

Ecological and biological features of *Gentiana septemfida* in the south of Western Siberia

Alexey S. Prokopyev

Siberian Botanical Garden, National Research Tomsk State University, 34/1 Lenina Ave., Tomsk, 634050, Russia

Tatjana N. Kataeva

Siberian Botanical Garden, National Research Tomsk State University, 34/1 Lenina Ave., Tomsk, 634050, Russia

Mikhail S. Yamburov

Siberian Botanical Garden, National Research Tomsk State University, 34/1 Lenina Ave., Tomsk, 634050, Russia

Gentiana septemfida Pall. is a montane species native to the Caucasus, Asia Minor, and Western Siberia. This protected plant species from the Siberian flora has significant medicinal and ornamental value. Field studies were conducted in the forest zone of the West Siberian Plain (Tomsk Region) and in the Altai highlands (Seminsky, Kuraisky and North Chuysky ridges of the Republic of Altai). It was found that the distribution of *G. septemfida* in the southern part of Western Siberia is closely associated with meadow cenoses. In the Altai Mountains, this species occurs near the upper boundary of the forest belt, in forest meadows, open glades, and bushy tundra with alpine and subalpine forbs. In the flat landscape, it is rarely encountered in river valleys among mesophilic tall grass meadows. The studied coenopopulations of *G. septemfida* are characterized as normal type, incomplete, ripening or mature. By morphological features were showed that coenopopulations from Seminsky Ridge and Tomsk Region have the most optimal conditions for plant growth and development. In nature, *G. septemfida* reproduces by seeds. However, in some areas seed productivity significantly reduced due to annual damage of fruits by insect pests. The lowest level of the reproductive potential was in Seminsky Ridge coenopopulation. The assessment of plant introduction in the southern part of the Tomsk Region classified *G. septemfida* as a stable plant. The gene pool established in the Siberian Botanical Garden, Tomsk State University, plays a crucial role in successful conservation of the species in ex situ conditions.

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Corresponding author: Alexey S. Prokopyev (rareplants@list.ru)

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Gentiana septemfida, coenopopulations, phytocoenotic habitat, demographic structure, morphology, reproductive biology, introduction, Republic of Altai, Tomsk Region

Introduction

Gentiana L. is one of the largest genera in the family Gentianaceae. The genus currently comprises 362 species (Ho and Liu 2001) distributed mainly in temperate, arctic and alpine habitats of the northern hemisphere, with only a few species occurring in the southern hemisphere (Grossheim 1952). The greatest diversity of *Gentiana* species is observed in mountain communities of Central Asia (79 species), where they play a significant role in the composition of the vegetation cover of highlands (Grubov 2002). The “Flora of the USSR” (Grossheim 1952) contains 93 species of the genus *Gentiana* s.l., with different interpretations of its scope by authors. The current trend in the systematics of the genus is to subdivide it into smaller taxa and continually refine their numbers and boundaries. For nomenclatural convenience, we adhere to classical understanding of the genus *Gentiana* accepted in the “Flora of the USSR” (Grossheim 1952).

The genus *Gentiana* comprises a number of valuable medicinal plants. One of the European species of this genus, *G. lutea*, is used in traditional and folk medicine in numerous countries (Allen et al. 2014). Other *Gentiana* species are widely used in folk medicine in Tibet, and China (Veysin 2004; Monographs ... 2012). A pharmacological study of Siberian *Gentiana* species revealed their potential as a source of raw materials for preparations with a wide range of therapeutic effects, including gastrointestinal, anti-inflammatory, wound-healing, choleric, antihelminthic, and anti-fever effects (Galinskaya 1978; Povydysh and Bityukova 2011). The majority of *Gentiana* species display outstanding ornamental features. Many relict and endemic species are found among *Gentiana* plants confined to highlands. Some of them show scarce, rare and very limited distribution. Therefore, *Gentiana* species are protected in most countries. In Europe, all *Gentiana* species native to Alpine highlands are protected (Hegi 1977; Allen et al. 2014). Wild plants *G. lagodechiana* and *G. paradoxa* are among the most beautiful flowers of the Caucasian flora (Kozlov 2023). In most cases, less abundant species are protected throughout their range. Widespread species (*G. cruciata*, *G. pneumonanthe*, *G. septemfida*, etc.) are typically protected at the local level.

The study of the biology and ecology of rare species that exhibit beneficial properties is of great theoretical and practical relevance for understanding their distribution and stability in natural phytocoenoses. This, in turn, helps to address issues related to biodiversity conservation and prospects for practical use of plants in various sectors of the economy.

Nowadays, the biological characteristics of rare and economically valuable species in *Gentiana* genus are actively studied in Russia and other countries. A significant part of the work is devoted to the study of natural populations of *Gentiana* species (Sirotyuk et al. 2016; Adams and Thompson 2017; Borovik and Revushkin 2018; Sirotyuk 2019) and the prospects for their practical use (Kataeva and Prokopyev 2017; Olennikov et al. 2019; Ponticelli 2023; Hou et al. 2022a). Some studies are devoted to the reproductive biology of species (Kozuharova et al. 2008; Cuenca-Lombraña et al. 2016; Hou et al. 2022b), micropropagation of the most valuable species (Devic et al. 2006; Huang et al. 2014), distribution and biodiversity conservation of Gentianaceae species in certain regions (Sirotyuk et al. 2015; Wai et al. 2024). The taxonomy of the genus *Gentiana* also remains relevant (Struwe and Albert 2002; Revushkin and Borovik 2019; Chen et al. 2024).

The aim of this work was to study *Gentiana septemfida* biological features in the southern part of Western Siberia and assessment of the success of species introduction in the Siberian Botanical Garden of Tomsk State University (SibBG TSU).

Materials and methods

Gentiana septemfida Pall. (= *Dasystephana septemfida* (Pall.) Zuev.) is a herbaceous perennial with short rhizomes; shoots elongate, erect, foliose; large dark blue flowers in clusters (Kataeva and Prokopyev 2023) (Fig. 1). This montane species is native to the Caucasus, Asia Minor, and Western

Siberia (Sirotyuk 2016) and exhibits two distinct geographical ranges. The first is the Caucasian range, which encompasses the Caucasus, northern Asia Minor, and northwestern Iran. The second is the Altai range, which extends across the mountain systems of the southern part of Western and Middle Siberia and Eastern Kazakhstan (Tsvelev 1978). In the literature, the Central Asian-South Siberian race of *G. septemfida* often regarded as a distinct species, *G. fischeri* Smirn. (Grubov 2002; Ebel 2012). The World Online (POWO) database indicates that *G. fischeri* is a synonym of *G. dschungarica* Regel. In the “Flora of Siberia” (Zuev 1997) and the “Conspectus of the Flora of Asian Russia” (Baykov 2012), *G. septemfida* and *G. fischeri* are considered synonymous with *Dasystephana septemfida* (Pall.) Zuev. The present study regards the species as *Gentiana septemfida*.

