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MONITORING OF VIRAL INFECTIONS IN VEGETABLE CROPS IN AGROECOSYSTEMS OF UKRAINE

*Information on the abundance and diversity of phytopathogenic viruses in Ukraine is very variable and limited. There is a high importance of a complex study of the species composition and ways of spreading crop viruses, as well as the development of epiphytotic forecasting systems, which will help to limit the ranges of these viruses and save crop yields. Consequently, the aim of our study was to explore the species composition and frequency of mono- and mixed virus infection of vegetable crops in Ukrainian agroecosystems and to identify the possible etiology of its occurrence. **Methods.** The samples were analyzed for the presence of viral antigens by enzyme-linked immunosorbent assay in sandwich and indirect modifications. For the detection of viral antigens in ELISA, test systems manufactured by Loewe were used. To identify the virus, the material was homogenized and purified, and then registered on a reader. **Results.** The frequency of vegetable crops damaged by diseases of viral etiology increased by 25—27% compared to the previous years of the study. Serological analysis showed that 59% of the studied samples of the Cucurbitaceae family and 54% of the Solanaceae family were affected by the main viral diseases most common in Ukraine. The seed way of transmission of vegetable viruses in Ukraine was demonstrated as one of the sources of viruses in agroecosystems. The presence of antigens to cucumber mosaic virus (CMV) in 14.3% of the studied seeds, zucchini yellow mosaic virus (ZYMV) — 11.2%, and tomato mosaic virus (ToMV) — 12.6% was shown. This allows us to suggest that sowing those seeds in the future will contribute to the spread of these viruses across Ukraine. Analysis of soil samples showed the presence of antigens of cucumber mosaic virus, tobacco mosaic virus, and potato virus X. The lowest level of antigens to CMV was detected in the soils of Vinnytsia region, to PVX — in the Kyiv and Cherkasy regions, and to TMV — in the Odesa region. **Conclusions.** Vegetable agroecosystems in Ukraine are more often affected by viruses belonging to the Tobamovirus, Cucumovirus, Potyvirus, and Tospovirus genera of the Bromoviridae, Potyviridae, and Bunyaviridae families. In addition to the increasing areas of viral monoinfection, there is an active spread of mixed infection, or «superinfection», in Ukrainian agroecosystems. Mixed infections are mainly formed during the growth and development of the tested vegetable crops. All of this leads to further significant spread of not only mono- but also mixed virus infection of vegetable crops.*

Keywords: cucumber mosaic virus, potato virus X, tomato mosaic virus, tobacco mosaic virus, vegetable crops, monoinfection, mixed infection, monitoring.

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The amount of vegetable production in Ukraine reaches about 9.5 million tons, which is almost 10% of the gross harvest of all crops. The distribution and mass spread of viral diseases lead to a significant decrease in crop yields, product quality reduction, and rapid degeneration of varieties, which makes it harder to ensure sustainable production of competitive agricultural products as the basis for Ukraine's food and national security. Affected plants are not only characterized by reduced protective functions but also become more susceptible to damage by other various pests and pathogens of fungal and bacterial etiology. Intensive agriculture under conditions of weather and climate instability, the use of new technologies, varieties and hybrids, active seed, and planting material exchange and transportation contribute to the spread of infection to new geographical regions and induce the processes of changing the species composition of pathogens (Shevchenko et al., 2018).

Changes in temperature and other indicators (rainfall, wind, greenhouse gas accumulation, and extreme weather conditions) due to global warming will affect the geographical distribution of viral hosts and vectors, and consequently, the epidemiology of viruses will change as well. Among such regions will also be Ukraine, which is already considered a zone of high spread of viral diseases, which, together with the low virus resistance of most common varieties and hybrids of vegetable crops, will lead to total re-infection (Shevchenko et al., 2015).

On the territory of Ukraine, vegetable crops (cucumber, tomato, potato, various pumpkin crops, etc.) are affected by the following viruses: cucumber mosaic virus (CMV), tobacco mosaic virus (TMV), pepper mild mottle virus (PMMoV), tobacco rattle virus (TRV), tomato mosaic virus (ToMV), tomato ringspot virus (ToRV), potato virus X (PVX), zucchini yellow mosaic virus (ZYMV), watermelon mosaic virus 2 (WMV-2), and turnip mosaic virus (TuMV) (Snihur et al., 2019).

It is important to note that most viral diseases run unnoticed due to the weak symptoms. However, in addition to mono infection, there are many cases of mixed infection, in which more serious disease symptoms are observed. Classic examples of increased disease symptoms due to mixed infection are potato mosaic disease caused by potato virus X (PVX) together with potato virus Y (PVY), potato virus X, and also potato virus A (PVA), significant symptoms of tomato stripe are caused by the combination of potato virus X (PVX) and tobacco mosaic virus (TMV) (Shevchenko et al., 2021). In some situations, the disease severity caused by mixed infection can lead up to 90% yield losses. In addition, the vast majority of these viruses spread rapidly over large areas, owing to efficient transmission pathways — insect vectors, infected seeds, and plant-to-plant contact (Pozhylov et al., 2019).

The presence of more than one virus in one plant results in the appearance of various symptoms at the same time, which causes difficulties in determining the etiology of the disease and, in particular, the ways to detect, identify, and eliminate viruses. To detect mixed virus infection, a number of scientists have developed several approaches based on multiplex PCR. The method involves identifying known viruses and sequencing the next generation of nucleic acid particles (Roossinck, 2008).

During a mixed infection, several types of interactions occur, which can be synergistic or antagonistic. The type of interaction that happens is highly dependent on the time and order of infection of the agricultural crop. When viruses infect plants at different times, the superinfection starts. In the case of simultaneous infection with several viruses, in the early stages, each virus can act as the main one since there is still a small number of viral particles in the plant and there is no competition between them. At later stages of infection, when the disease spreads, the number of viral particles in the plant increases, the number of uninfected cells decreases, and the superinfec-

tion becomes predominant and more frequent due to increasing competition (Gilbert, 2002). The type of interaction is also influenced by the order of infection, as it has been shown that contamination of papaya plants with papaya ringspot virus (PRSV) and papaya mosaic virus (PapMV) generates a synergistic effect, while the change in order leads to antagonism, mainly due to the activation of defense responses against PRSV infection (Silva-Rosales et al., 2018). The principle of superinfection laid the basis for the creation of the so-called «cross-protection», where early infection with a less aggressive strain prevents further infection with a more aggressive strain of the virus. The reliable protection of vegetable crops against viral infections can only be ensured by the application of a set of measures determined by the species composition of viruses, vectors, as well as their biological and environmental characteristics. To limit the spread of infection and its harmfulness, it is necessary to follow prevention standards at all stages of the vegetable growing process, including the use of proven planting and seed material (Rudneva et al., 2006).

