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# Ovaries with different heterozygosity levels of their genotypes have equal chances to reach maturity on a buckwheat plant: Is it the main condition for the start of the evolution toward selfing?

**Aleksey N. Fesenko, Ivan N. Fesenko**

*Federal Scientific Center of Legumes and Groat Crops, Orel, Russia*

***Corresponding author:*** Ivan N. Fesenko, ivanfesenko@rambler.ru

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**Background.** Inbreeding depression (ID) usually reduces the competitive ability of an individual compared to one of outbred origin. Such competition could be especially clear between different ovaries developing on the same plant. It can be assumed that ovaries with higher level of heterozygosity will have an advantage in competition for resources.
**Material and methods.** Homostylous buckwheat lines (*Fagopyrum esculentum* Moench with approx. 3% of closely related selfer *F. homotropicum* Ohnishi germplasm) of different inbred generations ($I_1$ – $I_6$) were grown adjacent to the heterostylous cv. 'Molva', and the share of seeds resulting from cross-pollination was assessed for each variant using the recessive marker *det* (genotypes of the seeds were visualized according to phenotypes of the resulting plants).
**Results and conclusions.** The proportions of seeds originated from cross-pollination were similar across the inbreeding generations, with small stochastic variations. Thus, the ovaries resulting from both self- and cross-pollination have equal chances to reach maturity on the same plant. It looks like a fundamental condition for the start of the evolution toward self-pollination. The levels of ID at other developmental stages, apparently, are less crucial for the possibility of such evolution. For example, the ID in the analyzed material was strong (> 0.5 for both vegetative development and seed productivity). It highly likely reflects the level of ID of the common ancestor of *F. esculentum* and *F. homotropicum*. However, the strong ID did not make impossible the speciation of the self-pollinator *F. homotropicum*.

***Keywords:*** inbreeding depression, developmental stage, self-pollination, outcrossing, buckwheat

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# Завязи с разным уровнем гетерозиготности генотипов имеют равные шансы достичь зрелости на растении гречихи: является ли это основным условием для начала эволюции самоопыления?

**А. Н. Фесенко, И. Н. Фесенко**

*Федеральный научный центр зернобобовых и крупяных культур, Орел, Россия*

***Автор, ответственный за переписку:*** Иван Николаевич Фесенко, ivanfesenko@rambler.ru

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**Актуальность.** Эволюция от перекрестного опыления к самоопылению – известное явление у растений. Основным фактором, препятствующим развитию самоопыления, является инбредная депрессия (ИД), и работы об эволюции системы размножения у растений посвящены главным образом этой проблеме. Для описания ИД можно использовать два критерия: 1) силу, то есть уровень снижения величины того или иного показателя по сравнению с аутбредным контролем, и 2) стадию развития, на которой она проявляется. Вероятно, сила и характер проявления ИД в начале и конце жизненного цикла растения могут по-разному влиять на вероятность эволюции в сторону самоопыления.
**Материал и методы.** Гомостильные линии гречихи (*Fagopyrum esculentum* Moench с примерно 3% зародышевой плазмы самоопылителя *F. homotropicum* Ohnishi) с детерминантным типом роста (мутация *det*) разных инбредных поколений ($I_1 – I_6$) выращивали смежно с растениями гетеростильного сорта ‘Молва’ с индетерминантным типом роста, и долю семян, полученных в результате перекрестного опыления, оценивали для каждого варианта с помощью рецессивного маркера *det* (генотипы семян определяли по фенотипам полученных растений).
**Результаты и заключение.** Доли семян, возникших в результате перекрестного опыления, были близки в разных поколениях инбридинга с небольшими стохастическими вариациями. Таким образом, завязи, возникшие в результате самоопыления и перекрестного опыления, имеют равные шансы достичь зрелости на одном и том же растении, несмотря на различия по уровню гетерозиготности. Это выглядит как фундаментальное условие начала эволюции самоопыления. Уровни ИД на других стадиях развития, по-видимому, менее важны для возможности такой эволюции. Так, ИД по вегетативному развитию и семенной продуктивности в анализируемом материале превышала 0,5. Вероятно, это отражает уровень инбредной депрессии, характерный для общего предка *F. esculentum* и *F. homotropicum*. Таким образом, исходно сильная ИД не сделала невозможным возникновение самоопылителя *F. homotropicum*.

