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Review

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THE TRANSMISSION OF PLANT VIRUSES

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Plant viruses are a threat to a sustainable economy because they cause economic losses in yields. The epidemiology of plant viruses is of particular interest because of their dynamic spread by insect vectors and their transmission by seeds. The speed and direction of viral evolution are determined by the selective environment in which they are found. Knowledge of the ecology of plant viruses is critical to the transmission of many plant viruses. Accurate and timely detection of plant viruses is an essential part of their control. Rapid climate change and the globalization of trade through free trade agreements encourage the transmission of vectors and viruses from country to country. Another factor affecting the emergence of viruses is the cultivation of monocultures with low genetic diversity and high plant density. Trade in plant material (germplasm and living plants) also cause the emergence of new viruses. Viruses have a fast adaptation and development in a new environment. Aphids are the most widespread and important vectors of plant viruses. *Myzus persicae* transmits more than 100 different plant viruses. In nature plant viruses are transmitted also by nematodes, fungi, mites, leafhoppers, whiteflies, beetles, and planthoppers. The symptoms of viral diseases are very diverse and are often confused with symptoms of abiotic stress. Control of viral diseases is based on two strategies: i) immunization (genetic resistance acquired by plant transformation, breeding, or cross-protection), ii) prophylaxis to limit viruses (removal of infected plants and control of their vectors). For management, we rely on quick and accurate identification of the disease.

Key words: transmission, plant viruses, epidemiology, management, seeds, viruses, infection

Plant viruses are important pathogens of many crops worldwide. Intensive epidemics of viral plant diseases have caused significant crop losses with potential social impact. Viruses threaten not only cultural crops but also ornamental flowers, the production of fibre, and medicinal products. Viruses cause up to 47% of plant diseases and epidemics. Globalization and the rapid growth of the human population contribute to the global intensification of viral diseases.

In the future, this can have serious consequences in the food chain, which can lead to famine. In agriculture, monocultures of annual plants were mainly grown, which led to regularly recurring crop viral diseases. Viral diseases occur less frequently in perennial plants because systemic invasion is slower, they are more difficult to detect, and they generally have inconspicuous and mild symptoms. Several facts have contributed to the worsening global situation of viral diseases, such as the rapid increase in trade in plants and plant products that are not normally found in the countries in question. Viral diseases are emerging more and more rapidly due to the movement of crops from centres of domestication to distant continents where they are grown as monocultures. Introduced crops are many times infected with plant viruses that spread from natural plants (Jones 2018; Jones 2020). Epidemics and pandemics caused by plant viruses are more difficult to control and manage due to climate change (global warming) (Trebicki 2020). Another fac-

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tor is the trade in plant seeds, which also be infected with plant viruses (Constable *et al*. 2018).

Plant viruses use different transmission routes to infect plants. Transmission has a major impact on the spread of diseases caused by viruses. The virus transmission cycle involves finding a host, feeding, transporting, and delivering the virus to a new host plant. Insect-borne viruses are classified as persistent (hours to days), semi-persistent (minutes to hours) and non-persistent (short retention time), viruses depending on the time during which the vector remains virulent. In the biology of animal vectors, the latent period is synonymous with the incubation period. We further divide viruses into non-circulating (associated with the mouthparts or the foregut) and circulating (they pass through several membrane barriers and are transported in the haemolymph of the vector). Viruses are further divided into circulating and non-circulating viruses. Plant virus species from genera such as *Luteoviridae*, *Nanoviridae* and *Geminiviridae* are transmitted in a non-circulative manner. Circulating viruses replicate in the tissues of the vector. Vector-borne plant viruses need a specific viral protein to transmit the viruses. Plant viruses have rather small genomes. Recombinant virus attachment protein (VAP) serves to reduce viral transmission by blocking viral binding via glycoproteins and subsequent spread in the vector and reduction of the vector population by the viral protein (Hogenhoug 2008). Vertical transmission involves transmission between parents and offspring, while horizontal is transmission to new plants. Horizontal transmission commonly includes vector transmission by insects, mites, ectoparasitic nematodes that attack roots, and contact transmission where mechanical damage occurs (Hull 2014; Jones 2018).

