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Ecological and biological features of *Polygala sibirica* from the southern part of Western Siberia

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Abstract

The paper reports data on the distribution and status of coenopopulations of the rare and valuable medicinal plant *P. sibirica* from the southern part of Western Siberia. The study investigated the phytocoenotic confinement, demographic characteristics of coenopopulations, seasonal patterns of growth, morphology, and reproductive biology. In mountainous areas, the species permanently inhabits rocky mountain steppes. In the plain of Western Siberia, its localities are fragmentary. *P. sibirica* coenopopulations are characterized by low density, ranging from 1.83 to 4.57 ind./m^2. The ontogenetic structure of coenopopulations shows a predominance of generative individuals (53.6–76.9%). The ontogenetic spectrum of coenopopulations is characterized as incomplete, unimodal (CP 1–3, CP 5, CP 7–9) or bimodal (CP 4 and CP 6), with a predominance of generative individuals and a low proportion of old age groups. The analysis of the morphological characteristics of *P. sibirica* indicates that the largest plants with long, branched shoots and large leaves and inflorescences are found at the range boundary. Coenopopulations differ significantly in LMA, leaf chlorophyll content and nitrogen status values. It is shown that vegetation indices CCI, CRI1, VREI1 and ZMI can be used to assess the physiological status of plants under different ecological and coenotic conditions. *P. sibirica* reproduces exclusively by seed. Most flowers develop into mature fruits (FFR = 77.1–93.5%). Real seed productivity varies considerably, ranging from 10.8 to 77.8 seeds per shoot. Most of the studied coenopopulations exhibit the above-average level of reproductive potential (C_p = 65.2–77.9%). Under anthropogenic pressure, *P. sibirica* coenopopulations retain self-sustaining ability and can survive for extended periods within the range.

Keywords
Rare species, *Polygala sibirica*, structure of coenopopulations, morphology, reproductive biology, physiology, Western Siberia, range boundary

Introduction

Polygala sibirica L. (family Polygalaceae Hoffmanns. & Link) is a well-known representative of petrophyte-steppe communities in the southern part of Siberia. Along with other representatives of the Siberian flora from the genus *Polygala* (*P. comosa* and *P. tenuifolia*), *P. sibirica* has gained significant attention in medicine, particularly as an expectorant for treatment of both acute and chronic respiratory tract infections. In Tibetan medicine, it is also used to treat gastrointestinal diseases. Saponins are major active components isolated from the roots and rhizomes of *Polygala* (Minaeva 1991). The roots also contain flavonoids, alkaloids, coumarins, xanthones, resinous and tannins, oligosaccharide esters, and ascorbic acid (Petrova et al. 2010, 2021; Olennikov et al. 2024), which possess a wide range of pharmacological activities, including neuroprotective, antidepressant, hypnotic, sedative, anti-inflammatory, antiviral, antitumor, antioxidant, rejuvenating, and antiarrhythmic effects. In traditional Chinese medicine, the species is widely used to treat insomnia, depression, cough, and rapid heart (Zhao et al. 2020).

In nature, the species is found in a narrow range of ecological and phytocoenotic conditions. It is characterized by low competitiveness, sporadic seed reproduction, and an insignificant soil seed bank. The primary threat to natural populations of *P. sibirica* is posed by increasing anthropogenic pressure on steppe phytocoenoses that encompass this species, including activities such as land plowing, road construction, excessive grazing, and harvesting for medicinal use. Yet, the species may be outcompeted by tall grasses or shrubs in the absence of grazing, haymaking or episodic grass fires (Ilyina 2018). It is considered rare throughout much of the European part of Russia. In Siberia, it is protected in Omsk, Tyumen and Tomsk regions, and in the Sakha Republic (Yakutia).

Modern studies of *P. sibirica* focus on the status of its coenopopulations in the European part of its range (Ilyina 2017, 2018; Shmaraeva et al. 2019; Maslennikov et al. 2023), as well as in Yakutia in Eastern Siberia (Egorova 2015; Ivanova and Borisova 2016). Extensive data are available on the phytochemical composition of the species (Zhou et al. 2014; Lacaille-Dubois et al. 2020; Petrova et al. 2021; Jing et al. 2024; Olennikov et al. 2024), its microclonal propagation *in vitro* (Okhlopkova et al. 2023), and the feasibility of its introduction into Siberian botanical gardens (Egorova 2022; Elisafenko and Kupriyanov 2024). However, data on this rare and economically valuable plant in Western Siberia are still meagre. So far, only a few publications on the status of the species in Tomsk region are available (Prokopyev and Kataeva 2017).

The main scope of the study was to investigate the ecological and biological features of *Polygala sibirica* in natural coenopopulations in the southern part of Western Siberia.

Materials and methods

Polygala sibirica L. is a monocentric taproot polycarpous plant with a multi-headed branched caudex and elongated shoots (Egorova 2022). Shoots are thin, up to 35 cm long, typically numerous, erect or recumbent, without rosettes, densely foliated from the base upwards. Leaves are oval or narrowly lanceolate, shortly pointed. Flowers are pale purple, grouped in sparse one-sided racemes. Fruit is a rounded obcordate two-seeded capsule (Fig. 1).

Figure 1. Generative shoots of *Polygala sibirica* (Tomsk region, environs of the Anikino village).

This mountain-steppe species of East European-Asian origin (Naumenko 2008) possesses a wide geographical range that extends from the Southern Carpathians in the west to Japan in the east (Kazakova and Tikhomirov 1984). It is widespread in Central and Eastern Europe, the Caucasus, Siberia, the Far East, Mongolia, China, Japan, India, and other regions of Asia (Peshkova 1996; Mayorov 2001; Gubanov et al. 2003). In Russia, its distribution is mainly confined to the steppe and forest-steppe regions of Siberia. The species occurs on open rocky southern slopes, in rocky gravelly and shrubby meadow steppes, in dry pine forests, and less frequently in open birch forests, growing on gravel and fallow soil (Peshkova 1996).

Field studies of *P. sibirica* were conducted repeatedly from 2018 to 2025 in the mountain-steppe belt of the Altai Mountains (Altai Republic), and along the northern border of the species range, particularly in the subtaiga and forest-steppe regions of the southern part of Tomsk region and the northern part of Kemerovo region.

