

Plant Viruses

Abbreviation: Plant Viruses

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Scope and target readership: *Plant Viruses* is dedicated to all aspects pertaining to viruses or viroids affecting plants at all levels of organization.

Plant Viruses will consider manuscripts that explore the following topics:

- 1) Assay of viruses and viral infectivity and the investigation of transmission and pathogenicity;
- 2) Detection and identification of viruses and viral infections;
- 3) Local response of infection (cells, organs, tissues), including local immunity and pathology;
- 4) Mechanism of natural and acquired host resistance against virus infections;
- 5) Methods for studying the morphology, assembly, replication, composition, function and physiochemical properties of viruses and their components;
- 6) Methods for investigating the suppression or inhibition of viral growth;
- 7) Molecular and cell biology of plant-virus interactions (molecular biology of virus multiplication, molecular pathogenesis, molecular aspects of control and prevention of viral infections);
- 8) Preparation and characterization of plant antiviral immunoglobulins;
- 9) Properties of viral antigens, production of antibody, and techniques for studying plant immune responses;
- 10) Purification of viruses and their components;
- 11) Safety and efficiency assessment and field trials;
- 12) Virus or viroid structure, replication, and pathogenesis: virus morphology, the function and antigenic analysis of virus structural components, virus genome structure and expression, analysis of virus replication processes, effects of viruses on their host cells, including oncogene activation and transduction, neoplastic transformation, and the pathogenesis of virus infections including tumour induction.

Findings of viruses infecting other organisms may be considered for *Plant Viruses* if they shed a new light on possible parallel mechanisms of functioning, action or defense in plants.

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Cover photo: Top left (two photos): Typical leaf symptoms induced by Chrysanthemum chlorotic mottle viroid, or CChMVd variant CM5 on chrysanthemum cv. 'Bonnie Jean' (right), compared with a healthy control of the same cultivar (left); More details in Flores *et al.*, pp 27-32. Middle, left: Sharka symptoms of leaves and fruits from *Prunus* trees infected with *Plum pox virus*; More details in García and Cambra, pp 69-79. Middle, right: Sweetpotato (NC-1554) showing purple ringspots and vein banding typical of those commonly seen in the field in the US in cultivars that normally have purple pigmentation on the leaves; More details in Valverde *et al.*, pp 116-126. Bottom right: Mosaic symptoms induced on *Lagenaria siceraria* leaves cause by *Watermelon mosaic virus*; More details in Ali and Natsuaki, pp 80-84.

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CONTENTS

Odon Thiébeauld (France), Mikhail M. Pooggin (Switzerland), Lyubov A. Ryabova (France) Alternative Translation Strategies in Plant Viruses	1
Zhong-Hui Zhang, Qi Xie, Hui-Shan Guo (China) Antiviral Defense in Plants	21
Ricardo Flores, Beatriz Navarro, Selma Gago, Marcos de la Peña (Spain) Chrysanthemum Chlorotic Mottle Viroid: a System for Reverse Genetics in the Family <i>Avsunviroidae</i> (Hammerhead Viroids)	27
Tony Remans (Australia/Belgium), Shazia Iram, Louise Shuey (Australia), Yasmina Jaufeerally-Fakim (Mauritius), Peer M. Schenk (Australia) Banana Streak Virus: a Highly Diverse Plant Pararetrovirus	33
Olga Chervyakova, Marina Keldish (Russia) Virus Diseases of <i>Sorbus</i> L.: Role in Biodiversity	39
Thierry Wetzel, Gabriele Krczal (Germany) Molecular Biology of <i>Raspberry ringspot nepovirus</i>	45
Baozhong Meng (Canada), Dennis Gonsalves (USA) <i>Grapevine rupestris stem pitting-associated virus</i> : A Decade of Research and Future Perspectives	52
Nuredin Habili (Australia), Petr Komínek (Czech Republic), Alan Little (Australia) <i>Grapevine Leafroll-Associated Virus 1</i> as a Common Grapevine Pathogen	63
Juan Antonio García, Mariano Cambra (Finland) Plum Pox Virus and Sharka Disease	69
Asad Ali (Pakistan), Tomohide Natsuaki (Japan) <i>Watermelon mosaic virus</i>	80
Ralf G. Dietzgen, Ben Callaghan, Paul R. Campbell (Australia) Biology and Genomics of <i>Lettuce necrotic yellows virus</i>	85
Safaa G. Kumari (Syria), Khaled M. Makkouk (Egypt) Virus Diseases of Faba Bean (<i>Vicia faba</i> L.) in Asia and Africa	93
Michael Schmitz, Gerhard Steger (Germany) Potato spindle tuber viroid (PSTVd)	106
Rodrigo A. Valverde, Christopher A. Clark (USA), Jari P.T. Valkonen (Finland) Viruses and Virus Disease Complexes of Sweetpotato	116
Pradeep Sharma, Narayan Rishi (India) Cotton Leaf Curl Disease, an Emerging Whitefly Transmissible Begomovirus Complex	127
Masamichi Isogai, Hajime Yaegashi, Nobuyuki Yoshikawa (Japan) The Multifunctional Roles of <i>Apple chlorotic leaf spot virus</i> 50KP Movement Protein	135

