Review
DOI: https://doi.org/10.17816/ecogen697772 EDN: PBXFTO

Naturally Transgenic Plants as a Model for Studying Delayed Environmental Risks of GMO Cultivation: New Evidence and Generalizations

Tatiana V. Matveeva[1,2]

[1] Saint Petersburg State University, Saint Petersburg, Russia;
[2] All-Russian Research Institute of Plant Protection, Saint Petersburg, Russia

ABSTRACT

Transgenic plants occupy an important place in modern agriculture in many countries. The global area under genetically modified crops continues to increase each year and currently exceeds 200 million hectares. Increasing attention in the scientific data is devoted to assessing the potential environmental consequences of cultivating transgenic plants. Particular concern is associated with the possible effects of insecticidal proteins on non-target fauna and on microbial communities of the rhizosphere and phyllosphere. Another important issue is the escape of transgenes into the environment, which may occur through the uncontrolled introduction of seeds of transgenic crops into biocenoses, as well as through cross-pollination between transgenic plants and non-transgenic varieties of the same species or related plant species. The emergence and spread of spontaneous hybrids of transgenic varieties have been monitored by several researchers over multiple years of experiments; however, conducting long-term studies of these processes remains problematic. In this context, naturally transgenic plants, which originated in nature as a result of genetic transformation hundreds of thousands to millions of years ago, may serve as an interesting model for studying the evolutionary fate of transgenes, both under stabilizing selection in their favor and in its absence. Recent studies have expanded the list of naturally transgenic plants. It currently includes more than two hundred. Of particular interest in this context are genera in which the diversity of natural transgene sequences has been studied in detail across a large number of species, ecotypes, and populations. These include *Nicotiana*, *Camellia*, *Arachis*, *Vaccinium*, *Cuscuta*, *Ipomoea*, and several others. Within representatives of these genera, different evolutionary trajectories of natural transgenes can be observed. Some transgenes remain intact and expressed, leading to the emergence of new biosynthetic pathways in plants. Others gradually lose their integrity, accumulate point mutations, and over time undergo more substantial rearrangements, up to complete elimination. Such trends have been reported for certain genes in species belonging to the genera *Nicotiana*, *Camellia*, *Arachis*, and *Vaccinium*. Taken together, these findings suggest that in the absence of selective pressure favoring traits controlled by transgenes, plants not only accumulate point mutations but may also gradually eliminate transgenes.

Keywords: transgenic plants; environmental risks; natural transgenes; mutations.

To cite this article
Matveeva TV. Naturally Transgenic Plants as a Model for Studying Delayed Environmental Risks of GMO Cultivation: New Evidence and Generalizations. *Ecological genetics*. 2026;24(1):9–14. DOI: 10.17816/ecogen697772 EDN: PBXFTO

Submitted: 04.12.2025 **Accepted:** 15.12.2025 **Published online:** 31.03.2026

Научный обзор
DOI: https://doi.org/10.17816/ecogen697772 EDN: PBXFTO

Природно-трансгенные растения как модель изучения отсроченных экологических рисков возделывания ГМО: новые факты и обобщения

Т.В. Матвеева[1,2]

[1] Санкт-Петербургский государственный университет, Санкт-Петербург, Россия;
[2] Всероссийский научно-исследовательский институт защиты растений, Санкт-Петербург, Россия

АННОТАЦИЯ

Трансгенные растения занимают важное место в современном сельском хозяйстве многих стран. Посевные площади под генно-инженерно-модифицированными культурами увеличиваются год от года и ныне составляют более 200 млн га. В научной литературе всё больше внимания уделяют оценке возможных экологических последствий возделывания трансгенных растений. Наибольшую обеспокоенность вызывают вопросы, связанные с возможностью действия инсектицидных белков на нецелевую фауну и сообщества микроорганизмов ризосферы и филлосферы, а также проблемы утечки трансгенов в окружающую среду вследствие бесконтрольного попадания семян трансгенных культур в биоценозы и вследствие переопыления трансгенных растений с нетрансгенными сортами того же вида или представителями родственных видов растений. Мониторинг возникновения и распространения спонтанных гибридов трансгенных сортов был исследован рядом авторов в течение нескольких лет эксперимента, однако проведение более долгосрочных исследований проблематично. В этой связи природно-трансгенные растения, возникшие в природе в результате генетической трансформации сотни тысяч – миллионы лет назад, могут выступать интересной моделью эволюционной судьбы трансгенов в случае стабилизирующего отбора в их пользу и в отсутствие такового. Исследования последних лет позволили расширить список природно-трансгенных растений. Сейчас он насчитывает более двухсот. Особый интерес в контексте данной проблемы представляют рода, в которых наиболее детально оценено разнообразие последовательностей природных трансгенов у большого количества видов, экотипов, популяций. К ним относятся *Nicotiana*, *Camellia*, *Arachis*, *Vaccinium*, *Cuscuta*, *Ipomoea* и некоторые другие. У представителей данных родов можно проследить различные эволюционные судьбы природных трансгенов. Часть из них остаётся интактной, экспрессируется, приводя к появлению у растений новых биосинтетических путей. Другая часть теряет свою интактность, накапливает точковые мутации, а со временем претерпевает более существенные перестройки, вплоть до полной элиминации. Такие тенденции отмечены для некоторых генов у видов в пределах родов *Nicotiana*, *Camellia*, *Arachis*, *Vaccinium*. Эти данные в совокупности наводят на мысль, что в отсутствие селективного отбора в пользу признаков, контролируемых трансгенами, растение не только накапливает точковые мутации, но и пытается избавиться от трансгенов.

