ISSN 1062-3590, Biology Bulletin, 2020, Vol. 47, No. 10, pp. 1277–1280. © Pleiades Publishing, Inc., 2020.
Russian Text © The Author(s), 2019, published in Povolzhskii Ekologicheskii Zhurnal, 2019, No. 1, pp. 106–113.

SHORT COMMUNICATIONS

# Variability of the Gender Spectrum in *Origanum vulgare* L. (Lamiaceae, Magnoliopsida)

**N. I. Gordeeva[a], * and E. K. Komarevtseva[a], ****

[a]*Central Siberian Botanical Garden, Siberian Branch, Russian Academy of Sciences, Novosibirsk, 630090 Russia*

**e-mail: nataly.gordeeva@gmail.com*

***e-mail: elizavetakomarevceva@yandex.ru*

Received June 1, 2018; revised October 19 , 2018; accepted November 21, 2018

**Abstract**—*Origanum vulgare* L. is a gynodioecious species, populations of which include hermaphroditic plants with bisexual flowers and female plants with pistillate flowers. This is a holarctic forest–steppe species belonging to herbaceous perennial plants. The variability of the female-to-hermaphrodite ratio in 26 coenopopulations of *O. vulgare* from different habitats has been studied. The data on eight populations were obtained in the course of the authors' studies in southern Siberia, while 18 populations from Eastern Europe were analyzed based on the published data of other researchers. For all habitats, the projective cover of the species was determined according to the standard geobotanical methods. The plants studied represented a long-rhizome life form, so a partial shoot or a partial shrub (ramets) was used as a countable unit. The gender structure of coenopopulations was studied by counting generative plants within transects with an area of 10 to 20 $m^2$. For each population, the total number of plants to be counted was at least 90. A significant positive correlation between the projective cover of *O. vulgare* in a phytocenosis and the percentage of female plants in coenopopulations was revealed (the Pearson correlation coefficient $r = 0.86$, $p = 0.001$). The ANOVA analysis showed no significant difference in the percentage of female plants in six different habitats ($F_{emp} = 3.36$; $F_{crit\ 5.5} = 5.1$; $p = 0.05$). Taking into account the morphological and reproductive features of different genders of *O. vulgare,* one can suggest that an increase in the projective cover of the species in a phytocoenosis and an increase in the percentage of female plants in the gender spectrum depend on successful seed regeneration in the phytocenosis.

*Keywords*: *Origanum vulgare*, gynodioecy, gender spectrum, projective cover

**DOI:** 10.1134/S1062359020100076

*Origanum vulgare* L. (Lamiaceae), or common origanum, is a gynodioecious plant, in which populations of hermaphroditic plants with bisexual flowers and female plants with pistillate flowers grow together (Darwin, 1948; Demyanova, 1990). Ginodioecy prevents self-pollination of plants and increases the intra- and interpopulation variability of a species. Gynodioecious species often demonstrate a significant variation in the ratio between female and hermaphroditic individuals in different habitats (phytocoenoses). To date, there is no clear understanding of the reasons influencing the proportion of gender forms of plants (Dufay and Billard, 2012).

The purpose of this study was investigation of the variability of the ratio between female and hermaphroditic plants in *O. vulgare* populations from different habitats.

*O. vulgare* is a holarctic forest–steppe species; the habitats of this herbaceous perennial plant include dry and steppe meadows, thin forests, shrubs, and rocky slopes (Doron'kin, 1997). To analyze the gender structure of *O. vulgare,* we used our own data on eight coenopopulations (CPs) from different habitats of western Siberia and Gornyi Altai (Table 1), as well as the published data on 18 CPs from Eastern Europe (Godin and Evdokimova, 2017). For all habitats, the projective cover of the species was determined according to common geobotanical methods. The gender structure was studied using transects with an area of 10–20 $m^2$. Since plants from the studied CPs represented a long-rhizome life form, a partial shoot or partial shrub (ramets) was considered as a countable unit (an individual). For each CP, the total number of individuals to be counted was no less than 90. To study the effect of growing conditions in different habitats (phytocoenoses) on the gender proportion of *O. vulgare,* a single-factor analysis of variance (ANOVA) was carried out using phytocoenoses variants as an independent variable and the percentage of female plants in a CP as a dependent variable. Since the studied variants of phytocoenoses were represented by different numbers of replications (2–10, see Table 1), for each of them, the ANOVA was performed using 2–3 replications characterized by the minimum, average, and