***Ключевые слова:*** инбредная депрессия, стадия развития, самоопыление, перекрестное опыление, гречиха

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## Introduction

The evolution of self-pollination is a common trend among plants (Takebayashi, Morrell, 2001; Igic, Busch, 2013; Wright et al., 2013). There are two main preconditions for such transition to be achievable. The first is a mutation that makes possible the setting of seeds as a result of self-pollination, and the second is a fairly high tolerance to inbreeding depression.

Self-fertile mutations occur sometimes, and their future depends on a number of environmental factors that have been widely discussed in the literature (Baker, 1955; Voylokov et al., 1998; Boggs et al., 2009; Cheptou, 2019; Cropano et al., 2021; Slatter et al., 2021). However, the main factor hindering the evolution of self-pollination is inbreeding depression (ID), and the works devoted to the evolution of the mating system in plants are focused mainly on this problem (Lande, Schemske, 1985; Husband, Schemske, 1996).

ID can be described in terms of its strength and also in terms of the plant's developmental stage at which it is expressed (Husband, Schemske, 1996). Some models suggest that ID greater than 0.5 prevents the transition to selfing (Lande, Schemske, 1985). However, it is likely that the strength and nature of the manifestation of the depression at the beginning and at the end of the plant's life cycle may have a different impact on the likelihood of evolution towards selfing.

An example of the recent evolution of selfing (apparently despite the initially very strong ID) is known in the genus *Fagopyrum* Mill. *F. esculentum* Moench (common buckwheat) is a heterostylous cross-pollinator cultivated as a grain crop (Figure).

**Figure. Flowers of buckwheat: A – long-styled (pin), B – short-styled (thrum), and C – homostylous**
(flower diameter is about 8–10 mm)

**Рисунок. Цветки гречихи: A – длинностолбчатый, B – короткостолбчатый, C – гомостильный**
(диаметр цветка – 8–10 мм)

Due to the almost complete range of homostyly mutations, most of which are self-fertile, buckwheat has become one of the objects for genetic studies of heterostyly (Fesenko, 1989). There were ideas to breed self-pollinating buckwheat cultivars using homostylous mutations. All attempts to create such cultivars failed due to severe inbreeding depression, which could not be overcome. However, a wild autogamous (i.e., highly tolerant to selfing) species was found to be very closely related to the cultivated common buckwheat (Ohnishi, Asano, 1999). The species was named *F. homotropicum* Ohnishi. Thus, the experiment that seemed impossible in the practice of buckwheat breeders and geneticists was successfully implemented in nature.

*F. homotropicum* was considered a useful resource for the development of inbreeding-tolerant material for buckwheat breeding. By now, a self-pollinating commercial cultivar of common buckwheat has not yet been released. However, some experiments with inbred lines allowed us to make some conclusions on the problem of the evolution of selfing, especially at early stages of such evolution, with special attention on inbreeding depression at various developmental stages. The results and relevant discussion are presented in this publication.

## Material and methods

*Plant material*

*F. esculentum* cv. 'Demetra' with a determinate growth habit based on *det*-mutation, and cv. 'Molva' with an indeterminate growth habit, both bred at the Federal Scientific Center (FSC) of Legumes and Groat Crops; and

*F. homotropicum*, accession C9139 (Kyoto University collection), the species discovered by Prof. O. Ohnishi in Yunnan Province, China.

*Obtaining a homostylous line through interspecific hybridization*

The interspecific hybrid *F. esculentum* (cv. 'Demetra') × *F. homotropicum* (accession C9139) was obtained using the conventional method (without embryo rescue technique). The flower homostyly locus of *F. homotropicum* is tightly linked (recombination frequency = 0–2.4%) with the dominant allele of *SHT* (seed shattering habit) (Fesenko et al., 2006). Within $F_2$ segregation, a plant with homostylous flowers (see Figure) and nonshattering seeds was selected. The plant was used for backcrossing on *F. esculentum* (cv. 'Demetra'). Three backcrosses were made to obtain self-fertile material with approximately 94% of *F. esculentum* germplasm and 6% of *F. homotropicum*. Morphologically, such plants did not differ from the cultivated *F. esculentum*, with the exception of flower homostyly. The progeny of a $BC_3F_1$ homostylous plant was used for hybridization with *F. esculentum* to produce lines for the evaluation of inbreeding depression. The line was designated HL11.

