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SEXUAL DIFFERENTIATION OF *RHODIOLA ROSEA* L. POPULATIONS IN THE HIGH-MOUNTAIN ZONE OF THE UKRAINIAN CARPATHIANS

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Background. Individual (morphological) and group parameters (the number of male and female individuals, their sex ratio, and the range of sex ratio displacement) are an important indicator of sexual differentiation of *Rhodiola rosea* L. populations. To date, indicators of these parameters in natural plant populations have not been studied sufficiently. Therefore, for the analysis of the state of the populations of the species, it is important to study the parameters of their sexual differentiation and the main trends of changes that affect the ability to recover in high-mountain conditions.

Methods. In order to obtain data, conventional stationary and route-based research methods were used. To record individuals of different sexes, long-term monitoring plots were used, which were laid in the characteristic habitats of the species' populations in 2000–2022. The ratio of male and female individuals is determined based on their quantitative distribution per unit area. The sexual potential index that determines the proportion of females and their participation in generative reproduction was used.

Results. The main differences in the morphological and quantitative parameters of male and female individuals in high-mountain conditions were determined. It was found that a characteristic feature during long-term research is a decrease in the number of generative individuals of both male and female sexes. In the studied populations, there is a shift in the sex ratio towards males (73 %) and this trend has been maintained over the last dozen of years. Therefore, the number of females compared to males is very small, which affects the sexual potential of populations.

Conclusions. The ratio of male and female individuals, the range of its displacement and potential participation in the realization of sexual potential in *R. rosea* was determined. The present study showed that the general trend in the populations of the

species is a decrease in the number of female individuals. Male biased sex ratio has an impact on sexual potential and ability to generative reproduction.

Keywords: *Rhodiola rosea* L., dioecious, individual and group parameters, sex ratio, prospects for recover

INTRODUCTION

In recent years, the high mountain areas of the Ukrainian Carpathians have undergone significant transformations as a result of the action of abiotic and biotic factors, which increasingly affect the populations of many rare and endemic plant species. Therefore, there are changes in the structural organization of their populations and their adaptive features (Grabherr *et al*., 2010; Czortek *et al*., 2018; Kyyak *et al*., 2018, 2022). The study of these changes is especially relevant in mountain conditions with a view to determining various possibilities for recovery of populations (Pauli *et al*., 2003; Ramming *et al*., 2010; Johnstone, 2021). According to previous research, the most vulnerable are species with the narrow ecological amplitude, which are confined to the high-mountain zone of the Ukrainian Carpathians (Didukh, 2009b; Stoyko, 2012). The different response of populations to changing habitat conditions prompts the study of the basic parameters of their structural organization (Grime, 1979; Walther *et al*., 2005; Dmytrakh, 2019, 2021).

Rhodiola rosea L. is a circumpolar, arctic-alpine relict species, of the ice age included in the Red Data Book of Ukraine (Didukh, 2009a) with the status of “vulnerable” among the plant species that require further study of the current state of populations. In the Ukrainian Carpathians, it occurs only in the high-mountain zone. It occupies isolated habitations on the tops and slopes of glacial caldera. This species gives preference to wet and cool living conditions, and thus it is cold-loving and highly specialized (Malinovskyi, 1980; Lovelius & Stoyko, 1990). In the past, *R. rosea* was a fairly common species in the high-mountain zone of the Ukrainian Carpathians (Zapałowicz, 1889; Deyl, 1935; Bradis & Zapjatova, 1954). Today, populations of the species are represented only by small isolated and fragmented groups of individuals.

Rhodiola rosea is a dioecious species, the populations of which are represented by male and female individuals (**Fig. 1**). Considering this, an important indicator of populations is the sexual differentiation of individuals, and their sex ratio in particular (Delf, 1999; Delf & Wolf, 2005).

According to the current assumption, the sex ratio of populations of dioecious plant species at the initial stage of the life cycle should consist of an equal number of individuals of the male and female sexes as a result of the selection action of the genetically determined primary ratio of 1:1 (Hardy, 2002). Both sexes have the same probability in reproduction processes. However, populations of dioecious species most often show a shift from a balanced sex ratio of 1:1 (Delf, 1999; Bisang & Hedenas, 2005; Field *et al*., 2013 a,b). The reasons for the shift in the sex ratio in natural plant populations are still an understudied problem. It is known that the sex ratio is influenced not only by genetic, but also by environmental factors. It was noted that variations in sex ratio shifts are associated with species adaptive strategies to habitat conditions (Munné-Bosch, 2015; Stehlik & Barrett, 2006; Timerman & Barrett, 2019). The sex ratio of the offspring is one of the important factors of the quality of the offspring and the occurrence of seed renewal (Stehlik *et al.*, 2008).

