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Sexual Forms and Their Ecological Correlates of Flowering Plants in Siberia

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Abstract—The flora of Siberia includes 4500 species, 815 genera, and 123 families of angiosperms. The causes of the relationship between sexual forms and such ecological and biological features of plants as the life form, the mode of pollination, pericarp's consistency, habitat type, zonal group, and the ecological group in relation to moistening were analyzed and discussed. For the first time, we demonstrated that gynomonoecy in the flora of Siberia was associated with a semiwoody growth form, pollination by wind, and propagation in zonal communities. It was revealed that gynodioecy in Siberia was associated with a semiwoody growth form, circumpolar or Eurasian distribution, and floodplain meadows. It was found that the ratio of dioecious and hermaphrodite plants in the ecological-biological complexes of species directly depends on the frequency of the abundance of species with endemic areas.

Keywords: sexual forms, Siberia, flora, ecological correlates
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INTRODUCTION

In recent decades, a large number of studies devoted to the detection of ecological correlations of sexual forms with a variety of morphological and biological features of plants have been produced [1–9]. The main attention in these studies is given to dioecy and monoecy. The identification of ecological correlations can contribute to an understanding of the origins of dioecy (and other sexual forms) and/or factors allowing the maintenance of dioecy in plant populations.

Many authors [1, 10–13] noted that, most often, dioecious species are woody plants of the tropical zone, with small flowers [3, 14] of green or white color [15], pollinated by unspecialized insects [16, 17], wind [2, 18, 19] or water [20]. We did not find studies dedicated to the identification of environmental correlations in the temperate zone and for other sexual forms. We determined the sex spectrum of the flora of Siberia earlier: hermaphroditism (3373 species, 75.0%), monoecy (336 species, 7.5%), gynomonoecy (269 species, 6.0%), gynodioecy (222 species, 5.0%), dioecy (181 Type, 4.0%), andromonoecy (108 species, 2.4%), androdioecy (five species, 0.1%), trioecy (five species, 0.1%), and trimonoecy (one species, 0.02%) [21, 22]. The purpose of this study was identification of the ecological correlations of sexual forms in the flora of Siberia.

MATERIALS AND METHODS

The list of species for study is based on the "Summary of the Flora of Siberia" [23]. According to the updated data, the flora of Siberia includes 4500 species, 815 genera, and 123 families of flowering plants. Sexual forms were determined in 4500 angiosperms with the use of herbarium specimens, literature sources, and field studies. The morphology of the flowers was studied on herbarium specimens stored in the herbarium of the Central Siberian Botanical Garden (Siberian Branch, Russian Academy of Sciences (NS)) for the verification of the sexual forms described in the literature and their determination for taxa with ambiguous or unknown data. Three types of literature sources were used: (1) "Flora of Siberia" [24], (2) a summary of P. Knuth [25], (3) the main systematic processing for taxa that were not considered in detail in "1" and "2." Plants were attributed to sexual forms based on modern approaches and recommendations [26]. Nine sexual forms were distinguished: hermaphroditism, monoecy, gynomonoecy, andromonoecy, trimonoecy, dioecy, gynodioecy, androdioecy, and trioecy. For each species, ecological-biological features are indicated based on the same literature sources that were used to determine sexual forms. The choice of certain ecological and biological features for analysis (life form, the mode of pollination, pericarp's consistency, habitat type, zonal group, the ecological group in relation to moistening) was associated with the traditional approach developed in the analysis of any flora and comparison of the obtained results with those available in the literature. In the absence of data on life forms, methods of pollination and types of fruits, herbarium specimens and field studies were used. For assessment of the degree of deviation of the actual values from the theoretically expected and the comparison of species frequency with sexual differentiation, the $\chi2$ criterion was used [27]. Point charts for the actual abundance/theoretical abundance of the studied sexual forms with certain ecological and biological features (see figure 1) are plotted.

All plants were classified into four groups of life forms (according to the classification of I.G. Serebryakova [28]): woody plants (trees, shrubs, dwarf shrubs), semiwoody plants (semishrubs, semidwarf shrubs), terrestrial (poly- and monocarpic), and hydrophytic grasses. The attribution of the species to a specific life form was carried out according to the data given in the "Flora of Siberia" [24], herbarium specimens stored in the herbarium of the Central Siberian Botanical Garden (Siberian Branch, Russian Academy of Sciences (NS)), and literary sources.