*Obtaining the set of lines for evaluating inbreeding depression*

Since HL11 was not always homozygous for the homostyly gene, the $F_1$ hybrids *F. esculentum*, pin × HL11 were both homostylous and pin. The homostylous plants produced seeds due to self-pollination, while the pin-plants due to hand cross-pollination with homostylous ones. Therefore, progenies of the homostylous plants were considered the first inbred generation ($I_1$). To obtain the lines of the second inbreed generation, the seeds from homostylous plants of every individual line were used. Five seeds of each line were sown. Among the obtained plants, one with homostylous flowers was selected, the seeds of which were used to obtain the next generation. Every following inbred generation was obtained in the same manner, using seeds from one homostylous plant of every line of the previous generation. The progeny of the pin $F_1$ hybrids *F. esculentum*, pin × HL11 was used as the cross-pollinated control to evaluate inbreeding depression in all generations studied.

*Evaluation of ID*

The lines of all inbreed generations ($I_1$ – $I_6$) were previously obtained in an insect-free greenhouse. The lines were sown in the field together with the cross-pollinated control (see above). Twenty seeds of each line were planted. Sowing dates were May 25, 2018, May 22, 2019, and May 19, 2020. Plants were cut on August 10, 2018, August 15, 2019, and August 10, 2020.

ID was evaluated for the characteristics listed in Table 1 (see Results). To measure the area of the largest leaf, photographs of the leaves were taken with a scale, on which measurements were made using the AxioVision software. The photos were taken on July 10, 2018, and July 7, 2019. For each line, the largest leaves from 3 randomly selected plants were measured; the average was calculated and used in statistics. To evaluate the 'dry weight of a mature plant' and 'weight of seeds per plant', after counting the plants of each line that survived until harvesting, they were cut and dried. Those dried plants were then weighed and threshed. The resulting seeds were also weighed. The results obtained were used for the calculations. The value of inbreeding depression (δ) was calculated as described by R. Lande and D. W. Schemske (1985), i.e., $\delta = (w_o - w_i)/w_o = 1 - w_i/w_o$, where $w_o$ is the trait value in the outcrossed progeny, and $w_i$ is the trait value in the selfed progeny.

*Evaluating competitive ability of ovaries*

The evaluation of competitive ability of ovaries on a plant depends on the genotype's heterozygosity level. It was conducted by analyzing results of spontaneous hybridization of the inbred lines with the heterostylous cv. 'Molva'. The approach is described in detail in the Results section.

## Results

### *Dynamics of inbreeding depression (ID) during long-term self-pollination of buckwheat*

Dynamics of ID was typical for such cases. The ID for the resulted trait, i.e., the weight of seeds per plant, was the highest, as expected. The value of the trait decreased sharply after the first selfing (ID = 0.66 and 0.59 according to the data obtained in 2018 and 2019, respectively). The additional changes after subsequent self-pollinations were exponential (see Table 1).

The ID for the weight of a mature plant was also strong after the first self-pollination and increased exponentially during the following selfing. A similar trend is seen in another trait reflecting the strength of the plant's vegetative development, i.e., the area of the largest leaf on a plant, although the level of ID was lower compared to that for the mature plant weight (see Table 1).

The field germination rate showed low ID with little changes across generations. In 2018, the ID increased slightly from 0.12 in $I_1$ to 0.18 in $I_4$; in 2019, the ID remained within similar range across generations (see Table 1). The manifestation of the minimal depression is not associated with seed germination, only with the reduced fitness of some seedlings.

**Table 1.** Characterization of buckwheat lines according to the manifestation of inbreeding depression (mean ± SE) in a series of self-pollination generations