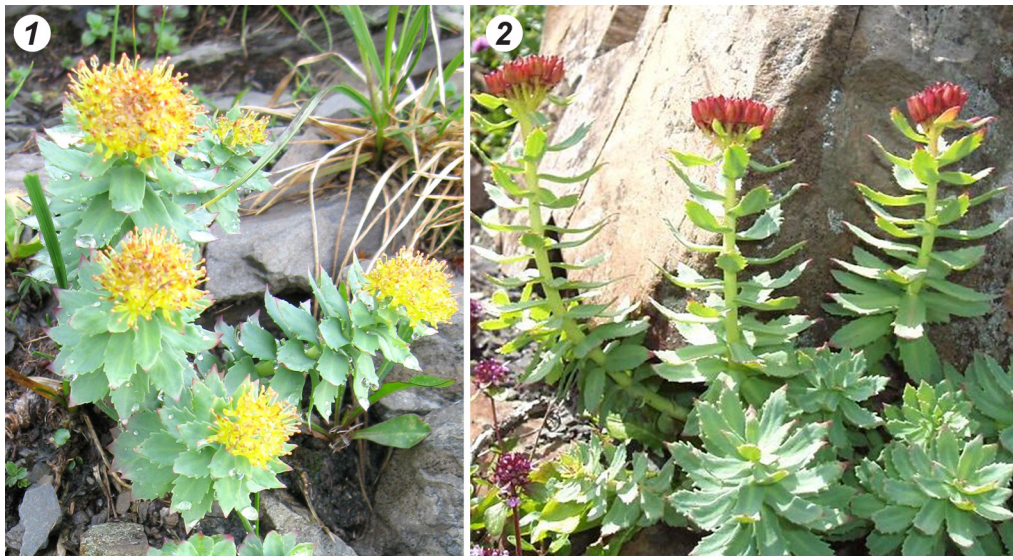

Fig. 1. *Rhodiola rosea* L.: ***1*** – male individuals; ***2*** – female individuals

Generative reproduction is important in the sexual differentiation of populations and their ability to recover (Falińska, 2021; Tsaryk *et al*., 2004; Dmytrakh, 2010). Plants form new reproductive organs every growing season, and this leads to the expression of the sexes. In this regard, the quantitative concept of gender and the probability of realizing sexual potential was introduced (Lloyd, 1979, 1980 a,b; Lloyd & Bawa, 1984). The share of genetic information that is transmitted to the next generation through male and female structures is estimated by the contribution of female individuals that affect the future prospects of seed offspring.

To characterize the sexual differentiation of *R. rosea* populations, it is important to obtain data on the number of male and female individuals and the range of shifts in their sex ratio during different years of vegetation (2000–2022). Therefore, this paper analyzes the changes in the sexual differentiation of populations of the species under study based on individual (morphometric) and group parameters. The share of female individuals is important in determining their sexual potential, which has an impact on the ability to generative reproduction and the seed renewal.

MATERIALS AND METHODS

Rhodiola rosea is a perennial, herbaceous, polycarpic plant of the *Crassulaceae* family. The main localities of the species are concentrated in the alpine and subalpine belts of the high-mountain zone (1600–2000 m a. s. l.). A characteristic feature of the species is the inclusion in open rock and meadow communities on the tops of ridges with rock outcrops, in refugia of glacial caldera and basins (Malinovskyi, 1980). Rock communities (terraces and ledges of rock) have a heterogeneous and mosaic character with open vegetation and occupy small areas. Meadows communities are formed on moist upper areas and hollows with outcrops of stone fragments.

The collection of material was carried out in the plant communities of *Saxifrage paniculata-Festuca supina*, *Luzuletum alpigo-pilosae*, *Festucetum pictae herbosum*,

Festucetum pictae luzuloidosum, *Festucetum supinae herbosum*, *Luzuletum alpigo-pilosa-Rolytririchum saxangulare-Gnaphalium supinum* on the mountains of Breskul, Hoverla, Petros, Rebra, Turkul, Shpytsy, Brebeneskul, Menchul (1730–1980 m a. s. l.) in the Chornohora mountain range.