However, information on the spread and species diversity of viruses affecting vegetable crops in Ukrainian agroecosystems is very limited. Therefore, it is necessary to comprehensively study the species composition and ways of spreading crop viruses, as well as to develop epiphytotic forecasting systems that will help limit the ranges of crop viruses and save crops and the quality of agricultural products (Furdychko et al., 2020). So the **aim** of our work was to study the species composition and the frequency of mono- and mixed virus infection of vegetable crops in agroecosystems of Ukraine and to identify the possible etiology of its origin.

Materials and Methods. The research was carried out on the basis of a systematic and integrated approach to assessing the condition of vegetable crops (cucumber, courgette, zucchini, tomato, pepper, melon, and watermelon) with symptoms of viral etiology. Laboratory studies

were carried out at the Laboratory of Ecology of Viruses and Biosafety named after Academician A.L. Boyko of the Institute of Agroecology and Environmental Management of the National Academy of Agrarian Sciences of Ukraine.

The objects of research were symptoms of viral etiology on vegetable crops and seeds (cucumber, courgette, zucchini, tomato, pepper, melon, and watermelon) collected from different agroecosystems of Ukraine. The plant samples were selected by visual examination of the plants for the presence of symptoms of viral damage. For the study, we used leaves of the middle or upper tier, fruits, and seeds of plants. Plants were collected from the open ground of the Forest-Steppe (Vinnytsia, Kyiv, Rivne, and Cherkasy regions) and the Steppe zones (Odesa region) of Ukraine.

For virus detection, soil samples were homogenized in 0.1 M PBS at a ratio of 1:2, followed by centrifugation at 5000 rpm for 15 min at 4 °C on a PC-6 centrifuge. The supernatant was removed, and the precipitate was dissolved again in 0.1 M PBS in a 1:1 ratio. Both fractions of the homogenate were tested in ELISA. For virus detection, the plant material (leaves, fruits) was homogenized in 0.1 M phosphate-salt buffer (pH 7.4) in a 1:2 ratio. Purification from plant components was carried out by centrifugation at 5000 rpm for 20 min at 4 °C on a PC-6 centrifuge (Boiko, 2000). The results were registered on a Termo Labsystems Opsi MR reader (USA) with Dynex Revelation Quicklink software at 405/630 nm. ELISA test systems manufactured by Loewe (Germany) were used to detect viral antigens in ELISA. Samples for the presence of viral antigens were analyzed by enzyme-linked immunosorbent assay (ELISA) in sandwich and indirect modifications (Crowther, 1995). The data on the optical density of the samples were processed by descriptive statistics, determining the mean and standard deviations of the data (Çağlayan et al., 2006). The threshold value of optical density, which distinguishes positive results of the enzymatic reaction from the background value, was

determined for each plate separately according to the recommendations (Curry et al., 2006).

Plant samples were analyzed for the presence of antigens of the following viruses: cucumber mosaic virus (CMV), tobacco mosaic virus (TMV), potato virus X (PVX), tomato mosaic virus (ToMV), zucchini yellow mosaic virus (ZYMV), watermelon mosaic virus 2 (WMV-2), and tomato spotted wilt virus (TSWV).

Mathematical analysis was performed and visualized using Statistica 10 (StatSoft. Inc., 2011) and Microsoft Excel 2010. Student's t-test was used to determine differences between average values. Comparison of large data sets to establish correlations was carried out based on the multivariate analysis of variance (ANOVA), and average values, variance, and deviations were determined.

Results. A number of sampling expeditions to the reference plots of agroecosystems in different soil and climatic conditions of Ukraine and further research allowed us to collect a sufficient amount of material for this study (during 2022–2023, 158 samples of plants of the *Solanaceae* and *Cucurbitaceae* families were collected).

The studies of agroecosystems have shown that vegetable agroecosystems in Ukraine are increasingly affected by diseases of viral etiology, and their frequency has increased by 25–27% compared to the previous years of research. For example, the studied agroecosystems in the Vinnytsia region, where nightshade crops were grown, were affected by symptoms of viral etiology by 14.2%. The habitus of such plants suffered from such symptoms as yellow-green mosaic, necrosis, and deformation of the leaf blade. At the same time, plants of the *Cucurbitaceae* family were affected by 16.1%. These plants exhibited symptoms such as light green mosaic on leaf blades, dark green mosaic of veins, threadlike leaf blades, green spotting, rounded yellow spots and deformation on leaf blades, deformation of fruits, etc. (Tsvigun et al., 2020).

In the vegetable agroecosystems of the Kyiv region, 12.5% of affected crops of the *Solanaceae* family and 17.3% of the *Cucurbitaceae* family

with similar symptoms were found. Vegetable fields where *Solanaceae* crops were grown in Kyiv and Rivne regions were affected by diseases of viral etiology by 10.5%, while *Cucurbitaceae* crops — by 17.1% and 14.5%, respectively.

The study of vegetable agroecosystems for the presence of viral diseases in the Steppe zone of Ukraine, on the example of the Odesa region, found that crops of the *Solanaceae* family were infected in 12.4% of cases, while plants of the *Cucurbitaceae* family — in 21%.

Therefore, in the agroecosystems of vegetable crops in both the Steppe and Forest-Steppe zones of Ukraine, a quite high percentage of plants with various lesions and symptoms of different nature is observed. The effect of these symptoms their intensity, and the level of development directly depends on the pathogenicity of the virus, environmental conditions, and the period of development of the plant itself.