Circulating transmission

This mode of virus transmission needs several hours to days to infect. The exact route of virus movement through the vector can vary between and within virus families. They are mostly located in the phloem, but inoculation can also take place in non-vascular tissues. Acquisition by aphids begins with the ingestion of phloem sap. The virus accumulates in the intestine when the aphid continues to feed. Part of the ingested virus actively moves through the intestinal wall into the hemocoel, and part is excreted. Once in the hemocoel, the virus can be transported in the haemolymph and accumulate in specific tissues, including phagocytic cells. Finally, the virus travels through the salivary system. Before the aphid leaves the plant, there is no effective transmission of the virus in the salivary system, the so-called latent period This is a short and variable period when the aphid starts transmitting the virus again. However, the amount of virus, available for transmission will be reduced (James & Keith 2004).

Non-circulating transmission

Most plant viruses are transmitted by non-circulatory transmission. We further divide these viruses into non-persistent, semi-persistent and persistent. It depends on how long the aphids have been feeding. Virus transmission consists of three steps:

1. Receiving the virus from an infected source (acquisition).
2. Stable retention of the obtained virions in the required places within the vectors.
3. Release of virions and their transport to the site of infection (inoculation) (James & Keith 2004).

Non-persistent transmission

Viruses carried by aphids are transmitted non-persistently. Aphids infect plants while feeding. They are transmitted with low vector specificity due to their short transmission time. These viruses are not circulating and are found only in the mouthparts of insects. The vector is only virulent for a short time, so it can only spread over short distances. Non- persistent viruses transmitted by aphids belong to the genera *Alfamovirus, Cucumovirus, Fabavirus, Macluravirus,* and *Potyvirus* (Bragard *et al*. 2013; Adams & Antoniw 2015; International Committee on Taxonomy of Viruses Executive Committee 2020).

Semi-persistent transmission

Semi-persistent viruses are concentrated in the phloem and surrounding tissues. These viruses do not enter the body, they are in the anus and their retention period lasts from several hours to days. Semi-persistent viruses transmitted by aphids belong to the genus *Caulimovirus*. The genus *Alexivirus* is transmitted in a semi-persistent manner by eriophyid mites. The genus *Crinivirus* is transmitted

by whiteflies, *Bromovirus* and *Comovirus* are transmitted by beetles (Bragard *et al*. 2013; Adams & Antoniw 2015; International Committee on Taxonomy of Viruses Executive Committee 2020).

Persistent transmission

Persistent viruses are restricted to the phloem only, meaning they need a longer feeding time to be transmitted to plants by the insect vector. Unlike non-persistent viruses, these viruses circulate in the vector´s body, passing through the insect´s tissues to penetrate multiple organs. They show a high degree of specificity for vectors that can remain virulent for several weeks or their lifetime. As a result, they can spread over long distances and a single virus can infect multiple plants. The viruses transmitted by aphids are from the genera *Capulavirus, Enamovirus, Luteovirus, Nanovirus,* and *Polerovirus.* Indirectly, circulating transmission refers to the genus *Umbravirus*, which uses the auxiliary genus *Luteovirus* for its transmission. *Begomovirus* is transmitted by whiteflies. *Orthotospovirus* is transmitted by thrips (Bragard *et al*. 2013; Adams & Antoniw 2015; International Committee on Taxonomy of Viruses Executive Committee 2020).

Transmission through seeds

Viruses in seeds can persist for a long time if the seeds are viable. Seed transmission allows viruses to spread over long distances. It represents an important source of primary inoculum for many vertically transmitted viruses (Jones 2016). The seed-borne viruses can survive long periods of drought in the seed. They facilitate the expansion of the geographical range of plant viruses. The increasing temperature associated with global warming increases the survival of infected seeds and their rate of transmission. Transmission of plant viruses by seeds is of great importance in virus epidemics, which will lead to food safety problems (Montes & Pagán 2019). The seed-borne virus has two mechanisms for reaching the seed. The first mechanism is a direct invasion of the embryonic tissues, and the second is through infection of the egg or pollen. Unlike animal viruses, plant viruses are confined to the intracellular symplast.

Their movement between cells takes place through plasmodesmata (symplastic channels). Invasion of gametes or embryos requires symplastic association with the parent plant.