Odon Thiébeauld (France), Mikhail M. Pooggin (Switzerland), Lyubov A. Ryabova (France) Alternative Translation Strategies in Plant Viruses (pp 1-20)

ABSTRACT

Special Feature: Plant viruses have evolved several unconventional translational strategies that allow efficient expression of more than one protein from their compact, multifunctional RNAs, as well as regulation of polycistronic translation in the infected plant cell. Here, we review recent advances in our understanding of these unconventional mechanisms, which include leaky scanning, ribosome shunting, internal initiation, reinitiation, stop codon suppression and frameshifting, and compare their characteristics with related phenomena in other systems.

Zhong-Hui Zhang, Qi Xie, Hui-Shan Guo (China) Antiviral Defense in Plants (pp 21-26)

ABSTRACT

Invited Mini-Review: RNA silencing is a conserved pathway and it may result in gene expression blockage in eukaryotic organisms. RNA silencing is also part of a highly adaptable immune system response against viruses in plants and animals. It is generally thought that virus-induced RNA silencing is that double-stranded replicative intermediates of RNA viruses, and/or double-stranded RNA produced from the viral RNA by host RNA-dependent RNA polymerases are recognized by Dicer-like proteins for the production of viral siRNAs (vsiRNAs). However, recent studies show that vsiRNAs originated predominantly from highly structured single-stranded viral RNAs is a general characteristic for RNA viruses, dsDNA virus as well as for sub-viral pathogens, e.g. viroid. Increasing lines of evidence has also shown that the plant antiviral response involves hierarchical action of DCLs. To counteract antiviral silencing, many viral genomes encode suppressor proteins to combat the defense pathway. The most common strategy for viral suppressors to inhibit RNA silencing is via binding to siRNAs. Some viral suppressor can also bind to long dsRNA and maybe compete with DCLs to access viral RNA substrates, or inhibit the activity of specific DCLs in the production of vsiRNAs. This review will give an update on the current view of these researches on antiviral silencing and defense in plants.

Ricardo Flores, Beatriz Navarro, Selma Gago, Marcos de la Peña (Spain) Chrysanthemum Chlorotic Mottle Viroid: a System for Reverse Genetics in the Family *Avsunviroidae* (Hammerhead Viroids) (pp 27-32)

