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RESEARCH ARTICLE

The current state of the introduction coenopopulation of Gymnospermium odessanum on the botanical-geographical plot "Steppes of Ukraine" at the M. M. Gryshko National Botanical Garden of the NAS of Ukraine

Victoria Gritsenko

M.M. Gryshko National Botanical Garden, National Academy of Sciences of Ukraine, Tymiryazevska str. 1, 01014 Kyiv, Ukraine; gritsenkoviktoria@gmail.com

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Abstract

Gymnospermium odessanum is a rare relict endemic plant species. The research was carried out during *G. odessanum* flowering in 2019–2021 at the botanical-geographical plot "Steppes of Ukraine" of the M.M. Gryshko National Botanical Garden, National Academy of Sciences of Ukraine (NBG). Ecological and coenotic conditions of introduction at the NBG differ from natural habitats of the species and are not optimal for its vegetation. However, this species demonstrated ecological-coenotic plasticity and, over the decades, has formed a stable homeostatic introduction coenopopulation here. As of 2021, the area of introduction coenopopulation of *G. odessanum* at the NBG was 2,075 m^2. It comprises 412 individuals of this species (including 40 seedlings, 241 juvenile, 45 immature, 40 virginal, 45 generative, and 1 sub-senile plants). Coenopopulation fragments with a high density of *G. odessanum* individuals are rare here, so the average density is low – only 0.2 individuals per 1 m^2. In 2021, in the spectrum of age states, the total percentage of pregenerative individuals was very high and reached 88.8 %; the share of generative individuals was 10.9 %.

In general, the age structure of the introduction coenopopulation of *G. odessanum* is characterized by long-term (2010–2021) stability. The spatial distribution of individuals in the introduction coenopopulation is of two kinds – random and in groups. This is due to combined myrmecochoric and barochoric propagation. Also due to myrmecochory, this coenopopulation tends to spread the area. Compared to natural coenopopulations, the introduction coenopopulation of *G. odessanum* at the NBG is characterized by a larger area, a much significant number, and, at the same time, a low average density of individuals. However, like in most of natural populations, its age spectrum is left-sided.

The conducted research testifies the successful formation of the introduction coenopopulation of *G. odessanum* in the meadow-steppe cultural phytocoenosis of the NBG. This introduction coenopopulation is an example of a successful multi-year scientific experiment and effective *ex situ* protection and preservation of *G. odessanum* on the northern border of the Right Bank Forest-Steppe of Ukraine, far beyond the natural range of this endemic plant species.

Keywords: *Gymnospermium odessanum*, rare endemic species, introduction coenopopulation, stable age structure, *ex situ* protection

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Introduction

Gymnospermium Spach (Berberidaceae Juss.) is a small genus (7–12 species) of early flowering tuberous herbs, distributed from east China to the Balkans (Rosati et al., 2018). *Gymnospermium odessanum* (DC.) Takht. is a relict endemic species with a narrow disjunctive distribution range (Scherbakova & Novosad, 2018). It is listed as a vulnerable species in the Red Book of Ukraine (Kritska & Novosad, 2009) and also protected by the Red Book of the Republic of Moldova (Kolomiychuk & Popova, 2018). This species is distributed in Dobrogea region of Moldova and North-Western part of the Black Sea region of Ukraine (Kritska & Novosad, 2009; Scherbakova & Novosad, 2018). It is also reported as a phyto-rarity for the Steppe zone of Ukraine (Sobko et al., 2013).

As a result of phylogenetic analyzes, it was found that *G. odessanum* is sister to *G. peloponnesiacum* (Phitos) Strid from South Greece. Both species are, in turn, sister to *G. altaicum* (Pallas) Spach (Barina et al., 2017; Rosati et al., 2018). However, despite small number of representatives, the taxonomy of the genus is not fully clear and well-established yet. In particularly, recently Rosati et al. (2018) discribed a new subspecies of the genus (*G. scipetarum* Paparisto & Qosja ex E. Mayer & Pulevic subsp. *eddae* Rosati, Farris, Fascetti & Selvi) for the flora of Italy.

In Ukraine, *G. odessanum* has been extensively investigated in the nature (Visjulina, 1953; Litvinenko, 1986, 2010; Melnyk, 1994, 2000; Scherbakova, 2005, 2008, 2010, 2011; Kritska & Novosad, 2009; Litvinenko & Shcherbakova, 2009; Kritska, 2012; Scherbakova & Barmak, 2013; Smetana et al., 2014; Trotner, 2016, 2017). This species has also been studied in Dobrogea (Doroftei & Mierla, 2007) and Moldova, in general (Izverskaya et al., 2013, 2017). In particular, is interesting that Izverskaya et al. (2017) predicted displacement of *G. odessanum* in the Dniester river basin in Moldova to the north due to climate change.

Scherbakova & Novosad (2018) comprehensively investigated the distribution, ecological and coenotic peculiarities, and some aspects of *G. odessanum* protection. After that, additional information about the distribution and ecology of *G. odessanum* in Ukraine was provided by Krasova et al. (2019), Ponomareva et al. (2019), and Shiryaeva et al. (2019, 2020).

Krasova et al. (2016) introduced *G. odessanum* on the dump of the mining quarry to restore phytodiversity in the anthropogenic landscapes of Kryvbas, which were decommissioned. Pavlenko et al. (2020), during a survey of post-mining quarry and dump complexes in the area of Kryvyi Rih, found that *G. odessanum* is naturalized here as a result of reclamation.

