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O.G. Kovalenko, I.S. Shcherbatenko, A.M. Kyrychenko, V.M. Vasylev

Zabolotny Institute of Microbiology and Virology, NAS of Ukraine,
154 Acad. Zabolotny St., Kyiv, 03143, Ukraine

THE RELATIONSHIP BETWEEN VIRUSES AND PLANT CELLS IN NATURAL ECOSYSTEMS AND SOME APPROACHES TO THEIR REGULATION

Viral diseases of plants cause considerable economic losses by lowering the harvest and deteriorating the production quality. To reduce the harm caused by viruses and to prevent their spreading, protective measures should be developed, including those that apply resistance genes, resistance inducers, and viral infection inhibitors.

The purpose of this article is to provide an up-to-date information on plant virology, mainly concerning virus-plant interactions and covering topics on biological and molecular characteristics of the most pathogenic viruses, viral host range, disease symptoms, and various antiviral defense strategies of host plants. We also attempted to highlight general characteristics and diagnostic methods for some plant viruses and to elucidate the virus-host interaction at the molecular level.

Economically important viruses, such as Bean yellow mosaic virus (BYMV), Beet necrotic yellow vein virus, Beet yellows virus, and Hosta virus X were investigated. Their genome sequences showed maximum identity with BYMV strains reported from Russia, Australia, and Argentina. The sequence data was submitted to NCBI, accession numbers: KT923790.1 for the soybean isolate and KT923791.1 for the bean isolate of BYMV. Using computational analysis, we first show that subgenomic tobamovirus promoters contain 9-nucleotide motives similar to those of the pol III promoter in tRNA genes. The results obtained suggest an existence of similar transcription initiation signals in promoters of viruses and eukaryotes. Glycans, obtained from Basidiomycota mushrooms, can inhibit viral infections and activate non-specific defense mechanisms in host plants at the gene or conformation levels. Some of them adsorb of virions, and thus an interaction between a virus and a cell is, probably, blocked resulting blocking of infection in general.

The study aims to promote economic and socially acceptable ways of protecting plants from viral diseases, as well as to improve the applicability of research in plant virus ecology for prediction and control of plant virus outbreaks.

K e y w o r d s: plant viruses, biosensors, plant resistance inducers, conservative nucleotide sites, amplification, sequencing, phylogenetic analysis.

Introduction. Viruses are obligate intracellular parasites that cause a significant influence on the life cycle, evolution of higher organisms, environment, plant and animal productivity, bio-security and people's health. In recent years viral diseases have received tremendous attention around the world. Investigation of the virus structure and its genome functions as well as the relationships between viruses and host cells are the key issues of plant virology and the fundamental problems of virology in general. Achievements in fundamental virology have a huge impact on other applied problems related to crop production, animal husbandry, medicine and provide tools for successful solutions of these problems.

The relationship between viruses and plant cells varies widely – from asymptomatic infections (extreme resistance) to severe systemic reactions

with typical viral symptoms leading up to the death of infected cells. The relationships between pathogenic viruses and their host plants and the mechanisms of their interaction are poorly understood. This causes some difficulties in theoretical understanding of the phenomena of resistance to viruses and disease pathogenesis.

However, it has been proven that the inheritance of resistance by the host and the parasite ability to cause a disease depend on the interaction between the resistance (R) gene and the avirulence (Avr) gene. Generally, it is consistent with the gene-for-gene concept [1].

It was shown, that most of R-genes encode nucleotide-binding sites of leucine-rich proteins capable to specific interaction with pathogen's proteins and carbohydrates. The carbohydrates can interact with host or virus factors and be involved in elicitor-mediated activation of plant defense through elicitor perception and subsequent signal generation. Endogenous oligosaccharides, glycoproteins, and cell membrane components can serve as elicitors under a viral infection. Soybean mosaic virus (SMV) has been identified as an elicitor of viral resistance [2, 3]. Nevertheless, the genetic nature of SMV elicitor activity still remains unclear. The relationship between viruses and hypersensitive plants is poorly understood until now [3]. "RNA silencing" mechanism, R-gene mediated resistance or a combined action of both of these play a critical role in plant resistance against viruses.

It is known that some glycoproteins, neutral and anionic glycans can increase N-gene mediated plant resistance and are capable to activate a plant's protective mechanisms against tobacco mosaic virus (TMV).