The types of habitats were classified according to the principles outlined by H. Walter [29], taking into account the entire habitat of the species. The name of the habitat type is based on the general configuration of the habitat (circumpolar, Eurasian, American-Asian, Asian, hemi- and endemics). Plants were attributed to a certain zone group (steppe, forest-steppe, forest, alpine, and azonal) according to the predominance principle using the study of L.I. Malyshev and G.A. Peshkova [30]. All plants were classified into five ecological groups according to the degree of humidity (xerophytes, mesoxerophytes and xeromesophytes, mesophytes, hygrophytes and hydrophytes) based on the study of A.Yu. Korolyuk [31]. The pericarp's consistency (dry or soft fruit) is presented according to the study of A.V. Bobrov et al. [32]. The mode of pollination and the flower color of most species are presented according to P. Knuth [25]. Three groups of plants were distinguished according to the mode of pollination: anemophilous, entomophilous, and hydrophilous. The distribution of species was characterized by the presence in floristic provinces composing flora of Asian Russia according to statistical convergent zoning [33].

RESULTS AND DISCUSSION

Association of sexual and life forms of plants. In the flora of Siberia, terrestrial herbs (86.9%) were predominant vital forms, woody plants occupy the second place (6.7%), and semiwoody plants and hydrophytic grasses composed 3.1 and 3.3%, respectively. The highest proportion of hermaphrodite species occurs in terrestrial grasses (77.9%), and the remaining groups of life forms had higher proportion of dioecious species (55.0–58.8%). The relationship between dioecy and woody plants ($\chi^2 = 611.98$; $P < 0.001$), gynomonoecy and semiwoody plants ($\chi^2 = 7.44$; $P < 0.01$), gynodioecy and semiwoody plants ($\chi^2 = 7.44$; $P < 0.01$), monoecy and hydrophytic grasses ($\chi^2 = 173.03$; $P < 0.001$), and hermaphroditism and terrestrial herbs ($\chi^2 = 8.06$; $P < 0.01$) (see figure 1) was detected.

Association of sexual plant forms with habitat types. The flora of Siberia consists mainly of species with Asian habitats (46.4%) and quite a few Eurasian (21.6%), circumpolar (13.7%), and endemic (14.8%) species. Plants with American-Asian habitats (3.4%) occur more rarely. Dioecious plants are most common among species with circumpolar and Eurasian habitats: 37.1 and 38.5%, respectively. On the contrary, among the species with Asian and endemic habitats, the proportion of nonhermaphrodite plants was extremely low: only 19.1 and 10.3%, respectively. The following positive association was identified: monoecious species most often had circumpolar habitats ($\chi^2 = 51.73$; $P < 0.001$), gynodioecious had circumpolar ($\chi^2 = 19.71$; $P < 0.001$) and Eurasian ($\chi^2 = 102.08$; $P < 0.001$), andromonoecious had Eurasian ($\chi^2 = 32.73$; $P < 0.001$), dioecious had Eurasian ($\chi^2 = 9.09$; $P < 0.01$) and American-Asian ($\chi^2 = 7.34$; $P < 0.01$), hermaphroditic had Asian ($\chi^2 = 8.96$; $P < 0.01$) and endemic habitats ($\chi^2 = 18.53$; $P < 0.001$) (see Fig. 1).

Association of sexual plant forms with the mode of pollination. Among the species of the flora of Siberia, plants with entomophilous pollination predominate (73.6%), the second place belongs to plants with anemophilous pollination (26.1%), and plants with hygrophilous pollination (0.3%) are extremely rare. The ratio of dioecious and hermaphrodite species depends on the mode of pollination of plants. In dioecious plants, pollen is most commonly transferred with water (86.7%) and less often by a variety of insects (19.1%). There is a link between gynomonoecy and anemophily ($\chi^2 = 30.02$; $P < 0.001$), monoecy with anemophily ($\chi^2 = 449.50$; $P < 0.001$) and hydrophily ($\chi2 = 55.44$; $P < 0.001$), dioecy with hydrophily ($\chi^2 = 19.12$; $P < 0.001$), and hermaphroditism with entomophily ($\chi^2 = 15.39$; $P < 0.001$) (see figure 1).