To obtain data on the sexual differentiation of *R. rosea* populations and their reproductive parameters, conventional stationary and route-based research methods were applied. The used methods aimed at studying the parameters of sexual differentiation of populations at the individual and group levels (Zlobin *et al*., 2013). The sexual status of male and female individuals was assessed based on a set of individual morphological features in the generative state (structure and size of flowers and shoots). Individual morphometric parameters of individuals of different sexes were obtained on the basis of a representative selection of 25 individuals in the localities of rocky and meadow communities during 2006, 2011, 2020 and 2022 years.

To record male and female individuals long-term, multi-year studies were applied during the years 2000–2022 at monitoring sites in species-specific plant communities. The location of the experimental plots was chosen in view of the heterogeneity of the population distribution of the species in order to obtain adequate variation in the data (Greig-Smith, 1992). Individuals were counted on 10 (15) permanent experimental plots, taking into account their sex distribution. The experimental plots had a size of (0.5) 1 × (10) 20 m, divided into squares of 0.5 × 0.5 or 1 × 1 m (Harper, 1977; Zlobin, 2009).

The Excel and Statistica programs were used the guarantee statistical processing of the obtained results. All experimental data reported are mean ± standard deviation (SD). Statistical significance of differences between samples was assessed using one-way ANOVA with Turkey post-hoc analysis. Statistical significance ($p < 0.05$) of the results was established by comparing the studied mean values of the sample and control mean values.

As an integral indicator, the proportion of females was determined by the sexual potential index, calculated by the formula: $I = \sum g♀ / \sum(g♀ + g♂)$, where g♀ is the number of females; g♂ – number of males. Similarly, indicators of the sexual potential of the number of generative shoots and flowers in inflorescences were calculated. If the value goes to zero, then the individuals transmit their genetic information through the male gender and, conversely, if the value goes to 1, then the individuals transmit the genetic information through the female gender.

RESULTS AND DISCUSSION

Individual and group parameters. Long-term studies showed that individuals of the male and female sexes in of rocky and meadow habitats are distinguished by individual morphological (height of generative shoots, thickness and annual growth of the rhizome) and group parameters (number of individuals, number of generative and vegetative shoots, number of flowers, etc.). On the basis of the conducted research, differences in the parameters of individuals from rocky and meadow localities were found (**Table 1**).

In the localities of rock communities, individual and group parameters of both male and female individuals are significantly smaller than in meadows. In particular, the number of males in the localities of rock communities is 2.9, while the number of males in meadows is 3.2. A similar situation is observed in females. Individuals have a smaller number of generative and vegetative shoots, the number of flowers in inflorescences and the power of rhizome development (thickness, annual growth).

Greater values of the size of generative and vegetative structures are observed in individuals of meadow localities, which are confined to places with a better structure of the substrate, where the outflow of surface water is delayed and deposited silt residues are concentrated. Thus, based on the influence of limiting factors (microclimate, substrate structure, moisture regime, etc.), different life forms of individuals are formed.

Table. 1. **Individual and group parameters of *Rhodiola rosea* in different types of habitats (♂– male individuals; ♀– female individuals), (M ± m), n = 5**

Parameters	Rocky habitats		Meadow habitats	
	♂	♀	♂	♀
Number of individuals / m²	2.9 ± 0.4*#	1.2 ± 0.3*#	3.2 ± 0.5	1.7 ± 0.4
Number of generative individuals / m²	1.9 ± 0.1*#	0.6 ± 0.02*#	2.2 ± 0.3	1.2 ± 0.3
Number of generative shoots	2.6 ± 0.3*#	1.5 ± 0.2*#	3.0 ± 0.3	2.5 ± 0.3
Number of flower on generative shoots	19.3 ± 1.5*#	12.7 ± 1.2*#	21.0 ± 1.5	18.5 ± 1.4
Number of vegetative shoots	5.5 ± 0.4*#	4.2 ± 0.3*#	6.5 ± 0.5	5.8 ± 0.4
Height of generative shoots (cm)	9.2 ± 0.5*#	14.0 ± 0.9*#	17.1 ± 1.5	25.0 ± 1.9
Rhizome thickness (cm)	0.6 ± 0.02*#	0.7 ± 0.03*#	0.7 ± 0.03	0.8 ± 0.04
Annual rhizome growth (cm)	0.6 ± 0.03*#	0.5 ± 0.02*#	0.7 ± 0.03	0.6 ± 0.02