Endogenous glycans as viral pathogenicity regulators and resistance elicitors, can inhibit the biological activity of plant viruses and induce plant resistance to viral infection. It has been well-proven in our experiments on plants with local and system reaction to viral infections [3]. Thus, the search for substances able to function as exogenous resistance elicitors is one of the possible ways of limiting viral infections in plants. As the role of these substances in triggering plant defense responses becomes clearer, the possibility of sensitizing a plant by prior application of elicitors has become a promising option for effective management of plant diseases.

Strong evidence that these functions can be controlled by substances viral genomes encoded is available among numerous examples of "genetically engineered" forms of plants resistant to viral diseases. Genetically engineered resistance to plant viruses is widely used in agriculture and is gradually being introduced on large areas of land. Transgenic plants, resistant to viruses, are obtained through genetic modification with structural genes of coat and transport proteins or with viral RNA polymerase gene. Genetic engineers also design plants resistant to other abiotic factors, including herbicides [3].

Consequently, the main research topic of the Plant Viruses Department in recent years is devoted to detection of new harmful viral infections in plants, determination of viral influence on host plant cells under different conditions and in various experimental systems; elucidation of plant defence mechanisms against viral infections and understanding how viruses circumvent or suppress host defense systems. Most of these activities focus on general and divergent signs of plant protective reactions and on the influence of different exogenous substances (mainly of natural origin) on them. The department performs

strategic research to promote economically and socially acceptable ways for protecting plants against viral diseases.

Environmental aspects. Different ecological regions of Ukraine – Kyiv region (experimental fields of the Institute of Microbiology and Virology), Vinnitsa region (stationary fields of the Institute of Feed, Vinnitsa) and Cherkassy region (Drabiv Experimental Field of Cherkassy Institute of Agricultural and Industrial Production) were investigated to explore the distribution and properties of viral diseases of soybean in these areas. It was established that the diseases in soybean plants, growing in the examined areas, have been caused by two major viruses – SMV (Soybean mosaic virus) and BYMV (Bean yellow mosaic virus). The results of field observations were confirmed using light and electron microscopy and ELISA.

The most virulent isolates of BYMV were purified and selected for detailed study as they differed in virulence, host range, biological, physical and chemical and antigenic properties. The results indicate that the Kyiv isolate of BYMV (BYMV-K) has some unique characteristics enabling to distinguish it from the typical strains and isolates studied previously in Ukraine by other authors [4]. The data obtained under BYMV-K study indicates a strong effect on some physiological processes in *Glycine soja* L. cultivated in the Dnipro right-bank forest-steppe regions. The pigment content, the amount of soluble proteins and water soluble carbohydrates were estimated and, as it was shown, were subjected to significant changes comparing with the control plants after an exposure to BYMV-K [5].

Two BYMV isolates, grouped based on the host reactions of *Chenopodium amaranticolor*, *C. quinoa*, *C. alba, Vicia faba, Tetragonia expansa*, *Gomphrena globosa, Lupinus luteus* and *Pisum sativum,* were identified as two different strains: the isolates from lupine and beans were assigned to necrotic strains of BYMV while an isolate from soybean – to the medium-pathogenic group [6].

An efficiency evaluation of different techniques for BYMV purification was carried out and a modified method was proposed. It provides a high yield of intact viral particles almost completely cleared from cellular components and is characterized by high infectivity [7]. The yield of purified virus comprised around 2.0 mg /100 g of infected *Pisum sativum* plants. Antisera to the BYMV-K isolate was prepared by applying seven weekly consecutive injections of the purified virus and the antiserum titer was measured with direct ELISA method. The prepared antiserum was also used to determine the antigen dilution end point of BYMV clarified sap using direct ELISA.

Different varieties of beans that passed probation in natural grounds of the UAAS Institute of Agriculture and some varieties listed in the State Register of Plant Varieties suitable for dissemination in Ukraine, were tested for resistance to BYMV. The most resistant varieties 702, 707- 710 and Mavka were recommended for cultivation in fields. Varieties with a fairly high degree of resistance to natural isolates of soybean mosaic virus were found among soybean varieties zoned in different regions of Ukraine.

Another problem, to which our department pays big attention, is the viral diseases of beet (*Beta vulgaris*). The main fields planted with beets were monitored for prediction of possible epiphytotic diseases and early detection of viral infections of sugar beet. Thus, sugar beet plants with rhizomania symptoms in their roots were detected in Khmelnitsky region

of Chemerovetsky area. The *Beet necrotic yellow vein virus* (BNYVV), a causative agent of sugar beet rhizomania disease, which results in a significant economic loss, was detected [8]. The virus was purified and its biological properties were investigated. BNYVV was isolated from leaf tissue of indicator plants with local lesions, and gene products of expected size were amplified by RT-PCR. Another pathogen affecting sugar beet is *Beet yellows virus* (BYV). In agrocenoses of Kyiv region, it was established that sugar beet yellowing is caused by BYV. Purification was performed and some properties of the isolate of BYV persistent in Ukraine were studied [9].