Gymnospermium odessanum is an ornamental spring ephemeroid growing and *ex situ* protected in several botanical gardens of Ukraine (Mashkovska, 2015; Scherbakova & Novosad, 2018). Namely, it is cultivated at the M.M. Gryshko National Botanical Garden, National Academy of Sciences of Ukraine (NBG); Donetsk Botanical Garden, National Academy of Sciences of Ukraine (Krokhmal & Netsvetov, 2015); Botanical Garden of Kherson State University; Botanical Garden of V.N. Karazin National University of Kharkiv; Botanical Garden of I.I. Mechnikov National University of Odesa (Yermolaieva, 2010); Botanical Garden of Ivan Franko National University of Lviv; Kryvyi Rih Botanical Garden, National Academy of Sciences of Ukraine (Trotner, 2016; Krasova et al., 2019); O.V. Fomin Botanical Garden of Taras Shevchenko National University of Kyiv (Peregrym et al., 2014).

In the Department of Natural Flora of the NBG, *G. odessanum* was introduced and partially studied on the botanical-geographical plots "Steppes of Ukraine" (Borodina, 1972, 1976) and "Forests of the plain part of Ukraine" (Melnyk, 1994), and the collection plot "Rare plants of the Ukrainian flora" (Sobko & Borodina, 1987; Sobko & Gaponenko, 1996). It was found that *G. odessanum* formed a stable homeostatic introduction coenopopulation on the botanical-geographical plot "Steppes of Ukraine" of the NBG (Gritsenko, 2009). Previously, only brief information on this introduction coenopopulation was known (Gritsenko, 2010, 2012, 2014, 2017a, 2019a, b; Gritsenko et al., 2017). Thus, there was a need for a more detailed and in-depth study of this introduction coenopopulation.

In 2021, the phenology of *G. odessanum* was studied on the botanical-geographical plot

"Steppes of Ukraine" of the NBG (Gritsenko, 2021). *Gymnospermium odessanum* grows here outside its natural range (far to the north). The introduction conditions at the NBG, which is located on the northern border of the Right Bank Forest-Steppe of Ukraine, significantly differ from those in the natural habitats of the species in the North-Western Black Sea region.

There are two specific directions of plant introduction – within and outside the natural range, both of which are strongly argued (Gaponenko & Gnatiuk, 2016) and can be successfully realized. In recent years, in both of dirrections, the experimental studies of introduction populations of different rare plant species were conducted at the Department of Natural Flora of the NBG (Melnyk et al., 2018; Gritsenko, 2020). In particular, it was found that the introduction coenopopulation of the rare early-spring ephemeroid *Crocus reticulatus* Steven ex Adam at the NBG (which is, by the way, located within the species' natural range) was in the phase of logistic growth in 2020. This confirmed the success of the introductory experiment (Gritsenko, 2020).

Hence, it was worthing to find out whether the introduction of *G. odessanum* has been also fruitful. We suggested this an example of successful multi-decade scientific experiment, and effective *ex situ* protection and preservation of *G. odessanum* on the northern border of the Right-Bank Forest-Steppe of Ukraine.

Material and methods

The studies were conducted during the time of *G. odessanum* flowering in 2019–2021 at the botanical-geographical plot "Steppes of Ukraine" of the NBG. *Gymnospermium odessanum* was introduced here from the natural habitats of Odessa surroundings in 1953 and, repeatedly, in 1964 (Borodina, 1972). These initial individuals served as a base to form the introduction coenopopulation of *G. odessanum*. Additional solitary individuals were collected in 2002 and 2010 (Gritsenko et al., 2017) and planted in the nursery – they did not participate in the formation of the main introduction coenopopulation of the species.

In this article, for coenopopulation description, author applies the term 'introduction' ('інтродукційна' in Ukrainian) instead of 'introduced' ('інтродукована' in Ukrainian), because it reflects the semantic meaning much more correctly.

The area of the introduction coenopopulation of *G. odessanum* was calculated with a precision of 1 m^2. The area's configuration was plotted on the satellite images of Google Maps (2021). According to standard methodology, phenomenological observations of *G. odessanum* were performed daily during its mass flowering (Beideman, 1974; Zaitsev, 1978). The plants were not excavated or damaged during the research; only aboveground parts were considered. The age states of *G. odessanum* were determined according to Litvinenko (2010). In general, the number of generative individuals (total amount of young, middle-aged, and old generative plants) was counted. The study of the coenopopulation structure was conducted according to Uranov (1976). The average density of individuals per 1 m^2 was determined as the individuals' number divided by the total area. When mapping the spatial location of generative individuals, the total area of the coenopopulation was subdivided into smaller 5×5 m plots, using cords and measuring tape. Deviations between two numerical data were calculated by the formulae: $Dev. = 100 - y \times 100 / x$, where 'x' is the first datum, and 'y' is the second one.

Plant names were verified and provided according to Euro+Med PlantBase (2021) nomenclature. Species were determined following Prokudin (1987). All photos were captured by the author using a Canon Power Shot SD 4000 IS digital ELPH camera.