Ключевые слова: трансгеные растения; экологические риски; природные трансгены; мутации.

Как цитировать
Матвеева Т.В. Природно-трансгенные растения как модель изучения отсроченных экологических рисков возделывания ГМО: новые факты и обобщения // Экологическая генетика. 2026. Т. 24, № 1. С. 9–14. DOI: 10.17816/ecogen697772 EDN: PBXFTO

Рукопись получена: 04.12.2025 **Рукопись одобрена:** 15.12.2025 **Опубликована online:** 31.03.2026

INTRODUCTION

Transgenic plants have become a significant aspect of modern global agriculture, as demonstrated by the annual increase in the area dedicated to genetically modified (GM) crops, which now exceeds 200 million hectares[1, 2] (Fig. 1). Transgenic plants (GMOs) can help solve global problems because they have a number of significant advantages over traditional varieties and hybrids, including: resistance to pests and diseases, resistance to herbicides, increased yield and stability, improved nutritional and consumer qualities, resistance to abiotic stress. This large-scale shift to biotechnological solutions has led the scientific community to focus not only on productivity but also on a thorough evaluation of potential environmental impacts. Key areas of concern include: 1) the effects of plant-produced insecticidal proteins on non-target organisms, such as beneficial insects and microorganisms in the rhizosphere and phyllosphere; 2) the risk of uncontrolled transgene spread in the environment. This can happen through mechanical seed dispersal outside of agroecosystems and through cross-pollination between GM, traditional varieties, and their wild relatives, posing a threat of genetic contamination to natural populations [1]. The consequences of such flow can be evaluated by examining natural GMOs plants whose ancestors underwent *Agrobacterium*-mediated transformation hundreds of thousands or even millions of years ago. Let's look at this topic in more detail.

GENE FLOW IS A KEY ECOLOGICAL RISK OF GMO CULTIVATION

One of the key environmental risks associated with GM crops is transgene escape (also known as "gene flow" or "genetic pollution")—the uncontrolled spread of genetically engineered traits from intended crops into natural ecosystems or traditional farmland. The main causes of transgene escape can be categorized into two broad groups: biological mechanisms and agronomic/anthropogenic factors. Biological mechanisms include cross-pollination (via pollen) and the dispersal of vegetative parts and seeds [2–4]. The riskiest scenario involves cross-breeding with wild relatives [3, 4]. If the region where the GM crop is grown contains wild or weedy relatives capable of cross-breeding, the transgene can "escape" into the wild population [4–6]. Agronomic and anthropogenic causes, including errors and accidents, involve mistakes occurring at various stages of agricultural production and regulatory violations. The consequences of transgene escape include the emergence of hybrids with increased resistance, which can become difficult-to-eradicate weeds, a reduction in the genetic diversity of wild ancestors of cultivated plants, and changes in competitive relationships between species [1].

All of the above highlights the importance of conducting monitoring studies and developing strategies to prevent transgene leakage. However, current research is limited to only a few years of observation. In 2015, we proposed a model, based on naturally transgenic plants, for studying the delayed risks of GMO cultivation [7]. A substantial body of evidence has since accumulated, allowing us to revisit this topic.