The species composition and structure of plant communities that encompass *P. sibirica* were determined based on geobotanical descriptions and then specified based on herbarium material. The analysis of the phytocoenotic confinement of *P. sibirica* coenopopulations employed conventional geobotanical approaches (Lavrenko and Korchagin 1964). The species quantitative abundance was assessed using the Drude scale (Drude 1890). The Latin names of the species are given in line with the modern online resource POWO (https://powo.science.kew.org/).

The population analysis was conducted using approaches employed in modern plant population biology (Zlobin et al. 2013; Osmanova and Zhivotovsky 2020; Ishmuratova 2020).

The ontogenetic stages of the species were identified with regard to a set of morphological and biological characteristics, based on the ontogenesis of the closely related species *P. tenuifolia*, described by A.Yu. Astashenkov and A.A. Guseva (2007).

To study the density and ontogenetic structure of coenopopulations in communities, transects were regularly laid out and divided into plots. In each coenopopulation, not less than 20 plots of 1 m^2 area were laid out. The ecological density of the coenopopulation was determined based on the total number of individuals per unit area. The ontogenetic spectra were developed based on the number of individuals in each age group. A morphologically isolated individual served as a counting unit.

The coenopopulation type was identified with regard to the 'delta-omega' classification by L.A. Zhivotovsky (Osmanova and Zhivotovsky 2020) that was constructed based on the age index (Δ) and the efficiency index (ω). The data determined included also the renewal index (I_r) (Zhukova 1995) and the senescence index (I_{sn}) (Glotov 1998). The completeness (incompleteness) of the coenopopulation was determined based on the degree of group representation in the ontogenetic spectrum.

The analysis of the morphological characteristics of *P. sibirica* was conducted primarily on living well-developed individuals at the generative stage, as well as on herbarium material. For measurement, one generative shoot was taken from 25–30 individuals in each coenopopulation. The characteristics primarily measured were as follows: number of generative shoots per g_2 individual, generative shoot length, number of lateral shoots, number of leaves, leaf size, total area of leaves per generative shoot, inflorescence length and number of inflorescences per generative shoot, etc.

For analysis of seasonal patterns of growth, the phenological observation method by I. N. Beydeman (1974) was employed.

Pollen fertility was analyzed using the M.P. Alexander staining method (Barykina et al. 2004). Fully opened anthers were used for the analysis. The fertility was determined based on the examination of not less than 300 pollen grains from each species. Fertile pollen was stained red, while sterile pollen was stained blue-green.

Seed productivity of *P. sibirica* was analyzed using the method by T.A. Rabotnov (1960) and recommendations by I.V. Vainagiy (1974) and R.E. Levina (1981). The main characteristics determined were as follows: number of flowers and fruits per inflorescence, fruits-to-flowers ratio (FFR), number of ovules per flower and seeds per fruit, potential seed productivity (PSP), real seed productivity (RSP), and the coefficient of productivity (C_p). PSP and RSP were determined as the average number of ovules and seeds per generative shoot. C_p was calculated as a percentage ratio of RSP to PSP.

Seed morphology was described based on the studies by Z.T. Artyushenko (1990), M.A. Plisko (2000), and V. Brouwer and A. Shtelin (2010). The morphological characteristics of seeds (size, shape, color) were studied using a Leica M165 C stereoscopic microscope. The weight of 1000 seeds was determined using a DX-200 electronic scale (A&D, Japan) with a division value of 0.001 g.

Seed germination was analyzed in laboratory conditions via the conventional method (Ishmuratova and Tkachenko 2009), with our modification. The seeds were germinated after six months of dry storage. After that, they were placed in Petri dishes (in 4 repetitions of 100 seeds each) on moist filter paper and germinated at 20–22°C with a photoperiod of 16/8 (light/dark). Seed germination was monitored throughout the entire period of seedling emergence (at least 30 days from the start of germination).

Plant physiological status was studied in the field using non-destructive testing devices. For measurement, one leaf was collected from one generative shoot of each of the 25 individuals. Chlorophyll $_{a+b}$ content, epidermal flavonoids and nitrogen balance index (NBI) were measured using a Dualex Scientific 4 (FORCE-A) device. Vegetation indices were assessed using a CI-710S leaf spectrometer (CID-BioScience). Table 1 presents the measured indices.

Table 1. Vegetation indices

Index	Abbrev	Equation	Reference
Anthocyanin Reflectance Index 2	ARI2	R800 × ((1 / R550) – (1 / R700))	Gitelson et al. 2001a
Carotenoid Reflectance Index 1	CRI1	(1 / R510) – (1 / R550)	Gitelson et al. 2001b
Chlorophyll Content Index	CCI	T931 / T653	Parry et al. 2014
Normalized Difference Vegetation Index	NDVI	(R800 – R680) / (R800 + R680)	Tucker 1979
Normalized Difference Greenness Index	NDGI	(R760 – R565) / (R760 + R565)	Klem 2008
Nitrogen Nutrition State	NNS	(NDGI – 0.25) × 250	PlantPen/N-Pen N 110 Instruction Guide 2021

Index	Abbrev	Equation	Reference
Vogelmann Red Edge Index 1	VREI1	R740 / R720	Vogelmann et al. 1993
Water Band Index	WBI	R900 / R970	Penuelas et al. 1997
Zarco-Tejada & Miller Index	ZMI	R750 / R710	Zarco-Tejada et al. 2001

Note: R means Reflectance, T means Transmittance.

To assess the morphological characteristics of leaves and the accumulation of dry matter, the leaves were pre-measured using appropriate devices, dried via a flat method, weighed to determine the air-dry mass, and photographed against a calibration ruler and using the AxioVision program (Carl Zeiss, Germany). Measurements were made for length, width and area of the leaf. The obtained results were used to calculate leaf mass per area (LMA) using the formula LMA = Dry Leaf Mass / Leaf Area.

For all studied characteristics, the mean value, the mean error (M ± m) and the coefficient of variation (CV) were calculated. Variation levels were estimated according to G.F. Lakin (1990): CV < 11% – low, CV = 11–25% – moderate, CV > 25% – high. Statistical data processing was conducted using MS Excel 2016. For some data, correlation analysis was performed and Spearman's correlation coefficient (R_s) was calculated. The statistical significance of differences in characteristics between populations was determined using one-factor analysis of variance (ANOVA) with Duncan's criterion at $p < 0.05$ in Statistica 10.

