DOI: https://doi.org/10.17816/ecogen89905
Review

Why do plants need agrobacterial genes?

Tat'yana V. Matveeva

Saint Petersburg State University, Saint Petersburg, Russia

Agrobacterium mediated transformation in nature is the cause of the development of diseases: crown galls and hairy roots. These neoplasms are transgenic tissues on a non-transgenic plant. However, in nature, full-fledged GMOs arise, containing agrobacterial transgenes in every cell and transmitting them in a series of sexual generations. These plants are called naturally transgenic plants or natural GMOs. Over the past 3 years, the list of natural GMO species has been significantly expanded. Due to this, it became possible to make certain generalizations and more substantively discuss the possible evolutionary role of this phenomenon. The presented mini-review is devoted to the generalization of data on the possible functions of genes of agrobacterial origin in plant genomes.

Keywords: naturally transgenic plants; cT-DNA; opine synthesis genes; plast-genes; horizontal gene transfer.

To cite this article:
Matveeva TV. Why do plants need agrobacterial genes? *Ecological genetics*. 2021;19(4):365–375. DOI: https://doi.org/10.17816/ecogen89905

Received: 07.12.2021 **Accepted:** 10.12.2021 **Published:** 29.12.2021

DOI: https://doi.org/10.17816/ecogen89905
Обзорная статья

Зачем растениям агробактериальные гены?

Т.В. Матвеева

Санкт-Петербургский государственный университет, Санкт-Петербург, Россия

Агробактериальная трансформация в природе является причиной развития заболеваний: корончатых галлов и косматых корней. Эти новообразования представляют собой трансгенные ткани на нетрансгенном растении. Однако в природе возникают полноценные генетически модифицированные организмы, содержащие агробактериальные трансгены во всех клетках и передающие их в ряду половых поколений. Эти растения называют природно-трансгенными или природными генетически модифицированными организмами. За последние 3 года список видов природных генетически модифицированных организмов был существенно расширен. Благодаря этому стало возможным сделать определенные обобщения и более предметно обсуждать возможную эволюционную роль данного явления. Представленный мини-обзор посвящен обобщению данных относительно возможных функций генов агробактериального происхождения в геномах растений.

Ключевые слова: природно-трансгенные растения; клТ-ДНК; гены синтеза опинов; *plast*-гены; горизонтальный перенос генов.

Как цитировать:
Матвеева Т.В. Зачем растениям агробактериальные гены? // Экологическая генетика. 2021. Т. 19. № 4. С. 365–375. DOI: https://doi.org/10.17816/ecogen89905

Рукопись получена: 07.12.2021 **Рукопись одобрена:** 10.12.2021 **Опубликована:** 29.12.2021

ЭКО•ВЕКТОР

INTRODUCTION

Agrobacteria are a group of soil bacteria consisting of representatives of several genera [1] able to transfer a fragment of their own DNA, called T-DNA (transferred DNA), and integrating it into the plant genome [2]. In the most cases, during such a transformation, only a part of the plant tissues is transgenic, as a rule, in the region of the root collar. Other tissues, including tissues of generative organs, remain nontransgenic [3].

There are examples of T-DNA occurring in the genome of a whole plant. When this happens, T-DNA is passed down for generations. Such T-DNA is called cellular T-DNA (cT-DNA), and plants containing it are called naturally transgenic or natural genetically modified organisms (nGMOs) [4]. In this study, we are dealing with horizontal gene transfer from agrobacteria to plants. The role of horizontal gene transfer in plant evolution has not yet been fully studied [5].

Based on our knowledge of the role of horizontal gene transfer in the evolution of prokaryotes, we can assume similar effects occur in eukaryotes, namely, the acquisition and inheritance of new traits that provide selective advantages, which can be divided into two groups:

1) improvement of existing functions, and
2) emergence of new functions in the recipient (for example, changes in nutrition, new protective functions) [6–8].

The first nGMOs resulting from ancient agrobacterial transformation were described in the genus *Nicotiana* L. [9], later they were detected by molecular genetic methods in two more genera, *Linaria* Mill. and *Ipomoea* L. [10–12]. In 2017, we published a review on the biological aspects of the naturally transgenic plants known at that time and the possible functions of genes obtained by plants from agrobacteria [13]. At that time, the functions of cT-DNA included the following:

- increase in root mass to adapt to plant growth in arid conditions,
- immunity to repeated agrobacterial infection,
- increased regenerative capacity,
- transition to earlier flowering and, as a result, transition to an annotinous life cycle, and
- influence on the communities of microorganisms of the rhizosphere and phyllosphere of the plant [13].

In recent years, the list of natural GMOs has increased substantially through the use of bioinformatic methods [14, 15]. Thus, the time has come for a new review of the functions of cT-DNA and the evolutionary role of the horizontal transfer of agrobacterial genes in plants. This review is focused on this subject.

New taxa of natural GMOs

The development of next generation sequencing methods has provided new opportunities for studying plant genomes, resulting in incremental growth of data on the their structure. Constantly updated databases are a valuable source for searching for new nGMOs [14].

Analysis of the sequenced genomes of land plants allowed us to identify homologues of agrobacterial genes only within the angiosperm division. At present, it is generally accepted that agrobacteria transform dicotyledons much more efficiently than they do monocotyledons [16]. This idea is supported by data on the distribution of natural GMOs. Among several dozen species of new natural GMOs, only two of them are monocotyledons. The systematic position of one of them (*Dioscorea alata* L.) is debatable, and the other species (*Musa acuminata* Colla) is assigned to natural GMOs only based on data obtained from the analysis of the root transcriptome [14]. Thus, these data require further research and careful interpretation.

Among the dicotyledonous plants, the confinement of naturally transgenic species to a specific taxonomic group was not noted. Natural GMOs are described within the orders Malpighiales, Fabales Rosales, Cucurbitales, Fagales, Brassicales, Myrtales, Sapindales, Caryophyllales, Cornales, Ericales, Lamiales, Solanales [14, 15]. The geography of distribution of naturally transformants is wide, ranging from the tropics and subtropics (neem, representatives of the genus *Camellia* L.) to forest-tundra and tundra (e.g., representatives of the genus *Vaccinium* L.), and covers all continents, except for Antarctica [14, 17–20]. The list of natural GMOs includes many cultivated plants used by people from different countries for food as well as medicinal plants. Such plants include tea, guava, peanuts, hops, sweet potatoes, and cranberries. According to preliminary estimates, about 7% of dicotyledonous plants may contain traces of agrobacterial transformation in their genomes. This estimate is based on data on the share of natural GMOs among dicotyledonous species with sequenced genomes [14].

Is it worth searching a single function of cT-DNA for all natural GMOs?

To answer this question, it is necessary to evaluate the cT-DNA structures of natural GMOs and the diversity of intact genes in them.