**Table 1.** Projective cover of *Origanum vulgare* and the percentage of female plants of the species in the habitats of western Siberia and Eastern Europe

| CP no. | Phytocoenosis, total PC, geographic location | PC of the species, % | Number of generative plants | % of female plants |
|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 |
| 1 | Burch–pine motley grass forest, 100%, Novosibirsk oblast | 1 | 112 | 18 |
| 2 | Dry motley grass–cereal meadow on a rocky slope, 100%, Altai Republic | 3 | 214 | 18 |
| 3 | Dry motley grass–cereal grazed meadow, 100%, Altai Republic | 3 | 104 | 24 |
| 4 | Dry motley grass–cereal meadow, 100%, Altai krai | 5 | 115 | 26 |
| 5 | Dry motley grass–cereal meadow, 100%, Altai Republic | 8 | 145 | 31 |
| 6 | Dry motley grass–cereal meadow on fallow land, 90%, Novosibirsk oblast | 10 | 253 | 36 |
| 7 | Dry motley grass–cereal meadow on fallow land, 100%, Novosibirsk oblast | 10 | 108 | 41 |
| 8 | Bushed motley grass–cereal meadow on a rocky slope, 100%, Altai Republic | 15 | 92 | 41 |
| 9* | Motley grass–cereal steppe meadow, 95%, Moscow oblast | 3 | 102 | 18 |
| 10* | Motley grass–cereal steppe meadow, 95%, Moscow oblast | 2 | 104 | 14 |
| 11* | Motley grass–cereal steppe meadow, 95%, Moscow oblast | 1 | 127 | 24 |
| 12* | Motley grass–cereal steppe meadow, 100%, Moscow oblast | 1 | 101 | 17 |
| 13* | Cereal–motley grass steppe meadow, 98%, Moscow oblast | 1 | 121 | 22 |
| 14* | Motley grass–cereal steppe meadow, 95%, Moscow oblast | 2 | 103 | 17 |
| 15* | Motley grass–cereal steppe meadow, 100%, Moscow oblast | 1 | 101 | 20 |
| 16* | Motley grass–cereal steppe meadow, 95%, Moscow oblast | 2 | 105 | 15 |
| 17* | Dry motley grass–cereal meadow, 100%, Moscow oblast | 2 | 107 | 13 |
| 18* | Dry motley grass–cereal meadow, 95%, Moscow oblast | 1 | 108 | 17 |
| 19* | Dry motley grass–cereal meadow, 100%, Moscow oblast | 1 | 101 | 16 |
| 20* | Motley grass–cereal forest meadow, 95%, Moscow oblast | 2 | 127 | 23 |
| 21* | Motley grass forest meadow on the after-forest slope, 100%, Moscow oblast | 1 | 256 | 23 |
| 22* | Cereal–motley grass steppe meadow, 100%, Moscow oblast | 1 | 195 | 23 |
| 23* | Motley grass–cereal steppe meadow, 95%, Moscow oblast | 2 | 130 | 21 |
| 24* | Motley grass forest meadow on the after-forest slope, 100%, Moscow oblast | 1 | 103 | 15 |
| 25* | Motley grass–cereal forest meadow, 90%, Moscow oblast | 1 | 249 | 23 |
| 26* | Dry motley grass–cereal meadow, 95%, Moscow oblast | 2 | 197 | 24 |

* According to published data (Godin and Evdokimova, 2017). CP, coenopopulation; PC, projective cover (%).

maximum values of the dependent variable (percentage of female plants). The statistical treatment of data was carried out using common methods (Zaitsev, 1984).

*O. vulgare* belongs to gynodioecious plants, so a significant variation in the ratio between two gender forms is observed: the percentage of female plants in CPs may vary from 18–25 to 40–45% (Anisimova and Demyanova, 2007; Gordeeva, 2015a). To determine the reasons for such variability, we earlier analyzed the peculiarities of the morphology, ontogenesis, and reproduction of female and germaphroditic plants in different habitats (Gordeeva, 2015a). The analysis showed that plants of different genders did not differ in their morphological traits, such as the number of generative shoots and growing rhizomes in a partial shrub, annual growth of plagiotropic rhizomes, conditional age of a partial plant, the length of the generative shoot