Results and discussion

Area of the introduction coenopopulation

From a landscape perspective, the botanical-geographical plot "Steppes of Ukraine" is an extensive glade covering 2.5 hectares and surrounded by forest vegetation (Fig. 1 A). The introduction coenopopulation of *G. odessanum* is located in the western part of this plot on the open area with a flat relief (Fig. 1 A–C). The coordinates inside of *G. odessanum* coenopopulation are following – N 50.412000°,

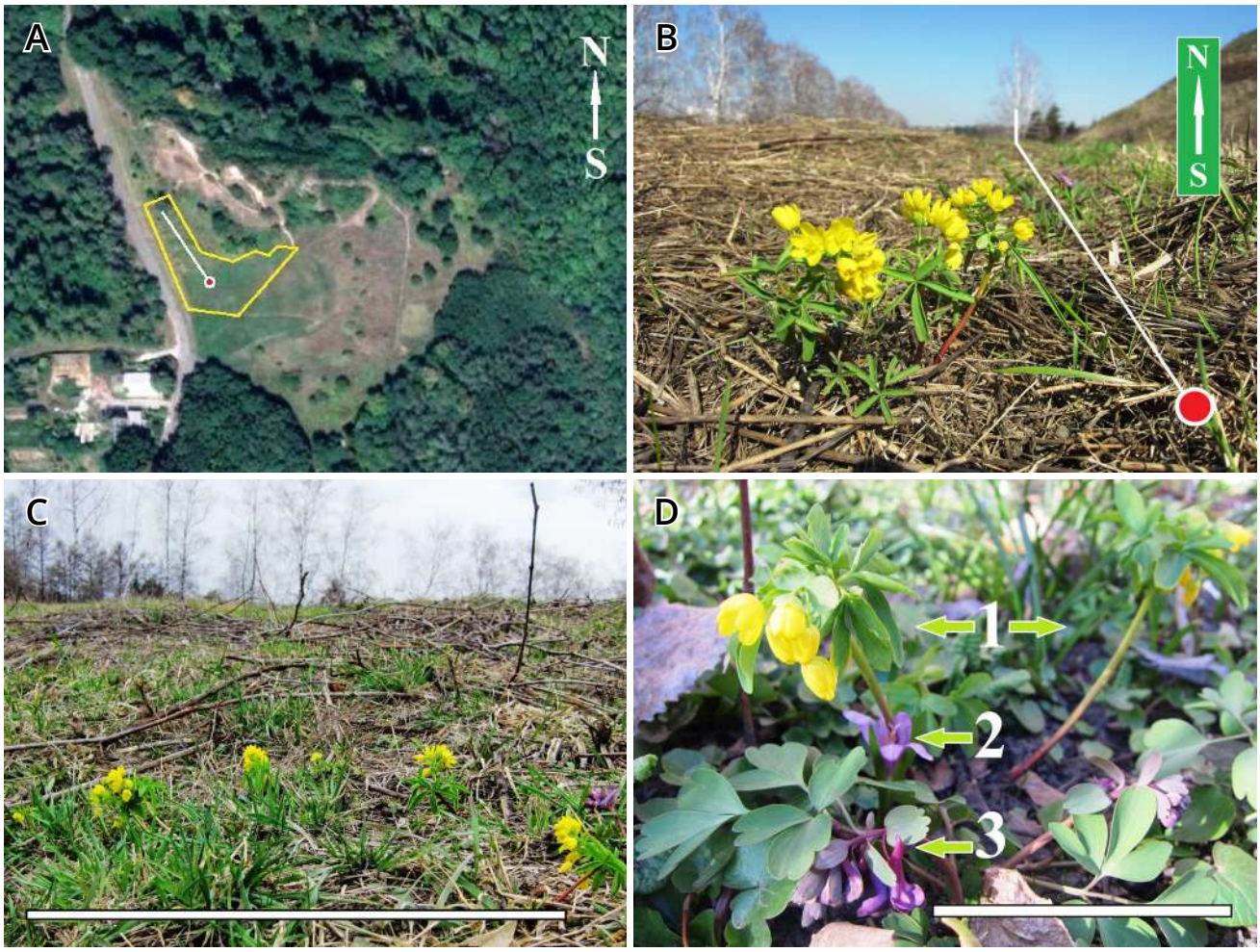

Figure 1. The introduction coenopopulation of *Gymnospermium odessanum* on the botanical-geographical plot "Steppes of Ukraine" at the M. M. Gryshko National Botanical Garden of the NAS of Ukraine: **A** – location and configuration (source: Google Maps; the **yellow line** indicates the boundaries of the coenopopulation; the **red point** indicates the coordinates inside of the coenopopulation); **B** – the fragment (the **red point** corresponds to A); **C** – the projective cover of the grass during the flowering time of *G. odessanum* and the beginning of vegetation of cereals; **D** – the fragment of spring synusia with the participation of *G. odessanum* (**1**), *Colchicum bulbocodium* subsp. *versicolor* (**2**) and *Corydalis solida* (**3**). Scales: **A–B** – 50 m; **C** – 0.5 m; **D** – 0.1 m.

E 30.565062°. The coenopopulation has polygonal (decagonal) outlines and area of 2075 m² (over 0.2 ha), bounded by earth roads (Fig. 1 A).

Scherbakova & Novosad (2018) generally characterized contemporary natural populations of *G. odessanum* as local and having small areas. Smetana et al. (2014) indicated that 27 natural populations of *G. odessanum* in the Ingulets river basin occupy areas from 0.5 m² to 500 m² and are confined to the slopes of the predominantly eastern exposure with 5–30° inclination. Thus, the introduction coenopopulation of *G. odessanum* at the NBG, compared to natural ones, is characterized by significantly larger area and is scattered on the flat relief.

Coenotic features

Gymnospermium odessanum grows on the botanical-geographical plot "Steppes of Ukraine" in the composition of artificially created meadow-steppe phytocoenosis (Gritsenko, 2017b). During the flowering time of *G. odessanum* (March – beginning of April) the soil surface is covered with a loose litter from the remnants of various plants of the previous year (Fig. 1 B). The projective cover of the grass stand reaches 60% (Fig. 1 C). In some places, the projective cover of *G. odessanum* can be up to 10%. The height of *G. odessanum* flowering shoots above the soil surface is 5–12 cm (Fig. 1 D).