NATURALLY TRANSGENIC PLANTS

The term "naturally transgenic plants" refers to plants that have acquired foreign genes from a species other than their direct ancestors through a natural, horizontal gene transfer (HGT) process, without human intervention. The most famous and well-documented examples of naturally transgenic plants are species that were transformed by *Agrobacterium/Rhizobium*, the very same bacterium that scientists use as a tool to create transgenic plants in the lab [8]. Hundreds of species of naturally transgenic plants are currently known, and it is generally accepted that traces of *Agrobacterium/Rhizobium*—mediated transformation (called cT-DNA, cellular T-DNA) exist in the genomes of seven percent of dicotyledons [9–11]. The rapid development of next-generation sequencing and bioinformatics methods enables large-scale genome sequencing of various species within specific genera, providing invaluable data for assessing the diversity of natural transgenes. This analysis can be used to track the fate of natural transgenes in evolutionarily related plant groups [12–15].

EVOLUTIONARY FATE OF NATURAL TRANSGENES

Research conducted by our group shows that transgenes integrated into plant genomes millions or hundreds of thousands of years ago can follow varying evolutionary paths. Our analysis reveals that most natural transgenes accumulate mutations that render them nonfunctional, leading to their gradual deletion. In contrast, some natural transgenes persist under stabilizing selection, resulting in groups of species that retain functional transgenes [16–18].

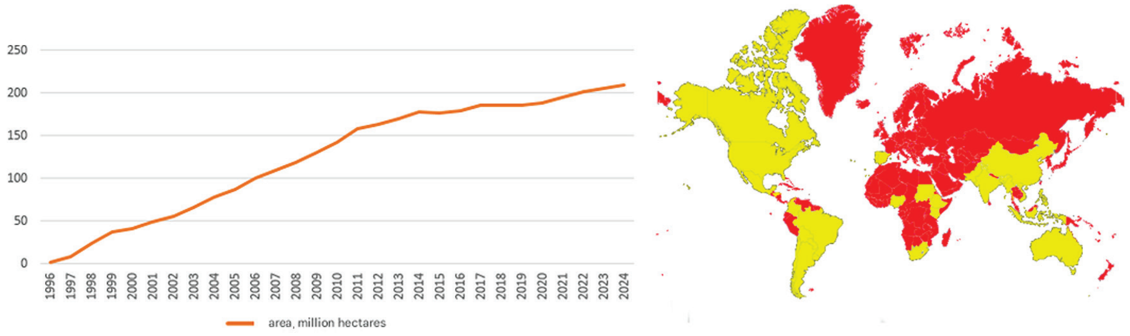
Now, let's examine specific examples of natural transgenes with different evolutionary outcomes.

In a study by Bogomaz et al. [17], 23 species of the genus *Arachis* were characterized, with some species represented by various forms. Within this genus, virtually all studied accessions contained in their genomes at least one intact copy of a gene homologous to the cucumopine

---

[1] AgbioInvestor GM Monitor Report [Internet]. 2025. Available from: https://gm.agbioinvestor.com (Accessed 01.12.2025).

[2] ISAAA. GM Approval Database [Internet]. 2025. Available from: https://www.isaaa.org/gmapprovaldatabase/default.asp (Accessed 01.12.2025).



a *b*

Fig. 1. Area under genetically modified crops (*a*) and countries cultivating them (highlighted in yellow) (*b*) (based on data from ISAAA).
Рис. 1. Площади под генномодифицированными культурами (*a*) и страны, выращивающие их (помечены жёлтым) (*b*) (по материалам ISAAA).