**Table 2.** Percentage of female plants of *Origanum vulgare* in different habitats of western Siberia and Eastern Europe

| No. | Phytocoenosis | Percentage of female plants | |
|---|---|---|---|
| 1 | Dry motley grass–cereal meadow, Gornyi Altai (CP2, CP5) | 18 | 31 |
| 2 | Motley grass–cereal steppe meadow, Moscow oblast (CP10, CP11) | 14 | 24 |
| 3 | Dry motley grass–cereal meadow, Moscow oblast (CP17, CP26) | 13 | 24 |
| 4 | Motley grass–cereal forest meadow, Moscow oblast (CP20, CP25) | 23 | 23 |
| 5 | Motley grass forest meadow, Moscow oblast (CP24, CP21) | 15 | 23 |
| 6 | Motley grass–cereal meadow on fallow land, Novosibirsk oblast (CP6, CP7) | 36 | 41 |
| | $F_{emp} = 3.3$, $F_{crit\ 5.5} = 5.1$ ($p = 0.05$) | | |

**Table 3.** Percentage of female plants of *Origanum vulgare* in western Siberia phytocoenoses with high and low projective cover of the species

| Phytocoenosis | Percentage of female plants | | |
|---|---|---|---|
| Dry motley grass–cereal meadow, Altai Republic (CP2, CP3, CP4) | 18 | 24 | 26 |
| Motley grass–cereal meadow on fallow land, Novosibirsk oblast (CP6, CP7, CP8) | 36 | 41 | 41 |
| $F_{emp} = 313$, $F_{crit\ 1.2} = 18.5$ ($p = 0.05$) | | | |

and inflorescence, and the number of paracladia per inflorescence. *O. vulgare* is characterized by a reproductive compensation; i.e., female plants have a higher seed productivity than hermaphroditic plants (Darwin, 1948). The real seed productivity of a generative shoot in female plants is 1.6 times higher than that in hermaphroditic plants (Gordeeva, 2015b). It is known that self-pollination of hermaphroditic plants results in the formation of a hermaphroditic progeny, while a progeny formed by crossing of female and hermaphroditic plants contains >40% female individuals (Lewis and Crowe, 1956). The higher seed productivity of female plants makes it possible to suppose a tendency toward an increase in the percentage of female plants in CPs.

In studying the gender structure of *O. vulgare* CPs, we found that an increase in the projective cover of the species causes changes in the percentage of female plants in CPs. Using our own data and data published by other authors (Godin and Evdokimova, 2017), correlation analysis for these two indices was carried out (Table 1). Calculation of the Pearson correlation coefficient ($r = 0.86$, $p = 0.001$) showed the presence of a significant correlation between the projective cover and the percentage of female plants in the CPs of the species studied.

To determine the reasons for such a correlation, we analyzed the peculiarities of plant renewal in the phytocoenoses studied. In earlier studies of the ontogenetic structure of *O. vulgare* CPs, it was found that the self-maintenance of CPs occurs mainly vegetatively; a seed origin was typical only for juvenile, immature, and single virginile individuals (Gordeeva, 2015a). In most of the CPs studied, the percentage of seed plants was less than 5% of the total number of plants. Germination of seeds and development of seedlings were hindered by accumulation of a thick layer of plant debris in the soil litter. A high percentage (61.1%) of seed reproduction was observed in the *O. vulgare* CP revealed on a bushed motley grass–cereal meadow located on a rocky slope (Table 1, CP8). Most likely, the conditions of this phytocoenosis were favorable for germination of plants due to the thin soil litter layer on a steep rocky slope.

The majority of CPs with a low seed reproduction (CP1–CP5) was characterized by a low projective cover and a low percentage of female plants in the total population (see Table 1). At the same time, CP8 (high seed reproduction) was characterized by a higher projective cover (15%) and an increased percentage of female plants (41%). Note that CP6 and CP7 located on disturbed fallow habitats were characterized by low seed reproduction, but a relatively high projective cover (10%) and percentage of female plants (36–41%). Most likely, due to the disturbed coenosis, this location earlier was favorable for mass seed reproduction of *O. vulgare,* but later the tillage was overgrown, and a large layer of plant debris was accumulated that prevented germination of seeds. A high percentage of female plants could have existed here since the time of the seed invasion of this species.

Thus, the results of our studies allow us to suppose that an increase in the projective cover and the percentage of female plants in *O. vulgare* CPs depends on the successful growth of seed reproduction of the species in the present or, probably, the recent past of the corresponding phytocoenoses. In this case, female

**Table 4.** Percentage of female plants of *Origanum vulgare* in western Siberia and Eastern Europe phytocoenoses with high and low projective cover of the species

| Phytocoenosis | Percentage of female plants | | |
|---|---|---|---|
| Dry motley grass–cereal meadow, Moscow oblast (CP17, CP18, CP26) | 13 | 17 | 24 |
| Motley grass–cereal meadow on fallow land, Novosibirsk oblast (CP6, CP7, CP8) | 36 | 41 | 41 |
| $F_{emp} = 93$, $F_{crit\ 1.2} = 18.5$ ($p = 0.05$) | | | |

plants characterized by higher seed productivity come over hermaphroditic plants.