In the Siberian mountains, *G. septemfida* is distributed along the entire vertical profile, extending from the forest to the alpine belt. It is found in forest meadows, glades, cedar and larch sparse forests, highland tundra, and among alpine and subalpine forbs (Zuev 1997; Zykova 2012). The plant is rare in the foothills of the West Siberian Plain (Kolyvan-Tom plateau), where it occurs in forest and floodplain meadows (Ebel 2012). The species is included in some local the Red Data Books of the Siberia (Tomsk region, Republic of Khakassia, Krasnoyarsk and Altai territories).

G. septemfida is a valuable medicinal plant. The aerial part of this species is composed of carbohydrates (genzianose, genziobiose), iridoids (septemphioside, helioside, and others), and flavonoids (glucoluteolin). Experimental evidence indicates that extracts derived from *G. septemfida* stimulate salivation and demonstrate vasodilating and hemostatic effects (Povydysh and Bitjukova 2011).

Field studies were conducted in 2023–2024 in the forest zone of the West Siberian Plain (Tomsk Region) and Altai highlands (Seminsky, Kuraisky and North Chuysky ridges of the Republic of Altai). We investigated four local coenopopulations (CP) of *G. septemfida*: three from the Republic of Altai and one from the Tomsk Region.

The species composition and structure of plant communities that include *G. septemfida* were identified based on geobotanical descriptions and subsequently specified based on herbarium material processing data. The phytocoenotic confinement of *G. septemfida* coenopopulations was determined using conventional geobotanical approaches (Lavrenko and Korchagin 1964). The quantitative abundance of species was estimated using the Drude scale (Drude 1890).



Figure 1. *Gentiana septemfida* (flowering plant)

Population studies were conducted using methods currently employed in contemporary plant population biology (Zlobin et al. 2013; Osmanova and Zhivotovsky 2020; Ishmuratova, 2020).

The ontogenetic stage of the individual was determined based on a set of qualitative morphological and biological characteristics and a biographical portrait of *G. septemfida* proposed by E.L. Nukhimovsky (Nukhimovsky 2002) in the territory of the Kuraisky Ridge as part of a subalpine meadow.

The density and ontogenetic structure of coenopopulations within the communities were studied based on transects divided into 1 m² plots. The total number of individuals per unit area was counted to determine the ecological and effective density of the coenopopulation, and the number of individuals in each ontogenetic group was counted to construct ontogenetic spectra. A morphologically distinct individual served as the counting unit.

The coenopopulation type was determined based on the “delta-omega” ($\Delta\text{-}\omega$) classification system by L.A. Zhivotovsky (Osmanova and Zhivotovsky 2020). In order to identify the demographic structure of the coenopopulation, age and efficiency indices were calculated. Additionally, the renewal index (I_r) was calculated for the analyzed coenopopulations (Zhukova 1995). The completeness (or incompleteness) of the coenopopulation was determined by evaluating the degree of representation of ontogenetic groups within the spectrum. The self-sustaining ability of the coenopopulation was evaluated based on the species capacity to produce viable seeds or vegetative propagules under specific habitat conditions.

The morphological characteristics of *G. septemfida* were primarily investigated through the study of living plants, complemented by herbarium specimens. In each coenopopulation, one generative shoot was collected from 30 generative individuals. On each shoot examined, the following measurements were made: length, number of leaves, foliate, and sizes of leaves, flowers, and inflorescences.

The seasonal rhythm of plant development was studied using the phenological observation method by I. N. Beydeman (1974).

Pollen viability was determined by Alexander staining method (Barykina et al. 2004). Non-viable pollen grains are stained green, while viable pollen grains are stained red.

Seed productivity was studied using the method by T.A. Rabotnov (1960), based on the recommendations of I.V. Vaynagay (1974) and R.E. Levina (1981). The calculated fruits-to-flowers ratio (FFR) was expressed as a percentage. The potential seed production (PSP) and real seed production (RSP) were determined as the mean number of ovules and seeds per generative shoot, respectively. In calculation of RSP, fruits damaged by insect pests were excluded, as they did not produce fully developed seeds. The productivity coefficient (Cp) was calculated as a percentage ratio of RSP to PSP.

The seed morphology was described based on studies by Z.T. Artyushenko (1990) and T.A. Fedotova (2010). The morphological characteristics of seeds, including size, shape, and coloration, were examined using a Leica M165 C stereoscopic microscope. The 1,000-seed weight was determined using an electronic balance (DX-200, A&D, Japan) with a resolution of 0.001 g. A total of 100 seeds were weighed in 4 repetitions in accordance with GOST 34221-2017 “Seeds of Medicinal and Aromatic Crops” (GOST 34221-2017 2017). The weight measurement data were multiplied by 10 and the resulting values were averaged.

Seed germination was studied in laboratory conditions using generally accepted methodology (Ishmuratova and Tkachenko 2009) with our modification. Before germination, some seeds were pretreated with 0.1% gibberellic acid solution for 24 hours or stratified at 0–2 °C for 4 weeks. The treated and untreated seeds were then placed in Petri dishes (in 4 repetitions of 100 each) on moist filter paper and germinated at 20–22 °C with 16/8 light/dark photoperiod. Seed germination was determined during the whole period of seedling emergence (not less than 30 days from the beginning of germination).

The mean value, mean error ($M \pm m$), and coefficient of variation (CV) were calculated for all the analyzed characteristics. The levels of variation were estimated in accordance with the method by G. F. Lakin (1990): CV < 11% indicates low variation, CV = 11–25% indicates average variation, and CV > 25% indicates high variation. The data were statistically processed using the MS Excel 2016 software. The statistical significance of the differences between the populations was determined by one-factor analysis of variance (ANOVA) based on Duncan’s criterion at $p < 0.05$ using Statistica 10.