Seed transmission via gamete infections requires invasion during gametogenesis prior to fertilisation. In autogamous plant species (eggs fertilised by pollen from the same flower), the virus must be present in the parent. However, this is less effective than seed infection from the parent plant (Bradamante *et al*. 2021). Very little is known about the function of plant genes involved in virus seed transmission. In *Glycine max* seed transmission of soybean mosaic virus is controlled by homologues of *Arabidopsis* host genes DCL3 and RDR6, they participate in the defence reaction in RNA silencing. Transmission of barley stripe mosaic virus and pea seed-borne virus is controlled by several unidentified loci. Genetic viral determinants involved in seed transmission have been analysed in several plant species. They are identified in the genome of the pea early browning virus and cucumber mosaic virus (Cobos *et al*. 2019).

Other types of transmissions

Viruses transmitted by nematodes belong to the genera *Cheravirus*, *Nepovirus* and *Tobravirus*. *Potexvirus*, *Sobemovirus*, *Soymovirus*, *Tombusvirus*, and *Tobamovirus* are transmitted by contact in the field. Viruses from the genera *Dianthovirus* and Tombusvirus are easily transmitted through the soil without a vector. The genus Ilarvirus is transmitted by pollen. However, not all virus vectors or modes of transmission are known, such as in viruses from the genus *Soymovirus* (Bragard *et al*. 2013; Adams & Antoniw 2015; International Committee on Taxonomy of Viruses Executive Committee 2020). A large number of viruses are transmitted through parasitic plants such as *Cuscuta* spp., *C. campestris* and *C. subinclusa.* Viruses are transmitted using variable organs (haustoria) of parasitic plants. The parasitic plant acquires the viruses from the phloem of the host. Parasitic plants are carriers of various viruses such as cucumber mosaic virus in cucurbit, beet curly top virus in sugar beets, tobacco mosaic virus in tobacco and potato stem mottle virus in tobacco (Singh *et al*. 2020).

Entry of plant viruses into plants

Accumulation of the virus at high levels throughout the plant is a necessary condition for the survival of the virus. A massive concentration of virions can facilitate virus transmission from one plant to

another, regardless of the mode of spread. Viruses depend on their hosts to complete their life cycle in the plant, cell-to-cell movement, encapsidation, and long-distance transport. Therefore, multiple compatible interactions must be formed between viral proteins and cellular factors. The plant responds to these pathogens with defence mechanisms. Viruses can overcome these defence mechanisms in different ways. Currently, some plants have evolved resistance genes that viruses cannot overcome (Hipper *et al*. 2013). The virus enters plants, mostly through the epidermis and mesophyll, virion uncoating and genome replication/translation occur in infected tissues. Subsequently, viral complexes move from cell to cell and continuous replication takes place in newly infected cells. Short-distance movement requires modification of plasmodesmata by viral movement proteins (Schoelz *et al*. 2011). Virus transport in phloem tissues involves translocation from mesophyll cells to sieve elements (SE) through a sequential crossing of the bundle sheath, vascular parenchyma cells, and companion cells. Once the virus in the SE is transported with the phloem sap to distant locations, it leaves the SE to initiate new sites of infection and spread throughout the plant (Figure 1). Viruses use existing plant transport pathways, including plasmodesmata and phloem vasculature, to carry out intercellular and long-distance transport, and they follow carbohydrate transport.

The nature of virus complexes transported in the SE from infected to uninfected leaves is an important question to be addressed to better understand the mechanisms by which viruses invade whole plants.

Management of plant viral diseases

To prevent the spread of viral diseases, it is most important to adopt and ensure strict regulations on the biological safety of plants. These regulations must prevent the spread of viral pathogens to other regions and continents. Quarantine measures must be used to prevent the entry of the virus not only in the exporting country but also at airports. If border and pre-border measures fail, we will achieve successful eradication, as the virus will spread slowly (a virus with a soil vector) while its vector is missing or adapted to different climatic conditions (Jones 2016).

