (Britton & Rose, 1919; Anderson, 2001; Rebman & Pinkava, 2001). Under natural conditions representatives of the genus are known from the American continent (Mahr, 2001; Nyffeler, 2002; Bulot, 2007; Majure & Ervin, 2008). Due to numerous xeromorphic adaptations most species are confined to arid habitats of subtropical and tropical natural belts. Mexico is a centre of the genus' diversity (Mahr, 2001; Rebman & Pinkava, 2001; Casas & Barbera, 2002; Majure & Ervin, 2008). Some *Opuntia* species are able to withstand temperatures below freezing during the winter period (Loik & Nobel, 1993; Nobel & Bobich, 2002). It allows them to penetrate into the colder regions. Plants may be found there mainly under the trees' canopy or on the slopes with a southern exposure or from their leeward side (Loik & Nobel, 1993). Thus, *Opuntia* plants are able to exist under a wide range of temperature conditions and in different plant communities: from deserts to tropical forests and alpine meadows (Mauseth, 2006).

Opuntia species have long been cultivated in some countries due to their taste and decorative qualities (e.g., Mahr, 2001; Casas & Barbera, 2002; Majure, 2007; Erre et al., 2009). They were firstly introduced from Mexico to Spain, and then – to other European countries (Erre et al., 2009). The moderate Mediterranean climate proved to be very favourable for their cultivation, distribution and naturalisation (Barbera et al., 1992; Casas & Barbera, 2002; Erre et al., 2009; Tashev, 2012). Then *Opuntia* species penetrated into the countries of Asia and Africa, and into Australia (Mahr, 2001). To date, of the 27 invasive *Opuntia* species, the largest number of naturalised ones has been recorded in Spain, South Africa and Australia (Novoa et al., 2014). There are cases where some *Opuntia* species caused significant economic damage to entire continents. The classic example is an invasion of *Opuntia stricta* (Haw.) Haw. and *O. vulgaris* Mill. into Australia (Frawley, 2007). For the first time *Opuntia* penetrated there in 1787, together with a Brazilian settler. And it gradually spread over a wide territory of pastures and farmlands. By the early 20th century the area occupied by *Opuntia* was several million hectares (Frawley, 2007). An ecological catastrophe was prevented only in 1925, when *Cactoblastis cactorum* (Berg, 1885) was brought in Australia in order to control the *Opuntia* invasion (Zimmerman et al., 2000; Frawley, 2007; Pemberton & Liu, 2007). This moth has become a biological barrier for the further spread of *Opuntia* plants. The invasion of *Opuntia ficus-indica* (L.) Mill. in South Africa in the 1990s has led to a significant agricultural crisis in this region (Dean & Milton, 2000).

Most likely, the history of *Opuntia*'s introduction in the Crimea began in the 19th century. In most cases, it was associated with the Nikitsky Botanical Garden. Although, there is an opinion that the introduction of *Opuntia* plants was induced by German colonists in the 18th century (Byalt et al., 2009). To date, *Opuntia* species have distributed over a significant territory of the southern coast of Crimea – from Sevastopol to Koktebel and in some areas of the Crimea steppe (Bagrikova & Ryff, 2014b). According to the latest published data (Bagrikova & Ryff, 2014b), eight *Opuntia* species are considered as self-renewing plants on the Crimean Peninsula.

From the published memoirs of Ye.A. Sludsky (son of the first director of the Karadag biological station) it has been found out that *Opuntia* appeared in Karadag at the beginning of the 19th century. They were planted by A.I. Bachinsky, who «walked through Karadag in forests, valleys and mountains, and in some places he planted *Opuntia* cacti to acclimatise them in the wild» (Sludsky, 2004–2005, p. 69). Later V.N. Wuczeticz planted them also near the biological station. According to some data (Voinov, 1930, 1968; Anisimova, 1939), there were attempts to introduce three *Opuntia* species. Of them, to date, we identified plants of two species, *Opuntia humifusa* (Raf.) Raf. (Fig. 1B) and the red-flowered form of *O. phaeacantha* Engelm. (Fig. 1D). Both species grow in the wild in the Karadag Nature Reserve, including the biostation territory.

It should be noted that many *Opuntia* species belong to taxonomically difficult groups. Even within the native range, researchers (e.g., Majure, 2007; Majure, Ervin, 2008; Majure et al., 2012) often distinguish many varieties within a single species. Many specialists indicate on objective problems associated with accurate identification of alien species within their secondary range. Among them is Yu.K. Vinogradova with co-authors (2010) who emphasise that most information about origin, type of range, ecological properties, etc. is associated with the taxon name.

And alien species are often represented by atypical forms within their secondary range. In addition, information about the herbarium specimens collected in natural habitats is hardly available.

Fig. 1. *Opuntia humifusa* (A, B, E, G) and *O. phaeacantha* (C, D, F, H) in the Karadag Nature Reserve. A, C – communities with participation of each *Opuntia* species (A – locality № 9, C – locality № 2); B, D – flowering plants; E, F – fruits; G, H – juvenile plants.