The biology of *G. septemfida* studied in SibBG TSU enabled assessment of the success of the species introduction in the forest zone of Western Siberia in accordance with the scale developed earlier for rare plants of the natural flora of Siberia (Prokopyev and Chernova 2020).

Results and discussion

Features of distribution and phytocoenotic habitat. In the Altai Mountains, *G. septemfida* was recorded near the upper boundary of forest belt. In the Seminsky Ridge, the upper boundary of the forest is formed by sparse stands of *Pinus sibirica* Du Tour. *Larix sibirica* Ledeb. with *Pinus sibirica* and *Abies sibirica* Ledeb. form dense stands covering the Kuraisky and North Chuysky

ridges. The species is rare in flat areas of the Tomsk Region, and it occurs among mesophilic meadow-forest grasses in the valley of the Tom River. At present, the locality is reliably confirmed only for *G. septemfida*; it grows in the vicinity of the village of Kolarovo, near the Kolarovo Wetlands natural complex (Kataeva and Prokopyev 2023).

CP 1. Bushy tundra with alpine and subalpine grasses surrounded by sparse cedar stands. Seminsky Ridge, Republic of Altai, Ongudai district. Coordinates: 51°02'44.2"N 85°37'15.7"E. Altitude 1,751 m a.s.l.

The shrub layer is composed of *Betula rotundifolia* Spach, *Salix glauca* L., and *S. krylovii* E.L. Wolf, with occasional occurrence of *Pentaphylloides fruticosa* (L.) O. Schwarz, *Lonicera altaica* Pall., and *Cotoneaster uniflorus* Bunge. *Betula humilis* Schrank, undergrowth *Pinus sibirica* and *Larix sibirica* are sporadically recorded. The total projective cover (TPC) of the herbaceous layer shows considerable variation, ranging from 30% in gravelly areas to 80% in grass-covered areas with good moisture and developed soil cover. Grass stands are predominantly low, averaging 15–20 cm, with some species up to 70 cm in height. It develops fragmentarily and exhibits very diverse and rapidly changing species composition, depending on habitat conditions. The habitat of *G. septemfida* located along a dirt road is grass-covered. TPC of the grass stand is 80%. The dominant grasses are *Festuca altaica* Trin., *Poa sibirica* Roshev., *Anthoxanthum odoratum* L., and *Milium effusum* L. Mixed grasses include *Aconitum krylovii* Steinb., *A. septentrionale* Koelle, *Alchemilla vulgaris* L. s. l., *Antennaria dioica* (L.) Gaertn., *Callianthemum sajanense* (Regel) Witasek, *Dracocephalum grandiflorum* L., *Galium boreale* L., *Gentiana grandiflora* Laxm., *G. septemfida*, *Ranunculus propinquus* C.A. Mey., *Sajanella monstrosa* (Willd. ex Spreng.) Soják, *Sanguisorba alpina* Bunge, *Schulzia crinita* (Pall.) Spreng, *Swertia obtusa* Ledeb., *Trifolium lupinaster* L., *Trollius altaicus* C.A. Mey., and *Viola altaica* Ker Gawl. In spring, *Erythronium sibiricum* and *Gentiana algida* contribute to bright colors of the community. The community comprises 47 species of vascular plants. The ground layer exhibits synusia of fruticose lichens and mosses. The area is used as pastureland.

CP 2. Shrubby steppe meadow of subalpine type surrounded by larch forests. Southern macro-slope of the Kuraisky Ridge, Republic of Altai, Kosh-Agach Region, vicinity of Kurai village. Coordinates: 50°12'24.1"N 88°06'28.3"E. Altitude 1,910 m a.s.l.

The shrub layer is not uniform. The most dense thickets with TPC of up to 40% are formed along the meadow periphery. *Betula rotundifolia*, *B. humilis*, and *Pentaphylloides fruticosa* dominate; *Spiraea media* Schmidt, and *Cotoneaster uniflorus* are found less frequently. *Lonicera altaica* and *Ribes altissimum* Turcz. ex Pojark grow closer to the edges of forest plantations. The maximum height of shrubs is 170 cm. The grass stand is low, averaging 35–40 cm in height, with low density of the aerial part and considerable grass cover. TPC of the grass stand is 85–90%. The species composition is notably diverse, comprising not only typical high-mountain species (*Aconitum altaicum* Steinb., *Aegopodium alpestre* Ledeb., *Dracocephalum grandiflorum*, *Trollius altaicus*, *Sajanella monstrosa*, *Swertia obtusa*), but also forest and steppe species from neighboring zones. The dominants are *Alchemilla vulgaris* L. s. l., *Artemisia macrantha* Ledeb., *Bistorta vivipara* (L.) Delarbre, *Bupleurum longifolium* ssp. *aureum* (Fisch. ex Hoffm.) Soó, *B. multinerve* DC, *Carex aterrima* Hoppe, *Festuca ovina* L., *Gentiana septemfida*, *Geranium krylovii* Tzvelev, *Iris ruthenica* Ker Gawl., *Ligularia altaica* DC., and *Seseli condensatum* (L.) Rchb. f. The community comprises 51 species. The area is used as pastureland.

CP 3. Forest meadow with subalpine grasses among cedar-larch forests. Northern macro-slope of the North Chuysky Ridge, Republic of Altai, Kosh-Agach district, road to the Aktru mountaineering camp. Coordinates: 50°06'46.5"N 87°48'13.4"E. Altitude 2,023 m a.s.l.

The shrub layer is not prominent, with *Spiraea media* and small groups of *Pentaphylloides fruticosa* and *Lonicera altaica* sporadically occurring along the edge of the community. The grass stand is largely low (60 cm on average), but dense, with 80–100% TPC. The dominant species are

meadow-forest species with typical plants of high-mountain formations occurring in small numbers and distributed sporadically. The dominants are *Alchemilla vulgaris*, *Bupleurum longifolium* ssp. *aureum*, *Calamagrostis langsdorffii* (Link) Trin., *Chamaenerion angustifolium* (L.) Scop., *Dianthus superbus* L., *Dracocephalum grandiflorum*, *Galium boreale*, *Gentiana septemfida*, *Geranium krylovii*, *Poa sibirica* Roshev., *Thalictrum minus* L., *Thesium repens* Ledeb., *Trollius altaicus*, and *Viola altaica*. The community comprises 37 species. There are lichens on the ground layer.