Note: * – the difference between the parameters of male and female individuals is statistically significant at $p < 0.05$; # – the difference between the parameters of individuals of different sexes in rocky and meadow (control) localities is statistically significant at $p < 0.05$

Morphological variability is also characteristic of individuals of different sexes. In males, there is a greater number of generative individuals, vegetative and generative shoots and flowers. However, females compared to males have larger generative shoot sizes and rhizome thickness, but the annual growth of the rhizome is somewhat smaller than that of males.

Sex ratio of generative individuals. The sex ratio in *R. rosea* populations reflects a different trend of changes in the number of generative individuals of the male and female sexes during 2000–2022 years. Long-term studies have shown a significant decrease in the number of generative individuals of both the male and female sexes (**Table 2**).

The number of generative individuals decreased in males from 2.8 (in 2000–2009 years) to 1.9 (in 2011–2022 years), and in females, from 1.3 to 0.4, respectively. Changes are also relevant to the number of generative shoots. In males, their number is from 4.1 to 2.3, and in females – from 2.8 to 0.9. The difference in the number of flowers on the generative shoot is somewhat smaller.

In the localities of both rocky and meadow habitats, there is a significant predominance of males (73 % on average). Compared to the previous years of research, changes concern females, whose number decreased from 31.7 % (in 2000–2009 years) to 17.4 % (in 2011–2022 years). The main trends of changes in the sex ratio during 2000–2022 years in rocky and meadow locations are presented in **Fig. 2**.

The obtained data prove the tendency for a shift towards male individuals has been a characteristic feature of the populations of the species during the recent decades.

The uneven distribution of individuals of different sexes determines their unequal reproductive positions and different ability to realize their sexual potential. In particular, this applies to females, whose number has decreased by 1.5 times.

Table 2. **Changes in generative parameters in *Rhodiola rosea* populations and their sex ratio during 2000–2022 years in rocky and meadow locations (♂ – male individuals; ♀ – female individuals), (M ± m), n = 10**

Year	Number of generative individuals, m²		Number of generative shoot		Number of flowers on the generative shoots	
	♂	♀	♂	♀	♂	♀
2000	2.9 ± 0.4	1.3 ± 0.2*	4.5 ± 0.3	3.0 ± 0.3*	18.2 ± 1.4	14.0 ± 1.2*
2001	3.0 ± 0.5	1.5 ± 0.3*	4.8 ± 0.4	3.1 ± 0.3*	18.5 ± 1.5	13.6 ± 1.2*
2003	2.7± 0.4	1.4 ± 0.3*	4.3 ± 0.3	2.9 ± 0.3*	18.0 ± 1.4	14.3 ± 1.3*
2006	2.5 ± 0.3	1.1± 0.2*	3.5 ± 0.3	2.5 ± 0.2*	17.4 ± 1.4	14.2 ± 1.3*
2009	2.7 ± 0.4	1.1 ± 0.2*	3.6 ± 0.3	2.3 ± 0.2*	19.0 ± 1.5	14.5 ± 1.3*
Average (2000–2009)	2.8 ± 0.4	1.3 ± 0.2	4.1 ± 0.3	2.8 ± 0.3*	8.2 ± 1.4	4.1 ± 1.3*
2011	2.3 ± 0.1	0.6 ± 0.03*#	2.8 ± 0.3	1.5 ± 0.2*#	16.5 ± 1.2	11.3 ± 1.2*#
2015	2.0 ± 0.1	0.5 ± 0.03*#	2.4 ± 0.2	0.9 ±.0.04*#	16.8 ± 1.3	12.0 ± 1.2*#
2017	1.7 ± 0.3	0.4 ± 0.02*#	2.0 ± 0.2	0.7 ± 0.03*#	17.2 ± 1.3	12.8 ± 1.3*#
2020	2.0 ± 0.1	0.4 ± 0.02*#	2.3 ± 0.2	0.8 ± 0.03*#	17.6 ± 1.4	12.9 ± 1.3*#
2022	1.5 ± 0.3	0.3 ± 0.01*#	2.0 ± 0.2	0.7 ± 0.03*#	17.0 ± 1.3	11.5 ± 1.2*#
Average (2011–2022)	1.9 ± 0.4*#	0.4 ± 0.02	2.3 ± 0.2	0.9 ± 0.03	17.0 ± 1.3	12.1 ± 1.3

