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FLOWERING DYNAMICS IN THE TRIMORPHIC SPECIES OF *LYTHRUM SALICARIA* L. (LYTHRACEAE)

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Flowering in the population of *Lythrum salicaria* in the Yavorivskiy district of Lviv region lasts for about 70 days from the end of June till the beginning of September. Flowering period of the long-styled individuals lasts 30 days, middle-styled individuals – 32 days, and short-styled individuals – 26 days. In the studied population, the ratio of flowering plants of different morphs changes in time: flowering long-styled individuals prevail at the beginning of the population flowering, middle-styled individuals – at the time of mass flowering and short-styled individuals – at the end of flowering period. The percentage of dominant flowering morph in each phase of the population flowering can reach about 70 %. The prevalence of the middle-styled morph during mass flowering and the longest flowering period seem to be the features responsible for maximal seed production of this morph and for the highest chance to be cross- and self-pollinated. Short flowering period of the short-styled morph and its prevalence at the end of the flowering in population could be regarded as the features enhancing autogamy and also is responsible for the lowest seed production. The differentiated flowering dynamics of the morphs is considered to be the mode which optimizes the legitimate pollination of each morph in the defined phases of the flowering period.

Keywords: purple loosestrife, trimorphism, flowering, morph ratio, pollination, xenogamy, autogamy.

INTRODUCTION

Lythrum salicaria L. – is a classical object for the study of tristylly, being firstly precisely investigated by Charles Darwin [8]. The features of this tristylous species revealed by Ch. Darwin [8] are: a) equal proportion of long-styled (LS), middle-styled (MS) and short-styled (SS) individuals in the population; b) anther, pollen and stigma trimorphism; c) high value of seed and capsule production under the legitimate pollination and low seed and capsule production under the illegitimate pollination. Some of these features were confirmed and more accurately studied lately [1, 2, 15, 20]. Nevertheless, some recent researches did not mention any differences between three morphs in the flower

and inflorescence structure [6], the flowering time [16], sporoderm development [19]. Obviously the authors had no intention to find these differences because the object was considered to be thoroughly studied.

We consider the phenomenon of tristily (and heterostyly in general) as a kind of flower and sexual polymorphism [3], because three hermaphrodite morphs reveal various sexual patterns (play male or female roles) in various kinds of breeding. The other kind of sexual polymorphism is the dioecy (presence of two kinds of individuals – male and female), the more investigated phenomenon for which some phenological, physiological and biological differences between sexual types were noted [3, 18].

The trimorphism in *Lythrum salicaria* is genetically determined [1, 5] and has a complex expression on flower morphology. We supposed that it may be revealed not only in the morphological traits but also in the flowering behavior as a kind of the mechanisms optimizing the legitimate pollination between the morphs.

The aim of this study was to find out the differences between morphs in a) time of the flowering period of the morph, b) duration of the individuals flowering, c) reveal the dynamics of the flowering period.

MATERIALS AND METHODS

The studied population of *Lythrum salicaria* was located in the Yavoriv district of the Lviv region, north-western locality of Stradtch village, near the turn of highway Lviv-Novoyavorivsk to the Gorodok town. The population is located in the wetland of Vereschytsia river and adjacent ponds. It contains about 100–200 generative individuals depending on a year, but in some years it can be significantly damaged by roasting or mowing. Observations were conducted in June–September 2008–2010 according to the recommendations of Ponomarev [17], Golubev and Volokitin [12–14]. For each morph, the flowering period in general and that of the defined model individuals were studied as well as the dynamics of the number of flowering individuals.

RESULTS

The flowering period in the studied population of *Lythrum salicaria* lasts about 2,5 months from the end of June till the beginning of September, mass flowering occurs at the second-third decades in July (Tab. 1). The flowering period of a flower for all morphs lasts about a day, but the receptivity period of a stigma is referred to be somewhat longer in SS-morph [20]. The SS-morph is characterized by the shortest period of the individual flowering, while the longest flowering period is revealed for MS-morph (Tab. 2).

According to the classification of Golubev and Volokitin [14], *Lythrum salicaria* is a long-flowered species by the flowering duration in population, middle-flowered by the duration of individual's flowering and one-day flowered by the duration of a flower flowering (anthesis).