As symptoms may have different sources, including stress, nutritional deficiencies, bacterial and fungal infections, etc., and symptoms of different viruses are often similar and do not allow identifying the virus clearly, the following research was aimed at identifying the type of virus using ELISA.

The results of ELISA of plant samples with characteristic features of viral etiology showed that in the vast majority of samples, viruses were detected in the form of mono-infection, with mixed virus infection occurring less frequently. The selected plant samples (tomato and vegetable pepper of different varieties and hybrids) of the *Solanaceae* family were tested for the presence of five viral antigens, namely cucumber mosaic virus (CMV), potato virus X (PVX), tomato spotted wilt virus (TSWV), tomato mosaic virus (ToMV), and tobacco mosaic virus (TMV) (Table 1).

The studies showed that cucumber mosaic virus (CMV) infected both tomato plants of different varieties and hybrids and vegetable pepper plants. The same dynamics was observed for tomato mosaic virus (ToMV). It should also be

noted that CMV and ToMV were the most frequently detected viruses on tomato plants, while tobacco mosaic virus (TMV) prevailed on vegetable pepper plants by almost 54%. The antigens of potato virus X (PVX) and tomato spotted wilt virus (TSWV) were detected only on tomato plants of certain varieties, which may be related to variety specificity.

It should be noted that according to the research, it was found that the same or similar symptoms on tomato and vegetable pepper plants were the result of the influence of different viruses. For example, the yellow-green mosaic on tomatoes was a symptom of both cucumber mosaic virus (CMV) and tomato spotted wilt virus (TSWV). Tomato varieties Sanka, De Barao, and Rozhevyi slon and vegetable pepper Ratunda were distinguished by a high frequency of detection of characteristic signs of viral infection. In addition, these varieties were identified with antigens for more than one virus, i.e. a mixed infection (or superinfection) was observed.

The analysis of the data obtained made it possible to conclude that 46% of the samples with classical signs of viral infection showed the absence of the tested viral antigens. This means that these plant samples had symptoms of either a different nature (bacterial, fungal) or an unknown viral nature, which puts researchers in a position to perform wider studies of these symptoms, in particular using molecular genetic methods.

Therefore, by the enzyme-linked immunosorbent assay of selected samples of vegetable crops of the *Solanaceae* family, 54% of the samples were contaminated with widespread viral pathogens. Among them, the vast majority were characterized by mono-infection: cucumber mosaic virus was detected in 23% of samples, tomato mosaic virus — 11%, tobacco mosaic virus — 7%, tomato spotted wilt virus — 3%, and potato virus X — 5% (Fig. 1).

In addition to mono-infection, mixed infection was also detected in tomatoes. Tomato

Table 1. Visual diagnostics and enzyme-linked immunosorbent assay of samples of affected vegetable crops of the *Solanaceae* family

| Variety/ hybrid | Visual symptoms on plants | Affected plants,% | Presence of viral antigens (E 405 nm) | | | | |
|--------------------|---|----------------------|--|-----|------|------|-----|
| | | | CMV | PVX | TSWV | ToMV | TMV |
| Tomato | | | | | | | |
| Sanka | Deformation of leaf blade, yellow-green mosaic | 15.1±1.2 | + | — | — | + | — |
| Rozhevyi slon | Necrosis and growth retardation | 11.2±1.1 | — | — | — | + | + |
| De Barao | Yellow-green mosaic | 10.5±1.3 | + | — | — | + | — |
| Chudo svitu | Yellow-green mosaic, rounded spots on the fruit | 5.1±1.2 | — | — | — | + | — |
| Malynovyi hihant | Necrosis on the leaf blades | 6.4±1.4 | + | — | — | — | — |
| Anastasiia | Dark green mosaic, deformation of leaf blades | 3.5±1.2 | + | — | — | — | — |
| Chornyi prynz | Yellow-green mosaic of leaf blades | 3.4±1.1 | — | — | + | — | — |
| Zoloty horikh | Necrosis and deformation of leaf blades | 5.1±1.2 | — | + | — | — | + |
| Pepper | | | | | | | |
| Vulkan | Yellow-green mosaic and leaf blade deformation | 2.0±0.9 | — | — | — | — | + |
| Mersedes | Yellow-green mosaic and fruit deformation | 5.2±1.0 | — | — | — | — | + |
| Ratunda | Rounded yellow spots on the leaf blades | 9.1±1.2 | — | — | — | + | + |
| Palanska babura | Necrosis on the leaf blades | 5.0±1.3 | + | — | — | — | — |
| Asti chervonyi | Yellow-green mosaic of leaf blades | 3.0±1.2 | — | — | — | + | — |

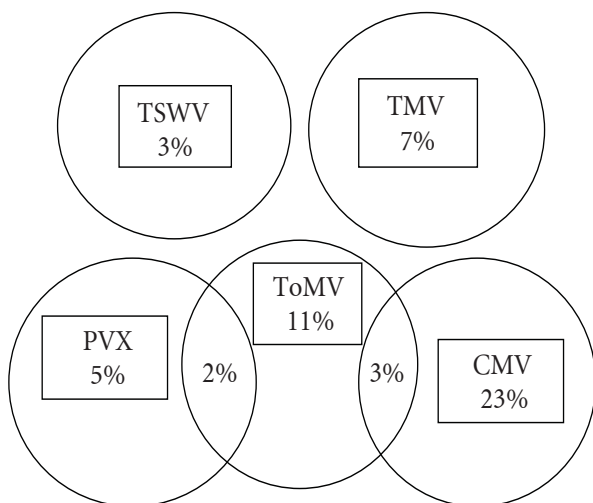


Fig. 1. Distribution of mono- and mixed infection among samples of affected plants of the family *Solanaceae* (according to ELISA results)

plants were infected with tomato mosaic virus (ToMV) + potato virus X (PVX) in 2% of cases and cucumber mosaic virus (CMV) + tomato mosaic virus (ToMV) in 3% of cases.

As the analysis of the symptoms of the viral nature of field vegetable crops showed that a great part of plants with such symptoms belong to the *Cucurbitaceae* family, samples (leaves, fruits) of such vegetable crops as cucumber, courgette, and zucchini of different varieties and hybrids were collected. The plant samples were tested for three main virus antigens — cucumber mosaic virus (CMV), watermelon mosaic virus 2 (WMV-2), and zucchini yellow mosaic virus (ZYMV) (Table 2).