Results and discussion

Distribution and phytocoenotic confinement. *P. sibirica* is one of the common species in mountain-steppe landscapes in the southern part of Western Siberia. It permanently inhabits rocky steppes developing on well-lit, poorly grass-covered slopes.

Its northern distribution boundary passes through Kemerovo, Tomsk, Omsk, Tyumen, Novosibirsk and Sverdlovsk regions. In the plain (West Siberian Lowland), this boundary coincides with the forest-steppe subzone, a narrow strip bordering the taiga zone to the south, which has been converted into agricultural cropland. Under these conditions, the localities of *P. sibirica* are scattered. It is rarely encountered, mainly in steppe meadows and in meadow forb-grass steppes, preserved fragmentally within river valleys along the slopes of floodplain terraces (Glazunov 2021; Bekisheva et al. 2003). Closer to mountainous regions (Altai-Sayan region), *P. sibirica* becomes more prevalent, often found in petrophytic steppes, on rocky outcrops, on poorly grass-covered slopes of meadow-steppe, and in dry pine and birch forests (Khmeleva 2012; Ebel 2012).

P. sibirica coenopopulations were studied in the following plant communities:

CP 1. Forb-grass meadow steppe with fragments of petrophytic vegetation (484 m a.s.l.). Altai Republic, Shebalinsky district, environs of the Cherga village (Bison nursery). Northern Altai, foothills of the Cherginsky Range within the Nizhny Aktel River valley. Southern steep (45^0) slope with rocky outcrops and glidders in the lower part. The average grass height is 70–80 cm; the total projective cover (TPC) is 60%. Dominant and co-dominant species: *Stipa capillata* L., *Poa angustifolia* L., *Carex pediformis* C.A.Mey., *Allium nutans* L., *Artemisia gmelinii* Weber ex Stechm., *A. laciniata* Willd., *A. macrantha* Ledeb., *Bupleurum multinerve* DC., *Fragaria viridis* Weston, *Iris ruthenica* Ker Gawl., *Nepeta multifida* L., *Psephellus sibiricus* (L.) Wagenitz, *Spiraea trilobata* L., *Thesium refractum* C.A.Mey., *Thymus jenisseensis* Iljin, *Ziziphora clinopodioides* Lam. A total of 63 species were recorded in the community.

CP 2. Forb-sedge-grass rocky steppe (1098 m a.s.l.). Altai Republic, Ongudaysky district, environs of the Kulada village (Uch-Enmek Nature Park). Central Altai, the Karakol River valley. Rocky gravelly steep (25^0) slope with western exposure. The average grass height is 15–20 cm; TPC is 30–40%. The area is used for grazing. Dominant and co-dominant species: *Pseudoroegneria geniculata* (Trin.) Á.Löve, *Koeleria pyramidata* (Lam.) P.Beauv., *Stipa glareosa* P.A.Smirn., *Cleistogenes squarrosa* (Trin.) Keng, *Carex pediformis*, *Artemisia frigida* Willd., *Goniolimon speciosum* (L.) Boiss., *Kitagawia baicalensis* (Redowsky ex Willd.) Pimenov, *Nepeta multifida*, *Polygala sibirica*, *Potentilla acaulis* L., *Psephellus sibiricus*, *Thymus petraeus* Serg. A total of 27 species were recorded in the community.

CP 3. Forb-caragana rocky gravelly steppe (1115 m a.s.l.). Altai Republic, Ulagansky district, environs of the Chibit village. Central Altai, the Chuya River valley. Rocky gravelly terraced scree on a steep (55^0) southern slope of a floodplain terrace. The area is used for grazing. The average grass height is 20 cm; TPC is 20%. Dominant and co-dominant species: *Caragana pygmaea* (L.) DC., *Artemisia frigida*, *A. stechmanniana* Besser, *Chamaerhodos erecta* (L.) Bunge, *Hedysarum gmelinii* Ledeb., *Polygala sibirica*, *Potentilla acaulis*, *Sibbaldianthe bifurca* (L.) Kurtto & T. Erikss., *Ziziphora clinopodioides*. A total of 19 species were recorded in the community.

CP 4. Forb petrophytic community (114 m a.s.l.). Kemerovo region, Yashkinsky district, environs of the Pisanaya village (Kuzbass Museum-Reserve 'Tomskaya Pisanitsa'). Steep (60^0) southern coastal slope of the Tom River with crumbling fine-earth-gravel soil and rock outcrops. The average grass height is 30 cm; TPC is 40%. Dominant and co-dominant species: *Artemisia pubescens* Ledeb., *Carex duriuscula* C.A.Mey., *Galatella angustissima* (Tausch) Novopokr., *Galium verum* L., *Gypsophila altissima* L., *Kitagawia baicalensis*, *Oxytropis campanulata* Vassilcz., *Phedimus hybridus* (L.) 't Hart, *Polygala sibirica*, *Stipa capillata*, *Thymus jenisseensis*, *Veronica incana* L. A total of 26 species were recorded in the community.

CP 5. Shrubby steppe meadow (107 m a.s.l.). Kemerovo region, Yashkinsky district, environs of the Pisanaya village ('Cossack Fortress' of the Tomskaya Pisanitsa Museum-Reserve). Lower part of a steep (40^0), grass-covered coastal slope of the

Tom River with southwestern exposure. The average grass height is 50 cm; TPC is 60%. Dominant and co-dominant species: *Caragana frutex* (L.) K.Koch, *Astragalus danicus* Retz., *Centaurea scabiosa* L., *Fragaria viridis*, *Medicago falcata* L., *Phedimus hybridus*, *Scutellaria altaica* Ledeb. ex Sweet, *Ziziphora clinopodioides*. A total of 32 species were recorded in the community.

CP 6. Forb-grass rocky steppe (120 m a.s.l.). Kemerovo region, Yashkinsky district, environs of the Slantsevy Rudnik village ('Tutalskie Rocks'). Steep rocky outcrops on the right bank of the Tom River. A rocky platform with southern exposure gently sloping toward the river at the top of the outcrop. The average grass height is 25 cm; TPC is 30–40%. Dominant and co-dominant species: *Artemisia pubescens*, *Koeleria pyramidata*, *Allium nutans*, *Androsace maxima* L., *Festuca pulchra* Schur, *Goniolimon speciosum*, *Polygala sibirica*, *Veronica incana*. A total of 27 species were recorded in the community.