Probably, difficulties in identification of *Opuntia* species have led to a situation where introduced and naturalised species in the Crimea were listed under different names in numerous publications. For example, the intraspecific taxonomic position has not been finally established for the red-flowered form of *O. phaeacantha*, which is cultivated in the vicinity of Koktebel and in Nikitsky Botanical Garden. But it is known in the wild in the Karadag Reserve. This is caused by the fact that it is most likely a cultivar, different from the ancestral taxon (or taxa) by one or more traits. These plants could be written out according to Western European catalogues of the early 20th century (where they appeared) as a variety of *Opuntia camanchica* Engelm. & J.M. Bigelow var. *rubra* (see Britton & Rose, 1919, p. 144). This *Opuntia* species has been noted under the mentioned name in many publications of Crimean researchers (Anisimova, 1939; Kamenskikh & Mironova, 2004; Emirsaliyev & Skopintseva, 2008; Kamenskikh & Potapenko, 2012). Plants growing in Karadag and Koktebel have been classified as a «f. *rubra*» within *O. phaeacantha* according to the monograph «Trees and Shrubs of USSR» (Zamyatnin, 1958). They have also been considered within *O. phaeacantha* var. *camanchica* (Engelm. & J.M. Bigelow) L.D. Benson, according to some web-sources: «Plantarium» (http://www.plantarium.ru/), «All Crimean Plants» (http://flora.crimea.ru/). Other specialists have considered this *Opuntia* species without the epithet «*rubra*»: either as an independent species *O. camanchica* (Voinov, 1930; Mironova & Kamenskikh, 1995; Byalt et al., 2009), or as a variety, *O. phaeacantha* var. *camanchica* (Voinov, 1968; Vasilyeva & Serov, 2009; Bagrikova, 2013a,b), or rarely – as *O. phaeacantha* without indicating its infraspecific status (Byalt, 2004, 2012; Yena, 2012). The origin and authorship of the epithet «*rubra*» are not clear; it is absent in the modern taxonomic databases such are «IPNI» (http://www.ipni.org/) and «Tropicos» (http://www.tropicos.org/). The diagnosis and location of the type for this taxon are not known. Therefore, further nomenclatural, morphological and molecular-genetic studies are needed in order to determine more accurate the status of the red-flowered form of *O. phaeacantha*. This applies to some other *Opuntia* species naturalised in the Crimea as well.

We have focused on the *Opuntia* invasion in the Karadag Nature Reserve because detailed investigations of this problem have not been carried out previously. The aim of the present study is to establish the invasion degree of two *Opuntia* species in different plant communities within the Karadag Nature Reserve.

Material and Methods

In order to estimate the distribution extent of *Opuntia* species within the Karadag Nature Reserve, we used our own data for 2014, as well as the results of fragmentary researches conducted in previous years. Population studies of two *Opuntia* species and geobotanical surveys of plant communities with their participation were carried out on 12 localities in October – November 2014. The localities were situated within the territory of the biological station and the areas of the Karadag Reserve adjacent to it (Fig. 2). In most cases, a studied plot had an area of the whole *Opuntia* locality. Only a geobotanical survey in locality №12 was carried out on five plots with an area of 25 m^2. In order to describe the plant communities, we investigated the general coverage (visually), the floristic composition and the species' abundance. We estimated the abundance of each species in according to the 7-point scale of Braun-Blanquet (Braun-Blanquet, 1964; Mirkin et al., 1989). Due to a lack of classification for the Karadag vegetation according to the ecological-floristic approach, we have carried out the identification of plant communities with *Opuntia* species in accordance with the existing syntaxonomy of the vegetation of Crimea (Korzhenevsky et al., 2003; Bagrikova, 2016) and Europe (Mucina, 1997; Rodwell et al., 2002; Mucina et al., 2016). Syntaxa names are given according to current requirements of phytosociological nomenclature (Weber et al., 2000).

In order to estimate the ontogenetic structure of populations, we distinguished three groups: a) generative individuals; b) virginile individuals, appearing from rooting of vegetative parts of parent plants; c) individuals of seed origin (juvenile and immature plants). Each individual or groups was considered as one counting unit. In order to determine the total number of *O. humifusa* and *O. phaeacantha* individuals, we used method of total counting. We noted the presence / absence of *Opuntia* seedlings in each locality without taking into account their number.

The identification of *Opuntia* species has been carried out according to both classical and modern monographs on taxonomy of the family Cactaceae (Britton & Rose, 1919; Anderson, 2001), as well as on the base of special web-sources (http://opuntiads.com/). Species names are provided according to «The Plant List» (http://www.theplantlist.org/). Names for other plant species of spontaneous Crimean flora are provided according to Yena (2012).