The whole period of the flowering in the population can be divided into three phases after prevalence of one of three morphs. At the beginning of the flowering period (first phase) the LS-morph was prevalent in three years of observation. At the middle of the flowering period the MS-morph prevailed (mass flowering, the second phase). At the end of flowering period the SS-morph prevailed (third phase) (Tab. 1). For the studied population of *Lythrum salicaria* in general, one can conclude that LS-morph is early-flowering, SS-morph is late-flowering.

Table 1. Number of flowering long-styled (LS), middle-styled (MSd) and short-styled (SS) plants of *Lythrum salicaria* L. during the flowering perio*

Таблиця 1. Кількість квітучих особин трьох морф *Lythrum salicaria* L. протягом періоду цвітіння*

Ten-day period of flowering	2008				2009				2010			
	LS-morph	MS-morph	SS-morph	Total	LS-morph	MS-morph	SS-morph	Total	LS-morph	MS-morph	SS-morph	Total
1	16	5	6	27	-	-	-	-	-	-	-	-
2	21	15	11	47	90	68	53	211	69	57	40	166
3	21	32	14	67	81	72	59	212	63	66	49	<u>178</u>
4	<u>27</u>	25	32	<u>84</u>	78	83	56	<u>217</u>	45	77	46	168
5	-	-	-	-	65	87	60	212	23	52	54	129
6	10	6	17	33	45	43	89	177	18	40	63	121
7	-	-	-	-	21	27	93	141	10	15	67	92

Comment: * Maximal number of the flowering LS-, MS- and SS-individuals for a ten-day period is marked in bold, maximal individuals number of a morph and population in total is underlined.

Примітка: * Максимальна кількість квітучих довгостовпчикових (LC), середньостовпчикових (MS) і короткостовпчикових (SS) особин на кожну декаду виділена жирним шрифтом; максимальна кількість квітучих особин для кожної морфи і популяції в цілому підкреслена.

Table 2. Flowering period of the model individuals of *Lythrum salicaria* L.

Таблиця 2. Тривалість цвітіння модельних особин *Lythrum salicaria* L.

Character	Flowering period of the individual, days		
	LS-morph	MS-morph	SS-morph
Mean value (n = 10, p>0.95)	30.3±1.6 Cv = 16.5%	32.2±1.5 Cv = 14.9%	26.9±1.5 Cv = 18.0%
Range of variation (min–max)	25–38	25–38	21–33

It was revealed that the ratio of the flowering individuals of LS-, MS- and SS-morphs often is not corresponding to the known ratio 1:1:1. However one morph at each flowering phase is dominant and reaches up to 70 % from the number of flowering individuals in population. It is most remarkable at the 1, 3 and 6 decades in 2008 and last two decades in 2009 and 2010 (Fig. 1). The part of LS-morph in flowering stage during the flowering period gradually decreased, the part of the SS-morph increased and the part of the MS-morph had a maximum at the middle phase of the flowering period.

DISCUSSION

According to the classical viewpoint on the pollination biology, one can make some assumptions about the reproductive system of *Lythrum salicaria*. Firstly, SS-morph has the lowest chance to be cross-pollinated because its stigma is hidden in the floral tube and situated beneath both stamens whorls. Secondly, LS-morph has the longest style and can be easily cross-pollinated by the mechanism of approach hercogamy. Consequently, the MS morph has high chances to be cross- and self-pollinated.