ABSTRACT

Invited Mini-Review: Viroids are small single-stranded circular RNAs able to infect plants. Chrysanthemum chlorotic mottle was one of the first viroid diseases reported, but identification and characterization of the causing RNA was delayed by its low accumulation *in vivo*. Chrysanthemum chlorotic mottle viroid (CChMVd) (398-401 nt) adopts a branched conformation instead of the rod-like secondary structure characteristic of most viroids. The natural sequence variability and the effects of artificial mutants support that the branched conformation is physiologically relevant and additionally stabilized by a kissing-loop interaction critical for RNA *in vitro* folding and *in vivo* viability. CChMVd shares structural similarities with peach latent mosaic viroid, with which forms the genus *Pelamoviroid* within the family *Avsunviroidae*. CChMVd adopts hammerhead structures that catalyze self-cleavage of the oligomeric strands of both polarities resulting from replication through a symmetric rolling-circle mechanism. The two CChMVd hammerheads display peculiarities: the plus has an extra A close to the central conserved core, and the minus an unusually long helix II. There are non-symptomatic strains (CChMVd-NS) that protect against challenge inoculation with severe strains (CChMVd-S). Introduction by site-directed mutagenesis of one of the CChMVd-NS specific mutations (UUUC→GAAA) is sufficient to change the symptomatic phenotype into non-symptomatic without altering the viroid titer. This pathogenicity determinant maps at a tetraloop of the CChMVd branched conformation. Co-inoculations with typical CChMVd-S and -NS variants showed that the infected plants remain symptomless only when the latter was in more than a 100-fold excess, indicating the higher fitness of the S variant. RNA silencing could mediate the observed cross-protection.

Tony Remans (Australia/Belgium), Shazia Iram, Louise Shuey (Australia), Yasmina Jaufeerally-Fakim (Mauritius), Peer M. Schenk (Australia) Banana Streak Virus: a Highly Diverse Plant Pararetrovirus (pp 33-38)

ABSTRACT

Invited Mini-Review: Plants are attacked by two major groups of DNA viruses: the single-stranded DNA viruses *Geminiviridae*; and the double-stranded DNA viruses which belong to *Caulimoviridae* (including the genera *Caulimovirus* and *Badnavirus*). Badnaviruses are frequently found in banana, rice, cacao, sugarcane and other plant species. Banana streak virus (BSV) is a badnavirus which typically is found integrated in the B genome of *Musa*. The integrated form is able to remain dormant for several years before viral replication starts and symptoms appear. The virus is known to be transmitted by at least three mealy bug species but it mainly spreads through vegetative propagation. *Banana streak Mysore virus* (BSMyV), *Banana streak GF virus* (BSGFV), and *Banana streak OL virus* (BSOLV) are the three major BSV species identified so far. BSV eradication from infected banana plants is very rare due to genome integration and clonal propagation practices. Interestingly, cryopreservation and use of selective inhibitors of *Hepatitis B virus* replication are currently the only two strategies which have been successfully used for this purpose.

Olga Chervyakova, Marina Keldish (Russia) Virus Diseases of *Sorbus* L.: Role in Biodiversity (pp 39-44)

ABSTRACT

Invited Mini-Review: Twenty years of experimental data under Main Botanical Garden conditions have been compiled to assess the spectrum of viral species, their combination character, nature of spread and resistance. For the first time in Russia monitoring of the distribution of viruses in the *Sorbus* genus complex in collections, dendrological and industrial types of plantations were carried out. In all virus diseases registered in 8 species and 17 varieties 3 *Ilar*-, 9 *Nepo*- and 16 non-specific viruses from 8 genera were revealed. For the first time on mountain ashes Raspberry ringspot virus, Prune dwarf virus, Grapevine fanleaf virus, Bean yellow mosaic, Soybean mosaic virus and Alfalfa mosaic virus were identified. Infection with a complex of viruses on mountain ash fruit crops, in particular industrial varieties, reaches 84-100%, and monoinfection is only registered in a small percentage of crops. A complex infection of more than 2 pathogens was registered on 75% of varieties. The evaluation of resistance to *Ilar*- and *Nepo*- viruses we conducted among 40 *Sorbus* species, and also 19 varieties and hybrids, has allowed us to select valuable genotypes of mountain ash *S. matsumurana* and *S. aucuparia* with complex resistance. We also established that all tested varieties appear susceptible, except for 5 with tolerance. There was a greater degree of infection in *S. aucuparia* including different forms of the species in creation.