Associations of sexual forms with zonal groups. In the flora of Siberia, two types of communities are the most common: steppe (25.7%) and highland (26.6%). There are many boreal species (18.6%), and the number of species of forest-steppe and azonal complexes is approximately the same: 14.0 and 15.1%, respectively. The ratio of dioecious and hermaphrodite species varied in different zonal groups: most often steppe and high-mountainous species are hermaphroditic plants (81.2 and 78.7%, respectively). The remaining groups had a lower abundance of hermaphroditic plants: from 68.0 to 71.6%. The abundance of hermaphrodite plants in steppe and alpine vegetation types was significantly higher than in other zonal complexes ($4.74 < \chi^2 < 17.62$; $0.03 < P < 0.001$). The following positive associations were identified: monoecy is asso-

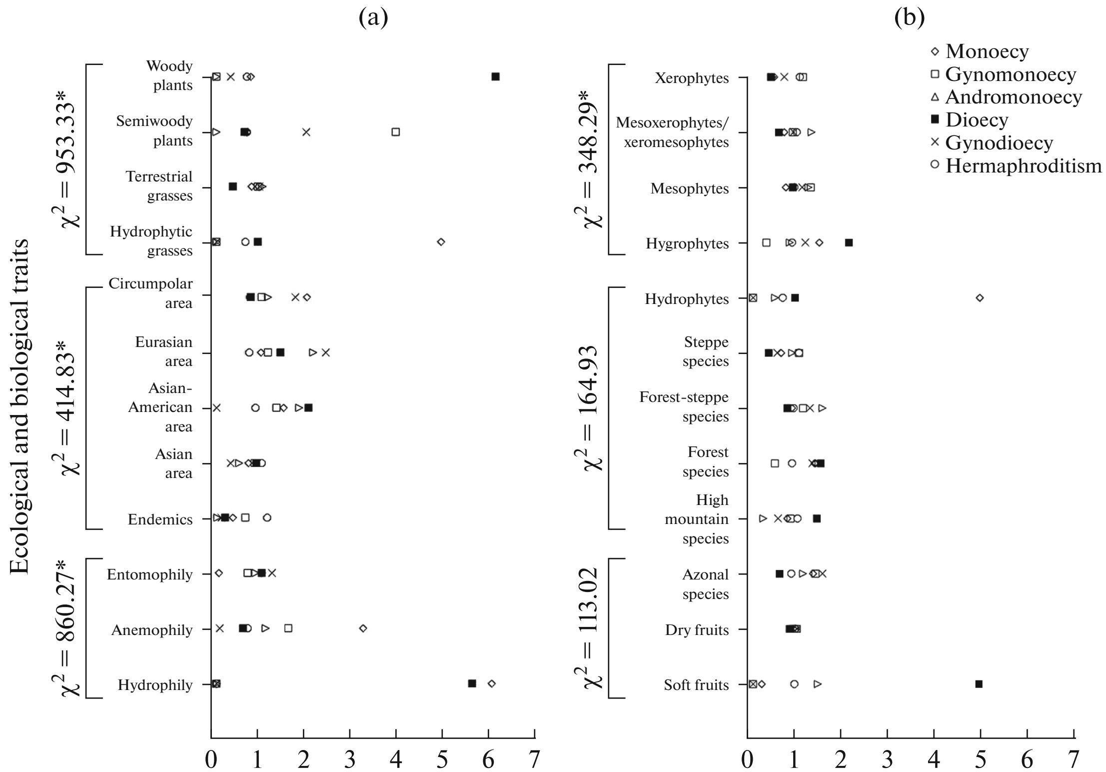

Fig. 1. Ratio of actual and expected abundance of different sexual forms with certain ecological and biological traits. The value of the ratio > 1 indicates that a particular sexual form is associated with this trait; χ^2 indicates the reliability of the differences; *$P < 0.001$; 1–7 are the ratio of actual and expected abundances of species.

ciated with boreal ($\chi^2 = 10.48$; $P < 0.01$) and azonal ($\chi^2 = 7.21$; $P < 0.01$) communities, dioecy with boreal ($\chi^2 = 10.04$; $P < 0.01$) and high-mountain ($\chi^2 = 10.01$; $P < 0.01$), gynomonoecy with azonal ($\chi^2 = 7.34$; $P < 0.01$), gynodioecy with azonal ($\chi^2 = 11.21$; $P < 0.001$) phytocenoses. Hermaphrodite plants were most often found in steppe communities ($\chi^2 = 6.11$; $P < 0.025$) (see Fig. 1).