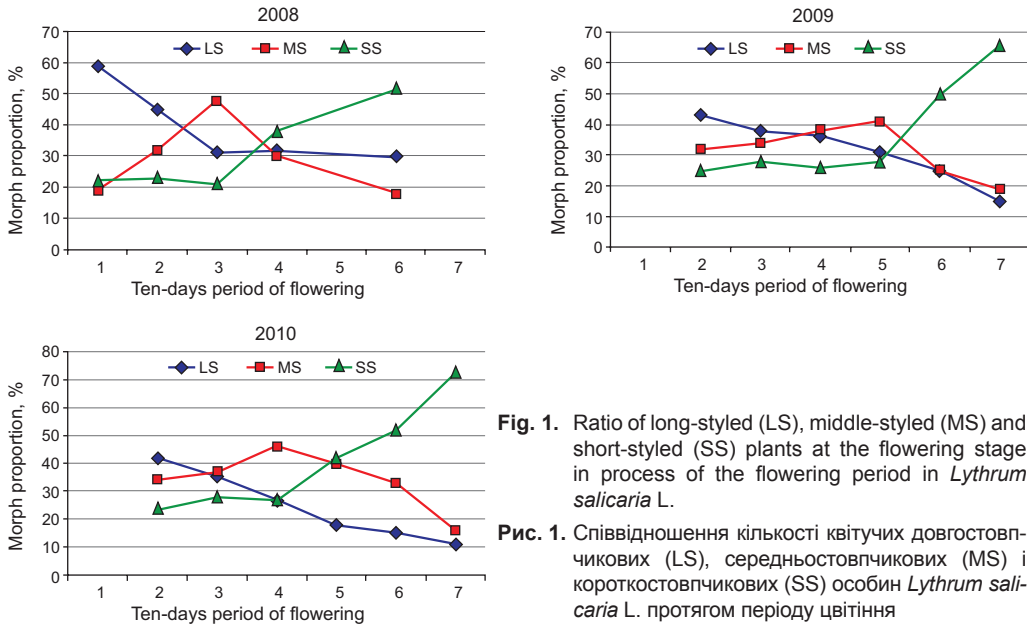


Fig. 1. Ratio of long-styled (LS), middle-styled (MS) and short-styled (SS) plants at the flowering stage in process of the flowering period in *Lythrum salicaria* L.

Рис. 1. Співвідношення кількості квітучих довгостовпчикових (LS), середньостовпчикових (MS) і короткостовпчикових (SS) особин *Lythrum salicaria* L. протягом періоду цвітіння

It was mentioned [11] that pollen grains of *Lythrum salicaria* are loaded on the insect body disassortatively. This fact obliges to think that reciprocal herkogamy (different length of stamens and styles in each morph) is not the only enhancing mechanism of cross-pollination. The revealed flowering dynamics may provide more effective assortative pollination for all the morphs in each phase of the flowering. According to the dynamic concept of flower ecology [12–14], morph's differentiation may be evident not only in the flower morphology (distant disposition of anthers and stigmas) but also in the changes of the functional role of a morph as male (pollen donor) or female (pollen acceptor) elements for other morphs. For example, at the first phase of the flowering, the LS-morph reaches 40-60 % of the total number of flowering individuals and ratio of the morphs LS:MS:SS can reach 2:1:1. It means that one LS-individual (having the longest style) as a pollen acceptor obtains one MS- or SS-individual as a pollen donor (with the longest stamens). At the same phase, the MS- or SS- individual as pollen acceptor has three individuals as pollen donors – two LS- and one SS- or MS- correspondingly (all having the middle or short stamens) (Fig. 2, A).

At the second phase of the flowering, the MS-morph (having the middle style) reaches maximal number prevalence (LS:MS:SS as 1:2:1). It means that one MS-individual as a pollen acceptor has one LS- or SS-individual as a pollen donor (with the middle-height stamens). The LS- or SS-individual as a pollen acceptor has three individuals as pollen donors (two MS- and one SS- or LS-individual correspondingly) (Fig. 2, B).

Finally, at the third phase of the flowering, the SS-morph (having the short style) has the same prevalence (LS:MS:SS as 1:1:2) and each SS-individual as a pollen acceptor has one MS- or LS-individual as a pollen donor (with the shortest stamens). At the same time, the MS- or LS-individual as a pollen acceptor has three individuals as pollen donors (two SS- and one LS- or MS- correspondingly) (Fig. 2, C).

It means that three morphs of *Lythrum salicaria* differ not only by morphological traits of the flower but also phenologically, by their behavior at the pollination. At the first phase

of the flowering the LS-morph plays mostly a male function for MS- and SS-morphs, at the second phase this role plays MS-morph and at the third phase – the SS-morph. Conversely, the effective female function for LS-morph occurs at the second and third phases of the flowering in population, for MS-morph – at the first and third phases and for the SS-morph – at the first and second phases. This assumption may be correct if we adopt that effectiveness of geitonogamy is equal for all the morphs at the all flowering phases (simultaneously a great number of flowers are open in LS-, MS- and SS-plants).