In the natural coenopopulations of *G. odessanum*, the projective grass cover varies

Table 1. Spring synusiae during the flowering of *Gymnospermium odessanum* on the botanical-geographical plot "Steppes of Ukraine" at the NBG in 2019–2021.

Nr	Plant species	Group	Phenophase
1	*Achillea millefolium* L.	N	I
2	*Adonis vernalis* L.	In	III
3	*Adonis volgensis* DC.	In	III
4	*Arrhenatherum elatius* (L.) J. Presl & C. Presl	A	I
5	*Bromopsis inermis* (Leyss.) Holub	N	I
6	*Calamagrostis epigejos* (L.) Roth	N	I
7	*Colchicum bulbocodium* Ker Gawl. subsp. *versicolor* (Ker Gawl.) K. Perss.	In	VI
8	*Corydalis solida* (L.) Clairv.	N	IV
9	*Dactylis glomerata* L.	N	I
10	*Delphinium sergii* Wissjul.	In	I
11	*Elytrigia intermedia* (Host) Nevski	In	I
12	*Elytrigia repens* (L.) Nevski	N	I
13	*Ficaria calthifolia* Rchb.	In	IV
14	*Ficaria verna* Huds.	N	IV
15	*Gagea liotardii* (Sternb.) Schult. & Schult. f.	N	IV
16	*Gagea minima* (L.) Ker Gawl.	N	IV
17	*Gagea pusilla* (F. W. Schmidt) Sweet	N	IV
18	*Gymnospermium odessanum* (DC.) Takht.	In	V
19	*Muscari neglectum* Guss. ex Ten.	In	III
20	*Ornithogalum boucheanum* (Kunth) Asch.	In	I
21	*Ornithogalum fimbriatum* Willd.	In	III
22	*Paeonia tenuifolia* L.	In	I
23	*Papaver orientale* L.	A	I
24	*Pulsatilla pratensis* (L.) Mill.	In	III
25	*Ranunculus illyricus* L.	In	I
26	*Scilla bifolia* L.	N	IV
27	*Scilla siberica* Haw.	In	III
28	*Tulipa biebersteiniana* Schult. & Schult. f.	In	I
29	*Veronica hederifolia* L.	N	V
30	*Viola odorata* L.	N	II

Note. Groups: N – native plant species; **In** – introduced plant species; **A** – alien plant species. **Phenophases: I** – beginning of vegetation; **II** – beginning of vegetation and budding; **III** – budding; **IV** – budding and beginning of flowering; **V** – mass flowering; **VI** – completion of flowering.

in a wide range from 20% to 95% (Smetana et al., 2014). *Gymnospermium odessanum* often dominates in the spring synusia (Scherbakova & Novosad, 2018). Krasova et al. (2016) observed a projective cover of *G. odessanum* reaching 50–60%. The height of *G. odessanum* in nature is 5–20 cm (Kritska & Novosad, 2009) or 10–15 cm (Trotner, 2017).

In the species composition of the artificially created phytocoenosis (Table 1), introduced plant species represent 50.0% (15 species), native – 43.3% (13 species), alien – 6.7%

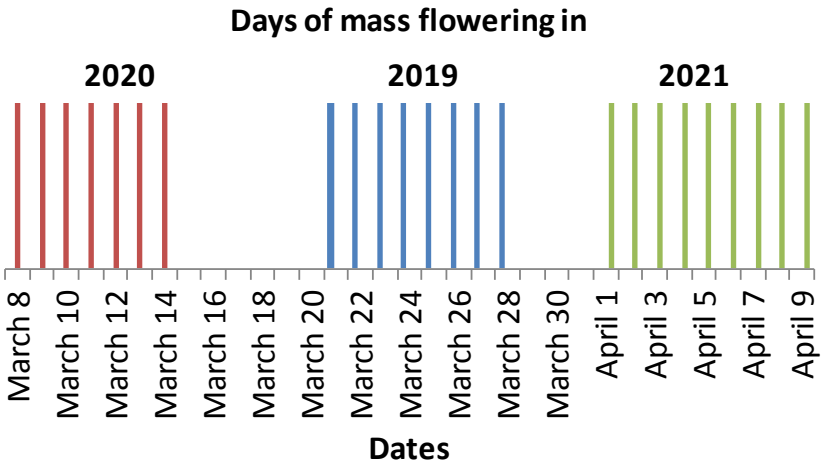

Figure 2. Dynamics of *Gymnospermium odessanum* mass flowering in the introduction coenopopulation at the NBG in 2019–2021.

(two species). At the same time, many plant species (13 species, 43.3 %) have not begun vegetation and therefore are not visible in the spring synusiae yet. In particular, cereals have just started their growth (Table 1; Fig. 1 C). From other hand, at this time, *Colchicum bulbocodium* Ker Gawl. subsp. *versicolor* (Ker Gawl.) K. Perss. already finishes its flowering (Table 1; Fig. 1 D). In this spring synusia, all plants are herbaceous (Table 1). Of course, such species composition of the spring synusia is possible only in introduction conditions and does not occur in natural phytocoenoses.

In Ukraine, the natural habitats of *G. odessanum* are located on the limestones, loess-limestones and granite slopes, ravines and gullies, in the phytocoenoses of shrub steppes, on the open areas of steppe slopes adjacent to shrubby thickets, and forest glades (Scherbakova, 2005; Kritska & Novosad, 2009; Kritska, 2012). Smetana et al. (2014) indicated a wide range of coenotic conditions for the *G. odessanum* existence, particularly shrubby, steppe, and rocky vegetation. Solomakha (2015) noted that in the Ukrainian Northern Black Sea region, *G. odessanum* occurs in the forest and shrub communities. Scherbakova & Novosad (2018) indicate that sylvatic communities (i.e., natural ravine forests, thickets of shrubs, and secondary forest phytocoenoses) are optimal for the existence of *G. odessanum* in Ukraine. In Moldova, this species occurs exclusively in light oak forests. It does not spread to open areas in Moldova, and therefore it is considered there a typical forest representative (Izverskaya et al., 2013).