Before considering the diversity of cT-DNA, we will briefly outline the main groups of genes in it. T-DNA usually contains genes for the synthesis of opines, the products of which are required for the nutrition of bacteria [21]. In addition to opine synthases, cT-DNA encodes oncogenes that cause neoplastic tissue growth and are represented by phytohormone synthesis genes and *plast* genes. The mechanism of influence of hormonal genes on plant morphogenesis has been known for a long time, while *plast* genes and the mechanisms of their action have been studied much less [22, 23].

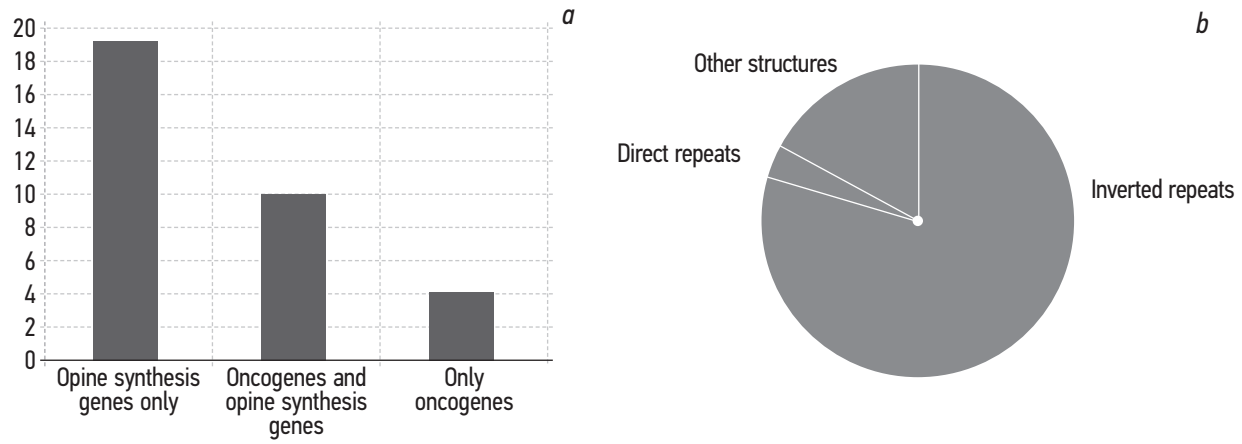

Fig. 1. Number of genera of natural GMOs with different cT-DNA structures (*a*) and types of extended cT-DNA structures (*b*)

The discussion on the functions of cT-DNA in natural GMOs started from the moment they were described. The discussion was centered on which of the genes (oncogenes or opine synthases) are the most important acquisitions of plants involved in evolution [4]. However, the discussion was hampered by a lack of factual material for research and generalizations. Now the situation has changed. By the beginning of 2021, 36 genera of angiosperms were already known, within which natural transgenic species were described [14, 15]. Among them, the most dominant are those whose cT-DNA contains only genes for the synthesis of opines (Fig. 1, *a*). This phenomenon can be explained in at least three ways. First, in currently known T-DNA, genes for synthesis of opines are located closer to the right border; therefore, they enter the plant cell first in the course of transformation. If T-DNA transfer is terminated untimely, than the opine synthesis genes could enter the recipient cel without oncogenes [21]. Second, we can expect the presence of strains of agrobacteria whose T-DNA contains only genes for opine synthase. Third, the possibility of transformation of plants with extended T-DNA and the loss of most of it during the evolution of the descendants of the natural transformants with the preservation of only opine synthesis genes cannot be excluded [24].

Species containing extended T-DNA fragments with oncogenes and genes for opine synthesis rank second in terms of abundance. Extended cT-DNA are mostly represented by inverted imperfect repeats (Fig 1b) and often contain well-known T-DNA genes and new poorly studied sequences, usually attributed to *plast* genes [14, 15, 25, 26], which indicates a wider variety of agrobacterial strains transforming plants than we previously believed.

The least abundant are cT-DNA containing only oncogenes [14, 15, 24]. Among them, special attention should be paid to *plast* genes found in representatives of the genera *Vaccinium* L. and *Nyssa Gronov* ex L. They are of interest because they are phylogenetically close to the *plast* gene sequences found in some basidiomycete fungi [14, 15].

Analysis of ORFs in all three types of cT-DNA for the presence of premature stop codons or mutations that cause frame shifts shows that some of the genes there remain intact, while others mutate [14–16]. More intact sequences have been preserved among opine synthases [15] but there are quite a lot of intact ones among *plast* genes as well.

We can, therefore, conclude that different natural GMOs have different sets of intact genes in their cellular T-DNA. This means that cT-DNA does not have a universal function. In different groups of plants, evolution used forms with various combinations of transgenes, and then far from all of them were preserved intact.

Possible functions of cT-DNA *plast* genes

Before discussing the cT-DNA *plast* genes, let us briefly consider what is generally known about this family of genes. The name *plast* genes comes from the words “developmental plasticity.” The term was coined to emphasize the ability of these genes to change plant morphogenesis in various ways during the transformation of wild-type plants [26]. Levesque et al. [27] suggest that *plast* genes may have similar functions associated with their common origin, and that their divergence may be an adaptation to different plant species. The best-known members of this family are the genes *rolA, rolB, rolC, ORF13*, and *ORF14* genes from *Rhizobium rhizogenes* (Riker et al. 1930) Young et al. (2001), gene *6b* from *Agrobacterium tumefaciens* (Smith and Townsend 1907) Conn 1942 (Approved Lists 1980) emend. Hördt et al. 2020 [26]. The analysis of their functions is complex due to the fact that some morphogenetic effects may coincide in different genes, while others may differ. For example, the *rolB* gene product is sufficient to induce root formation. *RolC* is not able to independently induce root formation, but exhibits a synergistic effect with *rolB* [26]. Transgenic plants containing only *rolB* or only *rolC* differ in leaf color (the former are dark green, the latter are light green), which indicates antagonism of the action of genes [26].

It is believed that *rolB* has meristem-inducing activity [28, 29], but it also causes necrosis of tobacco leaves [30] whereas *rolC* suppresses the necrotic effects induced by *rolB*. The introduction of *rolC* into the genome of cultivated tobacco and carnations (*Dianthus caryophyllus* L.) leads to the stimulation of shoot formation [26, 31], and in the cell culture of ginseng (*Panax ginseng* C.A. Mey.) it stimulates somatic embryogenesis [32]. The *ORF13* gene product enhances the effect of *rolB* in inducing root generation. However, the expression of orf13 in tobacco [33, 34], tomato [35], and arabidopsis [36] resulted in various changes in the height of transgenic plants up to dwarfism. *ORF14* does not have a clear phenotypic effect. However, the fact that the *rolA, rolB, rolC, ORF13, ORF14* genes are always located close to one another in T-DNA suggests their possible involvement in the control of the overall process [26]. Possibly, the different combinations of genes from this set function predominantly in different plants. That is, the "inclusion" of specific genes depends on the molecular genetic characteristics of the recipient.