**Таблица 1.** Характеристика линий гречихи по проявлению инбредной депрессии (X ± SE) в ряду поколений самоопыления

| Trait | Selfing generation | | | | | |
|---|---|---|---|---|---|---|
| | $I_1$ | $I_2$ | $I_3$ | $I_4$ | $I_5$ | $I_6$ |
| **Year 2018** | | | | | | |
| Lines studied | 50 | 50 | 50 | 50 | 50 | 50 |
| Field germination rate | 0.12 ± 0.014 | 0.15 ± 0.015 | 0.17 ± 0.015 | 0.18 ± 0.012 | 0.18 ± 0.013 | 0.17 ± 0.016 |
| Largest leaf area | 0.35 ± 0.014 | 0.38 ± 0.017 | 0.41 ± 0.013 | 0.54 ± 0.013 | 0.55 ± 0.010 | 0.58 ± 0.009 |
| Dry weight of a mature plant | 0.52 ± 0.023 | 0.72 ± 0.018 | 0.77 ± 0.017 | 0.81 ± 0.014 | 0.83 ± 0.014 | 0.85 ± 0.014 |
| Weight of seeds per plant | 0.66 ± 0.028 | 0.81 ± 0.020 | 0.87 ± 0.015 | 0.89 ± 0.013 | 0.92 ± 0.011 | 0.93 ± 0.009 |
| **Year 2019** | | | | | | |
| Lines studied | 37 | 37 | 37 | 37 | 37 | 37 |
| Field germination rate | 0.12 ± 0.020 | 0.13 ± 0.025 | 0.12 ± 0.025 | 0.14 ± 0.027 | 0.15 ± 0.022 | 0.16 ± 0.020 |
| Largest leaf area | 0.29 ± 0.022 | 0.33 ± 0.020 | 0.39 ± 0.019 | 0.50 ± 0.015 | 0.49 ± 0.014 | 0.53 ± 0.012 |
| Dry weight of a mature plant | 0.51 ± 0.015 | 0.57 ± 0.018 | 0.62 ± 0.016 | 0.69 ± 0.023 | 0.79 ± 0.017 | 0.81 ± 0.015 |
| Weight of seeds per plant | 0.59 ± 0.030 | 0.69 ± 0.025 | 0.73 ± 0.027 | 0.83 ± 0.024 | 0.88 ± 0.024 | 0.89 ± 0.014 |

This conclusion was suggested by the fact that ID was not detected when the seeds were germinated in Petri dishes, i.e., under controlled conditions. Inbreeding also had no noticeable effect on the survival of emerging seedlings before harvesting (ID was at the level of 0.02–0.05 across generations for both years).

### *Does competitive ability of ovaries on a plant depend on the heterozygosity level of their genotypes?*

ID usually reduces the competitive ability of an individual plant compared to a plant of the outbred origin. Such competition could be especially clear between different ovaries developing on the same plant. It can be assumed that if ID appears at the stage of ovary development, ovaries with higher level of heterozygosity will have an advantage in the competition for resources compared to those with more homozygous genotypes.

To assess this relationship, an experiment was conducted on the basis of the following assumptions: 1) the level of the line's (or plant's) homozygosity correlates with the generation of inbreeding; 2) on the given plant, ovaries resulting from self-pollination will obviously be more homozygous than ovaries resulting from cross-pollination; 3) all such lines have an equal tendency to cross-pollination with heterostylous *F. esculentum*, since they carry the same homostyly gene *S4*, introgressed from *F. homotropicum* C9139. So, if a higher level of heterozygosity in an ovary's genotype provides some advantages, the proportion of ovaries resulted from cross-pollination among ovaries that have turned into mature seeds should increase in later inbred generations.

The experimental design was as follows. Inbred lines $I_1 – I_7$ (= $F_2 – F_8$) with the determinate growth habit had been obtained previously under the conditions of an insect-free greenhouse using self-fertility of homostylous plants. In 2020, the lines were grown adjacent to the indeterminate cv. 'Molva' in the following order: 'Molva' – 'Molva' – inbred line – 'Molva' – 'Molva' – inbred line – 'Molva', etc. The length of the rows was 1.5 m. The distance between the rows was 30 cm. The sowing was manual. There were 30–35 plants of 'Molva' or 10–12 plants of one of the inbred lines in a row. Seeds were collected from all plants of each line. The number of seeds and number of plants of each line were taken into account to assess the average number of seeds per plant: the value was used for the across-lines statistics. The seeds were sown in 2021 to estimate the proportion of seeds resulted from cross-pollination using the morphological marker *det*: within the progenies, any plants with the indeterminate growth habit were hybrids with 'Molva', and the plants with determinate growth resulted from self-pollination. The results of the experiment are shown in Table 2.

Seed productivity, measured as the number of seeds per plant, decreased substantially with inbreeding. In the $I_1$ generation, the trait's mean value was 52.7 seeds per plant. This indicator dropped steadily across generations down to 13.2 seeds per plant in $I_7$: the decline confirms strong inbreeding depression for the trait.