Thierry Wetzels, Gabriele Krczal (Germany) Molecular Biology of *Raspberry ringspot nepovirus* (pp 45-51)

ABSTRACT

Invited Mini-Review: The *Raspberry ringspot virus* (RpRSV), first reported in raspberries (*Rubus idaeus*) in Scotland, is also a causative agent in Germany of the grapevine fanleaf disease and the Pfeffinger disease of sweet cherries. The RpRSV belongs to the genus nepovirus in the *Comoviridae* family, has polyhedral particles and is transmitted in the soil via nematodes. Different strains of RpRSV have been identified, from different types of hosts, and different types of nematode vectors have been found for the different strains of RpRSV. Furthermore, the different strains of RpRSV induce different types of symptoms on herbaceous hosts. The complete nucleotide sequences of the genomic RNAs 1 and 2 of two isolates of RpRSV infecting grapevine (RpRSV-grapevine and RpRSV-cherry), as well as partial sequences of other isolates of RpRSV from grapevine, raspberry, blackberry, were determined. In this paper, we report sequence comparisons and analysis between the different available sequences of RpRSV in relation to known and putative biological functions, and try whenever possible to correlate molecular and biological data.

Baozhong Meng (Canada), Dennis Gonsalves (USA) *Grapevine rupestris stem pitting-associated virus*: A Decade of Research and Future Perspectives (pp 52-62)

ABSTRACT

Invited Review: *Grapevine rupestris stem pitting-associated virus* (GRSPaV), a recently identified virus, is classified as a member of the *Foveavirus* genus within the *Flexiviridae* family. The genome of GRSPaV is a single-stranded RNA of positive polarity and encodes five open reading frames (ORFs). ORF1 codes for a replicase polyprotein, which contains sequence domains conserved among Alphavirus-like superfamily of RNA viruses. GRSPaV also encodes three movement proteins, a

feature distinct from most plant RNA viruses with a single movement protein. In this communication, we review the advancements that have been made on the virus over the past decade. GRSPaV has been demonstrated to comprise a family of molecular variants. Phylogenetic analyses reveal the presence of at least four distinct variant (lineage) groups. The genome of an isolate representing each of the viral variant groups has been sequenced. It is also demonstrated that commercial grape varieties are usually infected with mixtures of distinct viral variants, whereas rootstock varieties, at least those tested, are infected with a single variant. A specific relationship between some of the viral variant groups and distinct *Vitis* species seems to exist. Based on available information, a hypothetical model is proposed to explain the possible origin and evolution of different GRSPaV strains. The possible role of GRSPaV in the diseases Rupestris Stem Pitting and Vein Necrosis, as well as its economic importance are discussed. Lastly, we present our views on future directions for GRSPaV research.

Nuredin Habili (Australia), Petr Komínek (Czech Republic), Alan Little (Australia) *Grapevine Leafroll-Associated Virus 1* as a Common Grapevine Pathogen (pp 63-68)

ABSTRACT

Invited Mini-Review: *Grapevine leafroll-associated virus 1* (GLRaV-1) is a member of the genus *Ampelovirus*, family *Closteroviridae*. GLRaV-1 is one of the at least ten viruses causing grapevine leafroll disease worldwide, characterized by a typical downrolling of the leaf and its premature discoloration. It can cause delayed fruit maturity and reduced sugar content of the berries. GLRaV-1 naturally infects plants of the *Vitis* genus only. It is transmitted by infected propagation material and by the scale insects *Neopulvinaria innumerabilis* and *Parthenolecanium corni* and by the mealybugs *Heliococcus bohemicus* and *Phenacoccus aceris*. Virions are filamentous in shape, containing a coat protein of 35 kDa size. Within the virion the virus has a positive sense, single stranded RNA molecule of 17,647 nt in length and lacking a poly (A) tail. The genome contains 10 major ORFs encoding a putative RNA helicase, an RNA-dependent RNA polymerase and a homologue of the HSP70 family of heat shock proteins, which is a unique feature among plant viruses, being present only in closteroviruses. Further ORFs encode the viral coat protein and two diverged copies of the coat protein. Serology and molecular techniques such as RT-PCR and molecular hybridization are useful for the specific and sensitive detection of GLRaV-1.