CP 7. Forb-caragana steppe meadow (134 m a.s.l.). Tomsk region, Tomsky district, environs of the Anikino village. Right side of the Tom River valley, the upper part of a steep (40^0) slope with southwestern exposure. The area is subject to minor damage from grazing. The average grass height is 70 cm; TPC is 40%. Dominant and co-dominant species: *Phedimus hybridus*, *Artemisia glauca* Pall. ex Willd., *A. pubescens*, *A. gmelinii*, *Caragana arborescens* Lam., *Carex duriuscula*, *Dracocephalum nutans* L., *Festuca pulchra* Schur, *Galatella angustissima*, *Galium verum*, *Orostachys spinosa*, *Polygala sibirica*, *Stipa capillata*. A total of 23 species were recorded in the community.

CP 8. Forb-grass steppe meadow (109 m a.s.l.). Tomsk region, Kozhevnikovsky district, environs of the Safronovka village. A small ravine with steep (40^0) sides. On a southern slope. The average grass height is 70 cm; TPC is 60%. Dominant and co-dominant species: *Calamagrostis epigejos* (L.) Roth, *Poa angustifolia*, *Artemisia gmelinii*, *A. pubescens*, *Centaurea scabiosa*, *Dracocephalum nutans*, *Fragaria viridis*, *Galium verum*, *Medicago falcata*, *Polygala comosa* Schkuhr, *Potentilla argentea* L., *Trifolium pratense* L. A total of 47 species were recorded in the community.

CP 9. Shrubby forb steppe meadow surrounded by a birch-pine forest (124 m a.s.l.). Tomsk region, Tomsky district, environs of the Tomsk city. Steep (40^0) right side of the Malaya Kirgizka River valley with southern exposure. The average grass height is 40 cm; TPC is 60%. Dominant and co-dominant species: *Caragana arborescens*, *Cotoneaster laxiflorus* J.Jacq. ex Lindl., *Poa angustifolia*, *Fragaria viridis*, *Trifolium lupinaster* L., *Artemisia gmelinii*, *Iris ruthenica*, *Pulsatilla patens* (L.) Mill., *Phedimus aizoon* (L.) 't Hart, *Centaurea scabiosa*, *Polygala sibirica*. A total of 41 species were recorded in the community.

The analysis of the ecological and phytocoenotic confinement of *P. sibirica* revealed that at the border of its range, the species is found in steppe and shrubby communities, occupying steep slopes of watersheds with southern and southwestern exposure (CP 5, CP 7–9). It can also be found on rocky outcrops of coastal cliffs along the Tom River (CP 4 and CP 6). In the steppe belt of the Altai Mountains, it grows in petrophytic variants of meadow steppes (CP 1) and in rocky steppes, frequently exhibiting varying degrees of disturbance due to grazing (CP 2 and CP 3). The TPC generally does not exceed 60%. In rocky areas and poorly grass-covered, steep, crumbling slopes, the TPC decreases to 30–40%. Within these communities, *P. sibirica* often acts as a co-dominant species.

The species composition of the described communities can attain significant diversity, ranging from 19 to 63 species. The vegetation cover of steppe meadows (CP 5, CP 7–9) and meadow steppes (CP 1) on open, steep and grass-covered slopes is predominantly comprised of meadow and meadow-steppe species (*Allium nutans*, *Artemisia gmelinii*, *A. macrantha*, *Bupleurum multinerve*, *Carex pediformis*, *Fragaria viridis*, *Iris ruthenica*, *Medicago falcata*, *Poa angustifolia*, *Pulsatilla patens*, *Stipa capillata*, *Trifolium lupinaster*, etc.). Sporadically occurring species include typical xeropetrophytes (*Orostachys spinosa*, *Phedimus hybridus*, *Spiraea trilobata*, *Thymus jenisseensis*, *Ziziphora clinopodioides*). In true rocky steppes (CP 2, CP 3, and CP 6), the communities are primarily composed of plants from steppe and petrophyte complexes that are adapted to arid climate, intense lighting, and often possess a well-developed root system extending deep into the rocky soil. Dominant species in these communities include steppe rhizomatous grasses and low bunchgrasses (*Cleistogenes squarrosa*, *Festuca pulchra*, *Koeleria pyramidata*, *Pseudoroegneria geniculata*, *Stipa glareosa*), forbs (*Artemisia frigida*, *Goniolimon speciosum*, *Hedysarum gmelinii*, *Kitagawia baicalensis*, *Potentilla acaulis*, *Sibbaldianthe bifurca*, *Thymus petraeus*), and other species.

Structure of coenopopulations. In the natural conditions of the southern part of Western Siberia, *P. sibirica* coenopopulations are characterized by low ecological density. Depending on the type of habitat, the density varies from 1.83 to 4.57 ind./m^2 (Table 2). The minimum values of ecological density are characteristic of coenopopulations that develop on steep unstable slopes. Soil prone to erosion does not facilitate moisture retention, which leads to intensive elimination of seedlings and juvenile plants, and thereby decreases the total number of individuals in the area (CP 3 and CP 7). The maximum number of individuals is observed in communities with a relatively uniform moisture level throughout the season, accompanied by low grass cover (CP 6) or low grass height (CP 9).

The ontogenetic structure of *P. sibirica* coenopopulations is characterized by the predominance of individuals at the generative stage (g_1–g_3), with their proportion ranging from 53.6% in CP 4 to 76.9% in CP 2. In the ontogenetic spectrum, the maximum comes to g_2 individuals (CP 2–7) for most coenopopulations. The accumulation of mature generative plants is facilitated by the extended duration of this stage. In CP 1, CP 8, and CP 9, the maximum comes to g_1 individuals. The pre-generative stage (j–v) comprises juvenile, immature and virginile plants, with the proportion reaching 46.4% in coenopopulations at the boundary of the species range (CP 4). In the arid conditions of the Central Altai, the proportion decreases markedly to 12.8%, with no initial ontogenetic stages observed (CP 2 and CP 3). Additionally, seedlings and juvenile plants were not found in the Tomsk coenopopulation (CP 7) and in the Tutalskie Rocks coenopopulation (CP 6), which can be attributed to local edaphic conditions (high level of soil rockiness and steep, crumbling slope). Aging individuals are represented solely by the subsenile group (0.9–10.3%), the final ontogenetic stage for this species. Typically, individuals at this stage quickly drop out of the coenopopulation. Furthermore, no subsenile individuals were found in CP 3, CP 5, and CP 8. Consequently, the aging index for a significant portion of the studied coenopopulations approaches zero ($I_{sn} \leq 0.03$) (Table 2).