Thus, the coenotic conditions of *G. odessanum* habitats under introduction on the botanical-geographical plot "Steppes of Ukraine" differ from those in nature. This confirms the opinion of Scherbakova & Novosad (2018), who declared broad ecological and coenotic plasticity of *G. odessanum* in Ukraine.

Phenology features during *Gymnospermium odessanum* flowering

During the flowering of *G. odessanum*, the following phenophases were distinguished: the beginning of flowering, the mass flowering, and the completion of flowering. The mass flowering of *G. odessanum* in 2019 lasted eight days, in 2020 – seven days, in 2021 – nine days (Fig. 2). The earliest mass flowering occurred in March 2020, the latest – in early April 2021 (Fig. 2). The beginning of mass flowering in 2020 and 2021 differed significantly and resulted in 24 days of delay. This may be due to the significant differences in spring weather during these years. In 2021, the entire growing season of *G. odessanum* lasted from March 24 to May 22 and amounted to 60 days (Gritsenko, 2021). At the same time, mass flowering took up to 15 % of the entire vegetation period.

The flowering of *G. odessanum* occured in March-April both in the conditions of introduction at the NBG, and in nature (Visjulina, 1953; Kritska & Novosad, 2009; Trotner, 2017). During *G. odessanum* flowering, the composition of plant species in the spring synusia and phenophases of these plants were the same in 2019–2021 (Table 1). At different

Figure 3. *Gymnospermium odessanum* individuals: **A** – seedling; **B** – juvenile plant; **C** – immature plant; **D** – virginal plant; **E–F** – a generative plant with one (**E**) and three (**F**) flowering shoots; **G** – sub-senile plant. Scales: **A–D** – 2 cm; **E–G** – 10 cm.

dates of *G. odessanum* flowering, an associated shift of phenophases of other plant species in the spring synusia was observed. Therefore, the phenophases of these plants in different years were the same, too (Table 1).

Fruiting of *G. odessanum* in nature occurs from the middle of April to early May (Trotner, 2017). Ripening and dispersion of seeds of this species in the introduction conditions occur in May (Gritsenko, 2021). The seeds germinate in the spring of next year. Vegetative reproduction is not usual for *G. odessanum* (Litvinenko & Shcherbakova, 2009; Scherbakova & Barmak, 2013).

Ontogenetic aspect

Up to date, several generations of introduced *G. odessanum* were formed at the botanical-geographical plot "Steppes of Ukraine". During *G. odessanum* flowering, seedlings, as well as juvenile, immature, virginal, generative, and sub-senile individuals were observed (Fig. 3). In the introduction conditions, the principal parameters of the aboveground plant parts of *G. odessanum* corresponded to those registered in nature (Litvinenko, 2010).

Among the generative individuals, the most frequent were those with one flowering shoot (Fig. 3 E; Table 2). However, plants with two or three flowering shoots occasionally occurred too (Fig. 1 D; Fig. 3 F; Table 2). Plants with four, five, and six flowering shoots were quite rare (Table 2). In nature, usually occur plants with one-three flowering shoots, sometimes – with five or six flowering shoots (Trotner, 2017). Although, Litvinenko (2010) reported that generative individuals of *G. odessanum* in natural conditions could form up to 12 flowering shoots.

According to our long-term observations (2001–2021), the individuals of *G. odessanum* in the introduction conditions can persist in the generative state for over twenty years. Litvinenko (2010) indicated that the ontogenesis of *G. odessanum* typically lasts about 30 years, and the plants spend most of their life in a mature generative state. Thus, all individuals in the introduction coenopopulation of this species at the NBG today are direct descendants of initially introduced plants.

Table 2. The number of generative individuals of *Gymnospermium odessanum* with a different number of flowering shoots in 2019–2021.

Number of flowering shoots per plant	Generative individuals, number / %		
	2019	2020	2021
1	32 / 78.0	32 / 76.2	34 / 75.6
2	4 / 9.8	5 / 11.9	5 / 11.1
3	4 / 9.8	3 / 7.1	4 / 8.9
4	0 / 0	1 / 2.4	1 / 2.2
5	1 / 2.4	1 / 2.4	0 / 0
6	0 / 0	0 / 0	1 / 2.2
Total	41 / 100	42 / 100	45 / 100

Age structure

In the spectra of age states, the percentage of pregenerative individuals (i.e., seedling, juvenile, immature, and virginal) in 2019–2021 was very high (89.5% in 2019, 89.2% in 2020, and 88.8% in 2021). For this period, the percentage of generative individuals was low (10.0% in 2019, 10.3% in 2020, and 10.9% in 2021). The percentage of sub-senile individuals for this period was even much lower (0.5% in 2019, 0.5% in 2020, and 0.3% in 2021; Fig. 4).

In previous years (2010–2017), the overall percentage of pregenerative individuals of ontogenesis was also very high (about 90%), and the rate of generative individuals was low (about 10 %) (Gritsenko, 2010, 2014, 2017a). Thus, the age structure of the introduction coenopopulation of *G. odessanum* is characterized by long-term stability.

