

## Morphological Variability of *Nitraria* Species in Central and Southern Kazakhstan

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**Abstract**—The variability of metric traits has been studied in 20 Kazakhstan populations of three *Nitraria* species (*N. schoberi* L., *N. sibirica* Pall., and *N. komarovii* Iljin & Lava ex Bobrov). According to the results, *N. sibirica* differs from *N. schoberi* and *N. komarovii* in small leaves, fruits, and seeds, as well as in the structural features of inflorescences and flowers. *N. sibirica* is characterized by a greater number of flowers per inflorescence (25–66 on average) than *N. schoberi* and *N. komarovii* (14–28 on average). Additionally, *N. sibirica* differs from *N. schoberi* by narrower ( $1.3\times$ ) petals and smaller anthers ( $1.46\times$  in length and  $1.2\times$  in width) and pistils ( $1.25\times$  in length and  $1.44\times$  in width). *N. komarovii* differs from *N. schoberi* by narrower leaves ( $1.7\times$ ). *N. komarovii* is characterized by relatively large (especially in width) size of anthers that, together with smaller petals, makes it possible to distinguish this species during flowering. Flowers of *N. komarovii* are bright yellow, while those in *N. schoberi* and *N. sibirica* are white and light purple, respectively. *N. komarovii* fruits are orange, pale red, or bright red. Fruits of *N. schoberi* and *N. sibirica* are dark burgundy and black, respectively. At the intraspecific level, most of the studied metric traits (except for the habitus of *N. sibirica* plants) are stable and do not depend on the 16 climatic parameters of plant habitats. At the same time, a number of morphological features have been revealed in *N. sibirica* plants from the Ili Depression. In these populations, *N. sibirica* plants form shrubs up to 1.8 m in height with a large (up to 90) number of flowers per inflorescence, large petals (3.5 mm in length and 2.2 mm in width on average), small ( $\sim 0.6$  mm) anthers, small (5–5.5 mm in length) fruits, and small ( $\sim 4$  mm in length) narrow ovate stones. These features indicate the ecological–geographical differentiation of *N. sibirica* under the extra-arid conditions of the stony desert of the depression and evidence a separate taxonomic rank of these populations.

**Keywords:** *Nitraria sibirica*, *Nitraria schoberi*, *Nitraria komarovii*, Kazakhstan, intraspecific variability, interspecific differences, leaf, seed, petal, habitus

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### INTRODUCTION

The genus *Nitraria* L. consists of  $\sim 10$  species of halophytic shrubs from steppe, semidesert and desert regions of Asia, North Africa, Southeastern Europe (Romania), and Australia. Despite the smallness of the genus, scientists have no clear ideas about the number, chorology, or genesis of *Nitraria* species. Insignificant differences in the metrical traits of vegetative and generative organs serve as a reason for some authors to recognize extreme variants as independent species, while others consider them intraspecific forms or ecological races (Ilyin, 1944; Bobrov, 1946, 1965; Lukanenkova, 1964; Petrov, 1972; Vasilyeva, 1974).

Only two *Nitraria* species, *N. schoberi* L. and *N. sibirica* Pall., are mentioned in the special literature for the studied region (Pavlov, 1963; Abdulina, 1998; Baitenov, 1999, 2001). Petrov (1972) describes *Nitraria roborowskii* Kom. from Central and Middle Asia. According to the opinion of this author, this species is

rather widespread and grows together with *N. schoberi*. In our earlier study of the Balkhash-Alakol depression, we first discovered *N. komarovii* Iljin & Lava ex Bobrov on the territory of Kazakhstan (Tomoshevich et al., 2019).

*N. komarovii* is considered a relatively young modification of *N. schoberi* under halophilic conditions of the Caspian littoral (Ilyin, 1958; Bobrov, 1965). However, M.P. Petrov (1972) states that similar processes occur in other ecologically similar habitats located on the coasts of large saline Asiatic lakes. In connection with this, in his opinion, narrow-leaved forms identified as *N. komarovii* should be considered as a form of *N. schoberi* f. *komarovii* (Iljin & Lava) Petrov instead.

According to E.G. Bobrov (1965), *N. roborowskii* Kom. described by V.L. Komarov (1908) and differing from *N. schoberi* by greater leaves, inflorescences, and drupes, is an ecological form of *N. sibirica* (*N. sibirica* f. *majus*). He suggested considering the increased size of

vegetative and generative organs of this plant as a gigantism under favorable ecological conditions (moist clay-alkaline soil of oases, lake shores, and dry sandy reedbeds).

To understand the processes occurring in natural populations and to analyze taxonomic diversity, one should study the variability of organisms, because the number of species can be increased via their geographic variability (Gall and Popov, 1998). Morphological variability can result from uninheritable changes of traits caused by the variability of environmental conditions or from the process of evolutionary transformation of living things (Lukin, 1940; Mayr, 1974).

The purpose of the study was to investigate the variability of morphological traits in plants from the genus *Nitraria* to identify the environmental component of this variability and clarify their taxonomic rank.

## MATERIALS AND METHODS

Specimens of *N. sibirica* (nine habitats), *N. schoberi* (10 habitats), and *N. komarovii* were collected in 2012–2017 during field trips arranged on the territory of the Republic of Kazakhstan. For each population of plants, 25–30 herbarium sheets were collected, as well as specimens of flowers, fruits, and seeds, which were put into paper bags, marked, and delivered to the Novosibirsk laboratory for the morphometric analysis.

All samples collected during field trips were deposited in the NSC collection of the Central Siberian botanical garden of the Siberian branch of the Russian Academy of Sciences (Novosibirsk, Russia); they are also available in the digital herbarium of this botanical garden.

A comparative morphological analysis was carried out by the method used for studying the intraspecific variability of woody plants and developed by S.A. Mamaev (1972, 1975). Leaves, flowers, and fruits were measured using a Carl Zeiss Stereo Discovery V12 microscope equipped with a high-resolution Axio Cam digital camera. The images were obtained, treated, and analyzed using AxioVision v. 4.8 software. Morphological measurements of vegetative and generative plant parts were performed in 30 replications using a SIAMS Photolab program and a SIAMS MesoPlant module.

The analysis of climatic characteristics of *Nitraria* habitats included 16 parameters: average monthly temperatures in May, July, and January; annual air temperature amplitude; Conrad's index; frost-free period; average maximum and minimum of annual temperatures; number of days per year with  $T > 5^{\circ}\text{C}$ ; number of days per year with  $T > 10^{\circ}\text{C}$ ; sum of air temperatures for the period with  $T > 5^{\circ}\text{C}$ ; sum of air temperatures for the period with  $T > 10^{\circ}\text{C}$ ; annual precipitation, mm; precipitation–evaporation ratio; precipitations during April–October period; and air saturation insufficiency.