The enzyme-linked immunosorbent assay allowed us to identify that 59% of the *Cucurbitaceae* samples tested for the presence of the main

Table 2. Visual diagnostics and enzyme-linked immunosorbent assay of samples of affected vegetable crops of plants of the *Cucurbitaceae* family

| Variety/ hybrid | Visual symptoms on plants | Affected plants,% | Presence of viral antigens (E 405 nm) | | |
|--------------------|---|----------------------|--|-------|------|
| | | | CMV | WMV-2 | ZYMV |
| Cucumber | | | | | |
| Atlantis F1 | Light green mosaic on the leaf blades | 2.1±1.1 | + | — | — |
| Feniks F1 | Dark green vein mosaic on the leaf blades | 3.2±1.2 | — | + | — |
| Tsezar F1 | Necrosis | 2.0±1.1 | — | + | — |
| Paryzkyi | Rounded dark green spots on leaf blades, fruit deformation | 12.4±1.3 | + | + | — |
| Dzherelo | Filamentous leaf blades, retardation, fruit deformation | 23.3±1.4 | + | — | + |
| Kushchovi | Light green mosaic on the leaf blades | 15.1±1.2 | — | — | + |
| Zasolochnyi | Yellow-green mosaic, fruit deformation | 10.3±1.2 | + | — | — |
| Courgette | | | | | |
| Skvorushka | Yellow-green mosaic, leaf blade deformation | 9.1±1.4 | — | — | + |
| Anhelina F1 | Leaf threading, fruit deformation | 8.5±1.3 | — | + | — |
| Bilyk | Green spotting, vesicles, leaf blade deformity, fruit deformation | 21.6±1.7 | + | + | + |
| Haidamaka | Leaf blade deformation, fruit deformation | 16.4±1.2 | — | + | + |
| Hrybovskiy | Deformation of the leaf blade | 9.1±1.4 | + | — | — |
| Zucchini | | | | | |
| Holden | Dark green mosaic | 15.2±1.5 | — | — | + |
| Zolotivka | Green mosaic, filamentous | 10.3±1.5 | + | — | + |
| Chaklun | Filamentous leaf blades | 9.4±1.2 | — | + | — |
| Nefryt | Dark green mosaic, filamentous | 13.1±1.3 | — | + | — |

viral diseases most common in Ukraine were contaminated. The other samples (41%) were contaminated with either bacterial agents or viral particles for which the samples were not tested.

As a result of the research, it was found that cucumber plants were most often affected by cucumber mosaic virus (CMV) — 48.1%, and zucchini plants — by watermelon mosaic virus 2 (WMV-2) — 46.5%. The analysis also showed that zucchini plants were mostly affected by zucchini yellow mosaic virus (ZYMV) — 25.5% and watermelon mosaic virus 2 (WMV-2) — 22.5%. It should be noted that all of these viruses cause the same symptoms (in courgettes, leaf blade deformation was observed, while in cucumbers and zucchini, leaf blade mosaic was observed), and it is very difficult to separate them.

Together with general studies on the presence of virus infection, the variety specificity of cucumber, courgette, and zucchini varieties/hybrids was also researched. The research proved that the varieties/hybrids Dzherelo, Kushchovy cucumber, Bilyk courgette, and Holden zucchini were the most affected by virus diseases, and they showed the most symptoms.

It should be noted that the plants of the *Cucurbitaceae* family were contaminated not only by mono-infection (cucumber mosaic virus (CMV) — 18%, watermelon mosaic virus 2 (WMV-2) — 11%, and zucchini yellow mosaic virus (ZYMV) — 12%) but also by superinfection, which accounted for a significant part of all cases of damage — 15% (Fig. 2).

It was found that the samples of plants with mixed infection with cucumber mosaic virus (CMV) + watermelon mosaic virus 2 (WMV-2) accounted for 5% of the total. The incidence of samples contaminated with watermelon mosaic virus 2 (WMV-2) + zucchini yellow mosaic virus (ZYMV) was 3%, and cucumber mosaic virus (CMV) + zucchini yellow mosaic virus (ZYMV) — 7%. Also, we found cases when plant samples were contaminated with all three viruses, and their frequency of occurrence was 3%.

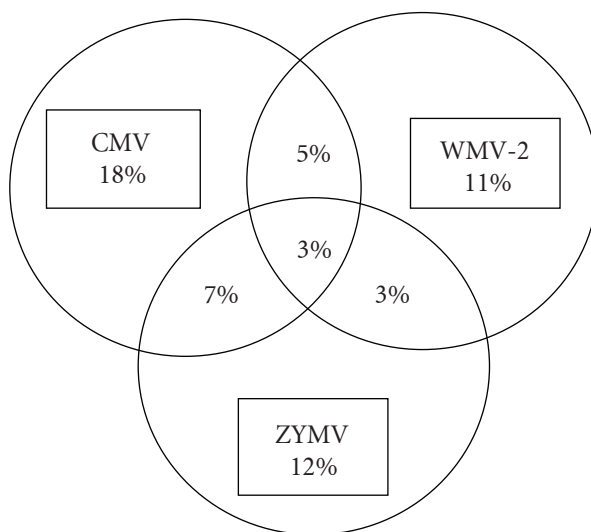


Fig. 2. Distribution of mono- and mixed infection among samples of affected plants of the family *Cucurbitaceae* (according to ELISA results)

The study of cultivar specificity showed that it was the plants of the zucchini variety Bilyk that were most affected by superinfection (Table 2). It should be noted that plants of the *Cucurbitaceae* family were more often affected by mixed infection than plants of the *Solanaceae* family.

The presence of such indicators of infections of viral etiology, as well as superinfections, indicates the development and existence of sustainable ways for viruses to enter agrocenoses in an orderly and active way (King et al., 2012). In addition to the traditional ways of virus transmission by plants and insect vectors (aphids, ticks, moths, etc.), it is known that about 18% of plant viruses are transmitted by contaminated seeds. A particularly high percentage of viruses spread in this way is observed when sowing freshly harvested seeds (Munkvold, 2009).