In the context of this experiment, the fact is significant because when a plant can form fewer seeds, the competition among the developing seeds for assimilates becomes greater. Therefore, if ovaries with more heterozygous genotypes were advantageous, the increased competition could further increase the proportion of non-aborted ovaries (i.e., mature seeds) resulting from cross-pollination. However, we did not observe such a trend: there was some variation in this indicator, but it was stochastic, and with the exception of some excess in $I_5$, the proportion of seeds resulted from cross-pollination among all the seeds formed on plants within the lines of different inbred generations after growing adjacent to the heterostylous cultivar was almost the same. Thus, the seeds set as a result of both self-pollination and cross-pollination have equal chances for development on the same plant.

**Table 2.** Seed productivity of inbred lines, and the dependence of the proportion of developed seeds from cross-pollination with the adjacent heterostylous cv. 'Molva' on the depth of inbreeding

**Таблица 2.** Семенная продуктивность инбредных линий и зависимость доли сформировавшихся семян, происходящих от переопыления с гетеростильным сортом 'Молва', от глубины инбридинга

| Inbreeding generation | Lines analyzed | Seeds per plant, Mean ± SE | Proportion of seeds from cross-pollination, Mean ± SE |
|---|---|---|---|
| $I_1$ ($F_2$) | 22 | 52.7 ± 2.75 | 16.2 ± 1.51 |
| $I_2$ | 21 | 34.6 ± 2.29 | 17.8 ± 1.27 |
| $I_3$ | 21 | 15.2 ± 0.81 | 17.9 ± 1.83 |
| $I_4$ | 21 | 15.1 ± 0.76 | 17.1 ± 2.09 |
| $I_5$ | 21 | 14.5 ± 0.70 | 21.7 ± 1.75 |
| $I_6$ | 21 | 13.6 ± 0.65 | 18.5 ± 1.75 |
| $I_7$ | 21 | 13.2 ± 0.70 | 15.5 ± 1.55 |

## Discussion

The cultivated cross-pollinator *F. esculentum* manifests a typical reaction to inbreeding. Main genetic load is eliminated mainly during two generations of selfing, and later the fitness continues reducing, down to a plateau, usually during three or four selfing generations. In the ontogenesis, ID was barely noticeable at the stage of seedling emergence, increased during further vegetative development (measured as the size of the largest leaf), and reached a maximum at the stage of grain filling, exceeding 0.5 (the level which allows the evolution of autogamy, according to some theoretical models). At the same time, the level of homozygotization does not influence competitive ability of developing seeds on a plant, i.e., the ovaries on the same plant resulted from both self- and cross-pollination have similar chances to reach maturity.

The phenomenon of ID enhancement during ontogeny has been documented for many species. Early-acting ID, i.e., ID at the stage of seed formation, also has been described in a number of published works; however, in most cases, the disturbances in seed development were due to strong deleterious recessives becoming homozygous. Such genetic load can be easily eliminated during self-pollination. In some cases, such mutations are maintained to provide early removal of selfed offsprings from a population and, therefore, to increase a share of outcrossed ones. It is especially useful when selfing prevention mechanisms are not very effective. Thus, selfing levels of aborted fruits of *Platypodium elegans* were 10% higher than those of seeds and seedlings; it was attributed to an early expression of genetic load (Hufford, Hamrick, 2003). Selfing levels of died seeds of *Caryocar brasiliense* were higher than those of viable seeds (Collevatti et al., 2009). Development of selfed seeds continuously varies in *Aconitum kusnezoffii*, i.e., the embryos are aborted at different stages; it was interpreted in terms of the expression of many deleterious alleles during seed maturation (Hao et al., 2012).

The embryonic lethality due to the homozygosity of strong deleterious recessives cannot be equated with the "true" ID. Such ovaries die in any case, regardless of the strength of competition for resources with other ovaries. The phenomenon of the effect of the genotype on competitiveness (if the competing genotypes do not carry embryonic lethals) has not yet been documented, apparently, for any plant species. In our work, the phenomenon of the absence of such competition was proved. This fact is very significant in the context of the evolution of self-pollination. So, if ovaries originated from outcrossing had advantages over the ones from self-pollination on the same plant, the evolution of autogamy would hardly be possible. Selfed ovaries would die off when any cross-pollination occurs, and mutations promoting selfing would tend to be eliminated from the population. When cross-pollination becomes impossible, self-pollinated ovaries might have a chance to develop. But if in a population that may have already partially adapted to selfing and reduced the level of ID the outcrossing is resumed, the outcrossed ovaries will prevent the development of selfed ones. On the other hand, if the heterozygosity level of the genotype of an ovary does not affect the probability that it will turn into a mature seed, less heterozygous ovaries have an opportunity to develop and, therefore, become the founders of self-pollinated lineages.