Association of sexual forms of plants with environmental groups. Among the plants of the flora of Siberia, mesophytes (34.0%) and xerophytes (25.3%) were found most often. The number of mezoxerophytes and xeromesophytes, as well as hygrophytes, is approximately the same: 18.6 and 18.8%, respectively. Less common species are hydrophytes (3.3%). The proportion of dioecious plants increases from 17.9% in xerophytes to 45.0% in hydrophytes with increase in humidity of habitats. The following positive associations were established: monoecy with hygro- and hydrophytes ($\chi^2 = 215.83$; $P < 0.001$), dioecy with hygrophytes ($\chi^2 = 60.94$; $P < 0.001$), and hermaphroditism with xerophytes ($\chi^2 = 20.08$; $P < 0.001$) (see figure 1).

Association of the sexual forms of plants with the pericarp's consistency. Plants with dry fruits dominate in the flora of Siberia (96.9%). The frequency index of dioecious species is approximately the same among plants with dry and soft fruits: 75.0 and 73.8%, respectively. A positive association was found between dioecy and soft fruits ($\chi^2 = 90.75$; $P < 0.001$) (see Fig. 1).

Ecological correlations in plants. Analysis of the associations between the ecological and biological characteristics of plants and the existence of one or another form of sexual differentiation showed that the sexual expression most often occurs in taxa with a combination of a certain set of characteristics [6, 9, 15, 34]. We can assume that this complex of ecological and biological traits was not the cause of the appearance of sexual differentiation in a given taxon. Most probably, the sexual differentiation in taxa with such a combination of traits is determined by advantages provided by the sexual form itself—the guaranteed predominance of outbreeding and the absence of significant decrease in the degree of inbreeding depression. As a result, taxa with a certain sexual differentiation and a listed set of traits are evolutionarily more successful, which is expressed as wide range of the species in comparison with the related taxa with hermaphrodite flowers.

Ecological correlations of dioecy. In the flora of Siberia, dioecy positively correlates with the woody growth form, soft fruits, Eurasian or American-Asian distribution, boreal or alpine communities, the transfer of pollen by water, and humidified habitats. The association of dioecy with woody growth form, soft fruits, and pollination by water was also described for tropical and sub-tropical floras [6]. The proportion of woody plants with dioecy in Siberia (32.7%; [34]) is comparable with similar data for tropical floras (36.0%).

For Siberia, the revealed correlations of dioecy with woody growth form, Eurasian or American-Asian distribution, boreal or high-mountain communities, and humid habitats were due to the widespread occurrence of the family Salicaceae in the temperate zone of the northern hemisphere (84 species). In places of increased humidity, along the banks of water reservoirs and in river valleys, willows almost everywhere belonged to the dominant plants. The participation of Salicaceae in the vegetation of the forest-tundra, tundra, in the subalpine and alpine belts of the mountains was especially high. According to our data, the increased proportion of dioecy (7.3–7.4%) in the three provinces (Siberian arctic-hyparctic, Siberian northeastern mountain- hyparctic, and Ural-West-Siberian boreal) was exclusively due to the wide distribution and dominance of Salicaceae in their vegetation.

In general, plants with soft fruits are quite rare in the flora of Siberia. Despite the approximately equal frequency of occurrence of dioeciousness in plants with dry and soft fruits (75.0 and 73.8%, respectively), a positive association between dioecy and the presence of soft pericarp was revealed. This association was explained by the presence of soft fruits in a number of dioecy species from the families Asparagaceae, Grossulariaceae, Rhamnaceae, Hydrocharitaceae, etc., although only 15.5% of dioecy plants had soft fruits in the flora of Siberia.

Ecological correlations of monoecy. In the flora of Siberia, a high frequency index of monoecy (7.5%), which, after hermaphroditism, is considered as the most common sexual form was noted. In tropical and subtropical flora, associations of monoecy with dry fruits and small, unattractive flowers was found [6]. The revealed correlations of monoecy with hydrophytic grasses, pollination by wind, and propagation in the boreal communities of the Holarctic region were due to the species of families Cyperaceae (184 species), Euphorbiaceae (34 species), Chenopodiaceae (26 species), Asteraceae (25 species), and Betulaceae (17 species). *Carex* species are most typical for the temperate and cold belts of the northern hemisphere. They occur almost everywhere and are largely involved in the formation of vegetation, especially in wet and swamp biotopes. Apart from the Euphorbiaceae family, all other monoecy species are anemophilous. Xenogamy of anemophilous monoecious plants provides definite protogyny (earlier flowering of pistillate flowers) and a mutual arrangement of staminate and pistillate flowers (pistillate flowers are usually located in the lower part of the inflorescence), and a self-incompatibility system. However, many of them are characterized by a combination of different modes of pollination (autogamy and xenogamy), which increases the probability of seed formation under unfavorable conditions. A high proportion of monoecy in hydrophilic plants (60.0%) is due to representatives of the families Zannichelliaceae, Najadaceae, and Ceratophyllaceae.