CP 4. Tall grass meadow on the edge of willow thickets. Tom River valley in flat areas of Western Siberia, Tomsk Region, Kolarovo Wetlands natural complex, vicinity of Kolarovo village. Coordinates: 56°19'31.6"N 84°58'00.3"E. Altitude 77 m a.s.l.

The studied community grows side by side with coastal thickets of *Salix viminalis* L., which separate it from the lake. From the other side, it is adjacent to the plot of cultivated arable land. Tree species *Betula pendula* Roth, *Pinus sylvestris* L., *Salix caprea* L. and shrubs *Rosa acicularis* Lindl., *Lonicera tatarica* L., *Spiraea media* are sporadically found along the edge. Grass cover is dense, with TPC of 85 % to 100 %. The average grass height is 50 cm, and the maximum height attains 170 cm. Abundant plant litter can be found in the ground layer. The dominant grasses include *Dactylis glomerata* L., *Calamagrostis epigeios* (L.) Roth, and *Brachypodium pinnatum* (L.) Beauv., and mixed grasses *Brunnera sibirica* Steven, *Equisetum pratense* Ehrh., *Fragaria viridis* Weston, *Galium boreale*, *Gentiana septemfida*, *Hemerocallis minor* Mill., *Inula salicina* L., *Ligularia glauca* (L.) O. Hoffm., *Thalictrum flavum* L., and *T. simplex* L. The community comprises 55 species.

Thus, the distribution of *G. septemfida* in the southern part of Western Siberia is closely associated with meadow communities. In the Altai Mountains, the species occurs at the upper boundary of the forest belt. It is confined to forest meadows, open glades, and bushy tundra with alpine and subalpine grasses. In the flat land-scape, the species is rarely encountered in river valleys among mesophilic tall grass meadows.

In the studied communities, *G. septemfida* is relatively abundant and sporadically distributed among the herbaceous layer without forming dense clusters. The herbaceous layer of phytocoenoses has a high TPC (80–100 %) and often low due to intensive grazing (CP 1, 2). Meadows with *G. septemfida* exhibit high species diversity and harbor a large number of species from different ecological-coenotic and belt-zonal groups. In Altai, the meadows located at the forest-mountain interface comprise numerous alpine and subalpine species, along with widespread meadow-forest species (CP 1, 3). A cover of bushy lichens and green hyphal mosses often develops on the soil surface. In the areas with sparse forest plantations (the southern macro-slope of the Kuraisky Ridge), high-mountain meadows are adjacent to steppes. As a result, widespread steppe species are found among the studied communities along with high-mountain species (CP 2). In flat areas of Western Siberia, meadows with *G. septemfida* exhibit tall (up to 170 cm) and dense grass stands dominated by forest and meadow species (CP 4).

Structure of coenopopulations. The study of the demographic structure of *G. septemfida* coenopopulations in different ecological and coenotic conditions of the southern part of Western Siberia revealed quite low values of ecological density (1.14–1.35 ind/m²) for this species. Values of effective density (0.85–1.01 ind/m²) insignificantly differ from those of ecological density, as coenopopulations include mainly well-developed virgin and generative individuals that can exert maximum impact on the environment (Table 1).

Generative individuals (g₁–g₃) dominate in the coenopopulations and make up the main proportion (77.8–95.8 %) in CP 2, CP 3, and CP 4. The pre-generative period (j–v) is mainly represented by virginile plants, the proportion of which increases markedly in open subalpine meadows with good moisture (CP 1, 22.7 %). CP 1 is formed by a small number of immature (13.6 %) and juvenile (7.4 %) individuals. The post-generative period (ss–s) is weakly expressed. A small number of subsenile individuals (2.4–3.7 %) are found in CP 2 and CP 4. No senile individuals are found (Table 1).

G. septemfida coenopopulations exhibit a centred ontogenetic spectrum with a maximum participation of mature generative individuals (CP 3) or approaching to the centred spectrum with a maximum participation of young generative individuals (CP 2, 4). However, CP 1 is characterized by a left-sided spectrum formed due to the predominance of young individuals (im-g₁) in the ontogenetic spectrum.

Indicator	CP 1	CP 2	CP 3	CP 4
Ontogenetic stage, %				
j	0	0	0	7.4
im	13.6	0	0	0
v	22.7	9.5	4.2	11.1
g ₁	36.4	47.6	29.1	33.4
g ₂	18.2	33.3	54.2	29.6
g ₃	9.1	7.2	12.5	14.8
ss	0	2.4	0	3.7
s	0	0	0	0
Demographic characteristics				
M, ind./m ²	1.29	1.14	1.14	1.35
Me, ind./m ²	0.85	0.92	1.01	1.00
Ir	0.57	0.11	0.04	0.24
Δ	0.29	0.38	0.45	0.39
ω	0.66	0.81	0.89	0.74
CP type	ripening	mature	mature	mature

Table 1. Distribution of the individuals by ontogenetic stages and demographic characteristics of *G. septemfida* coenopopulations in the territory of the Republic of Altai and Tomsk region

Note: CP – coenopopulation; ontogenetic stage: j – juvenile, im – immature, v – virginile, g₁ – young generative, g₂ – mature generative, g₃ – old generative, ss – subsenile, s – senile; M – ecological density, Me – effective density, Ir – renewal index, Δ – age index, ω – efficiency index, ind./m² – number of individuals per 1 m².

The self-sustaining ability of coenopopulations is assessed using the renewal index (Ir). In coenopopulations with young individuals (CP 1, 4), it can increase significantly. The highest renewal index (0.57) is found in CP 1, with virginile (22.7%) and immature (13.6 %) individuals in its demographic composition. In CP 2 and CP 3, the proportion of young individuals is low, i.e., the reproduction process is less successful and thus the index is markedly reduced (Table 1). It is evidently clear that the reproduction processes in natural coenopopulations of *G. septemfida* are rather complicated. We assume that the main constraints for successful seed reproduction are high level of fruit and seed damage by insect pests (CP 1, 3), considerable grass cover, and large amounts of plant litter that hinder the development of seedlings (CP 3, 4). Sporadic self-seeding is observed only in gravelly areas with low TPC (CP 1).

Thus, in the southern part of Western Siberia, the studied coenopopulations of *G. septemfida* are of normal type, incomplete (not all coenopopulations include individuals of the early stages of ontogenesis), and the post-generative period is not evident. According to the ‘delta-omega’ (Δ-ω) classification, coenopopulations are ripening (CP 1) or mature (CP 2-4).