Note: * – the difference between the parameters of male and female individuals is statistically significant at $p < 0.05$; # – the difference between the parameters of male and female individuals in different years is statistically significant at $p < 0.05$

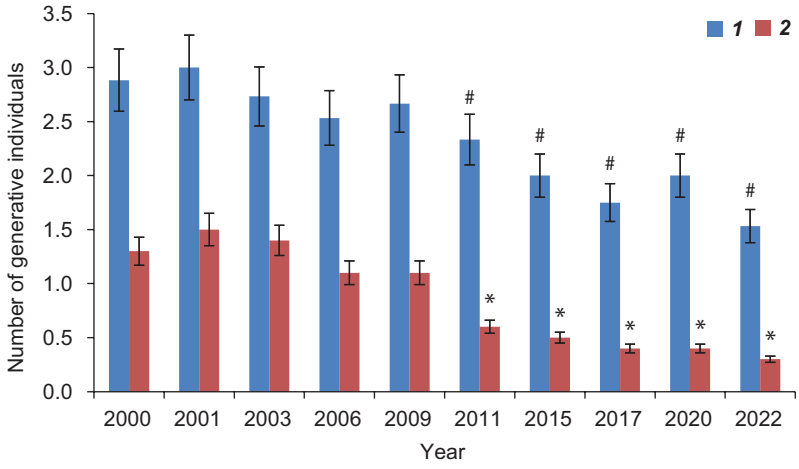

Fig. 2. The number of male (***1***) and female (***2***) generative individuals per m² of *Rhodiola rosea* during 2000 – 2022 years. * – the difference between the parameters of female individuals compared to the control (2001) is statistically significant at $p < 0.05$; # – the difference between the parameters of male individuals compared to the control (2001) is statistically significant at $p < 0.05$

The small number of females indicates that the index of sexual potential is quite low and was 0.32 in 2000–2009 years and 0.19 in 2011–2022 years. In particular, a significant decrease in this indicator is observed in the last period of research. A similar situation also applies to the number of generative shoots (from 0.40 to 0.27). The least prominent changes are in the number of flowers on a generative shoot (from 0.43 to 0.41) (**Table 3**).

Table 3. **Index of sexual potential of female individuals *Rhodiola rosea***

Year	Index of sexual potential		
	generative individuals	generative shoots	flowers
2000	0.32	0.40	0.43
2001	0.33	0.39	0.42
2003	0.34	0.40	0.44
2006	0.31	0.41	0.45
2009	0.30	0.39	0.43
Average (2000–2009)	0.32	0.40	0.43
2011	0.29	0.35	0.41
2015	0.20	0.27	0.42
2017	0.19	0.26	0.42
2020	0.17	0.25	0.43
2022	0.16	0.24	0.40
Average (2011–2022)	0.19	0.27	0.41

Indicators of the sexual potential of females in different growing seasons (2000–2022 years) and at different levels of the organization of the generative sphere are presented in **Fig. 3**.

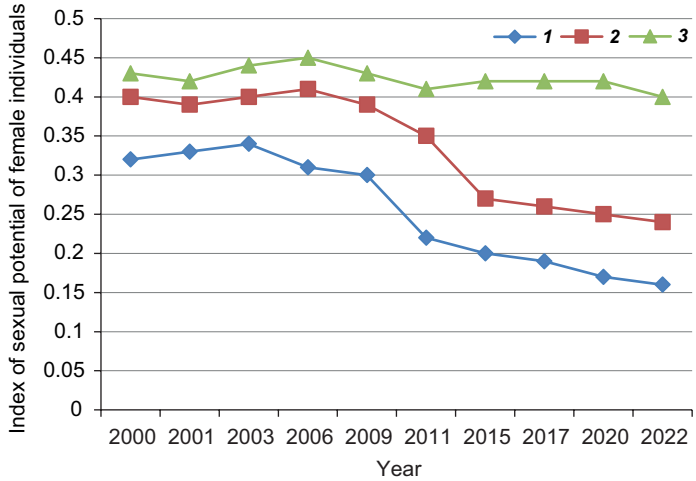

Fig. 3. Sexual potential of female individuals at different levels of organization of generative structures: generative individuals (***1***); generative shoot (***2***); flowers on a generative shoot (***3***)