Hosta Virus X (HVX) affects different host cultivars and causes problems in ornamental horticulture worldwide. Recently (in 2012) this viral disease was detected in Ukraine too. HVX was isolated from diseased hosta plants and its biological properties were studied. It was found that the virus disease-like symptoms in hostas were caused by at least two different viruses – *Hosta Virus X* and *Tobacco Rattle Virus* [10]. We recommended a system of measures for prevention and control of HVX in private farms and plant nurseries.

Molecular biological properties of pathogens. The isolates of BYMV from different regions of Ukraine originating from bean, soybean, and lupine were examined in regard to their molecular characteristics. With this aim, an analysis of specific primers was carried out to detect BYMV using reverse-transcription polymerase chain reaction (RT-PCR) [11]. The three pairs of primers used for BYMV detection were P1 (5′ttga atctgaactgaagtatt3′), P2 (5′ctcctttctacaaaatggaca3′); CPU (5′gtcgatttcaatccgaacaag3′), CPD (5′ggaggtgaaacctcactaatac3′) and BYMV1f (5′ccaacattccgccaaataat3′), BYMV2r (5′tctgttccaacattgccatc3′). It was shown that the primers BYMV1/BYMV2 were optimal for virus detection of BYMV isolated in Ukraine. The amplification regime was optimized and the optimal annealing temperature was determined. [6]. PCR amplification products were sequenced and compared with the corresponding sequences of different BYMV isolates obtained from GeneBank. The data obtained by phylogenetic analysis showed 98 % sequence identity among the studied isolates. According to the species demarcation criteria and the identification guidelines for potyviruses, it was suggested that Ukrainian isolates belong to one strain of BYMV. The sequence showed a high degree of sequence similarity with other BYMV isolates/strains and shared maximum identity with BYMV strains reported from Russia, Australia, and Argentina. Sequence data were submitted to NCBI, with the following accession numbers: KT923790.1 for the soybean isolate and KT923791.1 for the bean isolate of BYMV [12].

Molecular analysis of Ukrainian isolate of beet necrotic yellow vein virus was also performed. The partial nucleotide sequence of cDNA corresponding to RNA-2 of BNYVV isolates was analyzed and the Ukrainian isolate AG9 of BNYVV was assigned to type A strains. The nucleotide sequence of the gene encoding coat protein of the Ukrainian isolate of BNYVV was compared with appropriate nucleotide sequences present in the GeneBank and phylogenetic analysis of the investigated virus was conducted. It was shown that Ukrainian isolate AG9 of BNYVV is characterized by 100 % homology with the isolate originating from Sweden (accession number EU330452.1).

In our investigations of viral molecular properties, considerable attention is paid to the computational search of conservative nucleotide sites and secondary

structures in genomic sequences involved in virus reproduction, circulation, recombination and evolution, and in virus infection restriction and plant resistance [13].

To reveal and investigate different biologically significant sequences in genomes of plant viruses, highly specialized computational algorithms were used for structural and functional sites identification: an interactive graphical visualization of short identical or highly similar sites in the sequence sets of related viruses; visualization of position-linked clusters in short nucleotide sites; successive disposition of two genomic sequences with increasing displacement of their initial positions instead of a traditional alignment; conversion of graphic objects into the corresponding nucleotide or amino acid sequences followed by their output in a text file format.

Lately, we have been investigating some regulatory sequences, not studied or little studied on model viruses, such as the contexts of translation initiation and termination codons; transcription initiation signals in subgenomic and minus-strand RNA promoters; spontaneous nucleotide substitutions and codon usage bias in viral genomes; types and frequencies of spontaneous replacements of nucleotides.

We have shown for the first time that the movement and coat protein subgenomic RNA promoters of tobamoviruses contain 9-nucleotide motives ggttcgttt or gattcgttt, flanked with length-variable gc- and at-rich sequences [14, 15]. The 9-nucleotide motives are similar to those of the pol III promoter in tRNA genes (ggttcgantcc) and tobamovirus minus strand RNA promoter (gggattcgaattccc) suggesting similar transcription initiation signals in promoters of viruses and eukariotes [16].