The molecular mechanisms of action of genes remain completely incomprehensible. The fact that *plast* genes have been described not only in naturally transgenic plants but also in some fungi [22] suggests that if there is a certain common function of all *plast* genes, it should affect some basic biochemical processes characteristic not only for plants [26].

So far, there has been no direct evidence of the functioning of *plast* genes of cT-DNA in natural GMOs. However, some indirect arguments clearly indicate that *plast* genes can affect the growth of natural transformants. The *rolC, orf13,* and *orf14* genes often remain intact in naturally transgenic plants and are expressed [12, 22, 37]. A complete list of expressed genes can be reconstructed from the review [4] and article [14] that we published earlier.

The *plast*-gene-associated functions of cT-DNA previously discussed in the literature included an increase in root mass, an increase in regenerative capacity, and a transition to earlier flowering and one-year life cycles [13]. There is no clear evidence supporting the latter function. On the contrary, we detected the predominance of perennial forms among nGMOs in the presence of annual non-transgenic species, at least in toadflax [13]. The expanded list of nGMOs for 2021 is interesting in that among the carriers of *plast* genes, there were many ligneous plant forms, confirming that they are perennial plants [14, 15]. Thus, the new data supports our previous findings. Nevertheless, the identification of new nGMOs with this T-DNA function as a key function cannot be ruled out.

As for the increase in regenerative capacity and induction of root formation, the role of *plast* genes in the implementation of these functions should be discussed separately. At present, *plast* gene expression has been demonstrated by molecular methods in representatives of the genera *Nicotiana* (*NgrolC, trolC, Ngorf13*, and *torf13*) [22, 25, 38], *Linaria* (*rolC*) [39], *Ipomoea* (*rolB/C-like, orf13, gene c*) [10, 40]. When overexpressed in tobacco, *Ngorf13* causes the formation of dark green rounded leaves [41], overexpression of Ng*rol*C [42] and t*rol*C [43] leads to a dwarf phenotype and the formation of lanceolate, pale green leaves, whereas t*orf*13 induces green calli on carrot disks [44]. In naturally transgenic toadflax, tissue-specific expression of the Lv*rolC* transgene was demonstrated during plant regeneration from root explants on a hormone-free medium, which may indicate the involvement of the gene product in the regulation of this process [39]. In previous publications, we discussed the effect of *rol*-genes on the regenerative capacity of *Nicotiana* species [4, 13]. We concluded that the peculiarities of plant morphogenetic reactions can be determined, among other things, by a combination of intact *rol*-genes and their level of expression in a particular genotype.

Analysis of the transcriptomes deposited with the NCBI can be used for the primary search for the expressed genes of new natural GMOs. The currently available data can be interpreted in support of expression of *plast* genes in plants of the genus *Vaccinium* and *Diospyros* [14, 15].

The morphogenetic effects of *plast* genes, their role in the regulation of secondary metabolism and carbohydrate metabolism are discussed in the literature. The most common biologically active secondary plant metabolites include alkaloids, polyphenolic compounds (flavonoids, terpenoids, coumarins, saponins) and essential oils. All these compounds are efficiently synthesized in cultures of hairy roots [45, 46]. Under natural conditions, they are involved in the protection of plants from adverse abiotic factors as well as in the regulation of interaction of plants with other organisms.

Although there is no direct evidence of the involvement of cT-DNA genes in the control of the content of secondary metabolites, this role cannot be ruled out yet. Palazon et al showed that the *rolC* gene increases nicotine synthesis in transgenic tobacco obtained under laboratory conditions, and the introduction of a cassette from *rolA, rolB,* and *rolC* into the plant genome increases the nicotine level more than a single *rolC* gene does. So, far, no specific mechanisms of regulation of this process have been identified [47–49].

In tobacco, toadflax, and model transgenic arabidopsis plants, the effect of *rolC* and gene *6b* on sugar metabolism was revealed [43, 50]. This function is discussed as some common property of various *plast* genes, preserved by them from a common ancestral sequence. This hypothesis is confirmed by our preliminary data from the analysis of samples of cranberry (*Vaccinium macrocarpon* Ait. and *V. oxycoccos* L.), contrasting with the presence of a full

length *plast* gene previously unknown among agrobacterium strains. The content of monosaccharides is higher in shoots of cranberry forms with a full length *plast* gene compared to samples containing mutant alleles of the gene with a large deletion [51].

Thus, the involvement of *plast* genes in the control of plant morphogenesis cannot be ruled out although this process is not known yet. The regulation is probably implemented through the control of carbohydrate metabolism, and perhaps through other mechanisms. The control of plant secondary metabolism is an important component of the regulation of plant-microbial interactions, because secondary metabolites can both attract and repel microbes and insects [45, 46], demonstrating an important ecological role. However, there is another class of compounds that can attract specific microbes. These are opines.

Opine synthase

Opine synthases are the most common transgenes in natural transformants. The functions of opine synthases are quite clear and have been studied in detail in relation to agrobacterial strains of various origins.

In the case of natural GMOs, the greatest success was achieved in the study of opine synthases, for which not only expression at the RNA level was demonstrated in dozens of species [24], but also the ability of plants to accumulate the corresponding opines. Thus, deoxyfructosylglutamine was found in naturally transgenic cultivated tobacco plants, and mikimopine was revealed in the tissues of another nGMO, dodder, [52, 53]. Opines can be used as sources of carbon and nitrogen not only by bacteria, but also by fungi that have enzymes for their catabolism [54]. We can assume that opine synthases play a role in the regulation of the composition of microbial communities in the plant rhizosphere. This is supported by the fact that, in addition to natural GMOs, opine synthase genes have been described in many bacteria outside the group of agrobacteria and are also widely distributed in the genomes of ascomycete fungi [55]. In fungi, a certain mosaic structure was noted in terms of the location on the phylogenetic tree of species and isolates containing specific opine synthases in relation to the owners of other opine synthases within one larger taxon. This aspect can be interpreted in support of the role of horizontal gene transfer in the spread of opine synthases among fungi [55]. Most of the currently discussed opine synthases are annotated in sequenced genomes, based on their homology to known genes, and their real functions are yet to be studied using molecular and biochemical methods. The outcomes of these studies may include already known opines in organisms where they have not been studied before, and new variants of opines that have a certain structural similarity to previously known ones. In addition, new data on the role of opine synthases in the regulation of the formation of plant communities with bacteria and fungi can be expected in the coming years. To confirm this idea, the growing interest in the use of rhizopines to attract beneficial bacteria to the rhizosphere can be indicated. Rhizopines, although different from opines of agrobacteria, perform a similar function to them, attracting rhizobia, capable of metabolizing them, into the plant rhizosphere. In order to control the structure of the microbial community in the laboratory, successful attempts have been made to plants metabolic engineering. The study resulted in transgenic plants synthesizing rhizopines, which, in turn, attracted rhizobia [56]. In the case of natural GMOs, nature has done all the work for us.