Table 2. Distribution of the individuals by ontogenetic stages and demographic characteristics of *P. sibirica* coenopopulations in the southern part of Western Siberia

Indicator	CP 1	CP 2	CP 3	CP 4	CP 5	CP 6	CP 7	CP 8	CP 9
				Ontogenetic stage, %					
j	5.7	0	0	12.2	17.7	0	0	9.9	11.9
im	8.6	0	9.1	24.4	11.3	25.0	9.4	11.3	10.1
v	14.3	12.8	18.2	9.8	3.2	11.8	21.9	19.7	19.3
g_1	40.0	25.6	27.3	19.5	25.8	22.1	25.0	29.6	40.4
g_2	17.1	28.2	31.8	26.8	35.5	36.8	34.4	22.5	14.7
g_3	11.4	23.1	13.6	7.3	6.5	2.9	6.3	7.0	2.8
ss	2.9	10.3	0	0	0	1.5	3.1	0	0.9
				Demographic characteristics					
M, ind./m^2	3.50	3.90	1.83	2.56	3.88	4.57	2.29	3.94	4.36
M_e, ind./m^2	2.34	2.97	1.34	1.47	2.54	3.01	1.63	2.46	2.60
I_r	0.42	0.17	0.38	0.86	0.48	0.60	0.48	0.69	0.71
I_{sn}	0.03	0.10	0	0	0	0.01	0.03	0	0.01
Δ	0.32	0.48	0.36	0.27	0.31	0.30	0.34	0.27	0.24
ω	0.67	0.76	0.73	0.57	0.66	0.67	0.71	0.62	0.60
CP type	ripening	mature	mature	young	ripening	ripening	ripening	ripening	young

Note: CP – coenopopulation; ontogenetic stage: j – juvenile, im – immature, v – virginile, g_1 – young generative, g_2 – mature generative, g_3 – old generative, ss – subsenile, s – senile; M – ecological density, M_e – effective density, Ir – renewal index, Isn – senescence index; Δ – age index, ω – efficiency index, ind./m^2 – number of individuals per 1 m^2.

Thus, most coenopopulations of *P. sibirica* exhibit an incomplete, single-peaked ontogenetic spectrum characterized by a low proportion of old age groups. In CP 1, CP 8, and CP 9, the spectrum is left-sided, with a predominance of young generative individuals. CP 2, CP 3, CP 5, and CP 7 exhibit a centred spectrum, with a predominance of middle-aged generative plants. In coenopopulations with most intense renewal processes (I_r = 0.60–0.86), the second peak is observed in the young segment of the spectrum. In these conditions, the ontogenetic spectrum becomes bimodal (CP 4 and CP 6). According to the delta-omega (Δ–ω) classification, CP 4 and CP 9 are classified as young, CP 1 and CP 5–8 as maturing, and CP 2 and CP 3 as mature (Table 2).

Morphological and physiological characteristics. In the southern part of Western Siberia, mature generative plants of *P. sibirica* form between 5 and 73 generative shoots. Individuals with the highest number of shoots develop in good lightning conditions with low grass cover and consistent moisture during the growing season. These conditions are typical of the forest-steppe belt, which represents the northern boundary of the species range. The number of generative shoots reaches its maximum (on average 27.3 shoots per plant) in individuals growing on open steep slopes in the environs of the Anikino village (Tomsk), among steppe grasses with low TPC of the above-ground biomass (CP 7). Conversely, the lowest number of shoots is formed by plants growing among tall grasses and shrub thickets (5–9 shoots), which exert significant competitive pressure (CP 1, CP 8, and CP 9). High gravel content and insufficient moisture, characteristic of the central regions of Altai, reduce the ability of *P. sibirica* to form multi-shoot individuals (CP 2 and CP 3), with an average of 8.3 to 13.2 shoots per plant. Morphological characteristics such as branching of the generative shoot and the number of inflorescences do not strongly depend on the environmental conditions. However, plants confined to the range boundary possess more branched shoots (up to 5.2 lateral shoots) and a greater number of inflorescences (up to 7.8 per plant). Additionally, individuals from Kemerovo and Tomsk regions possess the longest inflorescences. All these characteristics demonstrate predominantly high coefficient of variation (CV = 35.5–78.9%) (Suppl. material 1: Table 3).

Individuals of *P. sibirica* growing among tall grasses exhibit the longest shoots and a greater number of leaves (CP 1, CP 5, CP 7–9). In contrast, on steep, dry slopes with sparse grasses (CP 4) and in rocky gravelly steppes (CP 2 and CP 3), these plants maintain a more compact morphology and produce fewer leaves. The size of the leaf blades varies significantly depending on moisture conditions, with larger blades found in plants confined to areas with consistent moisture (CP 1, CP 5, CP 7–9). In the arid conditions of Central Altai (CP 2 and CP 3) and on steep, crumbling slopes with poor soil-moisture content (CP 4), the plants develop the shortest and narrowest leaves. Furthermore, individuals growing in insufficient moisture conditions (CP 2 and CP 3) exhibit the smallest leaf area (0.46–0.64 cm^2) and the lowest total leaf area per generative shoot (15.6–21.8 cm^2). The foliage of the central shoot can also vary significantly (more than twofold) across different coenopopulations, regardless of moisture conditions. The minimum value for this characteristic was found in CP 1 (0.64 pcs/cm), while the maximum value was recorded in CP 2 (1.49 pcs/cm). In most coenopopulations, the size, area and number of leaves on the central shoot demonstrate moderate variation (CV = 12.1–24.3%). The total number of leaves on the generative shoot exhibits high variation across different coenopopulations (CV = 26.5–66.5%) (Suppl. material 1: Table 3).

The length-to-width ratio (L/W) indicates the leaf elongation parameters. The most elongated leaves (L/W = 4.2 and 4.7) were found in plants from Tomsk region, specifically in areas characterized by tall grasses or shrub thickets (CP 8 and CP 9). Conversely, low length-to-width ratios (L/W = 3.0–3.3) were recorded not in the most arid conditions of the Central Altai, but rather in Kemerovo region (CP 4 and CP 5) (Suppl. material 1: Table 3).