Currently, the Ukrainian market is represented by a huge array of commercial vegetable seeds of both Ukrainian and foreign production (Tsvihun et al., 2012). Testing of commercial seeds offered by the Ukrainian market for both farms and household plots for the presence of viral infection made it possible to check one of the ways

Table 3. Testing of seeds of plants of the families Solanaceae and Cucurbitaceae for the presence of viral antigens

| Variety/hybrid | Optical density of viral antigens (E 405 nm) | | |
|----------------------|--|--------------|--------------|
| | CMV | ZYMV | ToMV |
| Tomato | | | |
| Sanka | 0.405 | 0.098 | 0.093 |
| Rio Fueho | 0.099 | 0.100 | 0.523 |
| Andriivskiy siurpryz | 0.089 | 0.088 | 0.101 |
| Novichok | 0.091 | 0.094 | 0.498 |
| De-Barao chervonyi | 0.512 | 0.100 | 0.097 |
| Kobzar Tarasenko | 0.101 | 0.405 | 0.095 |
| Efymer | 0.503 | 0.092 | 0.100 |
| Hrusha chervona | 0.096 | 0.093 | 0.102 |
| Lahidnyi | 0.101 | 0.087 | 0.110 |
| Dzhyna | 0.094 | 0.089 | 0.099 |
| Pepper | | | |
| Lahidnyi | 0.103 | 0.091 | 0.099 |
| Zoloty fazan | 0.096 | 0.092 | 0.511 |
| Aivenho | 0.450 | 0.087 | 0.096 |
| Black diamond | 0.101 | 0.093 | 0.099 |
| Lahidnyi Druzhok | 0.098 | 0.100 | 0.497 |
| Cucumber | | | |
| Maliuk F1 | 0.089 | 0.099 | 0.091 |
| Kushchovy | 0.501 | 0.100 | 0.436 |
| Zasolochnyi | 0.498 | 0.098 | 0.088 |
| Feniks | 0.085 | 0.093 | 0.100 |
| Izid F1 | 0.087 | 0.102 | 0.094 |
| ALADYN F1 | 0.091 | 0.096 | 0.088 |
| Zasolochnyi-65 | 0.501 | 0.079 | 0.103 |
| Dalekoskhidnyi 27 | 0.100 | 0.093 | 0.087 |
| Courgette | | | |
| Lialiuk | 0.088 | 0.521 | 0.091 |
| Vodohrai | 0.086 | 0.099 | 0.089 |
| Haidamaka | 0.100 | 0.489 | 0.093 |
| Hrybovskiy | 0.093 | 0.101 | 0.098 |
| Watermelon | | | |
| Foton | 0.100 | 0.471 | 0.091 |
| Orfei | 0.087 | 0.099 | 0.101 |

of spreading the most common viral infections of vegetable crops. For the study, 35 varieties and hybrids of vegetable crops of the Solanaceae and Cucurbitaceae families were selected. The study was conducted by an enzyme-linked immunosorbent assay for the presence of antigens to such viruses as cucumber mosaic virus (CMV), zucchini yellow mosaic virus (ZYMV), and tomato mosaic virus (ToMV) (Table 3).

The study of widely distributed commercial seeds of cucumbers, tomatoes, courgette, zucchini, melon, and watermelon purchased in specialized stores for the presence of the most widespread vegetable virus infections showed that 38.1% of such seeds had viral particles. In general, the presence of antigens to cucumber mosaic virus (CMV) was observed in 14.3% of the seeds tested, zucchini yellow mosaic virus (ZYMV) — 11.2%, and tomato mosaic virus (ToMV) — 12.6% (Fig. 3). The data obtained allow us to assume that the sowing of such seeds in the future will contribute to the spread of these viruses in Ukraine.

The research showed that the seeds were mostly mono-infected with cucumber mosaic virus (CMV). The only exception was on the cucumber variety Kushchovy, where the presence of cucumber mosaic virus (CMV) and tomato mosaic virus (ToMV) was found. These results suggest that mixed infection is formed mainly by additional infection of plants in the field (another pathway of virus transmission).

Another significant route of virus transmission to plants is through soil, as it is known that

| Melon | | | |
|---------------|--------------|-------|-------|
| Zolotysta | 0.092 | 0.099 | 0.088 |
| Medovy aromat | 0.435 | 0.093 | 0.101 |
| Titovka | 0.095 | 0.094 | 0.101 |
| Zvaba | 0.088 | 0.100 | 0.093 |

* an optical density higher than 0.400 indicates that the sample is contaminated with a viral infection

viral particles of viruses such as cucumber mosaic virus (CMV), tobacco mosaic virus (TMV), potato virus X (PVX), barley yellow dwarf virus (BYDV) can be found for a long time (from 10 days to several years) in dead plant debris, fungi, and other particles (King et al., 2012).

The analysis of rhizosphere soil for the presence of viral antigens such as cucumber mosaic virus (CMV), tobacco mosaic virus (TMV), and potato virus X (PVX) proved the presence of these antigens in the soil, which means that these viruses have the ability to persist in the soil for a certain time. Subsequent research has shown that the structure, physical and chemical characteristics, as well as temperature and pH of soils, actively influence the timing and virulence of viral particles of a particular virus (Kimura et al., 2008). Thus, the soils of the Steppe zone of Ukraine, on the example of the Odesa region, due to soil and climatic features, are able to level the presence and time of activity of viral particles of potato virus X (PVX), while particles of tobacco mosaic virus (TMV) and cucumber mosaic virus (CMV) are stored in the soil and transmitted to other plants quite well. The soil type and climate conditions of the Forest-Steppe zone of Ukraine, as exemplified by the Vinnytsia region, were resistant to cucumber mosaic virus (CMV), while other viruses were quite actively persisting. The opposite data was obtained for the Kyiv, Rivne, and Cherkasy regions. These features, in our opinion, require special, additional research.