The ANOVA analysis was performed for six habitats (phytocoenoses) from western Siberia and Eastern Europe (Table 2); in addition, a comparison between the phytocoenosis pairs was made including three replications with a high projective cover from Western Siberia and three replications with a low projective cover from Eastern Europe or Western Siberia (Tables 3, 4). The result of this analysis showed that the difference in the percentage of female plants in six habitat variants was not significant: $F_{emp} = 3.36$ ($F_{crit\ 5.5} = 5.1$). However, phytocoenoses characterized by a high projective cover of *O. vulgare* significantly differed in the percentage of female plants from the communities with a low species participation; such a difference was observed in both the western Siberia ($F_{emp} = 93.93$, $F_{crit\ 1.2} = 18.5$) and Eastern Europe ($F_{emp} = 313$, $F_{crit\ 1.2} = 18.5$) variants.

Thus, this study showed that the variability of the gender spectrum of *O. vulgare* does not depend directly on different habitats (phytocoenoses). On the other hand, one can speak about the presence of a relationship between the percentage of female plants in a CP and the projective cover of the species in a phytocoenosis.

We revealed a reliable positive correlation between the projective cover and the percentage of female plants in CPs of *O. vulgare* (Pearson correlation coefficient $r = 0.86$, $p = 0.001$). The performed ANOVA did not show any significant difference between six different habitats in relation to the percentage of female plants ($F_{emp} = 3.36$, $F_{crit\ 5.5} = 5.1$, $p = 0.05$). A comparison of phytocoenoses with high and low projective cover of *O. vulgare* showed a significant difference between the variants from western Siberia and Eastern Europe in relation to the percentage of female plants in a CP ($F_{emp} = 93.93$ and $F_{emp} = 313$, respectively; $F_{crit\ 1.2} = 18.5$, $p = 0.05$). Taking into account the peculiarities of the morphology and reproductive biology of different *O. vulgare* genders, one can suppose that the increase in the projective cover of the species in a phytocoenosis and the percentage of female plants in the CPs depends on the success of seed reproduction in a coenosis.

## ACKNOWLEDGMENTS

This work was performed within the framework of a State Assignment of the Central Siberian Botanical Garden (project no. AAA-A17-117012610053-9).

## COMPLIANCE WITH ETHICAL STANDARDS

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

## REFERENCES

Anisimova, A.G. and Demyanova, E.I., Morphologic-anatomical features of *Origanum vulgare* (Lamiaceae) sex forms, *Rastit. Resur.*, 2007, vol. 43, no. 1, pp. 36–45.

Darwin, Ch., *Razlichnye formy tsvetov* (Different Forms of Flowers), Moscow: *Akad. Nauk SSSR*, 1948, vol. 7, pp. 31–251.

Dem'yanova, E.I., Sexual polymorphism of flowering plants, *Extended Abstract of Doctoral (Biol.) Dissertation*, Moscow, 1990.

Doronkin, V.M., Genus *Origanum* L., in *Flora Sibiri* (Flora of Siberia), Novosibirsk: Nauka, 1997, vol. 11, pp. 204–205.

Dufay, M. and Billard, E., How much better are females? The occurrence of female advantage, its proximal causes and its variation within and among gynodioecious species, *Ann. Bot.*, 2012, vol. 109, no. 3, pp. 505–519.

Godin, V.N. and Evdokimova, T.A., Sexual structure of *Origanum vulgare* populations in Moscow oblast, *Izv. Vyssh. Uchebn. Zaved. Povolzh. Reg., Ser. Estestv. Nauki*, 2017, no. 4, pp. 35–45.

Gordeeva, N.I., Ontogenetic and sexual structure of *Origanum vulgare* L. (Lamiaceae), . *Vestn. Mosk. Gos. Obl. Univ., Ser. Estestv. Nauki*, 2015a, no. 5, pp. 13–19.

Gordeeva, N.I., Seed productivity and germination of *Origanum vulgare*, Vestn. Altai. Gos. Agrar. Univ., 2015b, no. 11, pp. 87–90.

Lewis, D. and Crowe, L.K., The genetic and evolution of gynodioecy, *Evolution*, 1956, vol. 10, no. 2, pp. 115–125.

Zaitsev, G.N., *Matematicheskaya statistika v eksperimental'noi botanike* (Mathematical Statistics in Experimental Botany), Moscow: Nauka, 1984.

*Translated by N. Statsyuk*