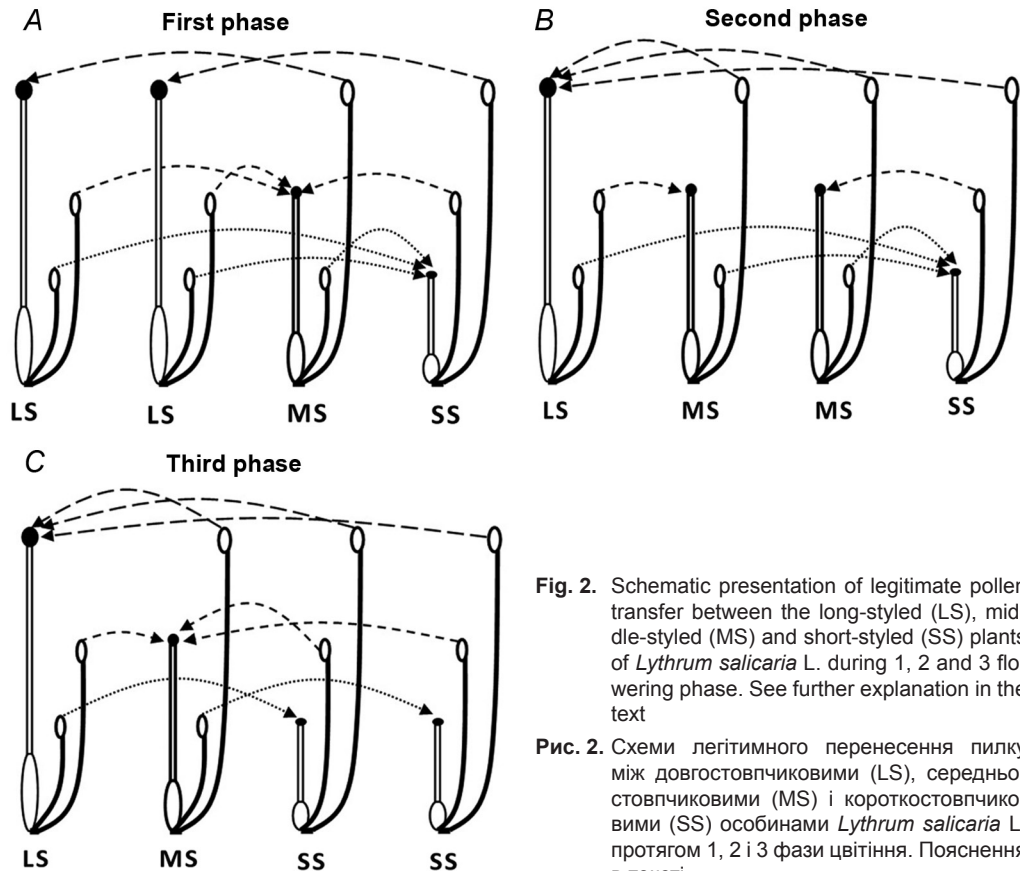


Fig. 2. Schematic presentation of legitimate pollen transfer between the long-styled (LS), middle-styled (MS) and short-styled (SS) plants of *Lythrum salicaria* L. during 1, 2 and 3 flowering phase. See further explanation in the text

Рис. 2. Схеми легітимного перенесення пилку між довгостовпчиковими (LS), середньостовпчиковими (MS) і короткостовпчиковими (SS) особинами *Lythrum salicaria* L. протягом 1, 2 і 3 фази цвітіння. Пояснення в тексті

The revealed differences of the morphs flowering provide some cautions on calculation of the morph ratio in the population. This calculation should be realized at the third phase of the flowering or just after the flowering period when all generative individuals reveal their morph identity, but not at the first or second phases of the flowering when the morph ratio will be declined from the proportion 1:1:1.

After Darwin [8], the MS-morph has the highest seed production after cross- and self-pollination, especially in the case of xenogenous pollination with pollen from long stamens [7]. This fact is explained by the less self-incompatibility (SIC) effect in this morph [20]. Our data show that the highest productivity of the MS-morph is maintained not only by the less developed SIC effect but also by the longest flowering period of

the individual and the prevalence at the second phase of the flowering when the mass flowering occurs. The least productivity and the shortest flowering period of the individuals of SS-morph confirm its high chances to be eliminated from the populations as was noted for both Europe and North America [1, 6, 10, 11].