The similarity or difference between the objects (habitats or populations) was determined by a cluster

analysis (Ward's method) using Euclidean distance as a measure of similarity.

## RESULTS

### *Morphological Variability of N. schoberi*

*N. schoberi* typically represents loose sprawling shrubs with arcuate stems and sparse large thorns. In most populations, plant height varied within 60–80 cm. Specimens with a greater height (up to 1–1.2 m) were reported for the Koktal and Basshi populations. The length of *N. schoberi* leaf in the studied populations varied from 2 to 4 cm, with an average value of 2.5–3 cm (Table 2). The smallest leaves were observed in *N. schoberi* plants belonging to the Aidarly, Basshi, and Koktal populations; their average length was ~2 cm. The leaf coefficient values varied from 0.14 to 0.26; the widest leaf part was localized above its middle. Thus, *N. schoberi* is characterized by oblong–spatulate and oblanceolate leaves (Fig. 1). Leaves of plants from the Aidarly population were linear–spatulate.

The number of flowers in *N. schoberi* inflorescences varied from 10 to 32; an increased value of this parameter (25 on average) was observed in southern populations, such as Saryozek, Basshi, Koktal, and Charyn (Figs. 2, 3). The internode length in *N. schoberi* inflorescences varied within 3.5–4.5 mm. The longest internodes (up to 10.7 mm) were observed in the Basshi population.

Petals in *N. schoberi* were ovate or (rarely) diamond-shaped, with short claws (Ak-Lama et al., 2017) (Fig. 4). The petal length varied from 3 to 4.5 mm (Table 3).

Fruits were dark-red or (rarely) black (Alakol, Lepsey, and Raz'ezd\_47), but could also be bright burgundy (Saryozek). The juice had a pale burgundy or pale pink color. The juice color significantly correlated with the peel color. Fruits were widely oval and usually did not exceed 1 cm in length and 7–8 mm in diameter. The weight of 100 stone varied from 220 to 440 g. The stone length in *N. schoberi* varied between 7 and 10 mm, being 8–9.5 mm on average. The stone width was 4.5–5.5 mm. In all studied *N. schoberi* populations, stones were ovate (Fig. 5).

### *Morphological Variability of N. komarovii*

The height and diameter of *N. komarovii* plants were 0.5–1 and 1.5–3 m, respectively. Shrubs were strongly branched from the base, shoots with relatively sparse thorns were slightly bent and elevated in the central part. The length and width of leaves were 2.5–3 and 0.3 cm, respectively. The leaf coefficient was 0.08–0.13.

The number of flowers per inflorescence varied from 17 to 30 (25 on average). The internode length in inflorescences varied within 4–7 mm (5.5 mm on aver-

**Table 1.** Collection sites of specimens from the genus *Nitraria*

Population name	Collection site	Voucher specimen number
<i>N. schoberi</i>		
Aidarli ( <i>N. schoberi</i> _Aidarly)	Kazakhstan, Almaty Region, Zhambyl District, village of Aidarli, 17 km from Aidarli	NSK3000958
Alakol ( <i>N. schoberi</i> _Alakol)	Kazakhstan, Zhambyl Region, Moyinkum District, shore of Lake Alakol	NSK3000964 NSK3000965 NSK3000942 NSK3000943
Balkhash ( <i>N. schoberi</i> _Balkhash)	Kazakhstan, Almaty Region, Sarkand District, eastern shore of Lake Balkhash, sandy desert	NSK3000959 NSK3000963 NSK3000948 NSK3000949
Basshi ( <i>N. schoberi</i> _Basshi)	Kazakhstan, Almaty Region, Kerbulak District, outskirts of the village of Basshi	NSK3000998 NSK3000982 NSK3000983
Karatal ( <i>N. schoberi</i> _Karatal)	Kazakhstan, Almaty Region, Karatal District, outskirts of the village of Ushtobe, Karatal River terrace	NSK3000923 NSK3000950 NSK3000951 NSK3000952
Koktal ( <i>N. schoberi</i> _Koktal)	Kazakhstan, Almaty Region, Panfilov District, outskirts of the village of Koktal	NSK3000999
Lepsy ( <i>N. schoberi</i> _Lepsi)	Kazakhstan, Almaty Region, Sarkand District, outskirts of the village of Lepsy, bank of the Lepsy river	NSK3000941 NSK3000997 NSK3000981
Raz'ezd_47 ( <i>N. schoberi</i> _Raz'ezd_47)	Kazakhstan, Almaty Region, Aksu District, outskirts of the village of Molaly	NSK3000944
Saryozek ( <i>N. schoberi</i> _Sariozek)	Kazakhstan, Almaty Region, Koksus District, 30 km to the north of the village of Saryozek	NSK3000995 NSK3000986 NSK3000969 NSK3000945 NSK3000946 NSK3000947
Charyn ( <i>N. schoberi</i> _Charin)	Kazakhstan, Almaty Region, Uigur District, Chunzha village, the Charyn river (10 km from the village of Koktal, beyond the Ili river)	NSK3000955 NSK3000956 NSK3000957
<i>N. sibirica</i>		
Balkhash ( <i>N. sibirica</i> _Balkhash)	Kazakhstan, Almaty Region, Sarkand District, eastern shore of Lake Balkhash, sandy desert	NSK3000921 NSK3001248
Basshi ( <i>N. sibirica</i> _Basshi)	Kazakhstan, Almaty Region, Kerbulak District, outskirts of the village of Basshi	NSK3001277 NSK3001249
Kainar ( <i>N. sibirica</i> _Kainar)	Kazakhstan, Karaganda Region, Karkaralinsk District, Karkaralinsk–Kainar highway, to the east of the village of Sholak-kayin	NSK3000918
Karatal ( <i>N. sibirica</i> _Karatal)	Kazakhstan, Almaty Region, Karatal District, outskirts of the village of Ushtobe, Karatal River terrace	NSK3000922 NSK3001272
Koktal ( <i>N. sibirica</i> _Koktal)	Kazakhstan, Almaty Region, Panfilov District, outskirts of the village of Koktal	NSK3000989 NSK3001236
Kurgan ( <i>N. sibirica</i> _Kurgan)	Kazakhstan, Karaganda Region, Karkaralinsk District, to the south of the village of Aybyz, burial mound	NSK3001285
Kurti ( <i>N. sibirica</i> _Kurti)	Kazakhstan, Almaty Region, Ili District, to the north of the village of Kurti, bank of the Kurti River	NSK3000990 NSK3001275 NSK3001241