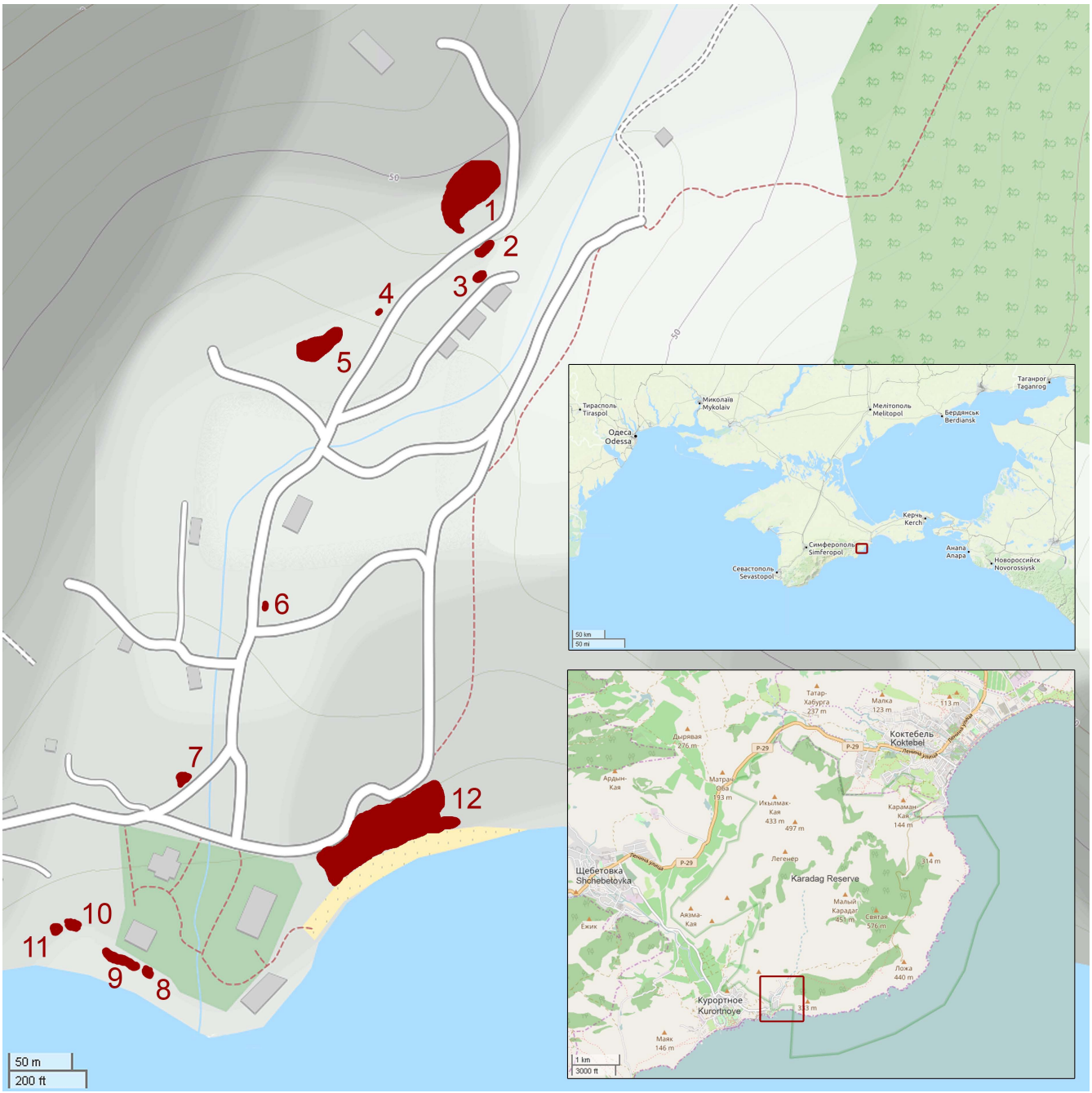

Fig. 2. Situation of the localities with *Opuntia humifusa* and *O. phaeacantha* within the «biostation» territory in the Karadag Reserve (explanations are in Table 1; background maps were taken from http://www.openstreetmap.org/).

Collected herbarium specimens were deposited into the Herbarium of the Nikitsky Botanical Garden (YALT). Live plants are preserved in the Succulents' collection of the Nikitsky Botanical Garden. Photographs were made using the digital cameras Sony DSC-H1, Sony DSC-HX200 and Canon PowerShot A570 IS.

Results

Only single individuals of both *Opuntia* species were found in the least disturbed habitats. These are 1) along the ecological path of the Karadag Reserve and 2) on the coastal clayey-gravelly slopes of the Beregovoy ridge adjacent to it. The largest coenopopulations in the Karadag Nature Reserve are situated within the territory of the biological station where 12 localities with *Opuntia* plants were studied. These are different on the base of phytocoenotic characteristics, areas (Table 1) and floristic composition (Table 2). *Opuntia humifusa* was found in seven localities, *O. phaeacantha* was found in four. In one locality, both species were registered. *Opuntia phaeacantha* was noted in the localities № 1, 2, 4, 5, 12, *O. humifusa* in the localities № 3, 6–12 (Table 1 and 2).

Table 1. General characteristics of studied localities in the Karadag Nature Reserve

Locality	Growing place	Co-ordinates; altitude	Steepness (degrees) / exposure of the slope	Area, m^2	Individuals'number per locality, units	Species
1	Below the house of the T.I. Vyazemsky's sanatorium complex	44º55.040′ N 35º12.239′ E; 50 m a.s.l.	5–10 / SSE	1115	219	*O. phaeacantha*
2	Above hostel	44º54.986′ N 35º12.227′ E; 39 m a.s.l.	10–15 / SE	70	25	*O. phaeacantha*
3	Above hostel	44º54.375′ N 35º12.235′ E; 37 m a.s.l.	20–30 / SE	20	10	*O. humifusa*
4	Between the road and the ridge Beshtash	44º54.957′ N 35º12.171′ E; 35 m a.s.l.	20 / W	10	2	*O. phaeacantha*
5	Under the ridge Beshtash	44º54.955′ N 35º12.125′ E; 32 m a.s.l.	25–35 / SE	125	19	*O. phaeacantha*
6	On the roadside near the boiler house	44º54.844′ N 35º12.108′ E; 22 m a.s.l.	5 / W	10	4	*O. humifusa*
7	Near the shop	44º54.844′ N 35º12.108′ E; 18 m a.s.l.	10–20 / SE	25	25	*O. humifusa*
8	To south of the laboratory building	44º54.695′ N 35º12.045′ E; 11 m a.s.l.	30 / SSW	100	88	*O. humifusa*
9	To south of the laboratory building	44º54.693′ N 35º12.031′ E; 12 m a.s.l.	30–40 / SSW	400	48	*O. humifusa*
10	Between the laboratory building and the meteorological station	44º54.703′ N 35º12.022′ E; 14 m a.s.l.	10–20 / SSW	160	62	*O. humifusa*
11	Below the meteorological station	44º54.712′ N 35º12.005′ E; 16 m a.s.l.	5–10 / S	100	51	*O. humifusa*
12	Seaside slopes above the beach	44º54.763′ N 35º12.195′ E; 15–19 m a.s.l.	25–40 / SSE	3200	299; 116	*O. humifusa*; *O. phaeacantha*