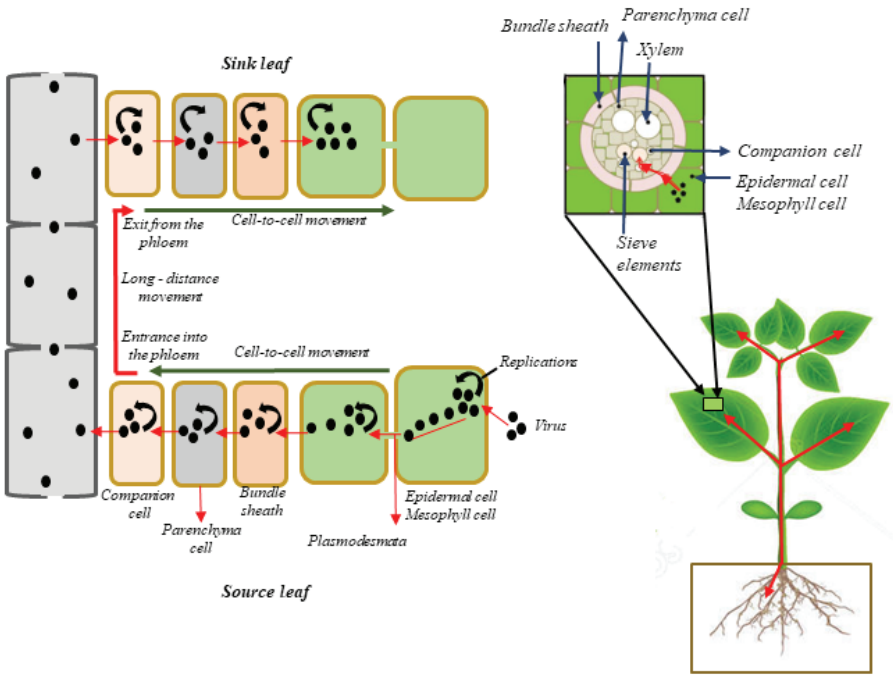


Figure 1. Virus movement between cells and over long distances in plant tissues. After inoculation, replication and translation of the viral genome occur in mesophyll and epidermal cells. Cell-associated viral proteins interact with the viral genome to form transport complexes that allow movement between cells via plasmodesmata. Viral replication and cell-to-cell movement continue in the nuclear phloem (sheath bundle, vascular parenchyma and companion cells). Movement complexes are stored in the SE, where they are ready for long-distance movement and are subsequently transported within the flow to the phloem. Invasion of distant cells begins with the release of the virus from the SE into host cells, then replication and cell-to-cell movement through bundle sheath and mesophyll cells (Figure taken from Seo & Kim 2016).

It is very important to observe border and pre-border measures that eliminate the transmission of viral pathogens (Constable *et al*. 2018). Early detection of seed-borne virus contamination before export is important. It is necessary to monitor the symptoms of the seeds before harvesting and take the leaves for the diagnosis of viral pathogens (Dombrovsky *et al.* 2017). From that, therefore, it is necessary to follow the conventional principles of mitigating the risk of spreading infection. Up to 90% of all crops are grown through seeds (the most important generative material). Testing seeds for the presence of a pathogen is a necessary step in the process of eliminating its proliferation. It has been proven that 20% of plant viruses are transmitted from generation to generation by seeds. Infected seed is considered to be one of the main sources of the Bean yellow mosaic virus (BYMV), so it is recommended to sow certified resistant seed. Monitoring and testing itself dealing with seed quality uses qualitative data relating to the presence or absence of a pathogen (Sevík & Tohumca 2011). The virus survives on the surface of the seed, rarely in the seed and endosperm (Pradhanang 2009). However, some authors state that the Bean common mosaic virus (BCMV) can survive on bean seeds for more than 20 years (Hrudova *et al*. 2006). Chemical treatment of crops against aphids is ineffective.

Due to cultivation, several alternative treatment methods have been proposed:

- soil sterilization using standard commercial steam equipment,
- sterilization of garden tools, hand hygiene,
- use of certified seeds obtained from healthy sources,
- germicidal emitters-disinfection using ultraviolet radiation of the spectrum C,
- thermotherapy – sterilization of seeds by applying a higher temperature (70°C) for 4 days or washing in a sterilizing solution,
- prevention of planting in areas with the detected presence of the virus,
- use of chemical substances – sodium phosphorate treatment for 15 minutes (Gooding 1976) (the pathogen is not completely removed), 5.25% sodium hypochlorite solution (Averre & Gooding 2000),
- thorough selection of healthy and infected plants.

Nanoparticles (NPs) are another prevention against viruses and other pathogens. These are small particles with nanoscale dimensions ranging from 1 nm to 100 nm (Khan *et al*. 2005; Srivastava & Singh 2021). They are classified based on their size, shape, and composition. Nanoparticles include individual classes such as fullerenes, polymer NPs, metal NPs, and ceramic NPs.