Morphological characteristics. The study of morphological characteristics of the species enables assessment of its ecological plasticity and identification of optimal conditions for plant growth and development. Table 2 presents morphometric and quantitative parameters of the generative individuals of *G. septemfida* in studied coenopopulations.

Indicator	CP 1	CP 2	CP 3	CP 4
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Number of generative shoots in g ₂ individual, pcs.	7.6±2.6 ^a /77.1	4.5±0.5 ^b /29.1	5.2±0.9 ^b /52.7	7.8±1.4 ^{ab} /55.6
Shoot length, cm	37.1±0.9 ^a /12.0	34.0±0.9 ^b /13.3	39.7±0.6 ^c /8.1	57.1±1.7 ^d /14.4
Number of leaves, pcs.	30.4±0.7 ^a /11.8	24.0±0.6 ^{ab} /12.0	21.8±0.4 ^b /10.2	40.0±1.5 ^c /17.5
Number of leaves per shoot length, pcs./cm	0.8±0.03 ^a /16.2	0.7±0.03 ^a /23.0	0.6±0.01 ^{ab} /12.5	0.7±0.03 ^{ac} /20.3
Leaf length, cm	4.9±0.1 ^a /10.2	4.2±0.1 ^b /9.2	4.6±0.1 ^{ab} /8.1	5.1±0.1 ^a /10.1
Leaf width, cm	2.4±0.1 ^a /11.5	2.1±0.1 ^a /15.0	2.3±0.1 ^a /12.1	2.4±0.05 ^a /9.3
Inflorescence height, cm	4.5±0.1 ^a /15.3	6.2±0.3 ^{ab} /20.7	8.0±0.6 ^b /36.0	5.8±0.2 ^{ab} /20.2
Inflorescence diameter, cm	3.7±0.1 ^a /14.6	3.7±0.1 ^a /13.2	4.5±0.2 ^a /23.5	4.4±0.2 ^a /16.9
Flower length, mm	31.4±0.5 ^a /8.0	37.4±0.2 ^b /3.2	35.9±0.4 ^b /5.5	36.9±0.7 ^c /9.2

Table 2. Morphological characteristics of the generative individuals of *G. septemfida* in natural coenopopulations in the territory of the Republic of Altai and Tomsk region

Note: Data are presented in the numerator $M \pm SEM$, in the denominator CV_{mean} . Identical letter indices show no differences between the indicators, different letter indices show that the differences are statistically significant at $p < 0.05$.

G. septemfida plants form shoots 34.0–57.1 cm long, which bear 21.8–40.0 leaves each. The longest shoots with the highest number of leaves are found in CP 4, which is apparently due to the plant's habitat between denser and taller herbaceous layer, forcing the plants to reach for light. The shortest shoots develop in plants from the steppe community with a low and sparse grass stand (CP 2). CP 2 and CP 3 also develop the lowest number of leaves per shoot. Indices have reliable differences in virtually all the coenopopulations studied. Shoot foliate keeps stable values and makes 0.6–0.8 pcs per 1 cm of shoot length. The largest leaves are observed in plants growing in the Seminsky Ridge (CP 1) and in the southern part of the Tomsk Region (CP 4). The most vigorous inflorescences are found in plants confined to the northern macro-slope of the North Chuysky Ridge (CP 3). Most of these characteristics have a low and medium variability level ($CV = 3.2$ –23.5%). The number of generative shoots of a middle-aged individual exhibits a significantly higher variability ($CV = 29.1$ –77.1%). The highest number of flowering and fruiting shoots is reported for CP 1 and CP 4 (7.6 and 7.8 shoots, respectively). In CP 2, this number does not exceed 4.5 pcs per individual, but it reliably distinguishes CP 1 from CP 2 and CP 3 (Table 2).

Morphological analysis of *G. septemfida* plants from different coenopopulations showed that the most developed plants (by most characteristics) are formed in bushy tundra with subalpine grasses (CP 1) and in tall grass meadows of the flat landscape (CP 4).

Reproductive biology. In nature, *G. septemfida* coenopopulations are propagated and maintained exclusively by seed. The main reproductive indicators of the species are pollen fertility, the number of flowers and fruits per inflorescence, the number of ovules per flower and seeds per fruit, and PSP and RSP. In addition, we considered the degree of damage to fruits and seeds by insect pests.

All the studied coenopopulations of *G. septemfida* exhibited high pollen fertility ranging from 86.7 % (CP 3) to 98.0 % (CP 4), which potentially makes this species highly pollinating and capable of setting viable seeds (Table 3).

Inflorescences are mostly few-flowered, with an average of 6–7 flowers and 5–7 fruits per shoot (Table 3). However, at the intrapopulation level, these indicators vary greatly from one individual to another. Thus, among plants growing in the forest belt of the North Chuysky Ridge (CP 3), the number of flowers and fruits per shoot varies significantly – from 3 to 19 flowers (fruits).

G. septemfida is characterized by a high fruits-to-flowers ratio (FFR) of 80–98%, i.e. most flowers in

the inflorescence develop into fruits. A significant number of ovules per flower (478.4–556.5) and correspondingly high potential seed production of the shoot (3,522.8–3,892.1) provide each coenopopulation with a large seed supply. However, our studies have shown that seed productivity of the species can be significantly reduced in some parts of its range due to annual damage of fruits and seeds by insect pests. The studies conducted in 2024 revealed a high degree of fruit damage in Altai plants, with the maximum percentage for CP 3 (57%). The minimum percentage of fruit damage (2%) was observed for Tomsk plants (CP 4). Accordingly, the productivity coefficient (Cp) for some Altai coenopopulations (CP 1, CP 3) is significantly lower than the average. CP 1 has the lowest reproductive potential (24.7 %) and seed setting rate (Table 3).