If we evaluate the diversity of opine synthases in natural GMOs, then the largest number of intact sequences is described for homologues of mikimopine synthases and cucumopine synthases. Although these are different genes, their products, mikimopine and cucumopine, are isomers [24]. Cucumopine and mikimopine synthases are the most attractive candidates for further research and development of approaches to modify microbial communities in the plant rhizosphere.

Do pGMOs become immune to re-transformation?

To date, species with multiple cT-DNA inserts have been described among natural GMOs. These species belong to the genera such as *Nicotiana* L., *Ipomoea* L., *Diospyros* L., *Parasponia* Miq., *Trema* Lour., *Silene* L. [14, 15, 25]. Among them, special attention should be paid to species of the genera *Nicotiana, Diospyros,* and *Parasponia*. Their genomes contain multiple cT-DNA organized as inverted repeats. In *Nicotiana tomentosiformis* L., all four cT-DNAs in the genome are organized as inverted repeats [25], in *Diospyros lotus* L., three out of seven are repeats [15], and in *Parasponia andersonii* Planch. eight out of nine are repeats [14]. Comparing the sequences of the right and left T-DNA arms, we can understand which of them diverged more. Thus, it is possible to perform a relative dating of transformational events (and reveal which of them happened earlier and which one happened later). This simple analysis enables us to draw an important conclusion that the transformational events in the evolution of these genera occurred sequentially, but not simultaneously. When the phylogeny of the genus is studied well by traditional methods, it is possible to link the relative dating to the time scale. Thus, it was revealed that hundreds of thousands of years passed between transformational events in tobacco [25]. Since repeated successive transformations took place in the evolution of representatives of three unrelated plant genera, we can state that the idea of a protective function of cT-DNA against repeated transformations is untenable. On the contrary, it can be assumed that there are species prone to transformation. By identifying their common characteristics and

introducing the identified traits into the genomes of other plants, it is possible to optimize further plant transformation protocols in the laboratory.

CONCLUSION

Our review has revealed that horizontal gene transfer from agrobacteria to plants has occurred and is occurring at a higher frequency than previously believed [14]. As a result of such a transfer, forms with various combinations of intact T-DNA genes are preserved in nature, while the other part of the genes mutates or is completely lost. If an extended T-DNA enters the genome during horizontal gene transfer, the forms with cT-DNA organized as an inverted repeat are taken by selection with a higher probability. Probably, this structure suppresses the expression of T-DNA genes, which softens the effect of agrobacterial oncogenes on plant morphogenesis. Further, under conditions of partial suppression of gene expression, selection starts in favor of specific gene combinations. In each case, the combination may be different, which is consistent with Levesque's idea on divergence of *plast* genes to different host plants. This results in a wide variety of natural GMOs.

In some plants, the process of such transformation can be repeated several times. It may result in the acquisition of new genes, such as additional opine synthases. Further, cT-DNAs within the same genome can evolve independently of each other.

Recently, evidence is accumulating in support of functioning of T-DNA genes. In the future, we can expect an increase in the number of scientific articles describing new opine synthases, their products, and their functional role in ecosystems.

In addition, the description of new representatives of *plast* genes can be predicted. This may become valuable material for elucidating the basic functions of the genes of this family.

The accumulated information on new natural GMOs is valuable for future studies of the role of genes obtained by plants from agrobacteria during evolution, for studies of the diversity of agrobacteria strains, and for studies of the function and evolution of cT-DNA genes in natural transformants.

ADDITIONAL INFORMATION

Author contributions. The author confirms that his authorship complies with the international ICMJE criteria.

Funding. This work was supported by the Russian Science Foundation (grant No. 21-14-00050).

REFERENCES

1. Ormeno-Orrillo E, Servín-Garciduenas LE, Rogel MA, et al. Taxonomy of rhizobia and agrobacteria from the *Rhizobiaceae* family in light of genomics. *Syst Appl Microbiol*. 2015;38(4):287–291. DOI: 10.1016/j.syapm.2014.12.002

2. Chilton MD. *Agrobacterium* Ti plasmids as a tool for genetic engineering in plants. In: Rains DW, Valentine RC, Hollaender A, editors. *Genetic Engineering of Osmoregulation, Basic Life Sciences*. Boston: Springer, MA, 1980;14:23–31. DOI: 10.1007/978-1-4684-3725-6_3

3. Nester EW. *Agrobacterium*: nature's genetic engineer. *Front Plant Sci.* 2014;5:730. DOI: 10.3389/fpls.2014.00730

4. Matveeva TV. *Agrobacterium*-mediated transformation in the evolution of plants. *Curr Top Microbiol Immunol*. 2018;418:421–441. DOI: 10.1007/82_2018_ 80

5. Aubin E, El Baidouri M, Panaud O. Horizontal Gene Transfers in Plants. *Life (Basel)*. 2021;11(8):857. DOI: 10.3390/life11080857

6. Koonin EV, Wolf YI. Evolution of microbes and viruses: a paradigm shift in evolutionary biology? *Front Cell Infect Microbiol*. 2012;13(2):119. DOI: 10.3389/fcimb.2012.00119

7. Richardson AO, Palmer JD. Horizontal gene transfer in plants. *J Exp Bot*. 2007;58(1):1–9. DOI: 10.1093/jxb/erl148

8. Husnik F, McCutcheon JP. Functional horizontal gene transfer from bacteria to eukaryotes. *Nat Rev Microbiol*. 2018;16(2):67–79. DOI: 10.1038/nrmicro.2017.137

9. White FF, Garfinkel DJ, Huffman GA, et al. Sequences homologous to *Agrobacterium rhizogenes* T-DNA in the genomes of uninfected plants. *Nature*. 1983;3012:348–350. DOI: 10.1038/301348a0

10. Kyndt T, Quispe D, Zhai H, et al. The genome of cultivated sweet potato contains *Agrobacterium* T-DNAs with expressed genes: an example of a naturally transgenic food crop. *PNAS*. 2015;112(18):5844–5849. DOI: 10.1073/pnas.1419685112

11. Matveeva TV, Bogomaz DI, Pavlova OA, et al. Horizontal gene transfer from genus *Agrobacterium* to the plant *Linaria* in nature. *Mol Plant Microbe Interact*. 2012;25(12):1542–1551. DOI: 10.1094/MPMI-07-12-0169-R

12. Matveeva TV, Kosachev PA. Sequences homologous to *Agrobacterium rhizogenes rolC* in the genome of *Linaria acutiloba*. Proceedings of 2013 International Conference on Frontiers of Environment, Energy and Bioscience (ICFEEB2013). China, Beijing: 2013. P. 541–546.