**Table 1.** (Contd.)

Population name	Collection site	Voucher specimen number
Matai ( <i>N. sibirica</i> _Matai)	Kazakhstan, Almaty Region, Aksu District, Motai–Taldykorgan highway, outskirts of the village of Koltaban	NSK3001273
Taskarasu ( <i>N. sibirica</i> _Taskarasu)	Kazakhstan, Almaty Region, Uigur District, outskirts of the village of Taskarasu	NSK3001244
<i>N. komarovii</i>		
Balkhash ( <i>N. komarovii</i> _Balkhash)	Kazakhstan, Almaty Region, Sarkand District, eastern shore of Lake Balkhash, sandy desert	NSK3000920 NSK3000926 NSK3000927 NSK3000920

**Table 2.** Variability of leaf, inflorescence, and seed traits in plants from the genus *Nitraria*

Population	Leaf length, mm	Leaf width, mm	Number of flowers per inflorescence	Internode length in an inflorescence, mm	Stone length, mm	Stone width, mm
<i>N. schoberi</i>						
Alakol	30.89 ± 0.70	5.44 ± 0.15	21.40 ± 0.98	5.8 ± 1.3	8.5 ± 0.19	4 ± 0.07
Balkhash	24.80 ± 0.52	5.30 ± 0.12	16.00 ± 3.03	6.0 ± 1.5	9.03 ± 0.18	5.40 ± 0.13
Lepsy	23.50 ± 0.96	5.50 ± 0.15	13.80 ± 2.20	3.8 ± 0.5	9.68 ± 0.12	4.87 ± 0.11
Karatal	30.40 ± 0.73	5.73 ± 0.12	17.50 ± 2.50	4.5 ± 0.5	8.95 ± 0.21	5.49 ± 0.13
Raz'ezd_47	26.75 ± 0.46	5.50 ± 0.11	27 ± 2.58	3.7 ± 0.4	7.4 ± 0.16	3.6 ± 0.10
Aidarly	22.10 ± 0.20	4.2 ± 0.12	18.80 ± 1.69	4.4 ± 0.5	7.1 ± 0.17	3.7 ± 0.09
Saryozek	25.25 ± 0.34	4.75 ± 0.08	24.75 ± 2.87	3.8 ± 0.8	8.62 ± 0.07	5.36 ± 0.09
Basshi	22.40 ± 0.49	4.70 ± 0.13	24.00 ± 1.61	10.7 ± 3.0	9.60 ± 0.14	4.97 ± 0.06
Koktal	22.20 ± 0.53	5.40 ± 0.18	27.50 ± 2.38	4.5 ± 0.5	8.59 ± 0.16	5.51 ± 0.10
Charyn	27.50 ± 0.46	6.17 ± 0.21	23.00 ± 1.79	4.6 ± 0.9	8.24 ± 0.15	4.95 ± 0.08
<i>N. sibirica</i>						
Balkhash	14.54 ± 0.55	3.83 ± 0.27	30.25 ± 3.82	2.5 ± 0.4	5.41 ± 0.11	2.79 ± 0.04
Basshi	16.50 ± 0.53	4.11 ± 0.11	42.80 ± 2.15	5.0 ± 1.5	4.21 ± 0.08	2.21 ± 0.04
Karatal	15.11 ± 0.41	4.06 ± 0.26	31.25 ± 4.27	5.3 ± 0.6	5.70 ± 0.11	2.64 ± 0.05
Koktal	14.75 ± 0.35	3.06 ± 0.09	66.40 ± 7.14	3.8 ± 0.8	4.44 ± 0.12	2.33 ± 0.05
Kurti	15.11 ± 0.48	4.28 ± 0.22	32 ± 3.03	3.8 ± 0.5	4.61 ± 0.06	2.05 ± 0.04
Matai	15.11 ± 0.48	4.11 ± 0.27	27.00 ± 3.49	5.8 ± 0.9	6.16 ± 0.09	3.14 ± 0.03
Taskarasu	14.00 ± 0.56	3.17 ± 0.18	25.00 ± 4.00	2.8 ± 0.5	4.61 ± 0.07	2.61 ± 0.05
Kurgan	10.35 ± 0.35	3.82 ± 0.21	25.70 ± 3.21	3.7 ± 0.3	5.75 ± 0.09	2.8 ± 0.05
Kainar	10.2 ± 0.39	3.98 ± 0.19	15 ± 2.30	3.1 ± 0.3	5.35 ± 0.08	2.4 ± 0.03
<i>N. komarovii</i>						
Balkhash	27.00 ± 0.50	2.83 ± 0.14	24.75 ± 2.49	5.5 ± 1.3	9.89 ± 0.18	5.39 ± 0.16

age). Petals were ovate; their average length and width were 3 and 2 mm, respectively.

Fruits were orange, pale red, or bright red, with a light pink juice. The weight of 100 stone varied between 370 and 530 g. Stones had a prolate–conical form with a typical tapered top; their length and width were 9–11 and 5–7 mm, respectively.

#### *Morphological Variability of N. sibirica*

*N. sibirica* had a variable habitus and was characterized by very thorny semibent shoots elevated in the central part of a shrub.

The leaf length varied slightly, being 1.0–1.5 cm on average. The smallest leaves were observed in the