In the natural populations of *G. odessanum*, there are present individuals of all age states (Scherbakova, 2005; Kritska & Novosad, 2009; Scherbakova & Novosad, 2018). The age spectra in the natural populations of this species are mostly left-sided, and only occasionally they are right-sided (Scherbakova, 2010; Scherbakova & Novosad, 2018). In particular, in the natural coenopopulations of *G. odessanum* in the Ingulets river basin, the share of generative individuals was high (about 50 %), and age spectra were right-sided (Smetana et al. 2014). The age spectra of the introduction coenopopulation of *G. odessanum* at the NBG in 2010–2021 were left-sided, like in the most of natural populations.

Spatial distribution and dissemination modes

The spatial distribution of particular individuals in the introduction coenopopulation of *G. odessanum* at the NBG is of two kinds – random and grouped. As a result of seed propagation and different dissemination modes, single individuals and groups of individuals of different age states occur within the same coenopopulation. *Gymnospermium odessanum* is a myrmecochorous plant (Litvinenko & Shcherbakova, 2009; Scherbakova & Barmak, 2013). Random distribution of its solitary individuals of different age states in the

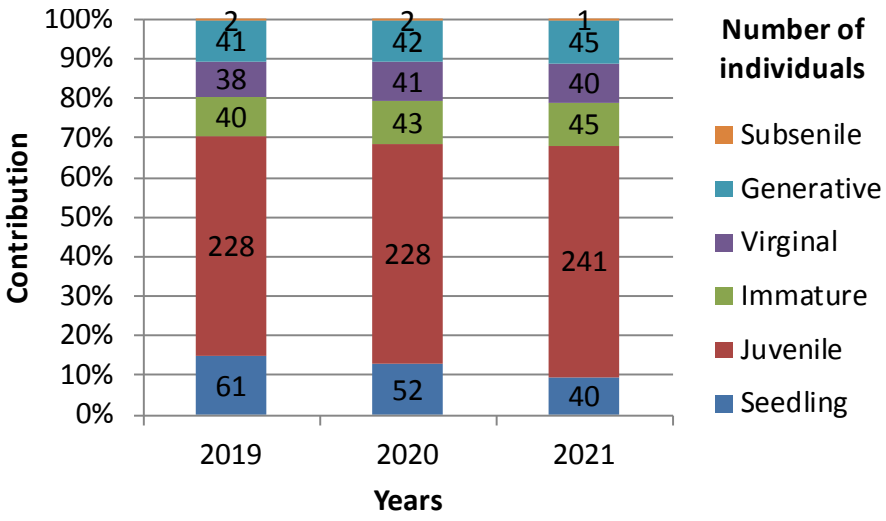

Figure 4. Age structure of *Gymnospermium odessanum* introduction coenopopulation at the NBG in 2019–2021.