Locality № 1 is situated below the house of the T.I. Vyazemsky's sanatorium complex, on the gently sloping plot in transformed pistachio sparse forest with trodden herb layer. Within the phytocoenosis, we found species (Table 2), which diagnose xerothermic and semi-xerothermic herbaceous communities of the class *Festuco-Brometea* Br.-Bl. & Tx. ex Soó 1947. Participation of synanthropic species and *Artemisia taurica* Willd. indicate the violation and transformation degree of the community in both this and other localities. Within this locality, there were 59 generative, 160 vegetative, and no less than 40 juvenile and immature individuals of *O. phaeacantha*. Young plants were found at a distance of 0.5–1.0 m from the main groups. We registered an abundant fruiting. At the time of observation, a part of the fruits has fallen off, but from 2 to 5 fruits have still remained on most segments (Fig. 1F).

Locality № 2 is situated above the hostel of the biological station, on a slope with a degraded steppe vegetation nearby locality № 1 and delimited from it by a dirt road (Fig. 1C). Within this locality, there are eight generative, 17 virginile (non-seeded) and at least six juvenile and immature individuals of *O. phaeacantha*. Young (seed origin) plants and single 2–4-segment vegetative individuals were found among stones below the main group (at least 10 m in diameter), as well as under the canopy of trees and shrubs on a fairly steep slope.

Table 2. Floristic composition and coverage of species according to Braun-Blanquet's scale in plant communities with *Opuntia* species in the Karadag Nature Reserve

Designation of locality	1	2	3	4	5	6	7	8	9	10	11	12a	12b	12c	12d	12e
General coverage, %	65	50	85	80	70	40	95	40	85	60	95	70	80	55	80	80
Total number of species per locality	30	22	27	9	17	17	22	11	13	20	20	14	12	13	10	13
Achillea nobilis L.						+	2				+	1				
Agropyron cristatum (L.) Gaertn. subsp. *pectinatum* (M. Bieb.) Tzvelev	1	2	1	+												
**Ailanthus altissima* (Mill.) Swingle								1	4	+						
Alcea taurica Iljin			r													
Alyssum tortuosum Waldst. & Kit. ex Willd.								+	r		+			+		
**Amaranthus retroflexus* L.							r									
Anisantha tectorum (L.) Nevski															+	
Artemisia lerchiana Stechm.				+	1	+				1	1					
Artemisia taurica Willd.	+	2	+	3	+	1	1	1	+	2	2	+	+		+	1
Asparagus verticillatus L.	r								r	+						
Asperula tenella Degen	r															
Atriplex aucheri Moq.									r		r					r
Atriplex micrantha C.A. Mey.							2		2	+	1				+	
Atriplex oblongifolia Waldst. & Kit.	r		1	+												
Bassia prostrata (L.) Beck		+														
Bassia sedoides (Pall.) Asch.		r				r	r								+	
Beta trigyna Waldst. & Kit.			+													
Bothriochloa ischaemum (L.) Keng	+															
Bupleurum brachiatum K. Koch	r										r					
Bupleurum exaltatum M. Bieb.														+		
Camphorosma monspeliaca L.	1			2	1		+			+	1	+			+	
Capparis herbacea Willd.		+	+						+	+						
Centaurea caprina Steven	r	r	+													
**Centaurea diffusa* Lam.	r	r	r													
Centaurea salonitana Vis.					r											
Centaurea sterilis Steven					+			+								
Chenopodium album L.			+				+									
Convolvulus cantabrica L.	r		+							+						
Crocus angustifolius Weston				+									r			
Cynanchum acutum L.												1				
Dactylis glomerata L.						+					+					1
Dasypyrum villosum (L.) P. Candargy						+										
**Descurainia sophia* (L.) Webb. ex Prantl							+									
Dianthus marschallii Schischk.		+														
Diplotaxis tenuifolia (L.) DC.		r														
Echium italicum L. subsp. *biebersteinii* (Lacaita) Greuter & Burdet			r			r						r				
Elytrigia caespitosa (K. Koch) Nevski subsp. *nodosa* (Nevski) Tzvelev	+							2		2			2	1	+	2
Elytrigia obtusiflora (DC.) Tzvelev										+	4					
Elytrigia repens (L.) Nevski							+									
Ephedra distachya L.	1	+	1		1		2						2	1		1
Erodium cicutarium (L.) L'Her.						+	r									
Erysimum cuspidatum (M. Bieb.) DC.					r						+					
Euphorbia myrsinites L.								+	3					+		r
Falcaria vulgaris Bernh.												r				
Festuca valesiaca Gaudin	1	+	+		2	1	1				1					
Galatella linosyris (L.) Rchb. f.					+						+					
Galatella villosa (L.) Rchb. f.	+	2	+	2	2	1	2				1	+			+	r
Galium humifusum M. Bieb.	r	r	r							+						
Galium xeroticum (Klokov) Pobed.														+		r
Hedera helix L.							+									
Heliotropium ellipticum Ledeb.			r													
Herniaria besseri Fisch. ex Hornem.	r	+														r
Jasminum fruticans L.	+															
Lactuca viminea (L.) J. Presl & C. Presl								+	+		r					
Lappula sp.										+						
Lepidium draba L.			r				r					+				
Limonium platyphyllum Lincz.			+										r			
Limonium scoparium (Willd.) Stank.	r					+				1	2					
Linaria genistifolia (L.) Mill.			+		+											
Medicago cretacea M. Bieb.								1	r						+	
Medicago falcata L.		+				+		+					r	+		
Medicago rigidula (L.) All.							+			+						