The absence of a noticeable effect of the level of heterozygosity in the ovary's genotype on its competitive ability during its development on a plant is very important for the start of the evolution towards self-pollination. The levels of ID at other developmental stages are apparently less crucial for a possibility of such evolution. Strong harmful recessives that cause selfed seeds to die off can be eliminated quite quickly after the process of such evolution has started. Further on, the elimination of weaker harmful alleles can gradually occur. This process can go on apparently for quite a long time. Ultimately, it is possible to obtain some optimal combination of genes, developing a sufficiently adapted self-pollinator, although complete disposal of ID at the later stages of ontogeny might fail to occur.

In this study, the selfed lines of *F. esculentum*, even the selfed interspecies hybrids *F. esculentum* × *F. homotropicum*, showed ID higher than 0.5. *F. esculentum* and *F. homotropicum* are very closely related species, obviously derived from a common ancestor. This ancestor had highly likely the same ID parameters as the cross-pollinator *F. esculentum*, i.e., ID > 0.5. However, it did not prevent the emergence of the autogamous species *F. homotropicum*.

Our experiment gives no answer to the question why the speciation of the self-pollinator *F. homotropicum* has started. The data presented do not allow us to speculate on this topic. It may have been the result of the isolation of small fragments of a crossbreeding population in mountains, where the self-fertility mutation became established. Apparently, it is not entirely correct to speculate how beneficial it is for a particular species to become a selfer. A more correct logic is that self-fertility mutations sometimes occur, but their evolutionary future, whether they will become founders of new species, or will be rejected by natural selection, depends on a number of conditions. Evidently, in most cases such mutations are eliminated from a population or maintained as a minor admixture. So, many self-fertile mutations of *F. esculentum* were isolated in a short time on experimental fields. It allows us to assume that such forms should arise quite often, but none of such mutants have become the basis for a new species in nature. However, there is an exception like *F. homotropicum*, when the one more self-fertile mutation was successfully combined with an increase in tolerance to ID.

## Conclusion

This study showed that ovaries differing in heterozygosity levels of their genotypes had an equal chance to become mature seeds on a buckwheat plant. It looks like a key preadaptation for the possibility of evolution towards selfing. The levels of ID at the stages of autotrophic development are less important for the possibility of such evolution. So, the ID of vegetative development and seed yield in the cross-pollinating species *F. esculentum* significantly exceeds 0.5. It is highly likely that the ancestral form of contemporary buckwheat species manifested a similar ID level. Despite this fact, the emergence of the autogamous species *F. homotropicum*, closely related to *F. esculentum*, became possible.

## References / Литература

Baker H.G. Self-compatibility and establishment after “long distance” dispersal. *Evolution*. 1955;9(3):347-349. DOI: 10.1111/j.1558-5646.1955.tb01544.x

Boggs N.A., Nasrallah J.B., Nasrallah M.E. Independent S-locus mutations caused self-fertility in *Arabidopsis thaliana*. *PLoS Genetics*. 2009;5(3):e1000426. DOI: 10.1371/journal.pgen.1000426

Busch J.W., Delph L.F. The relative importance of reproductive assurance and automatic selection as hypotheses for the evolution of self-fertilization. *Annals of Botany*. 2012;109(3):553-562. DOI: 10.1093/aob/mcr219

Cheptou P.O. Does the evolution of self-fertilization rescue populations or increase the risk of extinction? *Annals of Botany*. 2019;123(2):337-345. DOI: 10.1093/aob/mcy144

Collevatti R.G., Estolano R., Garcia S.F., Hay J.D. Seed abortion in the bat pollinated neotropical tree species, *Caryocar brasiliense* (Caryocaraceae). *Botany*. 2009;87(11):1110-1115. DOI: 10.1139/B09-054

Cropano C., Place I., Manzanares Ch., Do Canto J., Lübberstedt Th., Studer B. et al. Characterization and practical use of self-compatibility in outcrossing grass species. *Annals of Botany*. 2021;127(7):841-852. DOI: 10.1093/aob/mcab043

Fesenko N.N. The system of buckwheat reproduction: three types of flower homostyly inheritance. In: N.V. Fesenko, L.I. Gudin, L.P. Lomteva, S.A. Stefanina (eds). *Proceedings of the 4th International Symposium on Buckwheat, Orel, Russia, 11–15 July 1989*. Orel; 1989. p.193-201.