The differences in dry leaf mass among coenopopulations can exceed twofold. The minimum value was recorded in CP 2 (4.3 mg), while the maximum value was observed in CP 6 (10.1 mg). This characteristic demonstrates variation (CV = 19.6–22.4%) in CP 2–4, and high variation in other coenopopulations (CV = 25.7–31.7%).

The analysis of the morphological characteristics of *P. sibirica* revealed significant differences among individuals in different areas of the species range. The largest individuals with long, branched shoots, as well as larger leaves and inflorescences, often grow at the northern boundary of the range, particularly in humid areas. In the arid conditions of Central Altai, individuals exhibit a more compact morphology, developing fewer lateral shoots with smaller leaves and shorter inflorescences.

At the interpopulation level, the most statistically significant differences are observed in shoot length, the number of leaves per shoot, leaf size, leaf area, and dry weight. The most pronounced differences are found in individuals growing in the rocky steppe of Central Altai (CP 2) and at the northern boundary of the species range (CP 6–8).

The physiological characteristics of *P. sibirica* leaves in varying ecological and coenotic conditions were studied using the characteristics presented in Table 1.

LMA is an integral characteristic of the production process in leaves. *P. sibirica* coenopopulations exhibit nearly twofold difference in LMA values. The lowest accumulation of dry matter per unit of leaf area was observed in CP 1, CP 7, and CP 8 (4.9–5.5 mg/cm^2), while the highest values were recorded in CP 2, CP 3, and CP 6 (9.2–9.4 mg/cm^2). Low LMA values coincide with low content of the total chlorophylls a+b: 24.7–26.7 μg/cm^2 for CP 1, CP 7, and CP 8. However, high content of the total chlorophylls (30.6–44.5 μg/cm^2) was found not only in plants with the highest LMA values (CP 2 and CP 3) but also in those growing in CP 9 (Suppl. material 1: Table 3).

Low chlorophyll content is associated with low LMA values; however, there is no clear correlation with LMA for high chlorophyll content. For instance, in the population with high LMA values (CP 6), chlorophyll content is at a medium level, whereas in the population with high chlorophyll content (CP 9), the LMA value is at a medium level.

For *P. sibirica*, no clear correlation was observed between high and low LMA values and chlorophyll content in leaves, and most other morphological and reproductive characteristics, including the number of generative shoots, shoot length, number of lateral shoots, number of flowers, number of fruits, PSP, and RSP. It should be noted that plants with the highest values of LMA and chlorophyll content (CP 2 and CP 3) have short shoots, the lowest number of flowers and fruits, and low RSP. In most coenopopulations, chlorophyll content demonstrated moderate variation, while epidermal flavonoids exhibited low variation.

CP 1 and CP 7 exhibit the lowest epidermal polyphenol content (1.30–1.39 μg/cm²), while CP 4 and CP 6 show the highest content (1.69–1.70 μg/cm²) (Suppl. material 1: Table 3). This finding is somewhat unexpected, as epidermal polyphenol content typically increases under more stressful conditions (more arid conditions, excessive lightning, etc.) and decreases under more favorable conditions or when shaded by grasses. A number of components of the epidermal cuticle, such as phenolic compounds, protect it against excessive UV-radiation (Moreno 2022). The regulation of epidermal cuticle biosynthesis is known to be complex and involves interaction between signaling networks associated with environmental stress responses, pathogen responses, and feedback regulation based on the structure and integrity of the cuticle (Yeats and Rose 2013).

The Nitrogen nutrition state (NNS) of plants can be assessed using different vegetation indices. In this study, two devices were employed for the assessment: 1) Dualex Scientific device to calculate the NBI as the ratio of the sum of chlorophylls to the sum of epidermal polyphenols, and 2) SpectraVue leaf spectrometer to calculate the normalized difference greenness index (NDGI) to assess NNS. The NDGI has a strong correlation with NNS. In most coenopopulations, both indices demonstrated moderate variation (Suppl. material 1: Table 3). The analysis revealed that plants from different coenopopulations have different nitrogen status: the difference in the NBI between populations reached up to 69%, while the difference in NNS was up to 48%. The highest values of the NBI (28%) and NNS (92.7%) was found in CP 2. The highest NBI values (28%) and NNS (92.7%) were observed in CP 2, likely due to high grazing pressure. Cattle grazing exerts a complex effect on phytocoenosis; in addition to negative effects such as grass consumption and soil compaction, it also provides positive effects, including nutrient excretion from cattle grazing and enhancement of the soil microbiome (Magomedov 2015). The lowest nitrogen status for these indices was slightly different: the lowest NBI values (16.6–17.4) were found in CP 4, CP 5, and CP 8, while the lowest NNS values (62.8–66.1%) were recorded in CP 1, CP 3, and CP 8. Both nitrogen values demonstrated a weak positive correlation with LMA (R_s = 0.41–0.42).

In this study, the normalized difference vegetation index (NDVI), calculated across a broad spectral range and commonly used to assess vegetation status, exhibited extremely low variation (CV = 1.5–8.7) and low sensitivity. In coenopopulations, the index showed minimal differences, with values exceeding 0.66, indicating that plants in all populations are characterized as 'completely healthy'. The lowest NDVI value was recorded in CP 3 (0.69), while all other coenopopulations displayed the NDVI values ranging from 0.74 to 0.76 (Suppl. material 1: Table 3). No significant correlations were observed between the NDVI and other characteristics.

The chlorophyll content index (CCI) is also calculated across a wide spectral range. Unlike the NDVI, it is determined by the light transmitted through the leaf rather than by reflected light. The CCI demonstrated high variation across coenopopulations. The CCI values differ between populations by nearly fivefold, with the lowest values (8.4–10.1) recorded in CP 1, CP 7, and CP 8, and the highest values (15.9–41.9) observed in CP 2, CP 3, and CP 6. These coenopopulations exhibit the lowest and highest LMA values, respectively (Suppl. material 1: Table 3). The CCI shows a moderate positive correlation with LMA ($R_s = 0.68$), a strong correlation with the NBI (Rs = 0.87) and NNS ($R_s = 0.73$), and a very strong correlation with chlorophyll content ($R_s = 0.97$). The photosynthetic rate is closely related to leaf chlorophyll content, which positively correlates with the CCI (Ghasemi et al. 2011; Kaur et al. 2015; Lunagaria et al. 2015; Parry et al. 2014).