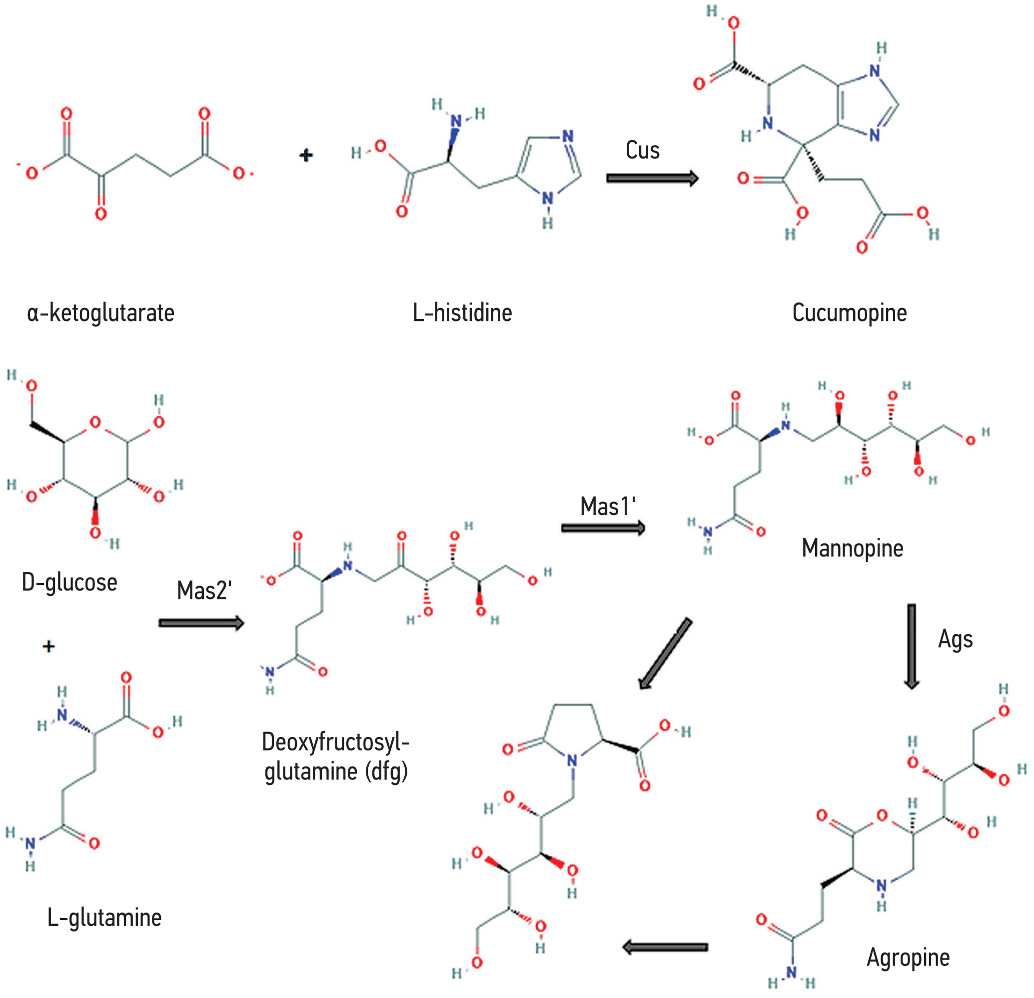


Fig. 2. Biosynthetic reactions of cucumopine and agropine (based on data from [19]).
Рис. 2. Реакции синтеза кукумопина и агропина (по материалам [19]).

synthase gene. This gene catalyzes the production of cucumopine (Fig. 2), a low-molecular-weight compound utilized by some bacteria for nutrition. Additionally, fragments of genes were identified in some peanut genomes, whose *Agrobacterium* homologs encode enzymes involved in the sequential synthesis of mannopine and agropine. Notably, none of the species retained all three genes, and none of the detected fragments were intact. In 14 species, the genes encoding the mannopine-agropine synthetase enzymes were completely absent. It can be inferred that the cucumopine synthase gene was preserved under the influence of stabilizing selection, while the genes for other opines lost their significance for the ancestor of peanuts and were gradually eliminated.

Another interesting example involves representatives of the genus *Vaccinium* [18]. Among the 22 species studied within this genus and its related species, damaged copies of the transgene were predominant only in *V. oxycoccos*. In the other species, the transgenes remained intact. The mutations in the damaged gene consisted of extensive deletions. This suggests that the species may have activated mechanisms to eliminate foreign DNA.

More extensive studies were conducted on plants from the *Nicotiana* and *Camellia* genera.

In the genus *Nicotiana*, eight distinct types of cellular T-DNA were analyzed (inside *Tomentosae* section they were named TA, TB, TC, TD, TE; in *Noctiflorae* section they are gT, NnT-DNA1, NnT-DNA) [12–14]. Attempts to trace their phylogenetic relationships during speciation revealed that cultivated tobacco did not inherit all copies of T-DNA from a single ancestral genome. One T-DNA (TC) was completely lost.

In addition to TC, TE also experienced chromosomal rearrangements throughout its evolution [14].

Within the genus *Camellia*, 12 variants of cellular T-DNA have been described. The most ancient of these are TA and TD. Phylogenetic studies suggest that the ancestral form that gave rise to the sections *Thea*, *Tuberculatae*, *Longipedicellatae*, and *Calpandria* lost TD. The stages of occurrence of deletions within TA were reconstructed based on a comparative analysis of the TA insertion in *C. fangchengensis* and the majority of representatives of the *Thea* section. Modern TAs do not contain intact genes; however, the mutation pattern indicates that species from the *Thea* section and *C. fangchengensis* diverged from an intact sequence, subsequently accumulating point mutations, followed by an inversion and two deletions of TA fragments in *C. fangchengensis*.