Indicator	CP 1	CP 2	CP 3	CP 4
Pollen fertility, %	91.5±1.4 ^a /3.7	88.8±1.3 ^b /4.0	86.7±1.5 ^b /5.6	98.0±0.3 ^a /0.6
Number of flowers, pcs.	6.9±0.4 ^a /30.9	6.9±0.4 ^a /31.5	7.4±0.6 ^a /42.9	6.4±0.6 ^a /32.4
Number of fruits, pcs.	6.6±0.5 ^a /34.5	6.7±0.4 ^a /29.5	7.0±0.6 ^a /43.1	5.1±0.7 ^a /46.0
Fruits-to-flowers ratio (FFR), %	96.1±2.2 ^a /11.7	97.8±1.3 ^a /6.5	96.0±2.1 ^a /10.8	79.6±7.1 ^b /29.6
Number of undamaged fruits, pcs.	3.2±0.4 ^a /62.8	4.6±0.5 ^a /52.4	3.0±0.4 ^a /63.8	5.0±0.6 ^a /51.7
Number of ovules per flower, pcs.	544.8±58.7 ^a /24.1	556.5±17.2 ^a /12.7	480.2±24.3 ^a /22.1	478.4±48.2 ^a /31.9
Number of seeds per fruit, pcs.	269.6±72.2 ^a /59.9	507.4±19.6 ^b /15.9	346.3±35.9 ^{ab} /45.1	366.0±61.6 ^b /20.2
Potential seed productivity (PSP) per shoot, pcs.	3748.2±231.8 ^a /30.9	3828.7±241.1 ^a /31.5	3892.1±352.0 ^a /39.4	3522.8±228.2 ^a /16.9
Real seed productivity (RSP) per shoot, pcs	855.7±112.0 ^a /62.8	2354.3±246.6 ^a /52.4	1077.4±176.8 ^a /69.6	1846.6±203.6 ^a /51.7
Productivity coefficient (Cp), %	24.7±3.0 ^a /58.6	61.3±5.1 ^a /41.6	31.2±5.3 ^a /71.9	52.0±4.6 ^a /41.6

Table 3. Reproductive indicators of the generative individuals of *G. septemfida* in natural coenopopulations in the territory of the Republic of Altai and Tomsk Region

Note: CP – coenopopulation. Data are presented in the numerator $M \pm SEM$, in the denominator CV_{mean} . Identical letter indices show no differences between the indicators, different letter indices show that the differences are statistically significant at $p < 0.05$.

Statistical data processing showed that most reproductive indicators of the species exhibit a high variability level. The most unstable indicators are number of flowers ($CV \geq 30.9\%$), number of fruits ($CV \geq 29.5\%$), number of undamaged fruits ($CV \geq 51.7\%$), number of seeds per fruit ($CV \geq 45.1\%$), PSP ($CV \geq 30.4\%$) and RSP ($CV \geq 45.1\%$), and Cp ($CV \geq 41.6\%$). The number of ovules per flower ($CV \geq 12.7\%$) and FFR ($CV \geq 6.5\%$) are less variable. Pollen fertility ($CV \geq 0.6\%$) is a slightly variable indicator. The variation coefficient attains its maximum for many plant characteristics in CP 1, CP 3, and CP 4 (Table 3). In CP 1 and CP 3, it is primarily associated with significant damage of fruits and seeds in inflorescences of individual plants. In CP 4, tall grass stands and competition with other species in some parts of the phytocoenosis (along willow thickets) may reduce the number of ripening fruits. A high variability level of generative indicators is determined by both permanent habitat factors (climatic, ecological-coenotic, etc.) and random factors related to damage of plants by insect pests (CP 1–3) or, possibly, by the impact of grazing (CP 2). Table 3 shows significant variations of most reproductive indicators at the intrapopulation level, which does not indicate statistically significant differences between the main integral indicators (PSP, RSP, Cp) of the studied coenopopulations of *G. septemfida*.

Seed morphology and germination. Seeds of *G. septemfida* are oblong, slightly sickle-shaped, light brown, 1.48 (1.25–1.73) mm long and 0.51 (0.43–0.70) mm wide, bluntly acuminate at the apex. The surface sculpture is oblong reticulate. The weight of 1,000 seeds is 0.147 g. For seed

germination, pre-sowing treatment is required: cold stratification for a month or soaking for one day in 0.1% gibberellic acid solution. After additional treatment, laboratory germination of seeds attained 87.0–99.5 % (Kataeva and Prokopyev 2017).

Assessment of introduction success. Observations of the seasonal rhythm of plant development in the southern part of the Tomsk Region (SibBG TSU) showed that *G. septemfida* is a long-vegetating spring-summer-autumn-green plant with a mid-late summer rhythm of flowering (Kataeva and Prokopyev 2017). The species starts growing as soon as the snow melts and the soil warms (the first half of April). Plants start flowering in the second half of July, which lasts three weeks on average. The period from fruit formation to seed maturation lasts about a month. Mass seed maturation occurs at the end of September. In early August, individual shoots begin to turn yellow and by early October they dry up completely.

The species prefers open or semi-shaded areas with fertile soils and good moisture. The plant regularly flowers and bears fruit. It is propagated by seeds and division. Regular moistening of plantings can induce abundant viable self-seeding. Self-seeded plants develop quickly; the generative phase can commence in the second year.

We conducted a comprehensive assessment of the success of *G. septemfida* introduction in the SibBG TSU according to the previously developed 4-point assessment scale for rare plant species of Siberia (Prokopyev and Chernova 2020). The scale is based on a set of biological and economic characteristics that indicate viability, reproductive indicators, completeness of the seasonal cycle of development, ontogenesis rate, longevity in culture, and resistance to biotic and abiotic factors.

It was found that *G. septemfida* passes all the main stages of ontogenesis, which are close to the natural ones; gives viable self-seeding; is capable of artificial vegetative propagation; is not damaged by pests and diseases; overwinters well and does not require strict compliance with agronomic practices. The assessment of introduction classifies *G. septemfida* as a stable plant (Table 4).

The gene pool established in the SibBG TSU contributes to successful ex situ conservation of the species.

I	II	III	IV	V	VI	Total	Plant tolerance
4	4	2	4	4	3	21	Stable

Table 4. Score assessment of successful introduction of *G. septemfida* in the southern part of the Tomsk Region

Note: I – passage of the main stages of ontogenesis; II – seed reproduction; III – vegetative reproduction; IV – damage by diseases and pests; V – overwinter mortality, desiccation or soaking; VI – demanding growing conditions.