Other vegetation indices of greenness calculated within a narrow spectral range demonstrated high sensitivity. The Vogelmann red edge index 1 (VREI1) exhibited extremely low variation (CV = 2.3–4.6) and insignificant (15%) difference between coenopopulations with minimum and maximum values. The lowest VREI1 values (1.25) were recorded in CP 1, CP 5, CP 7, and CP 8, while the highest value (1.43) was observed in CP 2. The high VREI1 value in CP 2 correlates with high LMA, CCI, chlorophyll content, and NNS. Conversely, low VREI1 values correlate with low LMA, CCI, chlorophyll content, and NNS in CP 1, CP 5, CP 7, and CP 8 (Suppl. material 1: Table 3). The VREI1 demonstrates a moderate positive correlation with LMA ($R_s = 0.57$), a strong correlation with the NBI ($R_s = 0.85$) and NNS (Rs = 0.89), and a very strong correlation with the CCI ($R_s = 0.94$) and chlorophyll content ($R_s = 0.96$).

The Zarco-Tejada and Miller index (ZMI) exhibited low variation and significant (32%) difference between coenopopulations with minimum and maximum values. The lowest ZMI values (1.69 and 1.70) were recorded in CP 1, CP 7, and CP 8, while the highest values (1.93 and 2.23) were found in CP 2 and CP 9. Low ZMI values correlate with low LMA, CCI, and chlorophyll content, whereas high ZMI values correlate with NNS. However, the ZMI does not fully correlate with high LMA, NBI, and CCI values (Suppl. material 1: Table 3). The ZMI demonstrates a moderate positive correlation with LMA ($R_s = 0.56$), a strong correlation with the NBI ($R_s = 0.85$), and a very strong correlation with the CCI ($R_s = 0.93$), chlorophyll content ($R_s = 0.96$), and NNS ($R_s = 0.91$).

Stress indices for plants from different coenopopulations were assessed separately. The studied coenopopulations of *P. sibirica* are confined to areas with different precipitation and insolation regimes. However, the water balance index (WBI) of the plants exhibited extremely low sensitivity, with index values differing by only 2% between coenopopulations. Additionally, no significant correlation was observed between this index and other characteristics.

The anthocyanin reflectance index (ARI2) is associated with anthocyanin content in leaves and indicates stress levels in plants, including under excessive insolation. In this study, the ARI2 demonstrated high variation (CV > 41%) and significant difference (threefold) among different coenopopulations. However, it did not correlate with the lighting or moisture conditions, nor did it demonstrate noticeable correlations with other characteristics. The lowest ARI2 values (0.08–0.09) were recorded in CP 3, CP 5, CP 6, and CP 8, while the highest values (0.21 and 0.25) were found in CP 7 and CP 9 (Suppl. material 1: Table 3).

The carotenoid reflectance index (CRI1), which is associated with carotenoid content, exhibited moderate variation across coenopopulations and showed a significant difference of 68%. High CRI1 values indicate an increase in carotenoid content in leaves relative to chlorophylls, reflecting a stronger stress response of the plants. The highest CRI1 values (0.057–0.062) were recorded in CP 1, CP 5, and CP 7, while the lowest values (0.040 and 0.037) were observed in CP 2 and CP 3 (Suppl. material 1: Table 3). The CRI1 demonstrates a moderate negative correlation with LMA (R_s = –0.65), chlorophyll content (R_s = –0.61), and CCI (R_s = –0.66), but shows no significant correlation with the NBI or NNS.

Seasonal patterns of growth. The seasonal patterns of growth for *P. sibirica* were investigated in natural populations in the southern part of Tomsk region. *P. sibirica* is a long-vegetating species characterized by spring, summer, and autumn greenness, with a mid-summer flowering cycle. The species begins to grow in early May. Flowering is extended from the second half of June until the end of July. Fruits are set simultaneously with flowering, and the period of fruit formation is extended. Seeds mature unevenly during July and August. The growing season lasts approximately 165 days until the first fall frost.

Reproductive biology. *P. sibirica* reproduces exclusively by seed. In natural conditions, this species is characterized by low seed germination efficiency, which can be attributed to both local edaphic and climatic conditions, as well as increasing anthropogenic pressure on steppe ecosystems (Ivanova and Borisova 2016; Ilyina 2018).

In this study, *P. sibirica* was found to exhibit high pollen fertility rates, ranging from 82.6% to 95.9%. (Fig. 2, Suppl. material 2: Table 4).

On average, each inflorescence contains between 4.4 and 8.4 flowers and between 3.6 and 7.4 fruits. The lowest numbers of flowers and fruits are formed in plants growing in the rocky steppes of the Central Altai (CP 2 and CP 3) with insufficient soil moisture and high grazing pressure. The most multi-flowered inflorescences develop in plants growing at the northern border of the species range (CP 4–6, CP 8, CP 9). In all coenopopulations, the fruit set percentage (FFR) remains high, ranging from 77.1% to 93.5%. However, the species ability to produce fruits is somewhat diminished in areas with active grazing (CP 2) (Suppl. material 2: Table 4).

Typically, each fruit contains no more than two seeds. Unfavorable environmental factors may reduce the seed count to as few as one, or the fruit may fail to set seeds. The lowest seed set per fruit (1.4 seeds) was observed in plants growing on dry, rocky gravelly scree with the signs of grazing by domestic animals (CP 3). Conversely, seeds are best set in areas with low anthropogenic pressure and moderate moisture (CP 1 and CP 7). A diverse combination of external environmental factors (phytocoenotic, climatic, edaphic, and anthropogenic) significantly increases variability in seed productivity indices (PSP and RSP). The highest number of seeds (54.5–77.8) was found in coenopopulations growing in communities with abundant grass cover (TPC 60%), sufficient moisture, and low anthropogenic pressure (local paths) (CP 5, CP 8, and CP 9). In contrast, on steep dry slopes and in rocky areas, where plants experience moisture deficiency and are often subjected to grazing, the number of viable seeds per shoot is significantly lower (10.8–32.1) (CP 2, CP 6, and CP 7). Overall, the species exhibits a relatively low RSP under natural conditions. Despite the high sensitivity of *P. sibirica* to external environmental factors, its reproductive potential is primarily realized at levels above the average (C_p= 65.2–77.9%), which supports more effective self-sustaining processes for the species in natural coenopopulations (Suppl. material 2: Table 4).