**Fig. 1.** Leaf shape in *N. schoberi*: (a) Aidarly and (b) Balkhash.



**Fig. 2.** Features of inflorescence structure in *N. schoberi*: (a) Balkhash, (b) Basshi, and (c) Lepsy.



**Fig. 3.** Grouping of *N. schoberi* populations according to the number of flowers per inflorescence.

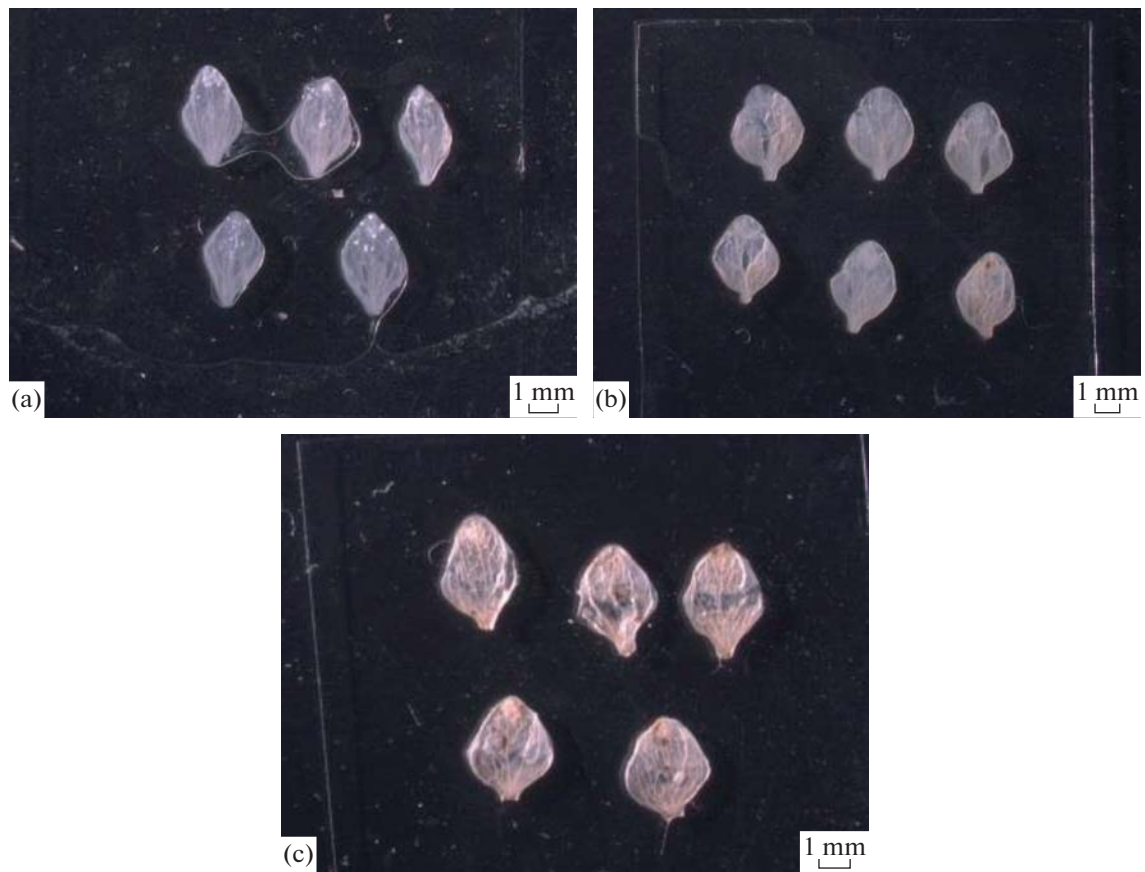


Fig. 4. Variability of petals in *N. schoberi*: (a) Charyn, (b) Basshi, and (c) Karatal.

Table 3. Individual variability of flowers in *Nitraria* plants

Population	Petal length, mm	Petal width, mm	Pistil length, mm	Ovary width, mm	Stamen length, mm	Stamen filament length, mm	Anther length, mm	Anther width, mm
<i>N. schoberi</i>								
Balkhash	3.76 ± 0.03	2.84 ± 0.04	4.04 ± 0.15	1.98 ± 0.13	3.27 ± 0.03	2.07 ± 0.03	1.32 ± 0.01	0.57 ± 0.01
Karatal	3.74 ± 0.03	2.75 ± 0.03	3.84 ± 0.13	1.84 ± 0.02	3.25 ± 0.04	2.00 ± 0.04	1.37 ± 0.03	0.74 ± 0.01
Lepsey	3.48 ± 0.03	2.66 ± 0.04	3.66 ± 0.10	1.58 ± 0.05	3.42 ± 0.07	2.31 ± 0.07	1.18 ± 0.02	0.58 ± 0.01
Saryozek	3.38 ± 0.03	2.36 ± 0.03	3.24 ± 0.05	1.68 ± 0.04	2.68 ± 0.06	1.93 ± 0.06	0.78 ± 0.01	0.46 ± 0.01
Basshi	4.04 ± 0.04	2.86 ± 0.03	—	—	—	—	—	—
Charyn	3.78 ± 0.05	2.31 ± 0.04	—	—	—	—	—	—
<i>N. sibirica</i>								
Balkhash	3.13 ± 0.03	1.74 ± 0.03	2.48 ± 0.09	1.13 ± 0.06	2.80 ± 0.02	1.85 ± 0.02	1.02 ± 0.01	0.50 ± 0.01
Kurti	3.39 ± 0.04	1.87 ± 0.03	2.87 ± 0.15	1.21 ± 0.20	3.06 ± 0.05	2.25 ± 0.04	0.85 ± 0.01	0.52 ± 0.01
Taskarasu	3.06 ± 0.02	1.78 ± 0.04	2.68 ± 0.04	1.04 ± 0.02	2.67 ± 0.03	1.94 ± 0.03	0.77 ± 0.01	0.51 ± 0.01
Karatal	3.55 ± 0.04	2.34 ± 0.04	3.29 ± 0.07	1.48 ± 0.04	3.16 ± 0.05	2.57 ± 0.05	0.62 ± 0.01	0.46 ± 0.01
Basshi	3.41 ± 0.04	2.20 ± 0.04	—	—	—	—	—	—
Koktal	3.50 ± 0.02	2.17 ± 0.03	—	—	—	—	—	—
<i>N. komarovii</i>								
Balkhash	2.97 ± 0.05	2.03 ± 0.04	2.40 ± 0.04	1.29 ± 0.05	2.70 ± 0.03	1.64 ± 0.02	1.29 ± 0.01	0.69 ± 0.01



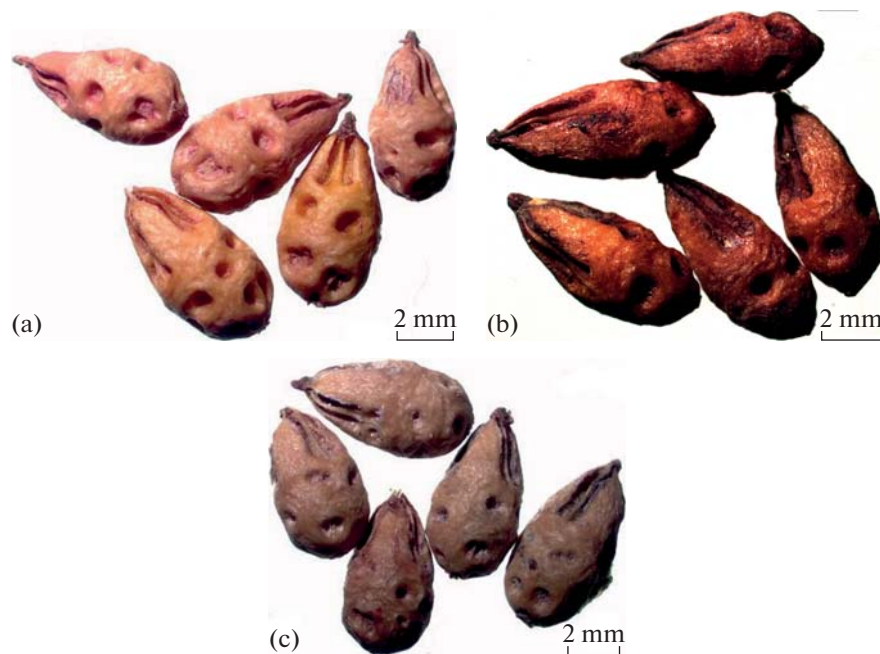


Fig. 5. Variability of *N. schoberi* seeds: (a) Balkhash, (b) Lepsy, and (c) Saryozek.

northern Kainar and Kurgan populations (Table 2). The leaf coefficient varied within 0.2–0.33; the widest part of the leaf was located above its middle, so *N. sibirica* leaves can be considered oblanceolate.