Juan Antonio García, Mariano Cambra (Finland) Plum Pox Virus and Sharka Disease (pp 69-79)

ABSTRACT

Invited Review: Sharka is a disease of fruiting, ornamental and wild *Prunus* species of great socio-economic relevance that has spread to most *Prunus*-growing nations. It is caused by *Plum pox virus* (PPV), a member of the genus *Potyvirus*. In recent years, there have been notable advances in our understanding of genome organization and expression, functions of gene products, and pathogenicity and host range determinants of PPV and other potyviruses. This knowledge is being applied to improve PPV detection and strain differentiation. In addition, the feasibility of engineering the PPV genome through cDNA cloning has opened the possibility of using PPV as a biotechnological tool. The combined application of classical breeding and genetic engineering techniques is yielding first results in the development of *Prunus* cultivars resistant to sharka disease.

Asad Ali (Pakistan), Tomohide Natsuaki (Japan) *Watermelon mosaic virus* (pp 80-84)

ABSTRACT

Invited Mini-Review: Potyviruses have been badly affecting crop yields in most parts of the world, with *Zucchini yellow mosaic virus* (ZYMV), *Watermelon mosaic virus* (WMV) and *Papaya ring spot virus* (PRSV) being of particular economic importance. *Watermelon mosaic virus* (WMV) causes severe economic losses in cucurbitaceous, leguminous, malvaceous and chenopodiaceous plants in temperate and mediterranean regions. It produces chlorosis, mottling, blisters on leaves and fruits, leaf distortion and stunting in watermelon, muskmelon, squash, pumpkin and cucumber. WMV has been shown to infect experimentally, more than 170 plant species belonging to 27 plant families. The biological variability of WMV has been well-documented. Serologically, it is close to *Soybean mosaic virus* (SMV) and *Papaya ringspot virus* (PRSV), but distantly related to *Potato virus Y* (PVY) and *Bean yellow mosaic virus* (BYMV). The genome of the reported WMV isolates is more than 10kb, flanked by untranslated regions at both the ends. The large open reading frame (ORF) encodes a putative polyprotein of 3217 aa, with a calculated Mr. of 366903.95. Sequence analyses of WMV isolates revealed close relationship with the reported isolates of SMV (84.7% to 85.8% aa identity). However, the N-terminal P1 protein encoding region was substantially different, presenting less than 35% identity. SimPlot analysis revealed that WMV arose through an ancestral event of inter-specific recombination between SMV and *Bean common mosaic virus* (BCMV)/ *Peanut stripe virus* (PSV) related potyviruses. Very little

genetic material resistant to WMV-2 is available. Cultural practices, crop rotation, cross-protection and genetic resistance have effectively been used against WMV. Coat protein transgenic resistance to WMV has also been reported in squash and cantaloupe.

Ralf G. Dietzgen, Ben Callaghan, Paul R. Campbell (Australia) Biology and Genomics of *Lettuce necrotic yellows virus* (pp 85-92)

ABSTRACT

Invited Mini-Review: Rhabdoviruses are important pathogens of humans, livestock, wildlife, fish and plants. *Lettuce necrotic yellows virus* (LNYV) is the type species of the genus *Cytorhabdovirus* in the family *Rhabdoviridae*. LNYV has characteristic bacilliform, enveloped particles with a single-stranded, negative-sense RNA genome of 12,807 nucleotides contained within an infectious nucleocapsid core. The viral genome encodes six proteins, namely the nucleoprotein (N), phosphoprotein (P), matrix protein (M), glycoprotein (G), 4b protein and large polymerase protein (L), the nucleotide and deduced amino acid sequences of which have recently been analysed in detail. LNYV naturally infects a narrow range of dicotyledonous and monocotyledonous host plants. It is transmitted in a persistent manner by aphids in which it also multiplies. This article reviews LNYV particle composition and structure, replication, purification, methods for identification and diagnosis, host range, symptoms, transmission and epidemiology. Recent advances in LNYV genome sequence analysis, genetic diversity and evolution, and potential transgenic control strategies are also discussed.