The search for similar nucleotide sites in viral genomes showed some similarity between viruses from different genera and families. The similarity can occur as clearly expressed clusters of relatively long nucleotide sites, as numerous short sites scattered along the viral genome, as diffuse clusters of short sites located in several genomic positions as well as as little clusters or single nucleotide sites located in a certain genome region [17, 18]. Distances between similar sites in these clusters are only equal to an integer number of triplet codons. These results suggest the functional importance of recombination in viral evolution.

Synonymous codon usage in the genes of the dwarf soybean virus and the potato X virus varies widely depending on the gene; amino acid and codon; gene overlapping; first two nucleotides in codons; mononucleotide context, located upstream and downstream of the codon; GC-content in virus-encoded genes and in the third codon positions [19, 22]. The overlapping of genes has an influence on the decrease in total nucleotide substitutions by 2.5-fold, in the number of synonymous substitutions in the third codon positions – by 2.8–4.3-fold, in dicodon content of genes – by 1.4–1.6-fold. The results obtained are consistent with the dicodon selection in viral genes.

The contexts of translation initiation codons (nucleotide sequences surrounding the AUG) were computationally analyzed in 15 tobamoviruses (45 genes) and 22 potexviruses (110 genes). The results [20] indicate both a few key similarities and some differences between Kozak's eukaryotic and viral AUG contexts. Distinctive features of viral translation initiation contexts include high frequency of +5C, -5Y and +10R components as well as high

variation of context elements between various viruses and/or genes. So, the frequency of +5C varies between 0 % (TGB1 genes) and 100 % (Re genes), of -5Y – from 22 % (TGB2 genes) to 86 % (Mp genes). The differences between Kozak's and viral AUG contexts may cause the difference in efficiency of virus and host genes translation.

Computational analysis of the frequency of stop codon reading through was performed for replicase and for coat protein genes of 118 plant virus strains, belonging to 68 species of 13 genera [21]. Although, most frequently weak (suppressive) terminal codons are followed by caauua, cgguuu, gggugc, ggaggc or guagac hexanucleotides, there are vast varieties of other nucleotide sites, located at different distances from the terminal codon. A characteristic feature of suppressive terminal codons of viral replicase genes is the presence of long clusters of identical nucleotide sites, located as far as several hundreds of bases away from terminal codons.

The results obtained support a hypothesis that termination of translation efficiency as well as stop codon reading may be determined at genome or gene level rather than by short nucleotide contexts surrounding stop codons.

It was shown that the frequency of nucleotide substitutions in viral genes depends on the nucleotide and strain pairs, the length and localization of gene regions as well as the substitution types and their codon positions [22]. The highest correlation of substitution frequency was shown for different nucleotide pairs (u→c/c→g, 1240), codon positions (third/second, 17,3) and substitution types (transitions/transversions, 5,8), the least – for forward and back substitutions in the same nucleotide pairs (1,03–1,6). Transversion frequencies are generally significantly lower but more variable than the ones of transition. The precise mechanisms and the possible biological role of a broad variation in nucleotide substitution frequency in viral genes are yet to be elucidated.

Glycans and glycan–glycolìpìd complexes as regulators of viral infections. Some species and strains of fungi (*Ascomycetes*, *Basidiomycota*) are the major source of pharmacologically active substances, therefore, they were selected for obtaining glycan preparations. Simple and effective methods for extraction and purification of antiviral factors were developed and mechanisms of their antiviral action were studied [23–26].

Based on the earlier developed protein-carbohydrate concept and receptor-inductor models, as well as the data published in this field of science, we proposed at least three mechanisms by which the substances of carbohydrate nature are able to inactivate viruses and prevent their pathogenic effects on plants:

a) to form complexes with viral components and thus inhibit the infectious activity of virions;
b) to activate non-specific protective mechanisms in host plant at the conformational level;
c) to activate non-specific protective mechanisms in host plant at the gene level.

To study the direct effect of glycans on viral particles, we used glucuronoxylomannan (GXM) and glucan, obtained from basidiomycetes *Tremella mesenterica* and *Ganoderma adspersum* respectively, which served as model glycopolymers [24, 25]. The glycans inhibited both local TMV

infection in hypersensitive tobacco plants and the virus reproduction in isolated protoplast system [23, 26].