Designation of locality	1	2	3	4	5	6	7	8	9	10	11	12a	12b	12c	12d	12e
General coverage, %	65	50	85	80	70	40	95	40	85	60	95	70	80	55	80	80
Total number of species per locality	30	22	27	9	17	17	22	11	13	20	20	14	12	13	10	13
Melica transsilvanica Schur	+		1		+					+		+				r
**Opuntia humifusa* (Raf.) Raf.			4			+	4	2	4	3	2	3	3			3
**Opuntia phaeacantha* Engelm.	3	2		+	1								4	3	4	
Ornithogalum pyrenaicum L.												+				
Otites densiflora (d'Urv.) Grossh.		+														
Phlomis herba-venti L. subsp. *pungens* (Willd.) Maire ex De Filipps	+		r											r		
**Pinus brutia* Ten. var. *pityusa* (Steven) Silba														1		
Pistacia mutica Fisch. & C.A. Mey.	3				r		r		r							r
Plantago lanceolata L.	+		r			+				+	1	+				
**Platycladus orientalis* (L.) Franco							4									
**Portulaca oleracea* L.			r													
Potentilla sp.	r	r														
**Prunus cerasifera* Ehrh.									r							
Pyrus elaeagrifolia Pall.	+															
Rapistrum rugosum (L.) All.						r										
Rosa sp.											r	r				
Salvia nemorosa L. subsp. *pseudosylvestris* (Stapf) Bornm.			r		+											
Scorzonera mollis M. Bieb.													r		r	
Securigera varia (L.) Lassen										+						
Seseli tortuosum L.	+	r	1	+	+	+	+	+		+		+	+	+		r
?*Solanum alatum* Moench							r									
Stachys cretica L. subsp. *velata* (Klokov) Greuter & Burdet													r	r		
Stipa capillata L.	1	r														
Taraxacum erythrospermum Besser					r	r										
Teucrium chamaedrys L.	1	r														
Teucrium polium L.	1	+	+				+						2			
Vicia anatolica Turrill														r		
Zygophyllum fabago L.										+	+					

Note: * – alien species of the Karadag Nature Reserve; ? – origin (native or alien) is uncertain; r – species is extremely rare, coverage is <1%; + – species rare, coverage is 1–2%; 1 – individuals are numerous, coverage is 2–5%; 2 – number of individuals is large, coverage is 5–25%; 3 – with any number of individuals, coverage is 25–50%; 4 – with any number of individuals, coverage is 50–75%; 5 – with any number of individuals, coverage is more than 75%.

Locality № 3 is situated below locality № 2, on a steep slope. It is characterised by a strongly damaged vegetation cover represented by plant species (Table 2), which diagnose synanthropic plant communities belonging to the classes *Artemisietea vulgaris* Lohmeyer et al. ex von Rochow 1951 and *Stellarietea mediae* Tx. et al. in Tx. ex von Rochow 1951 (according to Bagrikova, 2016) or *Chenopodietea* Br.-Bl. in Br.-Bl. et al. 1952 (according to Mucina et al., 2016). *Opuntia humifusa* is represented here by four large individuals, which reach up to 5.5 m in diameter. In addition, we found six pre-generative plants. Of them, four individuals had a vegetative (formed from broken segments) origin and two plants had a seed origin. The *Opuntia* individuals are characterised by an abundant fruiting (in average of 3–5 fruits per segment) (Fig. 1E). However, seedlings or juvenile plants were not found.

The primary vegetation in localities № 1–3 was presented by feather-fescue steppe communities belonging to the class *Festuco-Brometea*. They develop on heavy clays in conditions of the Karadag Nature Reserve. Low-growing annual and perennial herbaceous plants predominate in these phytocoenoses. The presence of *Atriplex oblongifolia*, *Limonium scoparium*, *Ephedra distachya* and species of the genus *Bassia* All. indicates the slight soil salinity. The transformation degree of these phytocoenoses is indicated by synanthropic species and also by *Artemisia taurica* which was registered with high constancy and abundance.

Locality № 4 is situated on a watershed slope, between the road and the ridge Beshtash. *Opuntia phaeacantha* occurs here in ruderal-steppe communities typical for badlands or semi-desert landscapes close to them. Perhaps, this phytocoenosis can be classified as the association *Atraphaco-Cappariderum* Korzhenevsky & Klyukin 1988 of the alliance *Atraphaco-Capparidion* Korzhenevsky 1988, described from Crimea (Korzhenevsky et al., 2003) within the Mediterranean class *Pegano harmalae-Salsoletea vermiculatae* Br.-Bl. & O. de Bolòs 1958 (Mucina, 1997; Rodwell et al., 2002; Mucina et al., 2016), although it has some similarities with plant communities of the Aral-Caspian class *Artemisietea lerchianae* Golub 1994 (Golub, 1994) too. This locality differs by both the smallest area and abundance of *Opuntia* plants. Only two *O. phaeacantha* individuals were found here. One plant is generative (with single fruits), another one is vegetative.

Locality № 5 is situated nearby locality № 4, on a desert-steppe watershed flysch slope below the ridge Beshtash. This phytocoenosis is less disturbed than the first four habitats abovementioned. It represents a basal group, because it contains fragments of several classes in accordance with the classification of Crimean vegetation (Korzhenevsky et al., 2003). There are petrophytic-steppe (*Festuco-Brometea*) and badland (*Pegano harmalae-Salsoletea vermiculatae*) classes with participation of separate elements of shale screes (*Thlaspietea rotundifolii* Br.-Bl. 1948). Nineteen generative *O. phaeacantha* plants were found here. Abundant fruiting (2–5 fruits per segment) was registered.