13. Matveeva TV, Sokornova SV. Biological traits of naturally transgenic plants and their evolutional roles. *Russian Journal of Plant Physiology*. 2017;64(5):635–648. (In Russ.) DOI: 10.1134/S1021443717050089

14. 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

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

16. Lutova LA, Matveeva TV. *Gennaya i kletochnaya inzheneriya v biotekhnologii vysshikh rastenii: uchebnik*. Tikhonovich IA, editor. Saint Petersburg: Eco-Vector, 2016. 167 p. (In Russ.)

17. https://www.plantarium.ru/ [Internet]. Plantarium. Rasteniya i lishainiki Rossii i sopredel'nykh stran: otkrytyi onlain atlas i opre-

delitel' rastenii [cited 1 November 2021]. Available from: https://www.plantarium.ru/. (In Russ.)

18. Morton J. Surinam cherry. In: *Fruits of warm climates*. Miami, 1987. P. 386–388.

19. Murav'eva DA. *Tropicheskie i subtropicheskie lekarstvennye rasteniya 2-e izd. pererab. i dop*. Moscow: Meditsina, 1983. 336 p. (In Russ.)

20. Elenevskii AG. *Botanika. Sistematika vysshikh, ili nazemnykh, rastenii*. Moscow: Akademiya, 2004. (In Russ.)

21. Vladimirov IA, Matveeva TV, Lutova LA. Opine biosynthesis and catabolism genes of *Agrobacterium tumefaciens* and *Agrobacterium rhizogenes*. *Russian Journal of Genetics*. 2015;51(2):137–146. (In Russ.) DOI: 10.1134/S1022795415020167

22. 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

23. Chen K, Otten L. Natural *Agrobacterium* transformants: recent results and some theoretical considerations. *Front Plant Sci*. 2017;8:1600. DOI: 10.3389/ fpls.2017.01600

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

25. Chen K, Dorlhac de Borne F, Szegedi E, Otten, L. Deep sequencing of the ancestral tobacco species *Nicotiana tomentosiformis* reveals multiple T-DNA inserts and a complex evolutionary history of natural transformation in the genus *Nicotiana*. *Plant J*. 2014;80(4):669–682. DOI: 10.1111/tpj.12661

26. Otten L. Natural *agrobacterium*-mediated transformation in the genus *Nicotiana*. In: Ivanov N, Sierro N, Peitsch MC, editors. *The Tobacco Plant Genome*. Springer, 2020. P. 195–209. DOI: 10.1007/978-3-030-29493-9_12

27. Levesque H, Delepelaire P, Rouze P, et al. Common evolutionary origin of the central portions of the Ri TL-DNA of Agrobacterium rhizogenes and the Ti T-DNAs of Agrobacterium tumefaciens. *Plant Mol Biol*. 1988;11:731–744. DOI: 10.1007/BF00019514

28. Altamura MM, Capitani F, Gazza L, et al. The plant oncogene *rolB* stimulates the formation of flower and root meristemoids in tobacco thin cell layers. *New Phytol*. 1994;126(2):283–293. DOI: 10.1111/j.1469-8137.1994.tb03947.x

29. Koltunow AM, Johnson SD, Lynch M, et al. Expression of *rolB* in apomictic *Hieracium piloselloides* Vill. causes ectopic meristems in planta and changes in ovule formation, where apomixis initiates at higher frequncy. *Planta*. 2001;214:196–205. DOI: 10.1007/s004250100612

30. Schmülling T, Schell J, Spena A. Single genes from *Agrobacterium rhizogenes* influence plant development. *EMBO J*. 1988;7(9): 2621–2629. DOI: 10.1002/j.1460-2075.1988.tb03114.x

31. Casanova E, Trillas MI, Moysset L, Vainstein A. Influence of rol genes in floriculture. *Biotechnol Adv*. 2005;23(1):3–39. DOI: 10.1016/j.biotechadv.2004.06.002

32. Gorpenchenko TY, Kiselev KV, Bulgakov VP, et al. The *Agrobacterium rhizogenes rolC*-gene induced somatic embryogenesis and shoot organogenesis in *Panax ginseng* transformed calluses. *Planta*. 2006;223:457–467. DOI: 10.1007/s00425-005-0102-2

33. Hansen G, Vaubert D, Heron JH, et al. Phenotypic effects of overexpression of *Agrobacterium rhizogenes* T-DNA ORF13 in transgenic tobacco plants are mediated by diffusible factor(s). *Plant J*. 1993;4(3):581–585. DOI: 10.1046/j.1365-313X.1993.04030581.x

34. Lemcke K, Schmülling T. Gain of function assays identify non-rol genes from *Agrobacterium rhizogenes* TL-DNA that alter plant morphogenesis or hormone sensitivity. *Plant J*. 1998;5(3):423–433. DOI: 10.1046/j.1365-313X.1998.00223.x

35. Stieger PA, Meyer AD, Kathmann P, et al. The orf13 T-DNA gene of *Agrobacterium rhizogenes* confers meristematic competence to differentiated cells. *Plant Physiol*. 2004;135(3):1798–1808. DOI: 10.1104/pp.104.040899

36. Kodahl N, Müller R, Lütken H. The *Agrobacterium rhizogenes* oncogenes rolB and ORF13 increase formation of generative shoots and induce dwarfism in *Arabidopsis thaliana* (L.) Heynh. *Plant Sci*. 2016;252:22–29. DOI: 10.1016/j.plantsci.2016.06.020

37. Matveeva TV, Lutova LA. Horizontal gene transfer from *Agrobacterium* to plants. *Front Plant Sci*. 2014;5:326. DOI: 10.3389/fpls.2014.00326

38. Aoki S, Kawaoka A, Sekine M, Ichikawa T, et al. Sequence of the cellular T-DNA in the untransformed genome of *Nicotiana glauca* that is homologous to ORFs 13 and 14 of the Ri plasmid and analysis of its expression in genetic tumours of *N. glauca* × *N. langsdorffii*. *Mol Gen Genet*. 1994 Jun 15;243(6):706–710. DOI: 10.1007/BF00279581

39. Matveeva TV, Bogomaz OD, Golovanova LA, et al. Homologs of the rolC gene of naturally transgenic toadflaxes Linaria vulgaris and Linaria creticola are expressed *in vitro*. *Vavilov Journal of Genetics and Breeding*. 2018;22(2):273–278. (In Russ.) DOI: 10.18699/VJ18.359

40. Quispe-Huamanquispe DG, Gheysen G, Yang J, et al. The horizontal gene transfer of *Agrobacterium* T-DNAs into the series *Batatas* (Genus *Ipomoea*) genome is not confined to hexaploid sweetpotato. *Sci Rep*. 2019;9:12584. DOI: 10.1038/s41598-019-48691-3