Together, these data suggest that the plant eliminates non-functional sequences while preserving intact genes that confer a selective advantage.

CONCLUSION

Similar consequences cannot be ruled out for transgenic plants created by humans, especially given their uncontrolled spread in the environment. *Brassica napus, Medicago sativa*, and *Agrostis stolonifera* warrant particular attention in this context, as all three crops are found in the wild worldwide. Transgenic lines resistant to herbicides have been developed from each of these species. When exposed to a selective agent, transgenic forms and their hybrids gain an advantage over non-herbicide-tolerant plants [1].

Consequently, monitoring is essential to prevent adverse developments. In recent years, new information has emerged regarding the spread of transgenes through cross-pollination within a species and interspecific hybridization. Although interspecific hybridization occurs infrequently, it can have significant consequences for the fixation of transgenes within new genome [7]. The history of naturally occurring transgenic plants shows that unwanted transgenes can be eliminated from populations by removing the influence of the selective agent. This can be accomplished by abandoning the use of pesticides to which specific GMOs are resistant in favor of other pesticides to which the escaped GMOs are not resistant.

ADDITIONAL INFO

Author contribution: T.V. Matveeva: conceptualization, investigation, writing—original draft; writing—review & editing. The author approved the version of the manuscript to be published and agreed to be accountable for all aspects of the work, ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Funding sources: The work was supported by the Russian Science Foundation, grant 25-26-00123.

Disclosure of interests: The author have no relationships, activities, or interests for the last three years related to for-profit or not-for-profit third parties whose interests may be affected by the content of the article.

Statement of originality: No previously obtained or published material (text, images, or data) was used in this study or article.

Data availability statement: All data obtained in this study are available in this article.

Generative AI: No generative artificial intelligence technologies were used to prepare this article.

Provenance and peer-review: This paper was submitted unsolicited and reviewed following the standard procedure. The peer review process involved one external reviewer, a member of the editorial board, and the in-house science editor.

ДОПОЛНИТЕЛЬНАЯ ИНФОРМАЦИЯ

Вклад автора. Т.В. Матвеева — определение концепции, проведение исследования; написание черновика рукописи; пересмотр и редактирование рукописи. Автор одобрил рукопись (версию для публикации), а также согласился нести ответственность за все аспекты настоящей работы, гарантируя надлежащее рассмотрение и решение вопросов, связанных с точностью и добросовестностью любой её части.

Источники финансирования. Работа выполнена при поддержке Российского научного фонда, грант 25-26-00123.

Раскрытие интересов. Автор заявляет об отсутствии отношений, деятельности и интересов за последние три года, связанных с третьими лицами (коммерческими и некоммерческими организациями), интересы которых могут быть затронуты содержанием статьи.

Оригинальность. При проведении исследования и создании настоящей статьи авторы не использовали ранее полученные и опубликованные сведения (данные, текст, иллюстрации). Доступ к данным. Все данные, полученные в настоящем исследовании, представлены в статье.

Генеративный искусственный интеллект. При создании настоящей статьи технологии генеративного искусственного интеллекта не использовали.

Рассмотрение и рецензирование. Настоящая работа подана в журнал в инициативном порядке и рассмотрена по обычной процедуре. В рецензировании участвовали один внешний рецензент, член редакционной коллегии и научный редактор издания.

REFERENCES

1. Matveeva TV. On the impact of GMOs on species diversity. http://www.rokson.nw.ru/ru/councils/ecology/school_science/gmo (accessed 10.10.2025).

2. Beckie HJ, Warwick SI, Nair H, Seguin-Swartz G. Gene flow in commercial fields of herbicide-re-sistant canola (*Brassica napus*). *Ecol Appl*. 2003;13(5):1276–1294. doi: 10.1890/02-5231

3. Bing DJ, Downey RK, Rakow GFW. Hybridizations among *Brassica napus*, *B. rapa* and *B. juncea* and their two weedy relatives *B. nigra* and *Sinapis arvensis* under open pollination conditions in the field. *Plant Breed*. 1996;115(6):470–473. doi: 10.1111/j.1439-0523.1996.tb00959.x

4. Sohn S-I, Thamilarasan SK, Pandian S, et al. Interspecific hybridization of transgenic *Brassica napus* and *Brassica rapa*—an overview. *Genes*. 2022;13(8):1442. doi: 10.3390/genes13081442