CONCLUSIONS

In the population of *Lythrum salicaria* in Lviv region (Ukraine), the number of flowering plants of LS-, MS- and SS-morphs changes in time, the LS-morph prevails at the beginning of the flowering period, the MS-morph prevails during mass flowering and the SS-morph – at the end of the flowering period in population. It should be retained that part of the LS-plants becomes lower, part of the SS-plants higher while the part of the MS-plants is maximal at the period of mass flowering. The prevalence of the MS-morph during mass flowering and the highest flowering period of the individual provide the highest chance to be cross- and self-pollinated and the maximal seed production of this morph. The differentiated flowering dynamics of the morphs is considered to be the mode enhancing the probability of the legitimate pollination of each morph in the defined phase of the flowering period. Our results confirm the assumption that the LS-morph is most adapted to the cross-pollination, SS-morph – to the self-pollination and the MS-morph has the advantages by the adaptation for both pollination modes.

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1. Barrett S.C.H. Heterostylous generic polymorphisms: model systems for evolutionary analysis. **Monographs on Theoretical and Applied Genetics. 15. Evolution and Functions of Heterostyly**. Ed. by S.C.H. Barrett. Berlin, Springer, 1992. 1–29.
2. Barrett S.C.H. The evolutionary biology of tristylly. **Oxford Surveys in Evolutionary Biology**. Eds. D. Futuyma & J. Antonovics. 1993. 9: 283–326. Oxford University Press, Oxford, U.K.
3. Barrett S.C.H. The evolution of plant sexual diversity. **Nature**, 2002; 3: 274–284.
4. Barrett S.C.H., Ness R.W., Vallejo-Marin M. Evolutionary pathways to self-fertilization in a tristylous plant species. **New Phytol**, (2009) 183: 546–556.
5. Barrett S.C.H., Shore J.S. New insights on heterostyly: comparative biology, ecology and genetics. V.E. Franklin-Tong (ed.) **Self-Incompatibility in Flowering Plants – Evolution, Diversity, and Mechanisms**. Berlin Heidelberg Springer-Verlag, 2008. 3–32.
6. Cheung M., Sattler R. Early floral development of *Lythrum salicaria*. **Can. J. Bot**, 1967; 45: 1609–1618.
7. Colautti R.I., White N.A., Barrett S.C.H. Variation of self-incompatibility within invasive populations of purple loosestrife (*Lythrum salicaria* L.) from eastern North America. **Int. J. Plant Sci**, 2010; 171(2): 158–166.
8. Darwin C. **The different forms of flowers on plants of the same species**. London: John Murray, 1877.
9. Eckert C.G., Barrett S.C.H. Stochastic loss of style morphs from populations of tristylous *Lythrum salicaria* and *Decodon verticillatus* (Lythraceae). **Evolution**, 1992; 46(4): 1014–1029.
10. Eckert C.G., Manicacci D., Barrett S.C.H. Frequency-dependent selection on morph ratios in tristylous *Lythrum salicaria* (Lythraceae). **Heredity**, 1996; 77: 581–588.
11. Faegri K., van der Pijl L. **The principles of pollination ecology**. London: Pergamon Press, 1979. 381 p.

