Sexual and ontogenetic structures of gynodioecious *Geranium pseudosibiricum* J. Mayer (Geraniaceae) in Altai Mountains

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Abstract. *Geranium pseudosibiricum* J. Mayer. is a gynodioecious North and Central Asian species. The study was conducted in a grass meadow on the edge of larch forest in the Altai Republic. The aim was to study the sexual and ontogenetic structures of the coenopopulation of *G. pseudosibiricum.* The generative individual consists of shoots of only one sexual form: hermaphrodite with bisexual flowers and female with pistillate flowers. There are significant differences in the length of corolla: the length of bisexual flowers is 12.2 ± 0.29 mm, pistillate flowers 6.7 ± 0.19 mm. The bisexual flower has well-developed stamens and anthers; the pistillate flower has stamens with underdeveloped anthers. There are no significant differences between hermaphrodite and female individuals in the number of generative shoots and the number of flowers per individual. The ontogenetic structure of the coenopopulation of *G. pseudosibiricum* is dominated by pregenerative individuals − 53%. Good seed germination contributes to maintenance of sexual structure of the coenopopulation. The female frequency is 55% of the total number of generative plants. The detected morphological differences between bisexual and pistillate flowers and the high female frequency may indicate a high degree of sexual differentiation of *G. pseudosibiricum*.

In the family *Geraniaceae*, gynodioecy is widespread − a sexual type of plant polymorphism in which hermaphrodite individuals with bisexual flowers and female individuals with functionally pistillate flowers co-exist in the population [1]. Gynodioecy prevents self-pollination of plants and is an adaptation to cross-pollination, which forms the basis of outbreeding of individuals, and therefore promotes to intra-and inter-population variability of species of plants. Of special interest when considering the sexual polymorphism of plants is the study of the sexual structure of species, the ratio of different sexual phenotypes in natural populations. The sexual structure of coenopopulations of gynodioecious species can be constant or vary in different habitats [2]. The different ratio of sexual phenotypes is determined by the species-specific characteristics of plants. The female frequency in different species can vary widely: from a few percent to 50% or higher. The female frequency depends on the ecological and phytocenotic conditions of the biotope [3]. One of the main mechanisms for maintaining of female frequency is the advantage in

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seed reproduction of female phenotypes compared to hermaphrodites [4]. To find out the reasons that affect the sexual spectrum in a population, it is informative to study the seed germination and the participation of pregenerative individuals in the ontogenetic structure of coenopopulations. The study of the sexual structure of gynodioecious species allows us to expand the understanding of the evolutionary processes of transformation of gynodioecy towards dioecy [2, 5].

The gynodioecious species of genus *Geranium* differ in the degree of sexual differentiation, such as *Geranium sylvaticum* L. and *Geranium asiaticum* Serg. (*Geranium bifolium* Patrin.) [6, 7]. In the taxonomic system of species of genus *Geranium*, together with these species, in the section *Geranium* includes *G. pseudosibiricum* J. Mayer, for which gynodioecy is also noted. Among the individuals of *G. pseudosibiricum*, there are forms with large flowers and well-developed stamens and forms with small flowers and underdeveloped stamens [8, 9].

The aim of the work is to study the sexual and ontogenetic structures of the gynodioecious *Geranium pseudosibiricum* J. Mayer. in Altai Mountains.

G. pseudosibiricum is a species with a North and Central Asian range, found in forest and forest-steppe mountain zones on forest edges, meadow and steppe slopes, in fellings, in brushwoods of shrubs [8] (Peshkova, 1996). The study of sexual polymorphism of the species was carried out in the coenopopulation of grass meadow on the edge of larch forest in the Altai Republic. The total projective cover of the phytocoenosis herbage was 90% (*Avenula pubescens* (Huds.) Dumort, *Koeleria cristata* Pers, *Potentilla chrysantha* Trevir., *Spiraea chamaedryfolia* F. Schmidt, *Fragaria viridis* Duch, *G. pseudosibiricum*); projective cover of *G. pseudosibiricum* 5%. To find out the differences between the sexual phenotypes, the generative sphere of plants was studied. The length of corolla was measured using an eyepiece micrometer at an 8 × 1 magnification; the sample consisted of 20 specimens of bisexual and pistillate flowers in different individuals. The number of generative shoots and flowers in the inflorescences of mature generative plants was determined on 40 different-sex individuals. The ontogenetic structure of the coenopopulation was studied by common methods on a 1 × 10 м^2 transect [10]. The ontogenetic states of *G. pseudosibiricum* were distinguished by the following morphological features: the form and pattern of the dissection into the segments of leaf blade, the type of root system, the formation of rhizome, the formation of generative semi-rosette shoots, the change in the growth of individual, the particulation. The sexual structure of coenopopulations was determined by counting all generative individuals of different sexual types on transect with an area of 15 м^2, the sample was 105 individuals. All the research results were statistically processed [11].