Ecological correlations of gynomonoecy. According to the number of species in the flora of Siberia (6.0%), ginomonoecy belongs to the third most common sexual form (after hermaphroditism and monoecy). We do not know the literature data on the ecological correlations of gynomonoecy with morphological or biological features of plants, which makes comparison with other floras impossible.

Ginomonoecy in the flora of Siberia is associated with a semiwoody growth form, pollination by wind, and distribution in azonal communities. The revealed correlations of gynomonoecy with a semiwoody growth form and pollination by wind were due to the large number of *Artemisia* (Asteraceae) and Chenopodiaceae species adapted to life in desert steppes and semiarid communities. Anemophily in these species is promoted by definite protogyny and a rather long preservation of viability of stigmas (from 3 to 8 days) of bisexual and pistillate flowers. The association with the azonal complex (floodplain meadows) was determined by the high number of oligotype genera of Asteraceae (*Achillea*, *Erigeron*, *Jacobea*, *Ligularia*, *Senecio*, etc.). These plants have entomophilous pollination. Geytonogamy is limited and xenogamy prevails due to the wide distribution of sporophytic self-incompatibility systems in Asteraceae [35].

Ecological correlations of gynodioecy. Special attention should be paid to the high proportion of gynodioecious species in the flora of Siberia (5.0%). Their share is very rarely indicated by researchers for different floras, which is, in most cases, due to the inclusion of this reproductive system in the widely understood group of dioecious plants (actually dioecious, gynodioecious ,and androdioecious species). X. Delannay [36] showed that 7.5% of the species in Belgium and Luxembourg were gynodioecious, and E.I. Demyanova [37] revealed a high proportion (10.8–11.9%) of gynodioecy in the forest-steppe and forest flora of the Urals. According to our data, in two provinces of Siberia (Ural-West-Siberian boreal and West Siberian hemiboreal), the abundance of gynodietic plants reaches 8.5%. The wide distribution of gynodioecy probably reflects the overall high proportion of this sexual form in angiosperms of the temperate zone of the Earth. Indirect confirmation of this assumption is the rare occurrence of gynodioecy in tropical floras: from 0.2% in the flora of New Caledonia [6] to 3.8% in the flora of Hawaii [38].

Gynodioecy in the flora of Siberia is associated with a semiarid growth form, circumpolar or Eurasian distribution, and floodplain meadows. The association with a semiwoody growth form was due to a large number of species of the genus *Thymus* (Lamiaceae). Distribution of thymes is associated with the mountain systems of Siberia (Altai, Sayan Mountains, etc.), where they were confined to open, stony, gravelly, and sandy substrates. The association of gynodioecy with circumpolar and Eurasian distribution was due to such genera as *Geranium*, *Metha*, *Campanula*, *Cirsium*, *Dianthus*, *Sinene*, *Stellaria*, etc. The association of gynodioecy with floodplain meadows was due to the wide distribution of a number of genera Lamiaceae (*Lycopus*, *Mentha*, *Stachys*, etc.) and Caryophyllaceae (*Silene*, *Stellaria*, etc.) in the humid biotopes.

Ecological correlations of andromonoecy. In the flora of Siberia, andromonoecy is associated with Eurasian distribution, forest-steppe, and boreal communities. The listed associations were due to the high proportion of umbellate and a number of grasses possessing such ecological and biological traits. Andromonoecy is more common in umbellate than it is reflected in systematic and floral studies [9].

Ecological correlations of hermaphroditism. The most common sexual form in plants of the flora of Siberia is hermaphroditism. It is associated with a grassy growth form, xerophytes, steppe communities, pollination by insects, Asian or endemic propagation. All these associations were due to the wide distribution of the genera *Oxytropis* (132 species), *Astragalus* (100 species), *Allium* (61 species), *Hieracium* (55 species), *Saussurea* (52 species), *Alchemilla* (50 species), etc. with hermaphrodite flowers in Siberia.

Endemism and hermaphroditism. In the flora of Siberia, there is a stable positive association between hermaphroditism of plants and their endemic condition. Almost 90% of the endemics of Siberia form exclusively hermaphrodite flowers.