Fesenko N.N., Fesenko I.N., Ohnishi O. Homostyly of two morphologically different lineages of *Fagopyrum homotropicum* Ohnishi is determined by locus *S4*, which is an *S*-locus related gene in the linkage group #4. *Fagopyrum*. 2006;23:11-15.

Hao Y.Q., Zhao X.F., She D.Y., Xu B., Zhang D.Y., Liao W.J. The role of late-acting self-incompatibility and early-acting inbreeding depression in governing female fertility in monkshood, *Aconitum kusnezoffii*. *PLoS One*. 2012;7(10):e47034. DOI: 10.1371/journal.pone.0047034

Hufford K.M., Hamrick J.L. Viability selection at three early life stages of the tropical tree, *Platypodium elegans* (Fabaceae, Papilionoideae). *Evolution*. 2003;57(3):518-526. DOI: 10.1111/j.0014-3820.2003.tb01543.x

Husband B., Schemske D.W. Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution*. 1996;50(1):54-70. DOI: 10.1111/j.1558-5646.1996.tb04472.x

Igic B., Busch J.W. Is self-fertilization an evolutionary dead end? *The New Phytologist*. 2013;198(2):386-397. DOI: 10.1111/nph.12182

Lande R., Schemske D.W. The evolution of self fertilization and inbreeding depression in plants. I. Genetic models. *Evolution*. 1985;39(1):24-40. DOI: 10.1111/j.1558-5646.1985.tb04077.x

Ohnishi O., Asano N. Genetic diversity of *Fagopyrum homotropicum*, a wild species related to common buckwheat. *Genetic Resources and Crop Evolution*. 1999;46(4):389-398. DOI: 10.1023/A:1008640522979

Slatter L.M., Barth S., Manzanares Ch., Velmurugan J., Place I., Thorogood D. A new genetic locus for self-compatibility in the outcrossing grass species perennial ryegrass (*Lolium perenne*). *Annals of Botany*. 2021;127(6):715-722. DOI: 10.1093/aob/mcaa140

Takebayashi N., Morell P.L. Is self-fertilization an evolutionary dead end? Revisiting an old hypothesis with genetic theories and a macroevolutionary approach. *American Journal of Botany*. 2001;88(7):1143-1150. DOI: 10.2307/3558325

Voylokov A., Korzun V., Börner A. Mapping of three self-fertility mutations in rye (*Secale cereal* L.) using RFLP, isozyme and morphological markers. *Theoretical and Applied Genetics*. 1998;97(1-2):147-153. DOI: 10.1007/s001220050879

Wright S.I., Kalisz S., Slotte T. Evolutionary consequences of self-fertilization in plants. *Proceedings. Biological Sciences*. 2013;280(1760):20130133. DOI: 10.1098/rspb.2013.0133

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### *Information about the authors*

**Aleksey N. Fesenko**, Dr. Sci. (Biology), Head of a Laboratory, Federal Scientific Center of Legumes and Groat Crops, 10, bldg. 1, Molodezhnaya St., Streletsky Settlem., Orel 302502, Russia, fesenko.a.n@rambler.ru, https://orcid.org/0000-0002-7658-3471

**Ivan N. Fesenko**, Dr. Sci. (Biology), Chief Researcher, Federal Scientific Center of Legumes and Groat Crops, 10, bldg. 1, Molodezhnaya St., Streletsky Settlem., Orel 302502, Russia, ivanfesenko@rambler.ru, https://orcid.org/0000-0002-3612-422x

### *Информация об авторах*

**Алексей Николаевич Фесенко**, доктор биологических наук, заведующий лабораторией, Федеральный научный центр зернобобовых и крупяных культур, 302502 Россия, Орел, пос. Стрелецкий, ул. Молодежная, 10, корп. 1, fesenko.a.n@rambler.ru, https://orcid.org/0000-0002-7658-3471

**Иван Николаевич Фесенко**, доктор биологических наук, главный научный сотрудник, Федеральный научный центр зернобобовых и крупяных культур, 302502 Россия, Орел, пос. Стрелецкий, ул. Молодежная, 10, корп. 1, ivanfesenko@rambler.ru, https://orcid.org/0000-0002-3612-422x

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