Safaa G. Kumari (Syria), Khaled M. Makkouk (Egypt) Virus Diseases of Faba Bean (*Vicia faba* L.) in Asia and Africa (pp 93-105)

ABSTRACT

Invited Review: Faba bean (*Vicia faba* L.) is the fourth most important pulse crop in the world. Consumed as dry seeds, green vegetable, or as processed food, its products are a cheap source of high-quality protein in the human diet, while its dry seeds, green haulm and dry straw are used as animal feed. This crop is naturally infected by around 50 viruses worldwide, and the number continues to increase. Fortunately only few are of major economic importance in Asian and African countries. This paper will not review the literature on all of these viruses, as there are already a number of comprehensive reviews. Rather will it deal with those of major importance in Asian and African countries and focus on the research progress made over the last two decades. Surveys conducted over the last two decades by ICARDA scientists have shown that the viruses of major economic importance on faba bean in Asia and Africa are: *Faba bean necrotic yellows*, *Bean leafroll*, *Bean yellow mosaic*, *Broad bean mottle* and *Pea seed-borne mosaic viruses*. Other viruses such as *Alfalfa mosaic*, *Beet western yellows*, *Broad bean wilt*, *Broad bean true mosaic*, *Broad bean stain*, *Chickpea chlorotic dwarf*, *Cucumber mosaic*, *Milk vetch dwarf*, *Pea early browning*, *Pea enation mosaic* and *Soybean dwarf viruses* are important in specific locations in specific countries. Significant progress has been made at ICARDA in virus characterization and diagnosis over the last 15 years. The availability of highly sensitive serological methods and specific diagnostic reagents currently permit more accurate detection of viruses. These accomplishments have a positive impact on screening for virus diseases resistance.

Michael Schmitz, Gerhard Steger (Germany) Potato spindle tuber viroid (PSTVd) (pp 106-115)

ABSTRACT

Invited Review: Potato spindle tuber viroid (PSTVd) is the type strain of the largest viroid family Pospiviroidae. PSTVd is a circular, single-stranded RNA molecule with a sequence length of about 359 nt and a rod-like native structure that causes infectious diseases in solanaceous plants. PSTVd does not code for any protein but replicates autonomously in the nucleus of infected plants and is systemically transported by host proteins using functional motifs encoded in its genome. Here we summarize the present knowledge about these motifs and their functional relationship to replication, processing, transport, and cause of symptoms.

Rodrigo A. Valverde, Christopher A. Clark (USA), Jari P. T. Valkonen (Finland) Viruses and Virus Disease Complexes of Sweetpotato (pp 116-126)

ABSTRACT

Invited Review: Sweetpotato is an important crop for food security in many developing countries. Surveys have consistently

listed virus diseases, especially sweetpotato virus disease (SPVD), as the most important diseases of this crop, yet they remain the most difficult diseases to manage. Much has been learned about sweetpotato viruses from independent research programs in different countries in recent years. Although there are indications that some viruses are yet to be isolated and characterized, there are at least 15 well characterized viruses now known from sweetpotato. It has become evident that sweetpotatoes are often infected by complexes of viruses and that interactions among these viruses influence the symptoms and yield losses. The crinivirus, *Sweet potato chlorotic stunt virus* (SPCSV), can greatly enhance the activity not only of the other key component of *Sweet potato feathery mottle virus* (SPFMV, a potyvirus), but also a number of other unrelated viruses. SPCSV will be the primary focus of future research to understand and control sweetpotato virus disease complexes. Sweetpotato begomoviruses are more widely distributed than previously recognized and may also require attention. International scientific exchange and collaboration could help determine why SPVD occurs in some countries but not others and provide insight to controlling this disease in the future.