Locality № 6 is situated at the roadside. This phytocoenosis is an anthropogenic derivative of the steppe community on heavy saline clays. Two generative and two vegetative *O. humifusa* plants were found on this locality. Fruiting (1–3 fruits per segment) was registered.

Locality № 7 is situated on a flowerbed near the shop. Therefore, the primary vegetation (steppe with elements of semi-desert vegetation of badlands) is highly anthropogenically transformed here. *Opuntia humifusa* had previously been planted here. And in time it spread under the crowns of *Platycladus orientalis* plantings. Fifteen generative and ten vegetative *Opuntia* plants were found on this locality. Individuals of seed origin and seedlings were not registered.

Locality № 8 is situated to south and east of the laboratory building, on the seaside on a gravelly-clayey denudation slope. It is characterised by a significant participation of semi-shrubs and gramineous plants in the herb layer composition. Apart from *O. humifusa*, another alien species, *Ailanthus altissima*, was found here.

Locality № 9 is situated to south of the laboratory building, on a steep gravelly-stony denudation slope. It is characterised by a high degree of anthropogenic transformation. *Ailanthus altissima* thickets occupy the upper part of the slope. Its lower part is almost completely covered by *O. humifusa* (Fig. 1A).

The floristic compositions of the plant communities in the localities № 8–9 are similar to the ones in the phytocoenoses of the seaside cliffs belonging to the order *Onosmo polyphyllae-Ptilostemonetalia* Korzhenevsky 1990 (Mucina, 1997; Rodwell et al., 2002; Mucina et al., 2016), which was described in Crimea. It is typical for the foothills and low-hill terrains of Southeastern Crimea and some points in the Southern coast. It contains open communities of xerophytic dwarf semishrubs on slopes, composed by various rock formations with weak and moderate anti-denudation resistance (Korzhenevsky et al., 2003). The plant community in locality № 9 is more anthropogenically transformed than the one in locality № 8.

Locality № 10 is situated west of locality № 9, in the zone of a seaside cliff. The phytocoenosis described here is an ecotone or derivative plant community. It is close to badlands' phytocoenoses. In accordance with classifications of the vegetation of Crimea (Korzhenevsky et al., 2003) and Europe (Mucina, 1997; Rodwell et al., 2002; Mucina et al., 2016), this phytocoenosis belongs to the Mediterranean halo-nitrophilic semi-desert shrub vegetation of the class *Pegano harmalae-Salsoletea vermiculatae*, although it has elements of plant communities belonging to the order *Onosmo polyphyllae-Ptilostemonetalia*, class *Festuco-Brometea*, etc.

Locality № 11 is situated on a relatively flat plot. Within its boundaries we distinguished the badland community with derivatives of steppe vegetation located on heavy saline clay soils. Its floristic composition is strongly different to the ones in other studied plant communities (Table 2).

In total, we registered 198 generative and 51 vegetative (13 plants have seed origin, 38 ones are a result of vegetative reproduction) *O. humifusa* individuals within the localities № 8–11. The plants are well-developed, with abundant fruiting. We registered seedlings and juvenile individuals.

Locality № 12 has the largest area (about 3200 m^2). It is situated on a denudation slope with a steppefied pistachio sparse forest and plantations of *Pinus brutia* var. *pityusa*. The vertical structure of the vegetation is pluristratal, the horizontal one is mosaic. On the base of floristic composition, plant communities described here with both *Opuntia* species may be classified as basal or derivative groups because these occupy ecotones and contain a complex of species from different Mediterranean types of vegetation. Some of them are phytocoenoses close to plant communities of the alliance *Artemision arborescentis* Géhu & Biondi in Géhu et al. 1986 (Rodwell et al., 2002) or *Atraphaco-Capparidion* (Korzhenevsky et al., 2003) from the class *Pegano harmalae-Salsoletea vermiculatae*, which include semi-shrub semi-desert halo-nitrophilic groups on clay soils in the Western Mediterranean (Rodwell et al., 2002) and in Crimea (Korzhenevsky et al., 2003). Furthermore, we found here species from plant communities of the alliance *Ptilostemonion* Korzhenevsky 1990, described in South-Eastern Crimea. These communities are typical for denu-

dation slopes on carbonate-free rocks (included in order *Onosmo polyphyllae-Ptilostemonetalia* Korzhenevsky 1990). In addition, we registered species of Mediterranean ephemere vegetation types (class *Thero-Brachypodietea* Br.-Bl. ex A. de Bolòs y Vayreda 1950), petrophytic steppes (class *Festuco-Brometea*), as well as synanthropic and alien species (Table 2). We would like to list species which were found outside the boundaries of the established plots. These plants were registered with low abundance (r, rarely +), but they characterise the described biotopes. These are *Agropyron cristatum* subsp. *pectinatum*, *Ailanthus altissima*, *Asparagus verticillatus*, *Capparis herbacea*, *Centaurea salonitana*, *Dianthus marschallii*, *Lactuca viminea*, *Rapistrum rugosum*, *Rosa* sp., *Salvia nemorosa* subsp. *pseudosylvestris*, *Scabiosa micrantha*, *Teucrium chamaedrys*, as well as *Aegilops ovata* L., *Camelina* sp., *Carduus pycnocephalus* L. subsp. *albidus* (M. Bieb.) Kazmi, *Lens nigricans* (M. Bieb.) Godr., *Lycopsis* sp., *Papaver* sp., *Scabiosa micrantha* Desf., *Senecio leucanthemifolius* Poir. subsp. *vernalis* (Waldst. & Kit.) Greuter and *Valerianella coronata* (L.) DC.