Conclusion

The distribution of *Gentiana septemfida* in the southern part of Western Siberia is closely associated with meadow communities. In the Altai Mountains, the species is found at the upper boundary of the forest belt. It grows in forest meadows, open glades, and bushy tundra with alpine and subalpine forbs. In the flat landscape, it is rarely encountered in river valleys among tall mesophytic plants. The study of the demographic structure of *G. septemfida* coenopopulations revealed substantially low ecological and effective density. The coenopopulations are of normal type, incomplete, mature, and ripening. Generative individuals make up a significant proportion of the coenopopulations. In nature, *G. septemfida* reproduces by seed. The species forms a large number of seeds. It was found that the values of most reproductive indicators of the species can significantly decrease due to notable damage of fruits and seeds by pests and ecological-coenotic

features of the communities. A high percentage of damaged fruits (31–57 %) and low reproductive potential were found for coenopopulations of the Altai Mountains. The lowest percentage of fruit damage (2 %) was observed in plants growing in flat areas of Western Siberia (CP 4). According to morphological characteristics, the most optimal conditions for plant growth and development were found in bushy tundra with subalpine forbs (CP 1) and tall grass meadows (CP 4). Based on the assessment of the seasonal rhythm of plant development, *G. septemfida* was classified as a long-vegetating spring-summer-autumn-green plant with a mid-late summer rhythm of flowering. In cultivation conditions of the southern part of the Tomsk Region, *G. septemfida* was classified as a stable plant promising for creation of stable populations in *ex situ* conditions.

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References

- Adams CA, Thompson RL (2017) Ecology of an endangered *Gentiana flavida* population in east-central Kentucky. *Phytoneuron* 83: 1–25.
- Allen D, Bilz M, Leaman DJ, Miller RM, Timoshyna A, Window J (2014) European Red List of Medicinal Plants. Publications Office of the European Union, Luxembourg, 63 pp.
- Artyushenko ZT (1990) Atlas of descriptive morphology of higher plants. Seed. Science, Leningrad, 204 pp. [In Russian]
- Barykina IP, Veselova TD, Devyatov AG (2004) Handbook of botanical microtechnology. Fundamentals and Techniques. Moscow State University Publ., Moscow, 312 pp. [In Russian]
- Baykov KS (Ed) (2012) Conspectus of the Flora of Asian Russia: Vascular plants. Publishing house SB RAS, Novosibirsk, 640 pp. [In Russian]
- Beydeman IN (1974) Methodology for studying the phenology of plants and plant communities. Science, Novosibirsk, 156 pp. [In Russian]
- Borovik TS, Revushkin AS (2018) Features of ontogeny and age structure of the population of *Dasystephana macrophylla* (Pallas) Zuev in the Altai Mountains. *Tomsk State University Journal of Biology* 41: 42–52. [In Russian]
- Chen T, Wang TT, Liu SY, Wang HC (2024) *Gentiana mopanshanensis* (Gentianaceae), a new species from Yunnan, southwest China. *PhytoKeys* 239: 215–228.
<https://doi.org/10.3897/phytokeys.239.119800>
- Cuena-Lombraña A, Porceddu M, Dettori CA, Bacchetta G (2016) *Gentiana lutea* L. subsp. *lutea* seed germination: natural versus controlled conditions. *Botany* 94: 653–659.
<https://doi.org/10.1139/cjb-2016-0030>
- Devic M, Momčilović I, Krstić-Milošević D, Maksimović V, Konjevic R (2006) In vitro multiplication of willow gentian (*Gentiana asclepiadea* L.) and the production of gentiopicrine and mangiferin. *Phyton-Annales Rei Botanicae* 46(1): 45–54.
- Drude O (1890) Handbuch der Pflanzengeographie. Vol. XVI. J. Engelhorn, Stuttgart, 582 pp. [In German]
- Ebel AL (2012) Abstract of the flora of the northwestern part of the Altai-Sayan province. *Irbis*,

Kemerovo, 568 pp. [In Russian]

Fedotova TA (2010) Gentianaceae. In: Takhtajan AL (Ed.) Comparative anatomy of seeds. Vol. 7. Dicotyledons. Lamiidae, Asteridae. Science, St. Petersburg, 53–75. [In Russian]

Galinskaya VD (1978) Flavonoid content in some Siberian species of gentian (genus *Gentiana* L. and *Swertia obtusa* Ledeb.). In: Krasnoborov IM (Ed.) Plant resources of Siberia and their use. Science, Novosibirsk, 50–56. [In Russian]

GOST 34221-2017 (2017) Seeds of medicinal and aromatic crops. Varietal and sowing qualities. General technical conditions. Moscow, 27 pp. [In Russian]

Grossheim AA (1952) *Gentiana* L. In: Shishkin BK, Bobrov EG (Eds) Flora of the USSR. Vol. 18. USSR Academy of Sciences, Moscow, Leningrad, 538–640. [In Russian]

Grubov VI (2002) Plants of Central Asia: based on materials from the Komarov Botanical Institute of the Russian Academy of Sciences. Vol. 13. Plumbaginaceae–Gentianaceae–Asclepiadaceae. Saint Petersburg State Chemical and Pharmaceutical Academy, Saint Petersburg, 132 pp. [In Russian]

Hegi G (1977) Alpenflora. Die wichtigeren Alpenpflanzen Bayerns, Osterreichs und der Schweiz. P. Parey, Berlin und Humburg, 196 pp. [In German]

Ho TN, Liu SW (2001) A worldwide Monograph of *Gentiana*. Science Press, Beijing, 694 pp. Hou QZ, Chen DW, Wang YP, Ehmet N, Ma J, Sun K (2022a) Analysis of endophyte diversity of two *Gentiana* plants species and the association with secondary metabolite. BMC Microbiology 22: 90. <https://doi.org/10.1186/s12866-022-02510-4>

Hou Qz, ur Rahman N, Ali A, Wang Yp, Shah S, Nurbiye E, Shao Wj, Ilyas M, Sun K, Li R, Said F, Fahad S (2022b) Range expansion decreases the reproductive fitness of *Gentiana ofcinalis* (Gentianaceae). Scientific Reports 12: 2461. <https://doi.org/10.1038/s41598-022-06406-1>

Huang SH, Agrawal DC, Wu FS, Tsay HS (2014) *In vitro* propagation of *Gentiana scabra* Bunge – an important medicinal plant in the Chinese system of medicines. Botanical Studies 55(1): 56. <https://doi.org/10.1186/s40529-014-0056-4>

Ishmuratova MM (Ed) (2020) Methodology for studying populations of rare and resource plant species in protected natural areas of the Republic of Bashkortostan. Bashkir encyclopedia, Ufa, 276 pp. [In Russian]

Ishmuratova MM, Tkachenko KG (2009) Seeds of herbaceous plants: features of the latent period, use in introduction and propagation *invitro*. Gilem, Ufa, 116 pp. [In Russian]