Pradeep Sharma, Narayan Rishi (India) Cotton Leaf Curl Disease, an Emerging Whitefly Transmissible Begomovirus Complex (pp 127-134)

ABSTRACT

Invited Review: In recent years leaf curl disease of cotton has become a major limiting factor in the production of cotton, which is an important fiber cash crop. In the last two decades or more, leaf curl disease in cotton took on epidemic proportions in Pakistan. In the early 1990's cotton leaf curl disease (CLCuD) appeared in the bordering parts of India in the states of Rajasthan and Punjab and spread to entire cotton growing areas in Rajasthan, Punjab and Haryana. The very early appearance of the disease devastated entire crops of susceptible varieties. This led to a ban on the cultivation of Barbados cotton and the collapse of several popular cotton varieties. The characteristic symptoms of CLCuD are general stunting, upward or downward curling of leaves and thickening of veins which turn dark green. Enations of various shapes and sizes numbering up to twelve develop on the thickened veins on the abaxial side of leaves. Fewer, smaller balls are formed which sometimes fail to open. In the field CLCuD is a complex problem that needs an integrated management approach. Six species of the genus *Begomovirus*, family *Geminiviridae* viz. *Cotton leaf curl Alabad virus* (CLCuAV), *Cotton leaf curl Gezira virus* (CLCuGV), *Cotton leaf curl Kokhran virus* (CLCuKV), *Cotton leaf curl Multan virus* (CLCuMV), *Cotton leaf curl Rajasthan virus* (CLCuRV) and *Tomato leaf curl Bangalore virus-Cotton* [Fat] associated with DNA- β and DNA-1 (genus *Nanovirus*) are reported to induce CLCuD. All these begomoviruses are monopartite DNA-A, transmissible by the whitefly *Bemisia tabaci*. Begomoviruses are recognized as the most abundant and most severe viral pathogens of cotton, worldwide. Yield losses due to CLCuD amount to 60% or more if the disease appears at a very early stage of the crop. The aim of this review is to discuss and understand our current knowledge of CLCuD complex of cotton, and epidemiology, management and future prospects.

Masamichi Isogai, Hajime Yaegashi, Nobuyuki Yoshikawa (Japan) The Multifunctional Roles of *Apple chlorotic leaf spot virus* 50KP Movement Protein (pp 135-141)

ABSTRACT

Invited Mini-Review: Diverse plant virus families encode movement proteins (MPs) in their genomes. MPs are required for cell-to-cell movement of the virus in host plants and modify plasmodesmata in the cell wall, allowing cell-to-cell movement of virus particles or infectious transcripts. In recent years, much progress has been made in determining cell-to-cell movement functions of MPs from herbaceous plant viruses. On the other hand, only a few studies have examined MPs of viruses infecting woody hosts. *Apple chlorotic leaf spot virus* (ACLSV), the type species of the genus *Trichovirus*, is graft-transmissible and causes topworking disease, which induces lethal decline in apple trees grown on Maruba kaido (*Malus prunifolia* var. *ringo*) rootstocks. ACLSV encodes a MP with a mol. wt of 50 kDa (50KP). In this review, we summarize the multifunctional roles of ACLSV MP which has the following characteristics: 1) it localizes to plasmodesmata in infected and transgenic cells, 2) it can spread from cells that initially produce it into neighboring cells, 3) it enables cell-to-cell trafficking of green fluorescent protein (GFP) when 50KP and GFP are co-expressed in the leaf epidermis, 4) it induces the production of tubular structures protruding from the surface of protoplasts, 5) it has two independently active, single-stranded nucleic acid binding domains, 6) it interferes specifically with the functions of the MP encoded by *Grapevine berry inner necrosis virus*, and 7) it acts as a suppressor of systemic silencing without interfering with local silencing, probably by inhibiting the movement of silencing signals.