The maximum number of flowers per inflorescence (up to 90) was observed in *N. sibirica* populations localized in the Ili depression (Koktal and Basshi; Fig. 6), whereas the typical average value of this parameter in this species was 25–30.

Petals were acuminate–elliptic; diamond-shaped and ovate petals were observed in some plants of the Basshi, Karatal, and Koktal populations (Fig. 7). The petal length varied from 2.5 to 4 mm. In three above-mentioned populations, petals had a greater size (3.4–3.5 mm on average; Table 3), while in the Balkhash and Taskarasu populations, the average value of this parameter was ~3.1 mm.

Ripe fruits of *N. sibirica* were always black; in the ripening period, they had a bright red color. The juice of ripe fruits was dark blue; the only exclusions were the Karatal and Kurti populations, in which we observed blackish green and light black juice of fruits, respectively. *N. sibirica* fruits were rounded (~5 mm in diameter). Small stone (4–6 mm) were observed in the Basshi and Karatal populations, while the largest ones (9 mm) were registered in the Matai population. The weight of 100 stone in the Matai population was 200–270 g; in the Basshi population, it was 50–80 g. In other populations, the value of this parameter varied within 100–200 g.

Small and narrow ovate stones with a narrow pointed tip were typical for the Basshi, Koktal, Kurti, and Taskarasu populations of *N. sibirica*. Greater ovate

stones were observed in the Balkhash, Karatal, and Matai populations (Fig. 8).

## DISCUSSION

An analysis of the data confirmed morphological differences between *N. sibirica*, *N. schoberi*, and *N. komarovii* (Banaev et al., 2017). *N. sibirica* was put into a separate cluster (Fig. 9) as a small-leaved and small-fruited species. In addition, *N. sibirica* differs from *N. schoberi* and *N. komarovii* in some details of the inflorescence structure. *N. sibirica* is characterized by a greater number of flowers per inflorescence (25–66 on average) compared to *N. schoberi* and *N. komarovii* (14–28 on average). Additionally, *N. sibirica* differs from *N. schoberi* by narrower (1.3-fold) petals, as well as smaller anthers (1.46-fold in length and 1.2-fold in width) and pistils (1.25-fold in length and 1.44-fold in width).

*N. komarovii* differs from *N. schoberi* by narrower leaves (1.7-fold); the leaf width in *N. schoberi* is ~5 mm on average, while that in *N. komarovii* is equal to 3 mm (Fig. 10). Leaves of both *N. schoberi* and *N. sibirica* are oblanceolate or oblong–spatulate with a blunt or slightly pointed apex. *N. komarovii* leaves are characterized by linear or sometimes linear–spatulate leaves with a sharply pointed, sometimes weakly pronounced, apex.

*N. komarovii* has a smaller length of the stamen (<3.5 mm) and stamen filament (<2 mm); at the same time, the length of the stamen, stamen filament, and anther in *N. schoberi* and *N. sibirica* reaches 4, 3, and almost 2 mm, respectively. At the same time, the

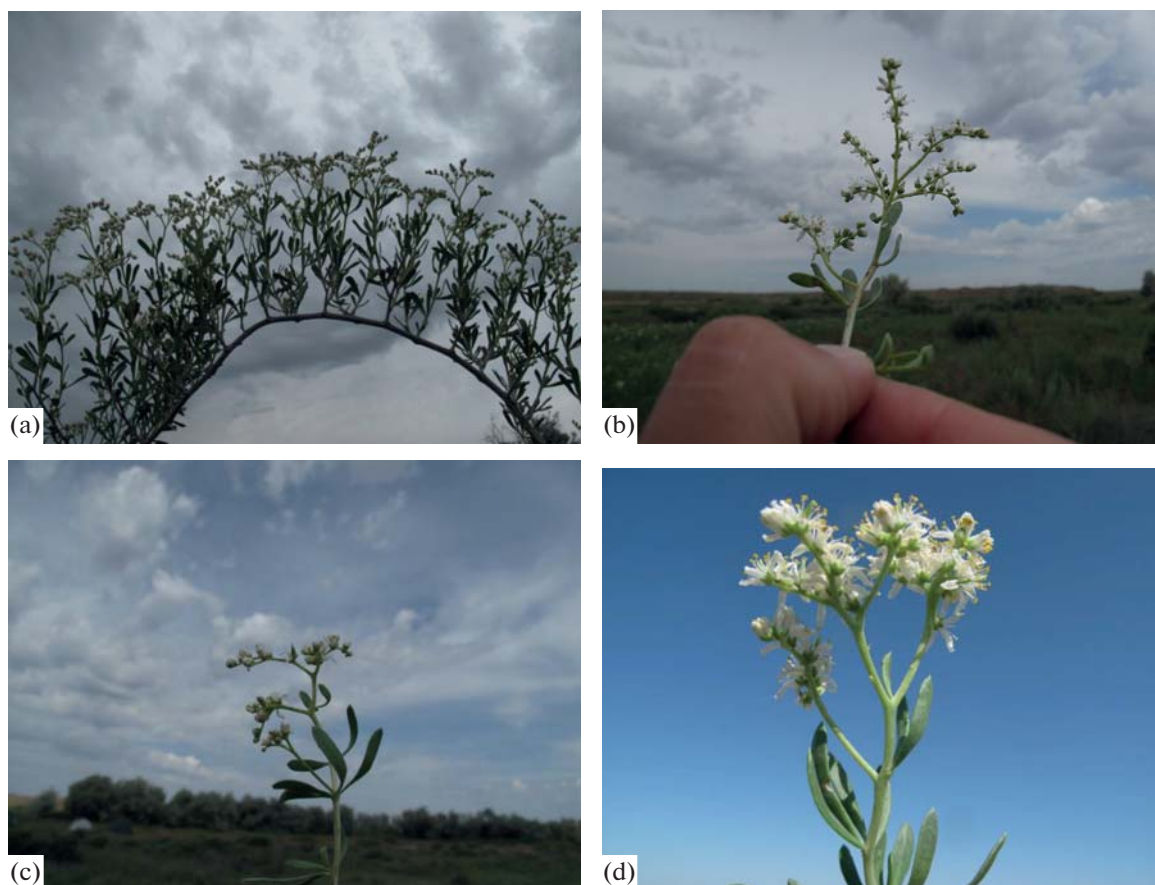


Fig. 6. Structure of the *N. sibirica* inflorescence: (a, b) Koktal, (c) Kurti, and (d) Matai.