Discussion. In nature, multicomponent virus systems exist for a long time, which can influence the development of pathological processes in plants and other organisms. These virus systems include several different species that can coexist in a common host, interact with each other, and influence the interaction between them and their host. This can have significant effects on the development of diseases in plants. For example, some viruses may be less harmful to plants when they infect a plant on their own, but when they interact with other viruses in a multicomponent

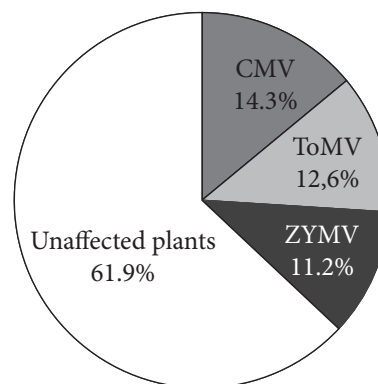


Fig. 3. Contamination of commercial vegetable seeds with pathogenic viruses: CMV — cucumber mosaic virus, ToMV — tomato mosaic virus, ZYMV — zucchini yellow mosaic virus, and unaffected plants

system, they will contribute to more dangerous disease symptoms. Such multicomponent systems can be formed for various reasons, such as certain interactions between viruses and plants (Roossinck, 2015). It is important to note that such virus systems can lead to significant consequences for the evolution of viruses and their hosts. They can promote the spread of genetic material through recombination and other mechanisms, which will lead to new variants of viruses with new properties. This is a complex and dynamic aspect of the interaction between viruses, hosts, and the environment, which still generates many questions (Khoury et al., 1993).

Mono-plants of the *Solanaceae* and *Cucurbitaceae* families from agroecosystems of some regions of Ukraine, a high frequency of signs of viral infection, including mono- and multicomponent infection, was found. Most of all, this indicates that viruses spread quite easily in these areas through several pathways, including through insects and the presence of quite powerful reservoirs of infection (most likely due to the lack of effective prevention of viral infections). The effects of climate change and intensive tillage techniques also reduce the conditions for growing vegetable crops, which in turn leads to the active spread of viral infection.

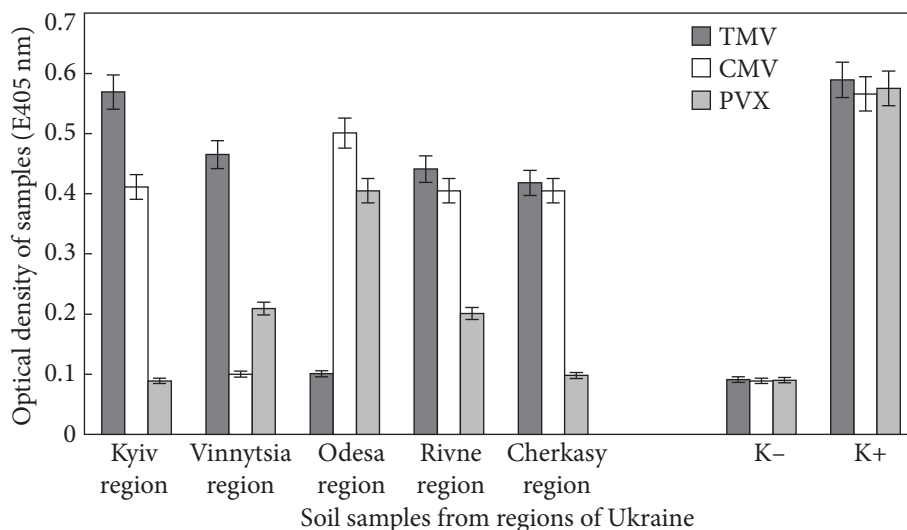


Fig. 4. The content of cucumber mosaic virus, tobacco mosaic virus, and potato virus X antigens in the soil. Controls: (K-) is a negative control, (K+) is a positive control

Obtained data showed that vegetable agrocenoses in Ukraine are more often affected by viruses belonging to the genera *Tobamovirus*, *Cucumovirus*, *Potyvirus*, and *Tospovirus* of the families *Bromoviridae*, *Potyviridae*, and *Bunyaviridae*, which is in line with the literature data of leading Ukrainian and foreign scientists (Shevchenko et al., 2021; King et al., 2012; Desbiez et al., 2020). This is because viruses of these families spread rapidly over large areas due to effective transmission pathways, namely mechanical contact, insect vectors, vegetatively, seeds, and pollen. Therefore, they are able to circulate in Ukrainian agrocenoses for a long time.

As known, plants of the *Solanaceae* family are affected by viral pathogens, specifically: cucumber mosaic virus (CMV), tobacco mosaic virus (TMV), pepper mild mottle virus (PMMoV), tobacco rattle virus (TRV), tomato mosaic virus (ToMV), tobacco ringspot virus (TRSV), turnip mosaic virus (TuMV), which correlates with our findings in this and previous studies (Pozhylov et al., 2019; Tsvigun et al., 2020; Furdychko et al., 2020). Research by Ukrainian scientists proves that in Ukraine, in particular in Poltava region, there is a spread of pepper mild mottle virus (PMMoV) — 14.3% of vegetable pepper crops and tobacco mosaic virus (TMV) — 7.1% of common

tomato crops. In the Zhytomyr region, fields with common tomato are 7.1% affected by pepper mild mottle virus (PMMoV), and in the Kyiv region, 21.4% of virus infection is observed in vegetable pepper and 7.1% in common tomato. Cucumber mosaic virus (CMV) has become widespread in the regions of Ukraine, where 25.7% of vegetable pepper and 21.4% of tomato crops were contaminated (Snihur et al., 2019; Shevchenko et al., 2021). We also obtained similar results: CMV was detected in 23% of tomatoes, PVX in 5%, ToMV in 11%, and TSWV in 3%, which indicates the systematic and sustainable presence of these pathogens in our agrocenoses. This may also be due to favorable weather and climatic conditions for the reproduction and spread of these types of viruses in our country. In different regions of the world, cucumber mosaic virus (CMV), watermelon mosaic virus 2 (WMV-2), and zucchini yellow mosaic virus (ZYMV) are the most commonly detected viral pathogens on plants of the *Cucurbitaceae* family (Desbiez et al., 2020). According to our research, cucumber plants were most often affected by Cucumber mosaic virus (CMV) — 48.1%, and courgette plants — by watermelon mosaic virus 2 (WMV-2) — 46.5%. The analysis also showed that zucchini plants were most often affected by two viruses: zucchini yellow mosaic virus (ZYMV) —