Female individuals at different levels of generative structures (individuals, shoots, flowers) make a differential contribution to the realization of sexual potential during pollination and seed dispersal. The subsequent reduction in the number of females affects the sexual potential, and therefore, reduces the likelihood of a potential contribution to generative reproduction and, as a result, the prospect of seed recovery.

CONCLUSIONS

It was established that individual (morphometric) and group parameters are important indicators of changes in the sexual differentiation of populations of *R. rosea*, in particular, male bias of sex ratio and potential participation in the realization the sexual potential of females. The dependence of morphological and quantitative parameters in individuals of different sexes on habitat conditions was revealed. Long-term studies have shown that the sex ratio of individuals in populations had a different range of distribution during 2000–2022. It was established that the general trend is a decrease in the number of generative individuals and a shift in their sex ratio towards male individuals. Their number ranges from 68.3 % to 82.6 %. The number of females compared to males in the last research period (in 20011–2022) was small (17.4 %). This affects the realization of their sexual potential and the ability to generative reproduction. Therefore, the sex ratio of individuals and, in particular, the number of female individuals is an important indicator of changes in the sexual differentiation of *R. rosea* populations and their ability to recover in high-mountain conditions.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest: the authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Animal Rights: this article does not contain any studies with animal subjects performed by any of the authors.

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СТАТЕВА ДИФЕРЕНЦІАЦІЯ ПОПУЛЯЦІЙ *RHODIOLA ROSEA* L. У ВИСОКОГІР'Ї УКРАЇНСЬКИХ КАРПАТ

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Вступ. Важливим показником статевої диференціації популяцій *Rhodiola rosea* L. є індивідуальні (морфологічні) та групові параметри (кількість особин чоловічої й жіночої статей, їхнє статеве співвідношення і діапазон його зміщення). Показники цих параметрів у природних популяціях рослин ще недостатньо вивчені. Відтак, для характеристики стану популяцій *R. rosea* важливим є дослідження параметрів їхньої статевої диференціації та основних тенденцій змін, які впливають на їхню здатність до відновлення в умовах високогір'я.

Методи. З метою отримання даних використано загальноприйняті стаціонарні й маршрутні методи досліджень. Для обліку особин різної статі застосовано багаторічні моніторингові ділянки, які закладені в характерних для популяцій виду оселищах високогір'я у 2000–2022 рр. Співвідношення особин чоловічої й жіночої статей визначено на основі їхнього кількісного розподілу на одиницю площі. Застосовано індекс статевого потенціалу, який визначає частку особин жіночої статі та їхню участь у генеративному розмноженні.

Результати. Визначено основні розбіжності у морфометричних і кількісних параметрах особин чоловічої й жіночої статей у різних умовах середовища існування. Виявлено, що характерною ознакою впродовж багаторічних досліджень є зменшення чисельності генеративних особин як чоловічої, так і жіночої статей. У популяціях виду спостерігають зміщення статевого співвідношення в бік особин чоловічої статі (73 %), і така тенденція утримується впродовж останніх десятиліть. Відтак, частка особин жіночої статі, порівняно з особинами чоловічої статі, є незначною, що має вплив на статевий потенціал популяцій і перспективи їхнього насіннєвого поновлення.

Висновки. Установлено, що важливими показниками змін у статевій диференціації популяцій *R. rosea* є співвідношення особин чоловічої й жіночої статей, діапазон його зміщення та потенційна участь у реалізації статевого потенціалу. Проведені дослідження встановили, що загальною тенденцією є зменшення кількості генеративних особин і, зокрема, особин жіночої статі. Значне зміщення у статевому співвідношенні особин впливає на статевий потенціал популяцій і їхню здатність до генеративного розмноження.

Ключові слова: *Rhodiola rosea* L., дводомність, індивідуальні та групові параметри, статеве співвідношення, перспективи відновлення

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