In total, within locality № 12 we registered 229 generative and 70 vegetative *O. humifusa* plants, as well as 72 generative and 44 vegetative *O. phaeacantha* individuals. The largest number of seedlings and juvenile plants of both *Opuntia* species were found here (Fig. 1G, H).

Thus, *Opuntia humifusa* was noted from different ecotopes. This species prefers plots with sparse and low herbage in semi-natural and anthropogenically damaged communities. The plants occur in compact groups which makes it often difficult or even impossible to distinguish the individuals within such a group. Therefore, curtains of plants often have not clear boundaries. *O. humifusa* propagates predominantly in the vegetative manner (by rooting of vegetative parts of plants). Seed reproduction occurs relatively rarely despite of abundant fruiting (in average, 4–7 fruits per segment). The total abundance of *O. humifusa* in all studied localities is more than 600 individuals.

Opuntia phaeacantha also grows in different ecotopes. In many of them, it becomes a dominant species. *Opuntia phaeacantha* propagates predominantly in the vegetative manner (by rooting of vegetative parts of plants). The plants abundantly bloom and fruit (in average, 3–6 fruits per segment are observed). Individuals of seed origin occur more common than in *O. humifusa* populations. The total abundance of this species in all studied localities is about 400 individuals.

Discussion

Opuntia humifusa plants were found in the Karadag Nature Reserve in the belt of pistachio and juniper sparse forests at an altitude of 2–205 m above sea level, while *O. phaeacantha* plants were found there at an altitude of 10–50 m above sea level. Thus, both studied *Opuntia* species inhabit the seacoast zone, predominantly on slopes of middle steepness of the south-east and south-west exposure, occupying the lower altitudinal belt of vegetation. This fact distinguishes the studied *Opuntia* populations of those known in more southern areas of the Mediterranean, where these are able to penetrate to altitudes up to 800 m (Erre et al., 2009).

Opuntia humifusa is the most common species on the Crimean Peninsula. It prefers well-aerated skeletal variants of dry clayey and loamy carbonate and carbonate-free soils. *Opuntia humifusa* often forms derivative groups in different vegetation classes, which include communities of stony outcrops (*Koelerio-Corynephoretea canescentis* Klika in Klika & Novák, 1941), sparse forests (*Quercetea pubescentis* Doing-Kraft ex Scamoni & Passarge 1959) and steppe phytocoenoses (*Festuco-Brometea* and *Thero-Brachypodietea*), as well as phryganoid communities floristically are close to phytocoenoses of the order *Onosmo polyphyllae-Ptilostemonetalia* (Bagrikova & Ryff, 2014a). In almost all studied localities in the Karadag Nature Reserve, *Opuntia* plants form derivational groups in degraded steppe, fryganoid-steppe and semi-desert badlands communities on heavy, slightly saline, gravelly-clay brown soils. Apart from *Opuntia* species, the main dominant species here is *Artemisia taurica*, in combination with various synanthropic plants, belonging predominantly to the family Chenopodiaceae (*Chenopodium alba*, *Atriplex micrantha*, *A. aucheri*, *A. tatarica*). The studied plant communities have a high invasibility, i.e. susceptibility to invasion of alien species (Mirkin & Naumova, 2014). These contain at least ten alien plant species (see Table 2). It is about 11% of the total number of alien plants in the Karadag Nature Reserve. Amongst these, apart from *Opuntia* species, *Ailanthus altissima* is considered as an invasive species. Our data are in accordance with results obtained for *O. humifusa* populations in Southern Bulgaria (Tashev, 2012) where this plant inhabits degraded oak sparse forest with secondary xerophytic groups in the herb layer. In the Karadag Nature Reserve, the largest *O. humifusa* coenopopulations were found on the territory of the biological station and steep denudation slopes adjacent to it. This species inhabits naturally or anthropogenically

disturbed phryganoid-steppe and badland communities, which are floristically close to phytocoenoses of the order *Onosmo polyphyllae-Ptilostemonetalia* and class *Pegano harmalae-Salsoletea vermiculatae*. Single *O. humifusa* individuals have already invaded in almost undamaged communities. They grow in juniper sparse forests with slightly degraded herbage on the ridge Karagach (western part of the ridge Beregovoy) (Fateryga & Fateryga, 2011). Also, *O. humifusa* plants are known in pistachio sparse forests on seaside gravelly-clay slopes. These phytocoenoses are floristically close to communities of the class *Thero-Brachypodietea* and order *Onosmo polyphyllae-Ptilostemonetalia*.

The invasion of the red-flower form of *O. phaeacantha* in Crimea is known in the Karadag Nature Reserve only. In this area, plants form derivative groups in phytocoenoses of different vegetation classes. The highest vitality of individuals was registered on watershed slopes of flysch low-hill terrains in degraded steppe communities of the class *Festuco-Brometea* in combination with elements of phytocoenoses belonging to the classes *Pegano harmalae-Salsoletea vermiculatae* and *Thlaspietea rotundifolii*.

Participation of *Opuntia* species in phytocoenoses of different vegetation classes and transitional nature of groups demonstrate the diversity of ecological, including climatic, conditions of the Karadag Nature Reserve. Most of the studied phytocoenoses with *Opuntia* species belong to xerothermic communities, attributing to Mediterranean vegetation classes. In general, they characterise the climate of the Karadag Nature Reserve. So, it is considered as very arid, hot, with very mild winters; it has the transitional character from the sub-Mediterranean climate typical for the western part of the southern coast of Crimea to the moderately continental and moderately hot arid climate, typical for the steppe part of the Crimean Peninsula (Kostenko et al., 2011).