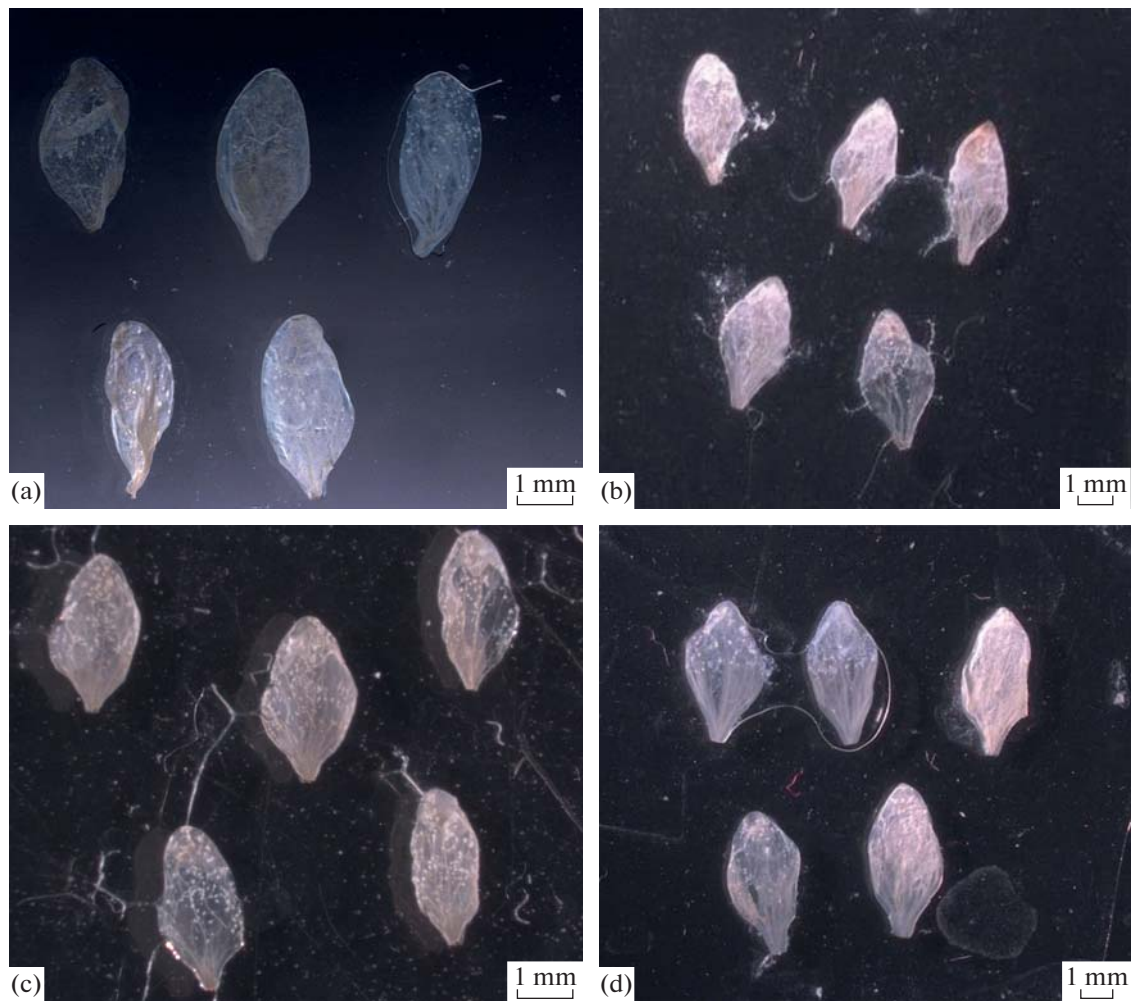
anthers of *N. komarovii* are relatively large (especially in width). This phenomenon, together with smaller petals, makes it possible to distinguish this species during flowering. Flowers of *N. komarovii* look bright yellow, while those of *N. schoberi* and *N. sibirica* are white and light purple, respectively. *N. schoberi* is characterized by the largest pistils (2.5–4.7 mm in length and 1.3–2.3 mm in width). The pistils of *N. sibirica* and *N. komarovii* flowers rarely exceed 3.5 mm in length and 1.8 mm in width.

Analyzing the connection between metric traits of plants and ecological–geographical parameters of their habitats, one should mention a high stability of such traits that agrees with our earlier observations of *N. sibirica* populations from Siberia (Banaev et al., 2017). In the case of *N. schoberi*, a weak correlation with climatic factors was observed only for leaf parameters. Smaller leaves were observed in *N. schoberi* plants from the Aidarly, Basshi, and Koktal populations, the habitats of which are characterized by a low precipitation–evaporation ratio (0.15–0.17), a high sum of positive air temperatures (for  $T > 5^{\circ}\text{C}$  it exceeds 3800, for  $T > 10^{\circ}\text{C}$  it exceeds 3500), and highly insufficient air saturation (8.4–9.7). Metric traits of *N. schoberi* vegetative organs are also influenced by microconditions

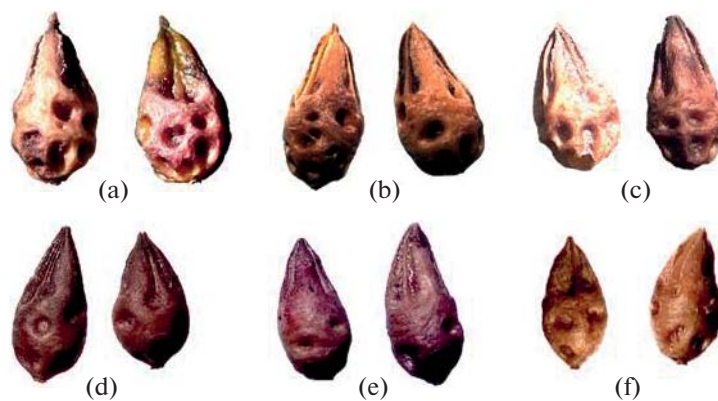
of their habitats, mainly by the groundwater availability. The Alakol population is located in the close vicinity of Lake Alakol. In Karatal and Charyn populations, *N. schoberi* plants grow on river terraces. Saryozek and Raz’ezd 47 populations are located on territories characterized by a high groundwater level or waterway presence. At the same time, the Aydarly population is located on the Bozoi plateau, at the roadside, where only temporary spring underflooding with meltwater occurs. Basshi and Koktal populations are located at an altitude of  $>1000$  m above sea level, in a stony desert with over-arid soils similar to the soils of Mongolian hamadas (Evstifeev and Rachkovskaya, 1976; Nasyrov and Sokolov, 1998).