The association between sexual forms and endemism was noted by other authors [6], except for tropical floras. It was shown that, for the studied tropical floras, the frequency index of dioecy and monoecy was not significantly different in nonendemic and endemic species. It can be assumed that allochthonous and autochthonous speciation under the given conditions (tropical flora) led to the appearance of a sufficiently high proportion of dioecy and monoecy in plants. In temperate latitudes, taxa with hermaphroditic flowers appeared more often, probably, due to the autochthonous speciation.

The proportion of endemism is particularly high in the steppe and high-mountain communities: 25.8 and 19.2%, respectively. In other types of communities (forest-steppe, boreal, and azonal), the frequency of endemism is much lower: from 6.3 to 8.9%. A high degree of endemism of the flora of steppes and highlands was associated with their geographical or ecological isolation.

Steppes of southern Siberia are confined to intermountain basins, extended valleys of rivers and foothills. There are no zonal steppes on the territory, except for a small strip on the border with Mongolia (Ubsunur Hollow). In the past, the steppes stretched as a continuous strip from the south of Europe to the coast of the Pacific Ocean [30]. Long-term isolation of steppe habitats, surrounded by a wide strip of forests, and the dissected character of the relief favored the formation of new species under given conditions. Genera *Oxytropis* (41 species), *Astragalus* (14), *Allium* (13), *Potentilla* (ten), *Eritrichium* (seven), *Leymus* (six), *Papaver* (six), *Corispermum* (six), etc. represented mainly or exclusively by the hermaphroditic species are among the steppe endemics of Siberia.

The flora of the high mountain regions is characterized by the high heterogeneity of its constituent species, combining alpine, arctoalpine, montane, and arctalpine plants. Among alpine plants, the share of endemism was almost 1.4 times higher than among arctoalpine and hyparctomontane plants. Alpine species were characterized by predominance of autochthonous speciation due to high ecological and geographic isolation, and, except for arctoalpine and hyparctomontane plants, allochthonous processes played an important role. Genera *Oxytropis* (20 species), *Alchemilla* (17), *Saussurea* (11), *Poa* (ten), *Draba* (ten), *Papaver* (ten), *Saxifraga* (nine), *Taraxacum* (nine), etc., represented almost exclusively by species with hermaphroditic flowers, are among the endemics of the high mountains of Siberia.

Moderate and arctic zones are most favorable for the appearance and existence of hermaphroditism. Most likely, it is a general pattern of distribution of sexual differentiation in plants by zones. Therefore, among the endemics in the temperate zone of Siberia, the proportion of hermaphroditic species is high. In addition, there are lot endemics in the steppe and high-arctic conditions; as a result, we observed an increased proportion of hermaphrodites there.

CONCLUSIONS

A number of ecological and biological features of plants of the flora of Siberia correlate with their sexual forms. The existence of such associations is determined by the prevalence of plants with a certain ecological and biological peculiarity among the representatives of one or another sexual form. In the flora of Siberia, the dioecy positively correlated with the tree growth form, soft fruits, Eurasian or American-Asian distribution, boreal or alpine communities, the transfer of pollen by water, and humid habitats, which is due to the widespread distribution of the Salicaceae family. The high abundance of representatives of the families Cyperaceae, Euphorbiaceae, Chenopodiaceae, Asteraceae, and Betulaceae determined the presence of a positive correlation between monoecy and hydrophytic grasses, pollination by wind or water, and distribution in the boreal communities of the Holarctic region. Gynomonoecy in the flora of Siberia is associated with a semiwoody growth form, pollination by wind, and distribution in azonal communities due to the ecological and biological characteristics of the representatives of the genus *Artemisia* (Asteraceae) and the family Chenopodiaceae. Gynodioecy in the flora of Siberia correlates with the semiwoody growth form (due to *Thymus* species), circumpolar or Eurasian distribution (many species of the genera *Geranium*, *Mentha*, *Campanula*, *Cirsium*, *Dianthus*, etc.), and floodplain meadows (for example, genera *Lycopus*, *Mentha*, *Silene*, *Stachys*, *Stellaria*, etc.). Andromonoecy in the flora of Siberia positively correlates with the Eurasian distribution and forest-steppe and boreal communities, since such features are characteristic for many representatives of the families Apiaceae and Poaceae. The ratio of dioecious and hermaphroditic plants in the ecological and biological complexes of species directly depends on the frequency index of species with endemic habitats in them, since, in the flora of Siberia, a stable positive association between hermaphroditism of plants and their endemic state was revealed.

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