They are characterized by unique physicochemical properties, high reactivity, biological systems, and interactions (Zhuang & Gentry 2011). Due to these properties, they have gained attention not only in agriculture (Srivastava *et al.* 2021) for the detection of plant diseases, and carriers of genetic materials (pesticides, fertilisers), but also in environmental science (Ripp & Henry 2011; Golobovič *et al*. 2012), medicine (Nikalje 2015; Loureiro *et al*. 2016) and energy research (Avasare *et al*. 2015; Ning *et al.* 2016; Wang *et al*. 2016). For plant protection, they are applied directly to the seeds, leaves, or soil. However, direct application to the soil affects soil micro-organisms, especially those that fix nitrogen and dissolve minerals. Silver nanoparticles were the first to be used in the fight against plant diseases and have proven their antimicrobial activity (Elbeshehy *et al.* 2015; Cordero *et al*. 2017; Hao *et al*. 2017). Another tool in plant protection is the utilization of clustered regularly interspaced short palindromic repeats (CRISPR), which is mediated by RNA or DNA interference of plants (Cao *et al*. 2020). CRISPR serves as adaptive immunity against invading nucleic acids. The simplified CRISPR system contains modified RNA (gRNA) and the effector protein Cas. CRISPR is divided into two different classes (Makarova *et al*. 2015; Makarova *et al*. 2017a; Makarova *et al*. 2017b). The CRISPR class 1 system contains types I, III and IV, which can utilize a multi-protein effector complex (Makarova *et al*. 2017a). CRISPR class 2 system includes II, V and VI, which achieve target editing using only one effector protein (Makarova *et al*. 2017b; Shmakov *et al*. 2017). The most suitable system for handling nucleic acids is the class 2 CRISPR system (Hsu *et al*. 2013; Garcia-Doval & Jinek 2017; Ji *et al*. 2019).

Cas type VI proteins are used for RNA editing and type II and V proteins for DNA editing. There are two main strategies for using CRISPR/Cas to control plant viruses:

1. It is directed to the target, interferes with and destroys the viral genome to inhibit infection and replication of invading viruses.
2. Manipulation of host susceptibility factors required for a viral infection to enhance plant immunity and block viral invasion (Cao *et al*. 2020).

Nowadays, gene editing technology has been rapidly introduced into plant genetic engineering to create resistance to other pathogens and viruses (Hadidi *et al*. 2016; Ma *et al.* 2016; Langner *et al.* 2018; Mahas & Mahfouz 2018; Li *et al*. 2019; Zhang *et al.* 2019b).

CONCLUSIONS

Viruses are among the most agriculturally important and biologically interesting groups of plant pathogens. Viral plant diseases cause serious economic losses in yields and serious threats to the global food society. Estimating economic losses caused by plant viruses is very difficult. Although viruses are relatively simple genetic entities, the mechanisms by which all disease symptoms are generated are still unknown. Genetic resistance is one of many approaches to protect crops from virus infection, which also include the use of virus-free seeds or plant materials and control of biotic vectors. Resistant varieties are considered the most cost-effective and reliable approach. A considerable amount of time and expense is required to develop resistant varieties. If resistance is persistent, then the use of resistant crop varieties is the preferred method of controlling agricultural losses. The advent of genomic and bioinformatics approaches has helped us to better understand plant-virus interactions, the ability to manipulate viral genes and genomes more precisely and quickly, and significant shifts in the structure and function of the genetic resources of resistance to plant viruses. Plant viruses are difficult to eliminate without damaging the host plant. Therefore, most strategies are focused only on the prevention of plant infection. Until now, most studies on plant viruses focused only on acute infection of cultivated plants. However, many wild plants are asymptomatic. Recently, molecular mechanisms have been elucidated that would support the development of potential new antiviral strategies. Viral infections of plants generally cannot be eliminated chemically. For this reason, it is necessary to follow conventional principles of mitigating the risk of spreading infection. One of the main measures is the use of resistant genotypes. The use of genetic resistance is the most effective and economical way to control plant diseases. There is a need for continuous assessment of plant genetic diversity in terms of interactions with viruses, as well as their closer characterization. To improve the management of viral diseases in agricultural production systems, a paradigm shift toward the implementation of integrated, ecological, and intelligent strategies is needed.

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REFERENCES

Adams, M. J. and Antoniw, J. F. 2005. DPVweb: an open access internet resource on plant viruses and virus diseases. *Outlooks on Pest Management, 16,* 268 – 270.