However, the effect of habitat conditions on the metric traits of vegetative and generative organs of *N. schoberi* is insignificant. These traits are also stable over the species range. For example, in Western Siberian populations of *N. schoberi*, the leaf length is comparable or sometimes slightly smaller ( $\sim 2$  cm) than those in Kazakh populations (Banaev et al., 2017). At the same time, sums of positive air temperatures ( $T > 5^{\circ}\text{C}$  and  $T > 10^{\circ}\text{C}$ ) at the eastern border of the species range are significantly (by  $1400^{\circ}\text{C}$ ) lower than those in Kazakhstan.





**Fig. 7.** Variability of petals in *N. sibirica*: (a) Balkhash, (b) Kurti, (c) Taskarasu, and (d) Karatal.



**Fig. 8.** Individual variability of *N. sibirica* seeds: (a) Balkhash, (b) Karatal, (c) Matai, (d) Basshi, (e) Koktal, and (f) Kurti.

Since the Aral–Caspian basin is considered the center of origin of *N. schoberi*, from which the species spread to the south and east into Central Asia and Western Siberia (Bobrov, 1946), one could expect an appearance of extreme morphotypes in the island

populations located at the border of the species range (Kulunda steppe). However, according to Komarov (1908), “the variability of *N. schoberi* is great, but poorly oriented” (p. 165) in the geographic sense. This is explained by the fact that *Nitraria* species are con-

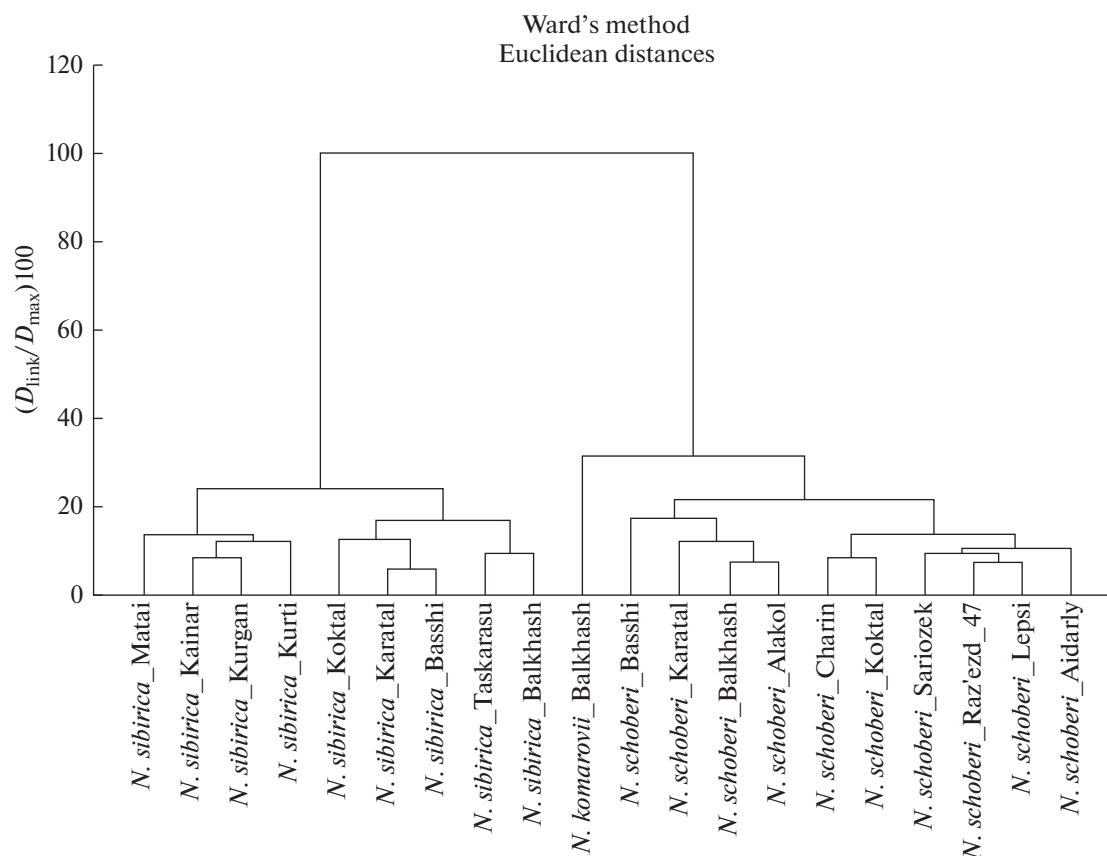


Fig. 9. Population similarity dendrogram for *Nitraria* species.

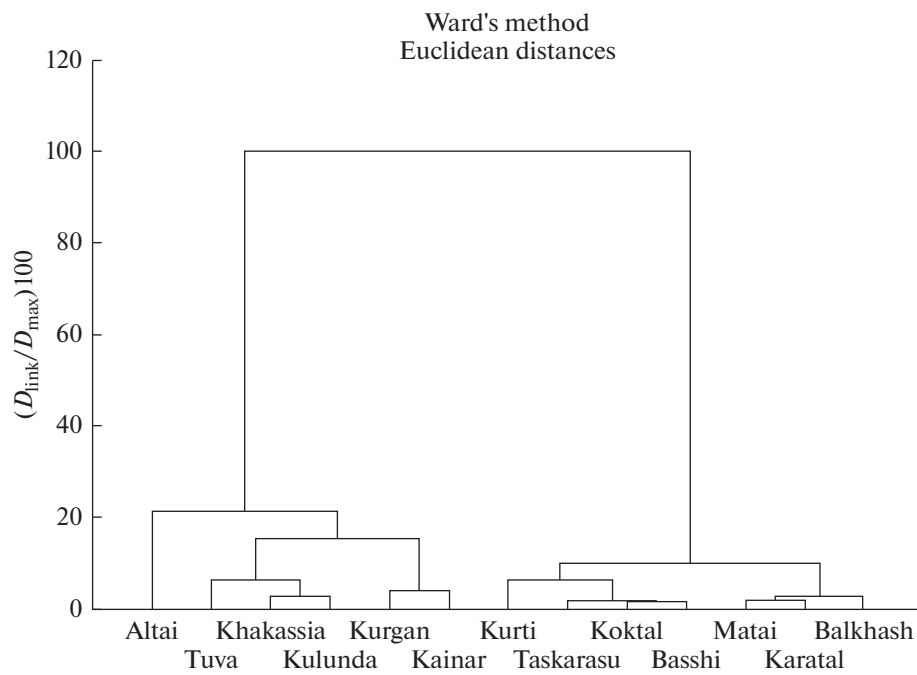


Fig. 10. Leaf variability in *Nitraria* species: (a) *N. komarovii*, (b) *N. shoberi*, and (c) *N. sibirica*.