5. Warwick SI, Legyre A, Simard M-J, James T. Do escaped transgenes persist in nature? The case of an herbicide resistance transgene in a weedy *Brassica rapa* population. *Mol Ecol*. 2008;17(5):1387–1395. doi: 10.1111/j.1365-294X.2007.03567.x

6. Warwick SI, Simard M-J, Legere A, et al. Hybridization between transgenic *Brassica napus* L. and its wild relatives: *Brassica rapa* L., *Raphanus raphanistrum* L., *Sinapis arvensis* L., and *Erucastrum gallicum* (Willd.) O.E. Schulz. *Theor Appl Genet*. 2003;107:528–539. doi: 10.1007/s00122-003-1278-0

7. Matveeva TV. Naturally transgenic plants as a model for the study of delayed environmental risks of cultivation of GMOs. *Ecological genetics*. 2015;13(2):118–126. doi: 10.17816/ecogen132118-126 EDN: TYRKIL

8. White FF, Garfinkel DJ, Huffman GA, et al. Sequences homologous to *Agrobacterium rhizogenes* T-DNA in the genomes of uninfected plants. *Nature*. 1983;301:348–350. doi: 10.1038/301348a0

9. Matveeva TV, Otten L. Widespread occurrence of natural genetic transformation of plants by *Agrobacterium. Plant Mol Biol*. 2019;101:415–437. doi: 10.1007/s11103-019-00913-y

10. Matveeva TV. New naturally transgenic plants: 2020 update. *Biol Commun*. 2021;66(1):36–46. doi: 10.21638/spbu03.2021.105

11. Shaposhnikov AD, Matveeva TV. The description of new naturally transgenic plants made it possible to estimate the time intervals of horizontal gene transfer from agrobacteria to plants. *Ecological genetics*. 2026;24(1):15-28. In Press. doi: 10.17816/ecogen693516

12. Chen K, Dorlhac de Borne F, Sierro N, et al. Organization of the TC and TE cellular T-DNA regions in *Nicotiana otophora* and functional analysis of three diverged TE-6b genes. *Plant J*. 2018;94(2):274–287. doi: 10.1111/tpj.13853

13. Chen K, Otten L. Natural *Agrobacterium* transformants: recent results and some theoretical considerations. *Front Plant Sci*. 2017;8:016. doi: 10.3389/fpls.2017.01600

14. Khafizova GV, Sierro N, Ivanov NV, et al. *Nicotiana noctiflora* hook. Genome contains two cellular T-DNAs with functional genes. *Plants*. 2023;12(22):3787. doi: 10.3390/plants12223787

15. Chen K, Zhurbenko P, Danilov L, et al. Conservation of an *Agrobacterium* cT-DNA insert in *Camellia* section *Thea* reveals the ancient origin of tea plants from a genetically modified ancestor. *Front Plant Sci*. 2022;13:997762. doi: 10.3389/fpls.2022.997762

16. Chen K, Liu H, Blevins T, et al. Extensive natural *Agrobacterium*-induced transformation in the genus *Camellia*. *Planta*. 2023;258(4):81. doi: 10.1007/s00425-023-04234-9

17. Bogomaz OD, Bemova VD, Mirgorodskii NA, Matveeva TV. Evolutionary fate of the opine synthesis genes in the *Arachis* L. genomes. *Biology*. 2024;13(8):601. doi: 10.3390/biology13080601

18. Zhidkin R, Zhurbenko P, Bogomaz O, et al. Biodiversity of *rolB/C*-like natural transgene in the genus *Vaccinium* L. and its application for phylogenetic studies. *Int J Mol Sci*. 2023;24:6932. doi: 10.3390/ijms24086932

19. Matveeva T, Otten L. Opine biosynthesis in naturally transgenic plants: Genes and products. *Phytochemistry*. 2021;189:112813. doi: 10.1016/j.phytochem.2021.112813

AUTHOR INFO

Tatiana V. Matveeva, Dr. Sci. (Biology), Professor;
address: 7–9 Universitetskaya Emb, Saint Petersburg, 199034, Russia; ORCID: 0000-0001-8569-6665; eLibrary SPIN: 3877-6598;
e-mail: radishlet@gmail.com

ОБ АВТОРЕ

Матвеева Татьяна Валерьевна, д-р биол. наук, профессор;
адрес: Россия, 199034, Санкт-Петербург, Университетская наб., д. 7–9; ORCID: 0000-0001-8569-6665; eLibrary SPIN: 3877-6598;
e-mail: radishlet@gmail.com