Avasare, V., Zhang, Z., Avasare, D., Khan, I., and Qurashi, A. (2015). Room-temperature synthesis of TiO2 nanospheres and their solar driven photoelectrochemical hydrogen production. *International Journal of Energy Research*, *39*(12), 1714 – 1719. DOI:10.1002/er.3372.

Averre, C. W. and Gooding (2000). Virus diseases of greenhouse tomato and their mangment. Available at: http://www.cesncsu.edu/depts./pp/notes/oldnites/vg15. htm.

Bradamante, G., Mittelsten, S. O. and Incarbone, M. (2021). Under siege: virus control in plant meristems and progeny. *Plant Cell, 33*(8), 2523 – 2537. DOI:10.1093/plcell/koab140.

Bragard, C., Caciagli, P., Lemaire, O., Lopez-Moya, J. J., MacFarlane, S., Peters, D., Susi, P., and Torrance, L. (2013). Status and prospects of plant virus control through interference with vector transmission. *Annual Review of Phytopathology*, *51*(1), 177 – 201. DOI:10.1146/annurev-phyto-082712-102346.

Cao, Y., Zhou, H., Zhou, X., and Li, F. (2020). Control of plant viruses by CRISPR/Cas system-mediated adaptive immunity. *Frontiers in Microbiology, 11*, 1 – 9. DOI:10.3389/fmicb.2020.593700.

Cobos, A., Montes, N., López-Herranz, M., Gil-Valle, M., and Pagán, I. (2019). Within-host multiplication and speed of colonization as infection traits associated with plant virus vertical transmission. *Journal of Virology*, *93*(23), 1078 – 19. DOI:10.1128/jvi.01078-19.

Constable, F., Daly A., Terras M.A., Penrose L., and Dall, D. (2018). Detection in Australia of cucumber green mottle mosaic virus in seed lots of cucurbit crops. *Australian Plant Disease, Notes, 13*(1), 18p. DOI:10.1007/s13314-018-0302-9.

Cordero, T., Mohamed, M.A., Lopez-Moya, J.J., and Daròs, J.A. (2017). A recombinant potato virus y infectious clone tagged with the rosea1 visual marker (pvy-ros1) facilitates the analysis of viral infectivity and allows the production of large amounts of anthocyanins in plants. *Frontiers in Microbiology*, 8*(611),* 1 – 11. DOI:10.3389/fmicb.2017.00611.

Dombrovsky, A., Tran-Nguyen, L.T.T. and Jones R.A.C. (2017). Cucumber green mottle mosaic virus: Rapidly increasing global distribution, etiology, epidemiology, and management. *Annual Review of Phytopathoogy, 55*, 231 – 256. DOI:10.1146/annurev-phyto-080516-035349.

Elbeshehy, E.K., Elazzazy, A.M. and Aggelis, G. (2015). Silver nanoparticles synthesis mediated by new isolates of *Bacillus* spp., nanoparticle characterization and their activity against Bean Yellow Mosaic Virus and human pathogens. *Frontiers in Microbiology*, *6,* 453. DOI:10.3389%2Ffmicb.2015.00453.

Garcia-Doval, C. and Jinek, M. (2017). Molecular architectures and mechanisms of Class 2 CRISPR-associated nucleases. *Current Opinion in Structural Biology*, *47,* 157 – 166. DOI:10.1016/j.sbi.2017.10.015.

Gooding, J.R. and Suggs, E.G. (1976). Seed borne tobacco mosaic virus in commercial sources of tomato seed. In *Plant Dissease Report*, *60,* 441 – 442.

Golobič, M., Jemec, A., Drobne, D., Romih, T., Kasemets, K., and Kahru, A. (2012). Upon exposure to Cu nanoparticles, accumulation of copper in the isopod Porcellio scaber is due to the dissolved Cu ions inside the digestive tract. *Environmental science & technology*, *46*(21), 12112 – 12119. DOI:10.1021/es3022182.

Hadidi, A., Flores, R., Candresse, T., and Barba, M. (2016). Next-generation sequencing and genome editing in plant virology. *Frontiers in Microbiology*, *7*(1325), 1 – 12. DOI: 10.3389/fmicb.2016.01325.

Hao, Y., Cao, X., Ma, C., Zhang, Z., Zhao, N., Ali, A., and Rui, Y. (2017). Potential applications and antifungal activities of engineered nanomaterials against gray mold disease agent Botrytis cinerea on rose petals. *Frontiers in Plant Science*, *8* (1332), 1–9. DOI:10.3389/fpls.2017.01332.