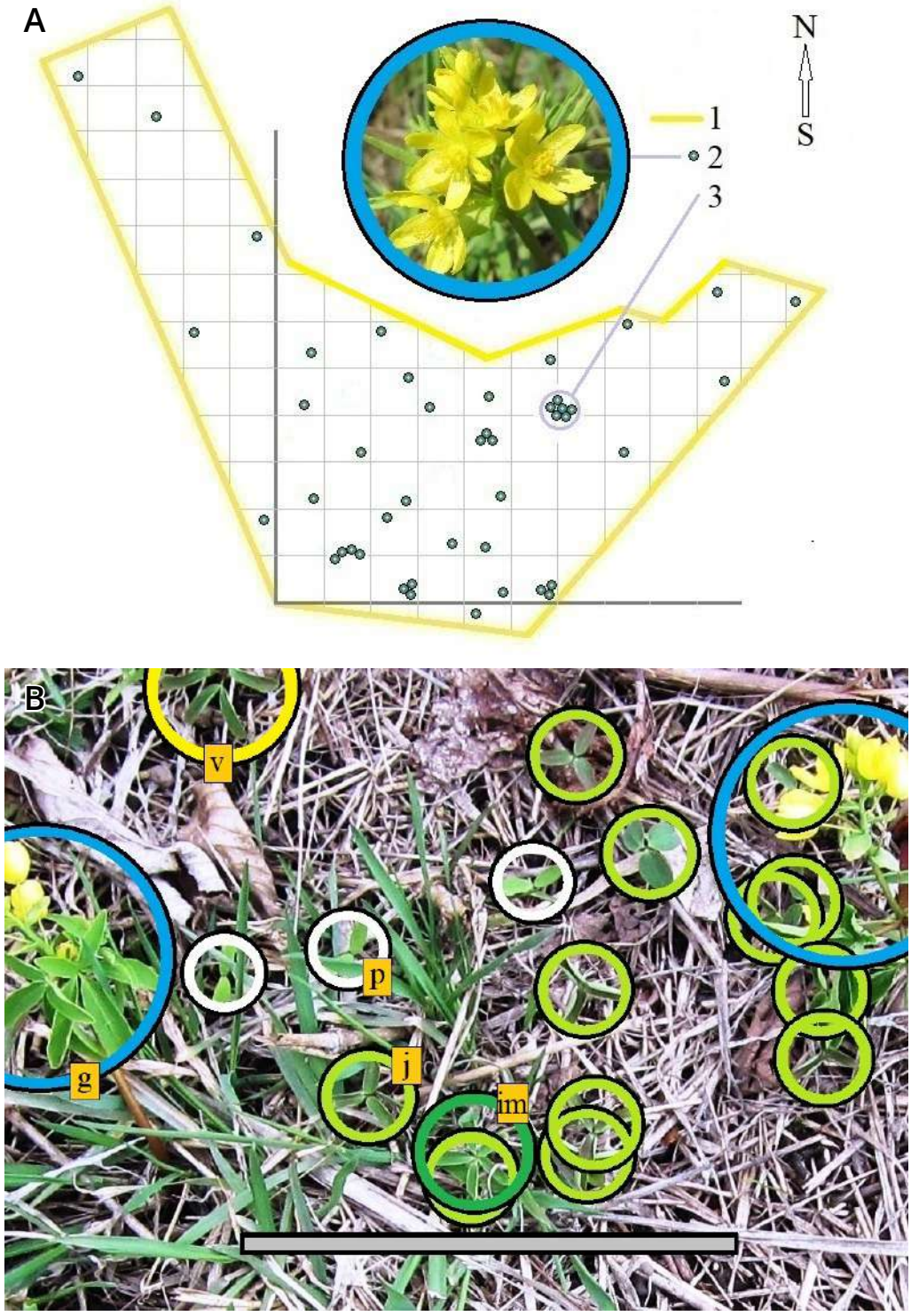

Figure 5. Spatial distribution of *Gymnospermium odessanum* individuals in the introduction coenopopulation at the NBG. **A** – boundaries of the coenopopulation (**1**), generative individuals in 2021 (**2**), and the fragment with the maximum density of generative individuals (**3**); scale – 50×50 m. **B** – individuals of different age states, including seedling (**p**), and juvenile (**j**), immature (**im**), virginal (**v**), and generative (**g**) plants; the **circles** indicate the phytogenic fields; scale – 10 cm.

introduction coenopopulation may be a result of myrmecochory. The spatial distribution of generative individuals illustrates their bivariate (random and grouped) nature (Fig. 5 A). Many pregenerative individuals were located near the maternal generative individuals (Fig. 5 B), evidencing the barochory. Individuals of different age states differed in height. As a result, the leaf blades of adjacent individuals were located one above other, and formed a

Table 3. The number of individuals of different age states in the introduction coenopopulation of *Gymnospermium odessanum* at the NBG in 2019–2021 (pairwise comparison).

Age states	Number of individuals, %		Deviation, %	Number of individuals, %		Deviation, %	Number of individuals, %		Deviation, %
	2019	2020		2019	2021		2020	2019	
Seedling	14.9	12.8	+14.09	14.9	9.7	+34.90	12.8	14.9	-16.41
Juvenile	55.7	55.9	-0.36	55.7	58.5	-5.03	55.9	55.7	+0.36
Immature	9.6	10.5	-9.38	9.6	10.9	-13.54	10.5	9.6	+8.57
Virginal	9.3	10.0	-7.53	9.3	9.7	-4.30	10.0	9.3	+7.00
Generative	10.0	10.3	-3.00	10.0	10.9	-9.00	10.3	10.0	+2.91
Subsenile	0.5	0.5	0.00	0.5	0.3	+40.00	0.5	0.5	0.00
	2020	2021		2021	2019		2021	2020	
Seedling	12.8	9.7	+24.22	9.7	14.9	-53.61	9.7	12.8	-31.96
Juvenile	55.9	58.5	-4.65	58.5	55.7	+4.79	58.5	55.9	+4.44
Immature	10.5	10.9	-3.81	10.9	9.6	+11.93	10.9	10.5	+3.67
Virginal	10.0	9.7	+3.00	9.7	9.3	+4.12	9.7	10.0	-3.09
Generative	10.3	10.9	-5.83	10.9	10.0	+8.26	10.9	10.3	+5.50
Subsenile	0.5	0.3	+40.00	0.3	0.5	-66.67	0.3	0.5	-66.67

vertical spatial pattern. Hence, phytogenic fields of individuals of different age states overlaped (Fig. 5 B).

Number and density of individuals

In 2019–2021, the total number and average density of *G. odessanum* individuals did not change significantly. The total number of individuals of different age states was 410 in 2019, 408 – in 2020, and 412 – in 2021 (Fig. 4). The most abundant were juvenile individuals, while sub-senile ones were very rare (Fig. 4). The number of individuals of other age states (seedlings, immature, virginal, and generative individuals) was not large and was commensurate with each other (Fig. 4). The largest number of seedlings was observed in 2019, the smallest – in 2021 (Fig. 4).

The number of seedlings and sub-senile individuals in the introduction coenopopulation at the NBG in 2019–2021 was characterized by the most extensive variation range. Simultaneously, juvenile, immature, virginal, and generative individuals demonstrated much lower variation ranges (Table 3).

Natural populations of *G. odessanum* predominantly consist of a pretty high number of individuals (Scherbakova, 2005). In particular, natural coenopopulations of this species in the basin of Ingulets river have from several tens to several hundreds of individuals (Smetana et al., 2014). Therefore, the number of individuals in the introduction coenopopulation of *G. odessanum* is significant compared with many natural coenopopulations.

Considering the density of individuals in the introduction coenopopulation of *G. odessanum* at the NBG, the following aspects were noted. In several different fragments of the coenopopulation, the density of individuals was high and reached up to 25 individuals per 1 m^2 (Fig. 5 B). At the same time, there were many fragments within the coenopopulation with low density (from one to several individuals) or even zero presence. Hence, the average density of *G. odessanum* here was only 0.1975 individuals per 1 m^2 in 2019, 0.1966 individuals per 1 m^2 in 2020, and 0.1985 individuals per 1 m^2 in 2021. Considering that fragments with a high density of *G. odessanum* individuals are rather rare, its average density within coenopopulation is relatively low.