With the method of surface plasmon resonance, it was shown that GXM interacts with viral particles in vitro. A decrease in the infectivity of viral particles in the presence of GXM can be explained by the virion aggregation, which was detected by centrifugation of the mixture in sucrose density gradient followed by transmissive electron microscopy [27, 28]. The results obtained showed that *in vitro* GXM forms a complex with virions. The evidence of this is found in the decrease in plasmon resonance signal (approximately 2-fold max) or in the change of its maximum position to 1: 800. Obviously, GXM interacts selectively with virus protein shell and, thus, reduces the number of possible binding sites of the antigen exposed to antibodies. On the other hand, it provides additional negative charge to the virus particle.

Later, similar studies were conducted with *G. adspersum* glucan [29, 30], although it is not yet proved that its glucan belongs to polyanions. As it was established, this polysaccharide also forms a complex with virions. This effect may, seemingly, play a certain role in the antiviral activity of this type of compounds. Glycans adsorb on virion surface, thus, blocking the interaction between virus particles and host cells and leading to an infection termination.

Activation of non-specific defense mechanisms in host plants at the gene or conformation levels was confirmed by experiments using TMV as a model on hypersensitive plants. It turned out that the tobacco plant resistance to TMV infection under glycan influence is formed *de novo* by the participation of actinomycin D – a specific inhibitor of RNA transcription from cellular DNA matrix – and by ά-methyl glycosides. ά-Methylglycosides block chemical signal in a cascade of reactions leading to an activation of protective mechanisms – localization of viral infection and induced systemic resistance development [23]. Therefore, these polymers have diverse effects on viral infections in plants, such as reduction of the infectious process in plants and induction of resistance to the virus both at the cell's genome and the conformational levels. So they change the activity of virus-induced and natural elicitors as biosensors in defense mechanisms [31].

It is known that therapeutic and prophylactic effects of drugs can be enhanced through a combination of agents with different mechanisms of action. We have observed this synergistic effect of antiviral agents in the application of microbial glycans and synthetic viral genome replication and/or translation inhibitors as well as glycolipids of *Pseudomonas* on sensitive and hypersensitive plants [32].

Unlike synthetic synergists, the last ones had not toxic effect on the host plant tissue. This prompted us to use this class of substances to create complex antiviral drugs that would have a practical interest along with a scientific one [33]. As a result of both theoretical calculations and experimental verification, we have developed complex preparations, which have no analogs in world literature and practice, to use in plant protection against viral diseases. The preparations were created based on the fungal and bacterial glycans and glycolipids using the principles of the supramolecular chemistry of hydrophobic-hydrophilic interactions [34, 35]. Recently, we have made successful attempts to include other classes of substances in our supramolecular structures, additionally to glycans and glycolipids, such as

thiosulfonates – chemical analogs of volatile components of garlic and onions. These volatile compounds are generally considered to be responsible for most of the pharmacological properties (antimicrobial and anticancer) of garlic, however, they are poorly water soluble or insoluble at all. Preliminary testing of these substances as protective (antiviral) drugs and effectors (adhesins) of legume-rhizobium plants showed some promising results towards such studies [36].

Considering the results of the theoretical research conducted at the Department of Plant Viruses and using the main principles of the supramolecular chemistry of hydrophobic and hydrophilic interactions, a new generation of drugs was created. These preparations can be used in crop production as the means of protecting plants against different pathogens with the aim of regulation or increasing the productivity of vegetable and horticultural crops and grapes.

О.Г. Коваленко, І.С. Щербатенко, А.М. Кириченко, В.М. Васильєв

Інститут мікробіології і вірусології ім. Д.К. Заболотного НАН України, вул. Академіка Заболотного, 154, Київ, 03143, Україна

ВЗАЄМОВІДНОСИНИ ВІРУСІВ З КЛІТИНАМИ РОСЛИН У ПРИРОДНИХ ЕКОСИСТЕМАХ ТА ДЕЯКІ ПІДХОДИ ДО ЇХНЬОГО РЕГУЛЮВАННЯ

Резюме

Вірусні інфекції рослин викликають значні втрати врожаю, погіршують якість сільськогосподарської продукції і все частіше розглядаються як серйозна загроза продовольчої безпеки. Необхідними заходами зниження шкодочинності вірусних захворювань та обмеження їх поширення є розробка та впровадження заходів захисту з використанням природніх генів стійкості, індукторів стійкості та інгібіторів вірусної інфекції.