Hipper, C., Brault, V., Ziegler-Graff, V., and Revers, F. (2013). Viral and cellular factors involved in phloem transport of Plant Viruses. *Frontiers in Plant Science, 4*(154), 1 – 25. DOI:10.3389/fpls.2013.00154.

Hogenhout, S.A., Ammar, E.D., Whitfield, A.E., and Redinbaugh, M.G. (2008). Insect vector interactions with persistently transmitted viruses. *Annual Review of Phytopathology, 46*, 327 – 359. DOI:10.1146/annurev.phyto.022508.092135.

Hrudova, E., Pokorny, R. and Vichova, J. (2006). *Integrated Plant Protection.* 1 st ed. Brno: Mendel University of Agriculture and Forestry in Brno. 151p. (in Czech).

Hsu, P., Scott, D., Weinstein, J., Ran, F., Konermann, S., Agarwala, V., et al. (2013). DNA targeting specificity of RNA-guided Cas9 nucleases. *Nature Biotechnology*, *31*(9), 827 – 832. DOI:10.1038/nbt.2647.

Hull, R. (2014). Chapter 12 – plant to plant movement. In Hull, R. (Ed.) *Plant Virology,* fifth ed. Academic Press, Boston. pp. 669 – 751.

International Committee on Taxonomy of Viruses Executive Committee (2020). The new scope of virus taxonomy: Partitioning the virosphere into 15 hierarchical ranks. *Nature Microbiology*, *5*, 668 – 674. DOI:10.1038/s41564-020-0709-x.

James, C.K. NG. and Keith, L.P. (2004). Transmission of plant viruse by aphid vector. *Molecular Plant Pathology*, *5*(5), 505 – 511. DOI:10.1111/j.1364-3703.2004.00240.x.

Ji, X., Wang, D. and Gao, C. (2019). CRISPR editing-mediated antiviral immunity: a versatile source of resistance to combat plant virus infections. *Science China Life Sciences*, *62* (9), 1246 – 1249. DOI:10.1007/s11427-019-9722-2.

Jones, R.A.C. (2016). Future scenarios for plant virus pathogens as climate change progresses. *Advances in Virus Research, 95,* 87 – 147. DOI:10.1016/bs.aivir.2016.02.004.

Jones, R.A.C. (2018). Chapter Six – Plant and insect viruses in managed and natural environments: Novel and neglected transmission pathways. *Advances in Virus Research, 101,* 149 – 187. DOI: 10.1016/bs.aivir.2018.02.006.

Jones, R.A.C. (2020). Disease pandemics and major epidemics arising from new encounters between indigenous viruses and introduced crops. *Viruses, 12*(12), 1388. DOI:10.3390/v12121388.

Khan, A.A., Naqvi, Q.A., Khan, M.S., Singh, R., and Raj, S.K. (2005). First report of a begomovirus infecting Calendula in India. *Plant Pathology*, *54*(4), 569 – 569. DOI:10.1111/j.1365-3059.2005.01220.x.

Langner, T., Kamoun, S. and Belhaj, K. (2018). CRISPR crops: plant genome editing toward disease resistance. *Annual Review of Phytopathology*, *56*, 479 – 512. DOI:10.1146/annurev-phyto-080417-050158.

Li, F., Liu, W. and Zhou, X. (2019). Pivoting plant immunity from theory to the field. *Science China Life Sciences*, *62* (11), 1539 – 1542. DOI:10.1007/s11427-019-1565-1.

Loureiro, A., Azoia, N.G., Gomes, A.C., and Cavaco-Paulo, A. (2016). Albumin-based nanodevices as drug carriers. *Current Pharmaceutical Design*, 22(*10)*, 1371 – 1390. DOI:10.2174/1381612822666160125114900.

Ma, X., Zhu, Q., Chen, Y., and Liu, Y. (2016). CRISPR/Cas9 platforms for genome editing in plants: developments and applications. *Molecular Plant*, *9*(7), 961 – 974. DOI: 10.1016/j.molp.2016.04.009.

Mahas, A. and Mahfouz, M. (2018). Engineering virus resistance via CRISPR-Cas systems. *Current Opinion in Virology*, *32,* 1 – 8. DOI:10.1016/j.coviro.2018.06.002.