12. Golubev V.N., Volokitin Y.S. Main principles and mechanisms of dynamical ecology of flowering plants pollination. **Collected Sci. Works of the State Nikitski Bot. Gard**, 1986; 98: 7–28. (In Russian).
13. Golubev V.N., Volokitin Y.S. **Instructions for the study of anthecological features of the flowering plants. Morphological description of the reproductive structure**. Yalta: Nikitskiy Botanical Garden, 1986. 43 p. (In Russian).
14. Golubev V.N., Volokitin Y.S. **Instructions for the study of anthecological features of the flowering plants. Functional-ecological organisation principles of the reproductive structure**. Yalta: Nikitskiy Botanical Garden, 1986. 37 p. (In Russian).
15. Hermann B.P., Mal T.K., Williams R.J., Dollahon N.R. Quantitative evaluation of stigma polymorphism in a tristylous weed, *Lythrum salicaria* (Lythraceae). **Amer. J. Bot.**, 1999; 86(8): 1121–1129.
16. Montague J. L., Barrett S. C., Eckert C. G. Re-establishment of clinal variation in flowering time among introduced populations of purple loosestrife (*Lythrum salicaria*, Lythraceae). **J. Evol. Biol.**, 2008; 21(1): 234–245.
17. Ponomarev A. N. The study of flowering and pollination. **Field Geobotany** / Ed. E.M. Lavrenko and A.A. Korchagin. Moscow; Leningrad: USSR Academy of Sciences, 1960; 2: 9–19. (In Russian).
18. Sheremetiev C. H. On the adaptive significance of the sexual dimorphism in flowering plants. **Botanical Journal**, 1983; 68(5): 561–571. (In Russian).
19. Volkova O.A., Severova E.E., Polevova S.V. Sporoderm development in *Lythrum salicaria* (Lythraceae). **Bull. Moscow Soc. of Naturalists. Biol. Ser.** 2012. 117(5): 57–63. (In Russian).
20. Waites A.R., Ågren J. Stigma receptivity and effects of prior self-pollination on seed set in tristylous *Lythrum salicaria* (Lythraceae). **Amer. J. Bot.**, 2006; 93(1): 142–147.

ДИНАМІКА ЦВІТІННЯ ТРИМОРФНОГО ВИДУ *LYTHRUM SALICARIA* L. (LYTHRACEAE)

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Цвітіння у популяції *Lythrum salicaria* у Яворівському районі Львівської області триває близько семи декад з кінця червня до початку вересня. Період цвітіння довгостовпчикової особини в середньому 30 діб, середньостовпчикової особини – 32 доби, короткостовпчикової особини – 26 діб. У дослідженій популяції *Lythrum salicaria* співвідношення кількості квітучих особин різних морф змінюється в часі: довгостовпчикова морфа переважає на початку цвітіння, середньостовпчикова – у період масового цвітіння, а короткостовпчикова – наприкінці цвітіння популяції. Кількість квітучих особин переважаючої морфи у кожній з трьох фаз цвітіння популяції може сягати 70 % від кількості генеративних особин. Переважання середньостовпчикової морфи під час масового цвітіння у популяції та найвища тривалість цвітіння особини зумовлюють найвищу насінневу продуктивність цієї морфи в результаті перехресного запилення і самозапилення. Коротка тривалість цвітіння особин короткостовпчикової морфи і переважання її наприкінці цвітіння у популяції узгоджується з її найбільш імовірною автогамією та найменшою насінневою про-

дуктивністю. Диференціація динаміки цвітіння різних морф розглядається як засіб підвищення імовірності легітимного запилення кожної морфи у певній фазі цвітіння у популяції.

Ключові слова: плакун верболистий, триморфізм, цвітіння, співвідношення морф, запилення, ксеногамія, автогамія.

ДИНАМИКА ЦВЕТЕНИЯ ТРИМОРФНОГО ВИДА *LYTHRUM SALICARIA* L. (LYTHRACEAE)

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Цветение популяции *Lythrum salicaria* в Яворовском районе Львовской области длится около семи декад с конца июня по начало сентября. Период цветения длинностолбчатой особи в среднем 30 суток, среднестолбчатой особи – 32 сутки, короткостолбчатой особи – 26 суток. В исследованной популяции *Lythrum salicaria* соотношение количества цветущих особей разных морф изменяется во времени: длинностолбчатая морфа преобладает в начале цветения, среднестолбчатая – в период массового цветения, а короткостолбчатая – в конце цветения популяции. Число цветущих особей преобладающей морфы в каждой из трех фаз цветения популяции составляет до 70 % от общего числа всех генеративных особей. Преобладание среднестолбчатой морфы в период массового цветения популяции и наибольшая продолжительность цветения особи обуславливают наибольшую семенную продуктивность этой морфы в результате как перекрестного, так и самоопыления. Короткая продолжительность цветения особи короткостолбчатой морфы и преобладание ее в конце цветения популяции соответствуют ее наиболее вероятной автогамии и наименьшей семенной продуктивности. Дифференциация динамики цветения разных морф рассматривается как способ повышения вероятности легитимного опыления каждой из них в определенной фазе цветения популяции.

Ключевые слова: дербенник иволистный, триморфизм, цветение, соотношение морф, опыление, ксеногамия, автогамия.

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