25.5% and watermelon mosaic virus 2 (WMV-2) — 22.5%. It should be noted that ZYMV was first detected in Ukraine more than 10 years ago. It is regularly detected on courgette and zucchini plants. The nature of the emergence and spread of these viral diseases depends on their biological and epidemiological features (Tsvigun et al., 2012). As seen from the latest data obtained by us, this virus continues to actively circulate in the agroecosystems of Ukraine. Along with the expansion of the areas of viral mono-infection in Ukrainian agroecosystems, there is an active spread of mixed infection (or superinfection). For example, the zucchini yellow mosaic virus (ZYMV), which we studied, is observed in 11—12% of both seeds and plants, has a rather narrow host range, and does not cause severe symptoms in plants that do not belong to the *Cucurbitaceae* family, and therefore can persist in natural reservoirs undetected (Delmiglio & Pearson, 2006). And because the narrow host range limits its ability to reproduce in plants outside the *Cucurbitaceae* family, it has to be more aggressive in maintaining its niche. This suggests that competition between viruses may be an important factor affecting their reproduction, transmission, and evolution in general. ZYMV often occurs in mixed infections with Watermelon mosaic virus 2 and less frequently with cucumber mosaic virus (Zeng et al., 2007). Watermelon mosaic virus 2 and ZYMV often coexist in the same pumpkin populations and have the same vectors (Salvaudon et al., 2013). That is why mixed infections of these three viruses are extremely common in Ukrainian agroecosystems. Mixed infection has been detected in both cultivated plants and wild species.

Watermelon mosaic virus 2 (WMV-2) and zucchini yellow mosaic virus (ZYMV) have host spectra that overlap, cause similar symptoms, and are transmitted non-persistently by the same aphid species, although with different efficiency. As already mentioned, they are often found in the same host populations and individual plants, which is typical for both cultivated and wild plants. It is also known that isolates of zucchini

yellow mosaic virus (ZYMV) isolates replicate at similar rates in mono- and mixed infections, while watermelon mosaic virus 2 (WMV-2) isolates accumulate to significantly lower levels in the presence of ZYMV (Shevchenko et al., 2016). In addition, ZYMV induces leaf discoloration and volatile production, which increases the attraction of aphids (*Aphis gossypii*) to infected plants. In comparison, WMV-2 does not have a strong effect on plant-phytophthora interactions. Nevertheless, WMV-2 can take advantage of mixed infection and be easily transmitted to other plants during it. Mixed infections of ZYMV and WMV 2 are quite frequent, due to the similar host range on the one hand and the same vector species (aphids) on the other (Zeng et al., 2007; Shevchenko et al., 2016).

The high abundance of CMV and ZYMV, combined with a moderate number of mixed infections, may indicate the presence of factors limiting their spread. Perhaps, one of these factors is the fact that pumpkins are one-year plants, and when several viruses enter a new ecological niche at the same time, in the initial stages of epiphytosis, when there are a large number of potential hosts not yet affected by any pathogen, the probability of mixed infections is extremely low but increases over time as the number of uninfected plants decreases, i.e. each year the epidemic outbreak starts from the beginning. However, certainly, at the levels of the organism and the ecosystem, species- and variety-specific features of CMV and ZYMV reproduction and species- and variety-specific features of the infected plant's defense mechanisms play an important role. Dense planting of vegetable crops and the presence of weeds in agroecosystems provide ideal conditions for the spread of infection by various aphid species (Salvaudon et al., 2013). In addition, viruses can be transmitted via seeds but with a lower transmission rate. All of these factors contribute to the spread of viral diseases in agroecosystems in Ukraine every year.

In the case of viral pathogens isolated from

plants of the Solanaceae family, mixed infection was observed in the complexes of CMV+ToMV and ToMV+PVX, which is in accordance with the literature (Roossinck, 2008; Tsvigun et al., 2012). However, the literature mainly reports the occurrence of mixed infection in the complex YVC+PVM+CMV+ PVM (Kimura et al., 2008; Desbiez et al., 2020).

According to some estimates, every third plant virus is capable of seed transmission (Munkvold, 2009). It is the ability to be transmitted by seeds that forms the genetic structure of viral populations. Active trade exchange between countries greatly facilitates and accelerates the spread of viral pathogens over long distances. Today, approximately 18% of plant viruses are known to be transmitted by seeds. A particularly high percentage of virus spread by seeds is observed when sowing with freshly harvested seeds (Tsvigun et al., 2021). Seed transmission can occur in several ways since the virus can be located inside the seed (e.g. cucumber mosaic virus) or on the surface of the seed coat (e.g. tobacco mosaic virus and cucumber green mottle mosaic virus). Every year, scientists increasingly detect 25 to 40% of commercial seeds infected with viral pathogens on the Ukrainian market (Tsvihun et al., 2012). The results of our research showed that 38.1% of the tested commercial seeds were contaminated with viral pathogens. The presence of antigens of cucumber mosaic virus (CMV) — 14.3%, zucchini yellow mosaic virus (ZYMV) — 11.2%, and tomato mosaic virus (ToMV) — 12.6%. As a result, new strains (or even species) of plant virus pathogens are being transferred to Ukrainian agrocenoses, which can lead to yield losses of 23 to 80% of agricultural products and the emergence of epiphytotic. Therefore, a necessary condition for working with seed material should be its advanced testing for viral contamination and neutralization of viral pathogens in case of their detection. To prevent the transmission of viral pathogens through seeds, certified seeds that are not contaminated with viruses should be

used for growing agricultural products. At the governmental level, it is necessary to conduct necessary inspections of all seed products that are imported and produced in Ukraine and to prohibit the sale of non-certified seeds.