Makarova, K., Wolf, Y., Alkhnbashi, O., Costa, F., Shah, S., Saunders, S., et al. (2015). An updated evolutionary classification of CRISPR-Cas systems. *Nature Reviews Microbiology*, *13*, 722 – 736. DOI:10.1038/nrmicro3569.

Makarova, K.S., Zhang, F. and Koonin, E.V. (2017a). SnapShot: class 1 CRISPR-Cas systems. *Cell, 168*(5), 946 – 946. DOI:10.1016/j.cell.2017.02.018.

Makarova, K.S., Zhang, F. and Koonin, E.V. (2017b). SnapShot: class 2 CRISPR-Cas systems. *Cell, 168*, 328. DOI:10.1016/j.cell.2016.12.038.

Montes, N. and Pagán, I. (2019). Light intensity modulates the efficiency of virus seed transmission through modifications of plant tolerance. *Plan Theory*, *8*(9), 304. DOI:10.3390/plants8090304.

Nikalje, A.P. (2015). Nanotechnology and its applications in medicine. *Medicinal Chemistry*, *5*(2), 1 – 9. DOI: 10.4172/2161-0444.1000247.

Ning, F., Shao, M., Xu, S., Fu, Y., Zhang, R., Wei, M., and Duan, X. (2016). TiO 2/graphene/NiFe-layered double hydroxide nanorod array photoanodes for efficient photoelectrochemical water splitting. *Energy & Environmental Science*, *9*(8), 2633 – 2643.

Pradhanang, P.M. (2009). Tomato mosaic virus: Does it transmit through tomato seeds? *Acta Horticulturae,* 808, 87 – 94.

Ripp, S. and Henry, T.B. (2012). *Biotechnology and Nanotechnology Risk Assessment: Minding and Managing the Potential Treats around US*. ACS symposium series, 1079. Publisher: American Chemical Society.

Sevík, M.A. and Tohumcu, E.K. (2011). The ELISA analysis results in tomato (*Lycopersicon esculenutm* MILL.) seed health testing fot Tobacco mosaic virus. *Žemdirbyste = Agriculture, 98*(3), 301 – 306.

Schoelz, J.E., Harries, P.A. and Nelson, R.S. (2011). Intracellular transport of plant viruses: finding the door out of the cell. *Molecular Plant, 4*(5), 813 – 831. DOI:10.1093/mp/ssr070.

Singh, S., Awasthi, L.P. and Jangre, A. (2020). Transmission of plant viruses in fields through various vectors. *Applied Plant Virology,* 313 – 334. DOI:10.1016/b978-0-12-818654-1.00024-4.

Shmakov, S., Smargon, A., Scott, D., Cox, D., Pyzocha, N., Yan, W., et al. (2017). Diversity and evolution of class 2 CRISPR-Cas systems. *Nature Reviews Microbiology*, *15*, 169 – 182. DOI:10.1038/nrmicro.2016.184.

Seo, JK. and Kim, KH. (2016). Long-distance movement of viruses in plants. In Wang, A. and Zhou, X. (Eds.) *Current Research Topics in Plant Virology.* Springer, Cham. pp. 153 – 172. DOI:10.1007/978-3-319-32919-2_6.

Srivastava, A. and Singh, R. (2021). Nanoparticles for sustainable agriculture and their effect on plants. *Current Nanoscience*, *17*(1), 58 – 69.

Trebicki, P. (2020). Climate change and plant virus epidemiology. *Virus Research, 286,* 198059. DOI:10.1016/j.virusres.2020.198059.

Wang, Y., Sun, C., Xu, C., Wang, Z., Zhao, M., Wang, C., Liu, L., and Chen, F. (2016). Preliminary experiments on nano-silver against tobacco mosaic virus and its mechanism. *Tobacco Science and Technology*, *49,* 22 – 30. DOI:10.16135/j.issn1002-0861.20160104.

Zhang, Y., Malzahn, A., Sretenovic, S., and Qi, Y. (2019b). The emerging and uncultivated potential of CRISPR technology in plant science. *Nature Plants, 5,* 778 – 794. DOI:10.1038/s41477-019-0461-5.

Zhuang, J. and Gentry, R.W. (2011). Environmental application and risks of nanotechnology: a balanced view. In Ripp, S. and Henry, T.B. (Eds.) *Biotechnology and Nanotechnology Risk Assessment: Minding and Managing the Potential Threats Around Us*. ACS Symposium Series, 1079. American Chemical Society, pp. 41 – 67.

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