Plants of *G. pseudosibiricum* form a short-rooted life form. Generative shoots are semi-netted, monocarpic, develop according to the dicyclic type. Synflorescence is a closed thyrsus of monohazia, paracladia are few, like synflorescence in plants of *G. sylvaticum* [12].

A study of the sexual differentiation of *G. pseudosibiricum* showed that each generative individual consists of shoots of only one sexual form: hermaphrodite with bisexual flowers and female with pistillate flowers. The bisexual flower is characterized by larger flowers with well-developed stamens and anthers; the pistillate flower is smaller and has stamens with underdeveloped anthers or without anthers. For the species, there is a significant difference in the length of the corolla in different types of flowers: the length of bisexual flowers is 12.2 ± 0.29 mm, pistillate flowers is 6.7 ± 0.19 mm. The size of the bisexual flower is 1.8 times larger than the pistillate flower.

Mature generative individuals of *G. pseudosibiricum* form from 1 to 7 reproductive semi-rosette shoots. Analysis did not reveal significant differences between hermaphrodite and female forms in terms of the number of generative shoots and the number of flowers

per individual. The number of shoots in hermaphrodites is slightly higher than in females and is, on average, 2.6 ± 0.38 pcs. and 2.1 ± 0.30 pcs., respectively. The number of flowers in hermaphrodites is also slightly higher than in females and averages 37.7 ± 4.70 and 33.9 ± 3.92, respectively. Thus, the hermaphrodite and female phenotypes are relatively similar in the ability to form reproductive organs.

The ontogenetic structure of the coenopopulation of *G. pseudosibiricum* was studied to determine the seed germination of plants (table). It is established that the coenopopulation is normal, individuals of all ontogenetic states are present in the population. Self-maintenance of the coenopopulation occurs by seed. In the ontogenetic structure, there is a significant predominance of individuals of the pregenerative state − 53%, well-represented immature and virginal individuals − 44%. Mature generative individuals have a significant share in the coenopopulation − 25%. A high percentage of immature and virginal individuals indicates the success of seed germination. Thus, we can conclude that *G. pseudosibiricum* is characterized by good seed germination, which contributes to maintenance of the sexual structure of the coenopopulation.

The study of the sexual structure of the coenopopulation of *G. pseudosibiricum* showed that the share of female is 55% of the total number of generative plants (table). This ratio of sexual phenotypes and the revealed morphological differences between bisexual and pistillate flowers of sexual individuals may indicate a high degree of sexual differentiation of *G. pseudosibiricum.*

Table 1. Ontogenetic structure and sexual structure of coenopopulation of *Geranium pseudosibiricum*

Ontogenetic groups, %*								Sexual forms, Pcs.	
j	im	v	g1	g2	g3	ss	s	hermaphrodites	females
9	22	22	7	25	2	10	3	47 (45%)	58 (55%)

Note. * − % of the total number of individuals. Ontogenetic states: j – juvenile, im – immature, v – virginal, g1 – young generative, g2 – mature generative, g3 – old generative, ss – subsenile, s – senile. In parentheses − % of the total number of generative individuals.

In the literature, there is information about gynodioecious species, such as *Gypsophila altissima* L., *Arenaria longifolia* L., which are characterized by a high female frequency about 50% [3]. Large-flowered hermaphrodite of these species form a small number of seeds, i.e. bisexual flowers are functionally male. The authors suggest that these gynodioecious species can be considered as close to dioecious plants [3]. In the taxonomic system of the relationship of genus *Geranium*, the species *G. pseudosibiricum* and *G. asiaticum* are united in one subsection of *Pseudosibirica* (section of *Geranium*) [9]. Previously, it was revealed that the gynodioecious *G. asiaticum*, based on the characteristics of hermaphrodite seed reproduction and female frequency in the coenopopulation of about 50%, belongs to species with a high degree of sexual differentiation [7]. Features of the morphology of different sexual flower types and the sexual spectrum of plants, namely, female frequency of about 50% in the coenopopulation, also suggest a high level of sexual differentiation for *G. pseudosibiricum*. The *Geranium* section also includes *Geranium sylvaticum* L., for which a low degree of sexual differentiation was revealed based on the characteristics of reproduction of different phenotypes and low female frequency [6, 7]. An additional comparison of the distribution of these species with different levels of gynodioecious traits showed that the widest range is indicated for *G. sylvaticum*: the Mediterranean, Northern and Eastern Europe, Northern, South-Western and Central Asia [8]. The species *G. pseudosibiricum* and *G. asiaticum* have

much narrower ranges: in Northern and Central Asia, respectively, and in Northern Asia [8].

Thus, the different degree of sexual differentiation of genus *Geranium* within the same taxonomic section suggests that evolutionary processes in expression of sexual polymorphism occur in genus *Geranium*. For further consideration of the issues related to gynodioecy of *G. pseudosibiricum*, additional studies of the seed reproduction of sexual phenotypes are necessary.

The results of the study further show that genus *Geranium* is a good model system for considering evolutionary transformations in plant reproduction systems.

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