The study of *Opuntia* species in the Karadag Reserve shows some features of their distribution in different biotopes. We observed both single plants and groups formed by individuals of vegetative and generative origin. Sometimes, the invasive plants formed curtains up to several meters in diameter. The structures of communities and populations' status indicate that both species being found in damaged habitats are invasive plants because these have overcome geographical and biological barriers. Participation of single *Opuntia* plants in natural communities indicates that both invasive species are able to overcome ecological-coenotic barriers. Therefore, these species will be classified as transformers if they will continue their expansion in future. To date, the *Opuntia* populations occupy insignificant areas in the Karadag Nature Reserve. That is why they do not cause any significant ecological damage to natural ecosystems. However, we should not underestimate the potential and opportunities for distribution of *Opuntia* species. It is enough only to look at the history of *Opuntia* dispersal in other countries and continents. For example, *Opuntia* plants were firstly brought in South Africa in 1656. In the late 18th century the plant was successfully entered into culture. In 1942, *Opuntia* plantations have covered an area of 9000 km^2 in the Karoo and the savannas of South Africa. And only in the late 20th century, this plant has become a real agricultural catastrophe (Dean & Milton, 2000). In order to spread over the Australian territory and to become a real ecological catastrophe there, *Opuntia* species took time about 140 years (from 1789 to 1925) (Frawley, 2007). At present, *O. humifusa* is the invasive species in Australia, South Africa and nine European countries. *Opuntia phaeacantha* is known from Australia and three countries of Central Europe (Tashev, 2012; Novoa et al., 2014). The term «lag-phase» means the time from the appearance of an alien species to its dispersal in conditions of a secondary range (Vinogradova & Mayorov, 2015). We suggest that on the Crimean Peninsula the lag-phase for *O. humifusa* is most likely 110 years, taking into account that the first reliable data on its self-reproduction dates back to the first half of the 20th century, while this species appeared in the Crimea in the early 19th century (Anisimova, 1939). The lag-phase for *O. phaeacantha* is most likely even shorter, because less than 80 years passed from its introduction to naturalisation in the Karadag Nature Reserve.

In order to get a better understanding of the invasion processes of representatives of the genus *Opuntia* into natural communities of the Crimea, complex studies are needed covering taxonomic, morphological, floristic, geobotanical and other approaches. Due to the fact that collection and herbarisation of cacti is a time-consuming and sometimes painful process, many botanists neglect representatives of this family during the preparation of herbarium collections of the flora of certain regions (Majure, 2007). Researchers should pay more attention to the collection of herbarium material of this genus since many *Opuntia* species belong to taxonomically difficult groups. Herbarium material is needed in order to avoid errors in determining and, subsequently, misinterpretation of the rate and degree of the distribution of certain taxa.

Conclusions

Based on the fact that the two studied *Opuntia* species were originally planted in Karadag in the early 20th century and since then their abundance increased, they have overcome the geographical, biological and partly ecological barriers. It can be stated that they are invasive species in the Karadag Nature Reserve, which sometimes demonstrates properties of the plants-transformers. This is caused due to their adaptation to the natural conditions of the secondary range, the ability to self-reproduce vegetatively (basic) and by seeds. They have a high invasive potential. The invasion degree of various cacti into the natural communities of Crimea has not sufficiently been studied yet. To date, it seems relevant to monitor the further expansion of both naturalised and, possibly, new species of the genus *Opuntia* over there.

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ИНВАЗИЯ *OPUNTIA HUMIFUSA* И *O. PHAEACANTHA* (CACTACEAE) В РАСТИТЕЛЬНЫЕ СООБЩЕСТВА КАРАДАГСКОГО ЗАПОВЕДНИКА

В. В. Фатерыга[1], Н. А. Багрикова[2]

[1]*Карадагская научная станция имени Т.И. Вяземского – природный заповедник РАН, Россия*
e-mail: valentina_vt@mail.ru
[2]*Ордена Трудового Красного Знамени Никитский ботанический сад – Национальный научный центр РАН, Россия*
e-mail: nbagrik@mail.ru

Представлены результаты изучения *Opuntia humifusa* и *O. phaeacantha*, натурализовавшихся на территории Карадагского заповедника (юго-восточная часть Крымского полуострова). Наибольшие по площади ценопопуляции представителей рода *Opuntia* приурочены здесь к территории биостанции (на границе с парком, административно-хозяйственными строениями и жилым фондом). Здесь описано двенадцать локалитетов, различающихся по фитоценотическим характеристикам, площади и флористическому составу. В семи локалитетах произрастает только *O. humifusa*, в четырех – только *O. phaeacantha*; в одном локалитете отмечены оба вида. В каждом локалитете подсчитана общая численность и демографическая структура каждого из видов. Общая численность *O. humifusa* на территории биостанции составляет более 600 особей, *O. phaeacantha* – около 400 особей. Исследования растительных сообществ проводили с использованием методики Браун-Бланке. Почти во всех описанных локалитетах опунции образуют дериватные группировки в составе деградированных степных, фриганно-степных и полупустынных бедлендовых сообществ. В них отмечено значительное участие синантропных видов, включая чужеземные растения. Опунции размножаются преимущественно вегетативным способом, реже самосевом. Обладая высоким адаптационным потенциалом, они являются инвазионными видами.

Ключевые слова: *Opuntia*, Карадагский заповедник, Крым, растительные сообщества, фитоинвазия, чужеземные растения