Метою даної роботи було висвітлити актуальні питання та представити основні результати, отримані у відділі вірусів рослин, зокрема тих, що стосуються біологічних та молекулярних характеристик найбільш поширених вірусів, механізмів їхньої взаємодії з рослинами, зокрема, висвітлити коло рослин-хазяїв, симптоми хвороб, а також різні противірусні стратегії рослин. Окрім того, в статті розглядаються загальні характеристики та методи діагностики деяких вірусів та показані основні результати щодо вивчення взаємодії вірусів і їхніх хазяїв на молекулярному рівні.

Нами було досліджено такі економічно важливі віруси, як вірус жовтої мозаїки квасолі, вірус некротичного пожовтіння жилок буряка, вірус жовтяниці буряка і Х-вірус хости. Встановлено значну гомологію українського ізоляту вірусу жовтої мозаїки квасолі з штамами із Росії, Австралії та Аргентини. Методом комп'ютерного аналізу ми вперше показали, що субгеномні промотори тобамовірусів містять консервативні мотиви, виявлені у промоторах еукаріот. Отримані результати свідчать про подібність сигналів ініціації транскрипції в промоторах вірусів і еукаріот.

Показано, що глікани з вищих грибів *Basidiomycota* здатні пригнічувати вірусну інфекцію і активувати неспецифічні захисні механізми в рослинах-хазяях на генному і конформаційному рівнях. Деякі з них можуть утворювати з вірусними частками зворотні комплекси, порушуючи інфекційність вірусу.

Дослідження, що проводяться у відділі, будуть сприяти розвитку економічно обґрунтованих і соціально прийнятних способів захисту рослин від вірусних інфекцій, а також дослідженням у галузі екології вірусів з метою прогнозування і контролю епіфітотій та спалахів вірусних інфекцій в агроценозах.

Ключові слова: віруси рослин, біосенсори, індуктори вірусостійкості, консервативні нуклеотидні сайти, ампліфікація, сиквенування, філогенетичний аналіз.

А.Г. Коваленко, И.С. Щербатенко, А.Н. Кириченко, В.Н. Васильев

Институт микробиологии и вирусологии им. Д.К. Заболотного НАН Украины, ул. Академика Заболотного, 154, Киев, 03143, Украина

ВЗАИМООТНОШЕНИЯ ВИРУСОВ С РАСТИТЕЛЬНЫМИ КЛЕТКАМИ В ПРИРОДНЫХ ЭКОСИСТЕМАХ И НЕКОТОРЫЕ ПОДХОДЫ К ИХ РЕГУЛИРОВАНИЮ

Резюме

Вирусные инфекции растений вызывают значительные потери урожая, ухудшают качество сельскохозяйственной продукции и все чаще рассматриваются как серьезная угроза продовольственной безопасности. Необходимыми мерами снижения вредоносности вирусных заболеваний и ограничения их распространения являются разработка и внедрение средств защиты с использованием природных генов устойчивости, индукторов устойчивости и ингибиторов вирусной инфекции.

Целью данной работы было осветить актуальные вопросы и представить основные результаты, полученные в отделе вирусов растений, в частности те, которые касаются биологических и молекулярных характеристик наиболее распространенных вирусов, механизмов взаимодействия вирусов и растений, включая круг растений-хозяев, симптомы болезней, а также различные противовирусные стратегии растений.

Нами были исследованы такие экономически важные вирусы, как вирус желтой мозаики фасоли, вирус некротического пожелтения жилок свеклы, вирус желтухи свеклы и вирус хосты X. Установлено значительную гомологию украинского изолята вируса желтой мозаики фасоли со штаммами из России, Австралии и Аргентины. Методом компьютерного анализа мы впервые показали, что субгеномные промоторы тобамовирусов содержат консервативные мотивы, обнаруженные в промоторах эукариот. Полученные результаты свидетельствуют о сходстве сигналов инициации транскрипции в промоторах вирусов и эукариот.

Показано, что гликаны из высших грибов *Basidiomycota* способны подавлять вирусную инфекцию и активировать неспецифические защитные механизмы в растениях-хозяевах на генном и конформационном уровнях. Некоторые из них также могут образовывать с вирусными частицами обратимые комплексы, нарушая этим инфекционные свойства вируса.

Исследования, проводимые в отделе, будут способствовать развитию экономически обоснованных и социально приемлемых способов защиты растений от вирусных инфекций, а также исследованиям в области экологии вирусов с целью прогнозирования и контроля эпифитотий и вспышек в агроценозах опасных вирусных болезней.

Ключевые слова: вирусы растений, биосенсоры, индукторы вирусоустойчивости, консервативные нуклеотидные сайты, амплификация, сиквенрования, филогенети-

ческий анализ.

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