Trotner (2017) also observed uneven distribution of *G. odessanum* individuals in natural conditions. However, the density was high for most part of the population. Natural populations of *G. odessanum* are generally characterized by high density

(Scherbakova, 2005) and comprise several dozen individuals per 1 m^2 (Kritska & Novosad, 2009). Thus, Shiryaeva et al. (2020) reported 15–25 individuals per 1 m^2. Krasova et al. (2016) counted up to 170 individuals of the species per 1 m^2 and registered its high projective cover. Similarly, Smetana et al. (2014) indicated from 1 to 44 *G. odessanum* plants per 0.25 m^2 for 27 natural habitats. Scherbakova & Novosad (2018) also noted the high number and density of *G. odessanum* individuals under conditions of ecological-coenotic optimum. Of course, the NBG conditions are far from such optimum.

Development trends of introduction coenopopulation

Gymnospermium odessanum on the botanical-geographical plot "Steppes of Ukraine" successfully reproduces and settles for decades. Introduction coenopopulation of *G. odessanum* here is steady in time (long-term existence) and space (occupy the stable area). In this coenopopulation, the species demonstrates a constant tendency to preserve its stable position in the meadow-steppe cultural phytocoenosis and, probably, to further area extension due to myrmecochory.

Conclusions

Ecological and coenotic conditions at the NBG differ from those in the natural habitats of *G. odessanum* and are not optimal for this species. It grows here on the botanical-geographical plot "Steppes of Ukraine" in the composition of artificially created meadow-steppe phytocoenosis. However, *Gymnospermium odessanum* demonstrated high eco-coenotic plasticity and, over the decades, has formed a homeostatic introduction coenopopulation here. Today all contemporary *G. odessanum* individuals in the introduction coenopopulation at the NBG are descendants of the initially introduced plants.

As of 2021, the area of introduction coenopopulation at the NBG was 2,075 m^2. It consisted of 412 individuals (40 seedlings, 241 juvenile, 45 immature, 40 virginal, 45 generative, and one sub-senile plants). Fragments with a high density of individuals were rare, so the average density was low, with only about 0.2 individuals per 1 m^2. In 2021, in the spectrum of age states, the total rate of pregenerative individuals of ontogenesis was high and amounted to 88.8%, while the share of generative individuals was 10.9%. In general, the age structure of this introduction coenopopulation is characterized by long-term (2010–2021) stability. Due to myrmecochoric and barochoric propagation, the spatial distribution of individuals in this introduction coenopopulation is uneven and of two kinds – random and in groups.

Compared to natural populations, the investigated introduction coenopopulation of *G. odessanum* is characterized by a large area, significant number, and low average density of individuals. Like in most natural populations, the age spectrum in this introduction coenopopulation is left-sided.

The conducted research testifies the successful formation of the introduction coenopopulation of *G. odessanum* in the meadow-steppe cultural phytocoenosis of the NBG. This introduction coenopopulation is an example of successful multi-decade scientific experiment and effective *ex situ* protection and preservation of *G. odessanum* on the northern border of the Right Bank Forest-Steppe of Ukraine, far beyond its natural range.

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Сучасний стан інтродукційної ценопопуляції *Gymnospermium odessanum* на ботаніко-географічній ділянці "Степи України" Національного ботанічного саду імені М. М. Гришка НАН України

Вікторія Гриценко

Національний ботанічний сад імені М. М. Гришка НАН України, вул. Тімірязєвська, 1, Київ, 01014, Україна; gritsenkoviktoria@gmail.com

Gymnospermium odessanum – це раритетний реліктовий ендемічний вид. Дослідження проведені під час цвітіння *G. odessanum* у 2019–2021 рр. на ботаніко-географічній ділянці "Степи України" Національного ботанічного саду імені М. М. Гришка НАН України (НБС). Еколого-ценотичні умови інтродукції у НБС відрізнялись від природних місцезростань і не були оптимальними. Зокрема, *G. odessanum* росте на ботаніко-географічній ділянці "Степи України" у складі штучно створеного лучно-степового фітоценозу. Втім, *G. odessanum* проявив еколого-ценотичну пластичність і, упродовж десятиліть, сформував тут стійку гомеостатичну інтродукційну ценопопуляцію. Станом на 2021 р. площа інтродукційної ценопопуляції цього виду становила 2075 м^2. У її складі налічувалось 412 особин *G. odessanum* (40 проростків, 241 ювенільних, 45 імматурних, 40 віргінільних, 45 генеративних та 1 субсенільна). Фрагменти з високою щільністю особин *G. odessanum* траплялися рідко, тому середня щільність була низькою і становила 0,2 особини на 1 м^2. У 2021 р. у спектрі вікових станів загальний відсоток особин прегенеративного періоду онтогенезу був дуже високим і становив 88,8 %, а частка генеративних особин становила 10,9 %.

В цілому, вікова структура інтродукційної ценопопуляції *G. odessanum* характеризується тривалою (2010–2021 рр.) стабільністю. Просторовий розподіл особин в інтродукційній ценопопуляції випадковий та груповий. Це пов'язано з мірмекохорним і барохорним поширенням. Ценопопуляція має тенденцію до подальшого збільшення площі, що обумовлено мірмекохорією. У порівнянні з природними ценопопуляціями, інтродукційна ценопопуляція *G. odessanum* характеризується великою площею, значною кількістю та низькою середньою щільністю особин. Вікові спектри, як і у більшості природних популяцій, є лівосторонніми.

Проведені дослідження свідчать про успішне формування інтродукційної ценопопуляції *G. odessanum* в лучно-степовому культур-фітоценозі НБС. Ця інтродукційна ценопопуляція є вдалим багаторічним науковим експериментом та представляє собою приклад ефективної *ex situ* охорони та збереження *G. odessanum* на північній межі Правобережного Лісостепу України, далеко за межами природного ареалу цього ендемічного виду.

Ключові слова: *Gymnospermium odessanum*, раритетний ендемічний вид, інтродукційна ценопопуляція, стабільна вікова структура, охорона *ex situ*