41. Aoki S, Syono K. Function of *ngrol* genes in the evolution of *Nicotiana glauca*: conservation of the function of NgORF13 and NgORF14 after ancient infection by an *Agrobacterium rhizogenes*-like ancestor. *Plant Cell Physiol*. 1999;40(2):222–230. DOI: 10.1093/oxfordjournals.pcp.a029531

42. Aoki S, Syono K. Horizontal gene transfer and mutation: *ngrol* genes in the genome of *Nicotiana glauca*. *PNAS*. 1999;96(23): 13229–13234. DOI: 10.1073/pnas.96.23.13229

43. Mohajjel-Shoja H, Clément B, Perot J, et al. Biological activity of the *Agrobacterium rhizogenes*-derived trolC gene of *Nicotiana tabacum* and its functional relationship to other plast genes. *Mol Plant Microbe Interact*. 2011;24(1):44–53. DOI: 10.1094/MPMI-06-10-0139

44. Fründt C, Meyer AD, Ichikawa T, Meins F. A tobacco homologue of the Ri-plasmid *orf13* gene causes cell proliferation in carrot root discs. *Mol Gen Genet*. 1998;259:559–568. DOI: 10.1007/s004380050849

45. Matveeva TV, Sokornova SV, Lutova LA. Influence of Agrobacterium oncogenes on secondary metabolism of plants. *Phytochem Rev*. 2015;14:541–554. DOI: 10.1007/s11101-015-9409-1

46. Matveeva T, Sokornova S. Agrobacterium rhizogenes Mediated Transformation of Plants for Improvement of Yields of Secondary Metabolites. In: Pavlov A, Bley T, editors. *Reference Series in Phytochemistry. Bioprocessing of Plant in vitro Systems*. Springer, 2016. 1–42 p. DOI: 10.1007/978-3-319-32004-5_18-1

47. Palazon J, Cusido RM, Gonzalo J, et al. Relation between the amount the *rolC* gene product and indole alkaloid accumulation in *Catharanthus roseus* transformed root cultures. *J Plant Physiol*. 1998a;153(5–6):712–718. DOI: 10.1016/S0176-1617(98)80225-3

48. Palazon J, Cusido RM, Roig C, Pino MT. Expression of the *rolC* gene and nicotine production in transgenic roots and their regenerated plants. *Plant Cell Rep*. 1998b;17:384–390. DOI: 10.1007/s002990050411
49. Amini G, Sokornova SV, Mohajjel-Shoja H, et al. Induced expression of rolC for study of its effect on the expression of genes associated with nicotine synthesis in tobacco. *Ecological genetics*. 2020;18(4):413–422. DOI: 10.17816/ecogen33768
50. Clément B, Perot J, Geoffroy P, et al. Abnormal accumulation of sugars and phenolics in tobacco roots expressing the Agrobacterium T-6b oncogene and the role of these compounds in 6b-induced growth. *Mol Plant-Microbe Interact*. 2007;20(1):53–62. DOI: 10.1094/MPMI-20-0053
51. Matveeva T, Berezina E, Isaeva I, et al. Influence of some *rol* genes on sugar content in *Nicotiana* and *Vaccinium*. *BIO Web of Conferences*. 2020;18:00020. DOI: 10.1051/bioconf/20201800020
52. Chen K, Dorlhac de Borne F, Julio E, et al. Root-specific expression of opine genes and opine accumulation in some cultivars of the naturally occurring GMO *Nicotiana tabacum*. *Plant J*. 2016;87(3):258–269. DOI: 10.1111/tpj.13196
53. Zhang Y, Wang D, Wang Y, et al. Parasitic plant dodder (*Cuscuta* spp.): a new natural *Agrobacterium*-to-plant horizontal gene transfer species. *Sci China Life Sci*. 2020;63:312–316. DOI: 10.1007/s11427-019-1588-x
54. Beauchamp CJ, Chilton WS, Dion P, Antoun H. Fungal catabolism of crown gall opines. *Appl Environ Microbiol*. 1990;56(1): 150–155. DOI: 10.1128/aem.56.1.150-155.1990
55. Sokornova SV, Matveeva TV. Phylogenetic Relationships of Ascomycetes Opine Synthases. *BMC Bioinformatics*. (accepted for publication)
56. Geddes BA, Paramasivan P, Joffrin A, et al. Engineering transkingdom signalling in plants to control gene expression in rhizosphere bacteria. *Nat Commun*. 2019;10:3430. DOI: 10.1038/s41467-019-10882-x