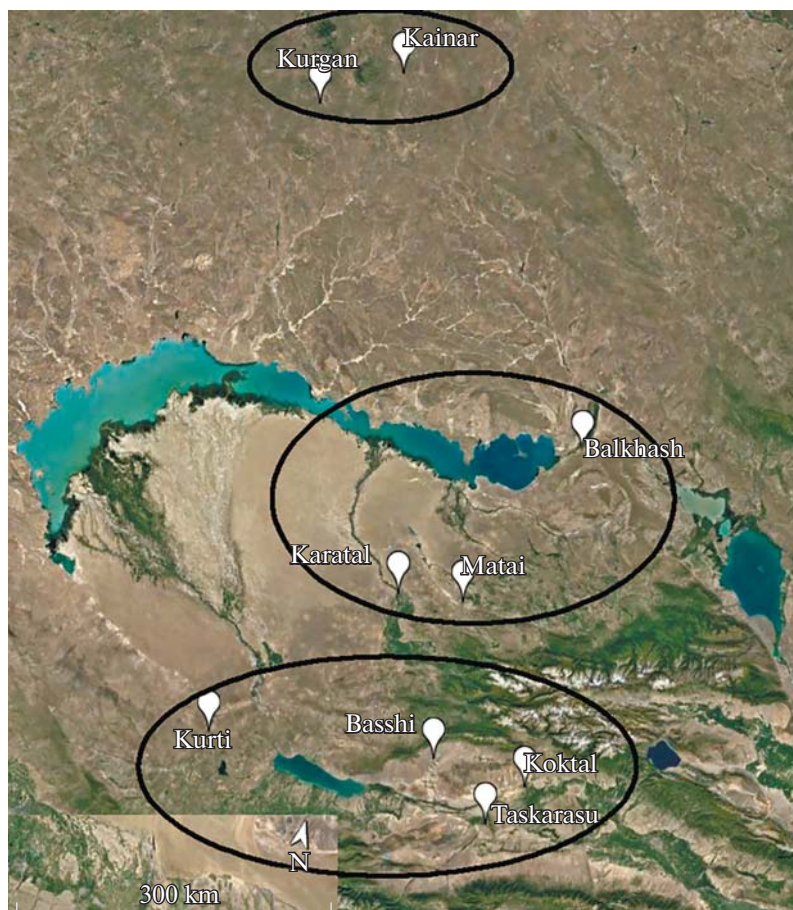
finned to local intrazonal habitats and can survive only under a combination of necessary soil and ground parameters, such as soil moisture and salinity (Khudyaev and Banaev, 2012). Both temperature and air humidity are not the main limiting factors for *N. schoberi* and *N. sibirica*. In connection with this, the clinal variability, which is inherent in many species with continuous ranges (Mayr, 1974), such as boreal woody plant species, is not typical for *Nitraria* species

(Banaev, 1997a, 1997b; 2009a, 2009b; Banaev and Shemberg, 2000; Banaev and Adelshin, 2009).

Climatic parameters of habitats influence only on the habitus of *N. sibirica* plants (Figs. 11, 12), as we have shown previously for Siberian populations of this species (Banaev et al., 2017). In Altai and Tyva republics, the height of *N. sibirica* plants does not exceed 20 cm, while the plant height in the Khakassia and Kulunda steppe populations is 50 cm on average. Sim-



**Fig. 11.** Dendrogram of similarity of *N. sibirica* habitats in 16 climatic parameters of temperature and humidity.



**Fig. 12.** Clustering of *N. sibirica* populations by the shrub habitus.





**Fig. 13.** Habitus of *N. sibirica*: (a) Kainar (up to 50 cm), (b) Matai (up to 70 cm), (c) Kurti (up to 1.4 m), and (d) Koktal (up to 1.8 m).

ilar bushes (about 50 cm in height) were observed in the *N. sibirica* populations of northern Kazakhstan (Kainar and Kurgan). Generative individuals from the Balkhash, Matai, and Karatal populations have a height of 70 cm; plant height in Taskarasu and Kurti populations reached 1.0–1.4 m. The highest *N. sibirica* plants were observed in the Basshi and Koktal districts (their height reached 1.8 m (Fig. 13)).

A number of morphological features was revealed in *N. sibirica* plants from the Ili depression (Basshi, Koktal, and Taskarasu populations). Plants from these populations have a greater number of flowers per inflorescence (up to 90), large petals (3.5 mm in length and 2.2 mm in width on average), small anthers (~0.6 mm), small fruits (5–5.5 mm in length), and small narrow ovate stones (~4 mm in length). In addition, *N. sibirica* plants from the Koktal and Taskarasu populations contain fewer phenolic components compared to those from the northern (Kurgan and Kainar) populations (Ak-Lama, 2020). The revealed features in the composition and content of phenolic compounds in *N. sibirica* plants from the Almaty district of Kazakhstan are confirmed by the results of a comparison of phenolic profiles of *N. sibirica* plants from other regions, including Siberia (Voronkova et al., 2017; 2020). The intraspecific heterogeneity of

*N. sibirica* was also revealed by an analysis of the ITS2 region of nuclear ribosomal DNA (Polyakova et al., 2020; Banaev et al., 2020). All these facts indicate the ecological and geographic differentiation of *N. sibirica* populations.

## CONCLUSIONS

Three species of the genus *Nitraria* (*N. schoberi*, *N. sibirica*, and *N. komarovii*) have been revealed in the Republic of Kazakhstan. *N. komarovii* grows on the Caspian Sea coast, as well as on coastal sands in the southeastern part of Lake Balkhash. *N. komarovii* reliably differs from *N. schoberi* by narrow linear or sometimes linear–spatulate leaves with a sharply pointed or sometimes weakly manifested apex. Additionally, *N. komarovii* is characterized by anthers of a greater size (especially in width), which, together with small petals, allow one to distinguish this species during flowering. Flowers of *N. komarovii* are bright yellow, while those in *N. schoberi* and *N. sibirica* are white and light purple, respectively. Fruits of *N. komarovii* are orange, pale or bright red; fruits of *N. schoberi* are dark burgundy, while in *N. sibirica* they are black.

Most morphometric traits of *N. schoberi* and *N. sibirica* are stable in different parts of their range,

which indicates the low dependence of these parameters on the air temperature and humidity at their habitats. Climatic parameters influence only on the habitus of plants, especially in *N. sibirica*.

The intraspecific differentiation of *N. sibirica* under conditions of the extra arid Ili depression evidences a separate taxonomic rank of these populations.

#### COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflicts of interest. This article does not contain any studies involving animals performed by any of the authors.

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