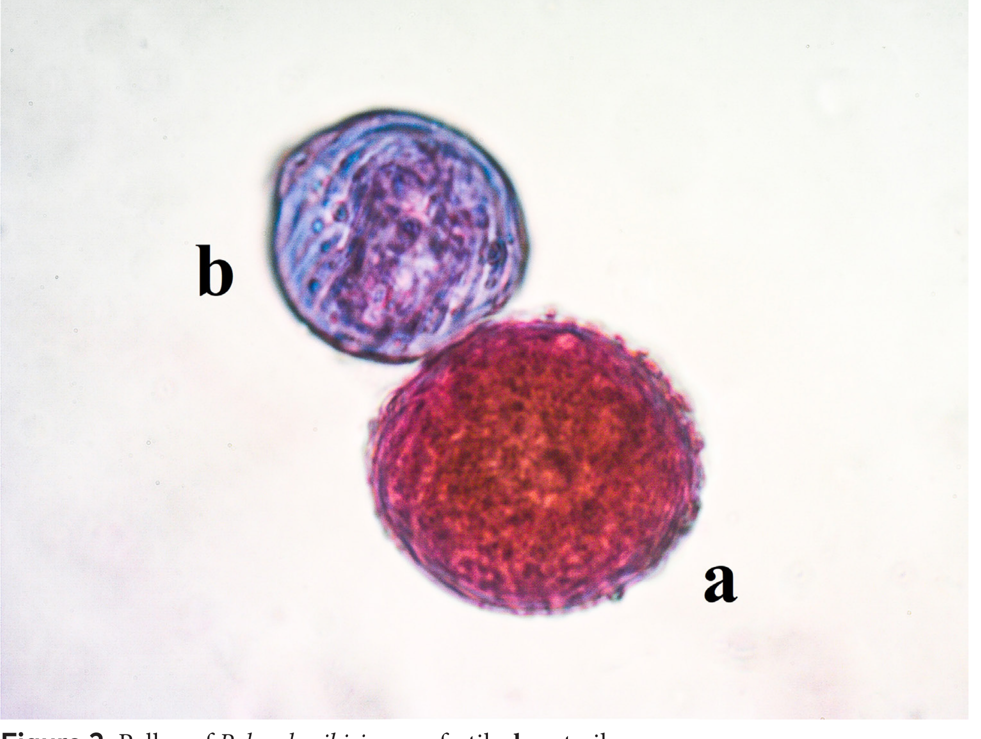

Figure 2. Pollen of *Polygala sibirica*: **a** – fertile, **b** – sterile.

Statistical data analysis revealed that the primary reproductive characteristics of the species exhibit high variability. The most unstable characteristics are the number of flowers and fruits, with CV ranging from 37.8% to 62.3%, as well as PSP and RSP, with CV ranging from 39.5% to 68.1%. The FFR is less variable, with CV ranging from 9.5% to 24.3%.

Comparison of coenopopulations revealed the most significant differences in individuals growing in rocky steppe (CP 2) and rocky gravelly scree (CP 3) areas subjected to considerable anthropogenic pressure. CP 2 shows significant differences in the number of flowers, fruits, shoot PSP, and RSP. Additionally, CP 3 exhibits reliable differences in the number of seeds per fruit and plant productivity (Cp). In both coenopopulations, these reproductive characteristics demonstrated the lowest values. Conversely, the maximum seed productivity indices (PSP and RSP) identified in CP 8 reliably distinguish it from the majority of the studied coenopopulations (Suppl. material 2: Table 4).

Morphology and germination of seeds. The seeds of *P. sibirica* are ovoid and slightly flattened, measuring 2.6 to 3.1 mm in length, 1.5 to 2.0 mm in width, and 0.9 to 1.3 mm in thickness, with a yellowish-white aril (Fig. 3, Suppl. material 2: Table 4). The seed surface is dark brown or black-brown, nearly smooth and matte, and covered with white hairs. The weight of 1,000 seeds ranges from 2.57 to 3.51 g.

Fresh seeds of *P. sibirica* did not germinate in our experiment, but after dry storage for 6 months they had high germination rates – from 87% to 100%.

Figure 3. Seeds of *Polygala sibirica*.

Conclusions

P. sibirica, a common species found in the steppe regions of southern Western Siberia, permanently inhabits rocky mountain steppes that develop on well-lit, poorly grass-covered slopes. However, at the northern boundary of the species range, its populations are fragmented. *P. sibirica* is characterized by low-density coenopopulations, which exhibit an incomplete ontogenetic spectrum that may be single-peaked or bimodal, with a predominance of generative individuals and a low proportion of old age groups. The studied coenopopulations include young, maturing, and mature plants. The analysis of the morphological characteristics of *P. sibirica* revealed significant differences among individuals in different parts of the species range. In the humid conditions of Tomsk and Kemerovo regions, the largest plants develop long, branched shoots, as well as larger leaves and inflorescences. In the arid conditions of Central Altai, individuals tend to have a more compact morphology, producing fewer lateral shoots with smaller leaves and shorter inflorescences. *P. sibirica* reproduces exclusively by seed. In natural conditions, most flowers form viable fruits, with a prolonged fruit formation period. Despite the above-average level of reproductive potential, the species is generally characterized by a relatively low seed yield per shoot. The analysis of coenopopulations based on a set of ontogenetic, morphological, and reproductive characteristics revealed their sufficient stability. Even under anthropogenic pressure, they maintain the self-sustaining ability and long-term persistence within their range. The application of vegetation indices to assess the status of *P. sibirica* plants across different coenopopulations revealed the NDVI, WBI and ARI2 as uninformative, while the CCI, CRI1, VREI1 and ZMI demonstrated high sensitivity. The greenness indices CCI, VREI1 and ZMI exhibited a moderate positive correlation with LMA, a high correlation with the NBI, and a very high correlation with chlorophyll content.

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Supplementary material 1

Table 3. Morphological and physiological characteristics of *P. sibirica* in natural coenopopulations in the southern part of Western Siberia

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Data type: tables

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Supplementary material 2

Table 4. Reproductive characteristics of *P. sibirica* in natural coenopopulations in the southern part of Western Siberia

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Data type: tables

Link: https://journal.asu.ru/biol/article/view/18263/15667