СПИСОК ЛИТЕРАТУРЫ

1. Ormeno-Orrillo E., Servín-Garciduenas L.E., Rogel M.A., et al. Taxonomy of rhizobia and agrobacteria from the *Rhizobiaceae* family in light of genomics // Syst Appl Microbiol. 2015. Vol. 38. No. 4. P. 287–291. DOI: 10.1016/j.syapm.2014.12.002
2. Chilton M.D. *Agrobacterium* Ti plasmids as a tool for genetic engineering in plants. In: Rains D.W., Valentine R.C., Hollaender A., editors. Genetic Engineering of Osmoregulation, Basic Life Sciences. Boston: Springer, MA, 1980. Vol. 14. P. 23–31. DOI: 10.1007/978-1-4684-3725-6_3
3. Nester E.W. *Agrobacterium*: nature's genetic engineer // Front Plant Sci. 2014. Vol. 5. ID730. DOI: 10.3389/fpls.2014.00730
4. Matveeva T.V. *Agrobacterium*-mediated transformation in the evolution of plants // Curr Top Microbiol Immunol. 2018. Vol. 418. P. 421–441. DOI: 10.1007/82_2018_ 80
5. Aubin E., El Baidouri M., Panaud O. Horizontal Gene Transfers in Plants // Life (Basel). 2021. Vol. 11. No. 8. ID857. DOI: 10.3390/life11080857
6. Koonin E.V., Wolf Y.I. Evolution of microbes and viruses: a paradigm shift in evolutionary biology? // Front Cell Infect Microbiol. 2012. Vol. 13. No. 2. ID119. DOI: 10.3389/fcimb.2012.00119
7. Richardson A.O., Palmer J.D. Horizontal gene transfer in plants // J Exp Bot. 2007. Vol. 58. No. 1. P. 1–9. DOI: 10.1093/jxb/erl148
8. Husnik F., McCutcheon J.P. Functional horizontal gene transfer from bacteria to eukaryotes // Nat Rev Microbiol. 2018. Vol. 16. No. 2. P. 67–79. DOI: 10.1038/nrmicro.2017.137
9. White F.F., Garfinkel D.J., Huffman G.A., et al. Sequences homologous to *Agrobacterium rhizogenes* T-DNA in the genomes of uninfected plants // Nature. 1983. Vol. 3012. P. 348–350. DOI: 10.1038/301348a0
10. Kyndt T., Quispe D., Zhai H., et al. The genome of cultivated sweet potato contains *Agrobacterium* T-DNAs with expressed genes: an example of a naturally transgenic food crop // PNAS. 2015. Vol. 112. No. 18. P. 5844–5849. DOI: 10.1073/pnas.1419685112
11. Matveeva T.V., Bogomaz D.I., Pavlova O.A., et al. Horizontal gene transfer from genus *Agrobacterium* to the plant *Linaria* in nature // Mol Plant Microbe Interact. 2012. Vol. 25. No. 12. P. 1542–1551. DOI: 10.1094/MPMI-07-12-0169-R
12. Matveeva T.V., Kosachev P.A. Sequences homologous to *Agrobacterium rhizogenes rolC* in the genome of *Linaria acutiloba* // Proceedings of 2013 International Conference on Frontiers of Environment, Energy and Bioscience (ICFEEB2013). China, Beijing: 2013. P. 541–546.
13. Матвеева Т.В., Сокорнова С.В. Биологические особенности природно-трансгенных растений и их роль в эволюции // Физиология растений. 2017. Т. 64, № 5. С. 323–336. DOI: 10.1134/S1021443717050089
14. Matveeva T.V., Otten L. Widespread occurrence of natural genetic transformation of plants by *Agrobacterium* // Plant Mol Biol. 2019. Vol. 101. P. 415–437. DOI: 10.1007/s11103-019-00913-y
15. Matveeva T.V. New naturally transgenic plants: 2020 update // Biol Commun. 2021. Vol. 66. No. 1. P. 36–46. DOI: 10.21638/spbu03.2021.105
16. Лутова Л.А., Матвеева Т.В. Генная и клеточная инженерия в биотехнологии высших растений: учебник / под ред. И.А. Тихоновича. Санкт-Петербург: Эко-Вектор, 2016. 167 с.
17. https://www.plantarium.ru/ [интернет]. Плантариум. Растения и лишайники России и сопредельных стран: открытый онлайн-атлас и определитель растений [дата обращения 1.11.2021]. Доступ по ссылке: https://www.plantarium.ru/.
18. Morton J. Surinam cherry. In: Fruits of warm climates. Miami, 1987. P. 386–388.
19. Муравьева Д.А. Тропические и субтропические лекарственные растения: 2-е изд. перераб. и доп. Москва: Медицина, 1983. 336 с.
20. Еленевский А.Г. Ботаника. Систематика высших, или наземных, растений. Москва: Академия, 2004.
21. Владимиров И.А., Матвеева Т.В., Лутова Л.А. Гены биосинтеза и катаболизма опинов // Генетика. 2015. Т. 51, № 2. С. 137–146. DOI: 10.1134/S1022795415020167
22. 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. Vol. 94. No. 2. P. 274–287. DOI: 10.1111/tpj.13853
23. Chen K., Otten L. Natural *Agrobacterium* transformants: recent results and some theoretical considerations // Front Plant Sci. 2017. Vol. 8. ID1600. DOI: 10.3389/fpls.2017.01600