Recently, more and more plant viruses have been detected in soil. It is known that viral particles can remain in dead plant residues for a long time (from 10 days to several years) and still retain their infectivity (Furdychko et al., 2020). A wide range of viral pathogens are transmitted through soil, namely cucumber mosaic virus, tobacco mosaic virus, tomato mosaic virus, potato virus X, barley stripe mosaic virus, and others. Plant pathogens of a viral nature can enter the soil in various ways. The most likely is the introduction of viruses with infected plants or plant residues. From these, viruses can enter the soil directly or indirectly (King et al., 2012). It is worth noting that viruses contained in plant residues tend to remain infectious longer than viruses in the soil as «free» vibrios. ToMV can persist in soil and plant residues for many years. The stability of viruses in soil is particularly dependent on adsorption and desorption processes (Castello et al., 1995). The adsorption of viruses by soil particles is influenced by factors such as their acidity, ionic concentration, organic matter, mechanical composition, and muddy minerals, as well as the properties of the viruses themselves and the time of interaction between viruses and soil particles. Decreasing soil moisture reduces the infectivity of phytopathogenic viruses, as shown by the example of the tomato bushy stunt virus. It is known that tobacco necrosis virus in root residues is infectious for 130 days, while it loses its infectivity after drying the soil for one day (Thomas, 1973). We tested the rhizosphere soil for the presence of viral antigens and found the presence of such viral antigens as cucumber mosaic virus (CMV), tobacco mosaic virus (TMV), and potato virus X (PVX). The soils of the Steppe zone of Ukraine, on the example of the Odesa region, due to soil and climatic conditions, are able to level the pres-

ence and time of activity of viral particles of potato virus X (PVX), while the particles of tobacco mosaic virus (TMV) and cucumber mosaic virus (CMV) are retained in the soil and transmitted to other plants quite well. The soil type and weather and climatic conditions of the Forest-Steppe zone of Ukraine, as exemplified by the Vinnytsia region, were resistant to cucumber mosaic virus (CMV), while other viruses were quite actively persisting. Thus, our results confirm that the soil is a reservoir of viral pathogens, which, due to their species characteristics and weather and climate conditions, have the ability to persist for a long time in agroecosystems of Ukraine.

Conclusions. Summarising the obtained results, it can be noted that there is a significant number of viral infections in the fields of vegetable crops in Ukraine. It was shown that vegetable agroecosystems in Ukraine are increasingly affected by diseases of viral etiology, and the frequency of their appearance has increased by 25—27% compared to previous years of research. The serological analysis made it possible to determine that 59% of the studied samples of the *Cucurbitaceae* family and 54% of the *Solanaceae* family were affected by the main viral diseases most common in

Ukraine. It should also be noted that a fairly high percentage of commercial seeds on the Ukrainian market are contaminated with viral antigens. All this complicates the diagnosis of plant diseases and contributes to their further spread. It has been shown that mixed infections are formed mainly during the growth and development of the studied vegetable crops, which leads to the further wide spread of not only mono- but also mixed virus infection of vegetable crops.

All of the above research results serve as the best confirmation of the need for an integrated approach to protecting crops from viral infections — from pre-sowing seed testing to monitoring the condition of crops at different stages of vegetation.

Given the current trend in virology, it is important to note the relevance of monitoring viruses in cultivated plants because of the possible emergence of new isolates and viruses, changes in environmental conditions, and the need for their systematic identification. The monitoring of phytopathogenic viruses is of strategic importance for the biosecurity of the government sustainable production of plant products and food, and thus human health.

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МОНІТОРИНГ ВІРУСНИХ ІНФЕКЦІЙ ОВОЧЕВИХ КУЛЬТУР В АГРОЦЕНОЗАХ УКРАЇНИ

Інформація про поширення та різноманіття фітопатогенних вірусів на території України є дуже мінливою і обмеженою, тому завжди існує необхідність комплексного вивчення видового складу і шляхів поширення вірусів сільськогосподарських культур, а також розвиток систем прогнозування епіфітотій, що сприятиме лімітуванню ареалів вірусів сільськогосподарських культур та збереженню врожаїв. Тому **метою** нашої роботи було дослідити видовий склад та частоту трапляння моно- та змішаної вірусної інфекції овочевих культур в агроценозах України та виявити можливу етіологію її походження. **Методи.** Для детекції вірусу матеріал гомогенізували та очищували, після чого реестрували на рідері. Для детекції вірусних антигенів у ІФА використовували тест-системи виробництва Loewe. Зразки на наявність вірусних антигенів аналізували імуноферментним аналізом у модифікаціях сандвіч та непрямий. **Результати.** Частота трапляння уражень овочевих культур хворобами вірусної етіології, порівняно з попередніми роками дослідження, збільшилася на 25-27%. Серологічний аналіз показав, що 59% досліджуваних зразків родини *Cucurbitaceae* та 54% — *Solanaceae* є ураженими основними найпоширенішими в Україні вірусними хворобами. Продемонстровано насіннєвий шлях передачі вірусів овочевих культур в Україні як одне з джерел вірусів в агроценозах. Показано наявність антигенів то CMV у 14,3% дослідженого насіння, ZYMV — 11,2% та ToMV — у 12,6%. Враховуючи ці показники, можна припустити, що висів такого насіння в майбутньому сприятиме поширенню вірусів територією України. Дослідження зразків ґрунту показало наявність антигенів вірусу огіркової мозаїки, вірусу тютюнової мозаїки та X-вірусу картоплі. Найнижчий рівень антигенів до CMV виявлявся в ґрунтах Вінницької області, до PVX — у Київській та Черкаській, а до TMV — в Одеській. **Висновки.** Овочеві агроценози України частіше уражуються вірусами, що належать до родів *Tobamovirus*, *Cucumovirus*, *Potyvirus*, *Tospovirus* родин *Bromoviridae*, *Potyviridae* та *Bunyaviridae*. Поряд з розширенням ареалів вірусної моноінфекції в агроценозах України спостерігається активне поширення змішаної інфекції або ж «супер інфекції». Змішані інфекції утворюються переважно в процесі росту та розвитку досліджених овочевих культур. Усе це призводить до подальшого широкого розповсюдження не лише моно-, а й змішаної вірусної інфекції овочевих культур.

Ключові слова: *cucumber mosaic virus*, *potato virus X*, *tomato mosaic virus*, *tobacco mosaic virus*, овочеві культури, моноінфекція, змішана інфекція, моніторинг.