Kataeva TN, Prokopyev AS (2017) Biological features of the genus *Gentiana* (Gentianaceae) representatives when introduced in the south of Tomsk region. Tomsk State University Journal of Biology 38: 45–67. [In Russian]

Kataeva TN, Prokopyev AS (2023) On the distribution of the rare species *Gentiana septemfida* Pall. (Gentianaceae Juss.) in the Tomsk region. Systematic notes on the materials of P.N. Krylov Herbarium of Tomsk State University 128: 45–49. [In Russian]

Kozlov AA (2023) On approval of the List of flora objects included in the Red Book of the Russian Federation. Order No. 320 of 23.05.2023. Ministry of Natural Resources and Ecology of the Russian Federation, Moscow, 27 pp. [In Russian]

Kozuharova E, Anchev ME, Popov P (2008) The pollination ecology of *Gentiana*

cruciata (Gentianaceae) – specifics of a Bulgarian population in comparison to Dutch populations. Nordic Journal of Botany 23(3): 365–372. <https://doi.org/10.1111/j.1756-1051.2003.tb00407.x>

Lakin GF (1990) Biometrics. Graduate School, Moscow, 352 pp. [In Russian]

Lavrenko EM, Korchagin AA (Eds) (1964) Field geobotany. Vol. 3. Science, Moscow, Leningrad, 530 pp. [In Russian]

Levina RE (1981) Reproductive biology of seed plants: a review of the problem. Science, Moscow, 96 pp. [In Russian]

Monographs on the Use of Traditional Medicine in Primary Health Care (2012) National Institute of Traditional Medicine, Thimphu, 127 pp.

Nukhimovsky EL (2002) Fundamentals of biomorphology of seed plants. Habitus and growth forms in the biomorph organization. Vol. 2. Nedra, Moscow, 864 pp. [In Russian]

Olennikov DN, Gadimli AI, Isaev JI, Kashchenko NI, Prokopyev AS, Kataeva TN, Chirikova NK, Vennos C (2019) Caucasian *Gentiana* species: untargeted LC-MS metabolic profiling, antioxidant and digestive enzyme inhibiting activity of six plants. Metabolites 9(11): 271. <https://doi.org/10.3390/metabo9110271>

Osmanova GO, Zhivotovsky LA (2020) Ontogenetic spectrum as an indicator of the state of plant coenopopulations. Izvestia RAS. Biological Series. 2: 144–152. <https://doi.org/10.31857/S0002332920020058>[In Russian]

Ponticelli M, Lela L, Moles M, Mangieri C, Bisaccia D, Faraone I, Falabella R, Milella L (2023) The healing bitterness of *Gentiana lutea* L., phytochemistry and biological activities: A systematic review. Phytochemistry 206: 113518. <https://doi.org/10.1016/j.phytochem.2022.113518>

Povydysh MN, Bityukova NV (2011) Gentianaceae Dumort. In: Budantsev AL (Ed) Plant resources of Russia: wild flowering plants, their component composition and biological activity. Vol. 4. Family Caprifoliaceae – Lobeliaceae. KMK, St. Petersburg, Moscow, 56–67. [In Russian]

Prokopyev AS, Chernova OD (2020) Assessment of the success of the introduction of some rare plant species in the Siberian Botanical Garden of Tomsk State University. IOP Conference Series: Earth and Environmental Science 421: 1–6. <https://doi.org/10.1088/1755-1315/421/5/052034>

Rabotnov TA (1960) Methods for studying seed production of herbaceous plants in communities. In: Lavrenko EM, Korchagin AA (Eds) Field geobotany. Vol. 2. USSR Academy of Sciences, Moscow, Leningrad, 20–38. [In Russian]

Revushkin AS, Borovik TS (2019) Genus *Dasystephana* Adans. (Gentianaceae Juss.) in the flora of Southern Siberia. Turczaninowia 22(4): 133–137. [In Russian]

Sirotyuk EA (2019) The population ecology of *Gentiana oschtenica* (Kusn.) Woronow in the highlands of the Republic of Adygea. Ecologica Montenegrina 23: 27–33. <https://doi.org/10.37828/em.2019.23.4>

Sirotyuk EA, Ayba EA, Gergiya IG (2016) Ecologic and geographical variability of *Gentiana septemfida* Pall. in mountain phytocenoses of Abkhazia. Bulletin of Adygea State University. Natural, mathematical and technical sciences 3(186): 47–54. [In Russian]

Sirotyuk EA, Gergiya IG, Ayba EA (2015) Distribution and ecological-coenotic features of Abkhazian species of the Gentianaceae family. Pedagogical Education in Russia 3: 153–161. [In Russian]

Struwe L, Albert VA (Eds) (2002) *Gentianaceae: Systematics and Natural History*. Cambridge University Press, Cambridge, 652 pp.

Tsvelev NN (1978) *Gentiana* L. In: Fedotov AA (Ed.) *Flora of the European part of the USSR*. Vol. 3. Science, Leningrad, 64–74. [In Russian]

Vaynagiy IV (1974) On the methodology for studying seed productivity of plants. *Botanical Journal* 59(6): 826–831. [In Russian]

Veysin U (2004) *Encyclopedia of Chinese Medicine: The Healing Power of Nature*. Neva, Saint Petersburg, 448 pp. [In Russian]

Wai TH, Liang X, Xie H, Liu L, Pan Y, Xu Y, Zhao L, Xu X (2024) Global richness patterns of alpine genus *Gentiana* depend on multiple factors. *Ecology and Evolution* 14: e11366. <https://doi.org/10.1002/ece3.11366>

Zhukova LA (1995) *Population life of meadow plants*. Lanar, Yoshkar-Ola, 224 pp. [In Russian]

Zlobin YuA, Sklyar VG, Klimenko AA (2013) *Populations of rare plant species: theoretical foundations and study methods*. University Book, Sumy, 439 pp. [In Russian]

Zuev VV (1997) *Gentianaceae*. In: Malyshev LI (Ed) *Flora of Siberia*. Vol. 11. Science, Novosibirsk, 56–85. [In Russian]

Zykova EYu (2012) *Gentianaceae*. In: Krasnoborov IM, Artemov IA (Eds) *Key to plants of the Altai Republic*. Publishing house SB RAS, Novosibirsk, 334–343. [In Russian]