24. Matveeva T.V., Otten L. Opine biosynthesis in naturally transgenic plants: Genes and products // Phytochemistry. 2021. Vol. 189. ID112813. DOI: 10.1016/j.phytochem.2021.112813
25. Chen K., Dorlhac de Borne F., Szegedi E., Otten L. Deep sequencing of the ancestral tobacco species *Nicotiana tomentosiformis* reveals multiple T-DNA inserts and a complex evolutionary history of natural transformation in the genus *Nicotiana* // Plant J. 2014. Vol. 80. No. 4. P. 669–682. DOI: 10.1111/tpj.12661
26. Otten L. Natural *agrobacterium*-mediated transformation in the genus *Nicotiana*. In: Ivanov N., Sierro N., Peitsch M.C., editors. The Tobacco Plant Genome. Springer: 2020. P. 195–209. DOI: 10.1007/978-3-030-29493-9_12
27. Levesque H., Delepelaire P., Rouze P., et al. Common evolutionary origin of the central portions of the Ri TL-DNA of Agrobacterium rhizogenes and the Ti T-DNAs of Agrobacterium tumefaciens // Plant Mol Biol. 1988. Vol. 11. P. 731–744. DOI: 10.1007/BF00019514
28. Altamura M.M., Capitani F., Gazza L., et al. The plant oncogene rolB stimulates the formation of flower and root meristemoids in tobacco thin cell layers // New Phytol. 1994. Vol. 126. No. 2. P. 283–293. DOI: 10.1111/j.1469-8137.1994.tb03947.x
29. Koltunow A.M., Johnson S.D., Lynch M., et al. Expression of *rolB* in apomictic *Hieracium piloselloides* Vill. causes ectopic meristems in planta and changes in ovule formation, where apomixis initiates at higher frequency // Planta. 2001. Vol. 214. P. 196–205. DOI: 10.1007/s004250100612
30. Schmülling T., Schell J., Spena A. Single genes from *Agrobacterium rhizogenes* influence plant development // EMBO J. 1988. Vol. 7. No. 9. P. 2621–2629. DOI: 10.1002/j.1460-2075.1988.tb03114.x
31. Casanova E., Trillas M.I., Moysset L., Vainstein A. Influence of rol genes in floriculture // Biotechnol Adv. 2005. Vol. 23. No. 1. P. 3–39. DOI: 10.1016/j.biotechadv.2004.06.002
32. Gorpenchenko T.Y., Kiselev K.V., Bulgakov V.P., et al. The *Agrobacterium rhizogenes rolC*-gene induced somatic embryogenesis and shoot organogenesis in *Panax ginseng* transformed calluses // Planta. 2006. Vol. 223. P. 457–467. DOI: 10.1007/s00425-005-0102-2
33. Hansen G., Vaubert D., Heron J.H., et al. Phenotypic effects of overexpression of *Agrobacterium rhizogenes* T-DNA ORF13 in transgenic tobacco plants are mediated by diffusible factor(s) // Plant J. 1993. Vol. 4. No. 3. P. 581–585. DOI: 10.1046/j.1365-313X.1993.04030581.x
34. Lemcke K., Schmülling T. Gain of function assays identify non-rol genes from *Agrobacterium rhizogenes* TL-DNA that alter plant morphogenesis or hormone sensitivity // Plant J. 1998. Vol. 15. No. 3. P. 423–433. DOI: 10.1046/j.1365-313X.1998.00223.x
35. Stieger P.A., Meyer A.D., Kathmann P., et al. The orf13 T-DNA gene of *Agrobacterium rhizogenes* confers meristematic competence to differentiated cells // Plant Physiol. 2004. Vol. 135. No. 3. P. 1798–1808. DOI: 10.1104/pp.104.040899
36. Kodahl N., Müller R., Lütken H. The *Agrobacterium rhizogenes* oncogenes rolB and ORF13 increase formation of generative shoots and induce dwarfism in *Arabidopsis thaliana* (L.) Heynh // Plant Sci. 2016. Vol. 252. P. 22–29. DOI: 10.1016/j.plantsci.2016.06.020
37. Matveeva T.V., Lutova L.A. Horizontal gene transfer from *Agrobacterium* to plants // Front Plant Sci. 2014. Vol. 5. ID326. DOI: 10.3389/fpls.2014.00326
38. Aoki S., Kawaoka A., Sekine M., et al. Sequence of the cellular T-DNA in the untransformed genome of *Nicotiana glauca* that is homologous to ORFs 13 and 14 of the Ri plasmid and analysis of its expression in genetic tumours of *N. glauca* × *N. langsdorffii*. Mol Gen Genet. 1994;243(6):706–710. DOI: 10.1007/BF00279581.
39. Матвеева Т.В., Богомаз О.Д., Голованова Л.А., и др. Гомологи гена rolC природно-трансгенных льнянок *Linaria vulgaris* и *Linaria creticola* экспрессируются *in vitro* // Вавиловский журнал генетики и селекции. 2018. Т. 22, № 2. С. 273–278. DOI: 10.18699/VJ18.359
40. Quispe-Huamanquispe D.G., Gheysen G., Yang J., et al. The horizontal gene transfer of *Agrobacterium* T-DNAs into the series *Batatas* (Genus *Ipomoea*) genome is not confined to hexaploid sweetpotato // Sci Rep. 2019. Vol. 9. ID12584. DOI: 10.1038/s41598-019-48691-3
41. Aoki S., Syono K. Function of *ngrol* genes in the evolution of *Nicotiana glauca*: conservation of the function of NgORF13 and NgORF14 after ancient infection by an *Agrobacterium rhizogenes*-like ancestor // Plant and Cell Physiol. 1999. Vol. 40. No. 2. P. 222–230. DOI: 10.1093/oxfordjournals.pcp.a029531
42. Aoki S., Syono K. Horizontal gene transfer and mutation: *ngrol* genes in the genome of *Nicotiana glauca* // PNAS. 1999. Vol. 96. No. 23. P. 13229–13234. DOI: 10.1073/pnas.96.23.13229
43. Mohajjel-Shoja H., Clément B., Perot J., et al. Biological activity of the *Agrobacterium rhizogenes*-derived trolC gene of *Nicotiana tabacum* and its functional relationship to other plast genes // Mol Plant Microbe Interact. 2011. Vol. 24. No. 1. P. 44–53. DOI: 10.1094/MPMI-06-10-0139
44. Fründt C., Meyer A.D., Ichikawa T., Meins F. A tobacco homologue of the Ri-plasmid *orf13* gene causes cell proliferation in carrot root discs // Mol Gen Genet. 1998. Vol. 259. P. 559–568. DOI: 10.1007/s004380050849
45. Matveeva T.V., Sokornova S.V., Lutova L.A. Influence of Agrobacterium oncogenes on secondary metabolism of plants // Phytochem Rev. 2015. Vol. 14. P. 541–554. DOI: 10.1007/s11101-015-9409-1
46. Matveeva T., Sokornova S. Agrobacterium rhizogenes Mediated Transformation of Plants for Improvement of Yields of Secondary Metabolites. In: Pavlov A., Bley T., editors. Reference Series in Phytochemistry. Bioprocessing of Plant *in vitro* Systems. Springer: 2016. P. 1–42. DOI: 10.1007/978-3-319-32004-5_18-1
47. Palazon J., Cusido R.M., Gonzalo J., et al. Relation between the amount the *rolC* gene product and indole alkaloid accumulation in *Catharanthus roseus* transformed root cultures // J Plant Physiol. 1998a. Vol. 153. No. 5–6. P. 712–718. DOI: 10.1016/S0176-1617(98)80225-3
48. Palazon J., Cusido R.M., Roig C., Pino M.T. Expression of the *rolC* gene and nicotine production in transgenic roots and their regenerated plants // Plant Cell Rep. 1998b. Vol. 17. P. 384–390. DOI: 10.1007/s002990050411
49. Amini G., Sokornova S.V., Mohajjel-Shoja H., et al. Induced expression of rolC for study of its effect on the expression of genes associated with nicotine synthesis in tobacco // Ecological genetics. 2020. Vol. 18. No. 4. P. 413–422. DOI: 10.17816/ecogen33768
50. Clément B., Perot J., Geoffroy P., et al Abnormal accumulation of sugars and phenolics in tobacco roots expressing the Agrobacterium T-6b oncogene and the role of these compounds in 6b-induced growth // Mol Plant Microbe Interact. 2007. Vol. 20. No. 1. P. 53–62. DOI: 10.1094/MPMI-20-0053
51. Matveeva T., Berezina E., Isaeva I., et al. Influence of some *rol* genes on sugar content in *Nicotiana* and *Vaccinium* // BIO Web of Conferences. 2020. Vol. 18. ID00020. DOI: 10.1051/bioconf/20201800020
52. Chen K., Dorlhac de Borne F., Julio E., et al. Root-specific expression of opine genes and opine accumulation in some cultivars of the naturally occurring GMO *Nicotiana tabacum* // Plant J. 2016. Vol. 87. No. 3. P. 258–269. DOI: 10.1111/tpj.13196

53. Zhang Y., Wang D., Wang Y., et al. Parasitic plant dodder (*Cuscuta* spp.): a new natural *Agrobacterium*-to-plant horizontal gene transfer species // Sci China Life Sci. 2020. Vol. 63. P. 312–316. DOI: 10.1007/s11427-019-1588-x

54. Beauchamp C.J., Chilton W.S., Dion P., Antoun H. Fungal catabolism of crown gall opines // Appl Environ Microbiol. 1990. Vol. 56. No. 1. P. 150–155. DOI: 10.1128/aem.56.1.150-155.1990

55. Sokornova S.V., Matveeva T.V. Phylogenetic Relationships of Ascomycetes Opine Synthases // BMC Bioinformatics. (accepted for publication).

56. Geddes B.A., Paramasivan P., Joffrin A., et al. Engineering transkingdom signalling in plants to control gene expression in rhizosphere bacteria // Nat Commun. 2019. Vol. 10. ID3430. DOI: 10.1038/s41467-019-10882-x

AUTHOR'S INFO

Tat'yana V. Matveeva, Dr. Sci. (Biol.), Professor; address: 7-9, Universitetskaya emb., Saint Petersburg, 199034, Russia;
ORCID: https://orcid.org/0000-0001-8569-6665;
eLibrary SPIN: 3877-6598; Scopus: 7006494611;
e-mail: radishlet@gmail.com

ОБ АВТОРЕ

Татьяна Валерьевна Матвеева, д-р биол. наук, профессор;
адрес: Россия, 199034, Санкт-Петербург, Университетская наб., д. 7-9; ORCID: https://orcid.org/0000-0001-8569-6665;
eLibrary SPIN: 3877-6598; Scopus: 7006494611;
e-mail: radishlet@gmail.com