Rajarshi Kumar Gaur · Nikolay Manchev Petrov Basavaprabhu L. Patil Mariya Ivanova Stoyanova *Editors*

Plant Viruses: Evolution and Management



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Preface

The current trends of environmental diversity and emerging virus species are becoming an increasing threat to our way of life economically and physically. Plant viruses are particularly significant as they affect our food supply and are capable of rapidly spreading to new plant species. In basic research, plant viruses have become useful models to analyze the molecular biology of plant gene regulation and cell-cell communication. The small size of DNA genome of viruses possesses minimal coding capacity and replicates in the host cell nucleus with the help of host plant cellular machinery. Thus, studying virus cellular processes also forms the best system in understanding the DNA replication, transcription, mRNA processing, protein expression and gene silencing in plants. A better knowledge of these cellular processes will help us in designing the antiviral strategies in plants.

This book will focus on the plant virus evolution, their molecular classification, epidemics and management. It covers topics on evolutionary mechanisms, viral ecology and emergence, appropriate methods for analysis and the role of evolution in taxonomy. This edited book also provides the in-depth knowledge of plant virus gene interaction with host, localization and expression. This book is expected to provide the most recent information regarding advances in plant virus evolution, their responses and crop improvement.

This book will be beneficial for molecular biologist and plant virologist because it combines characterization of plant viruses and disease managements. When these topics are present together, it is easy to compare all aspects of resistance, tolerance and management strategies.

Sikar, Rajasthan, India Sofia, Bulgaria New Delhi, India Sofia, Bulgaria Rajarshi Kumar Gaur Nikolay Manchev Petrov Basavaprabhu L. Patil Mariya Ivanova Stoyanova

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Plant Viruses: History and Taxonomy

Surabhi Awasthi, Reshu Chauhan, and Raghvendra P. Narayan

Abstract

Viruses are very small pathogenic particles made up of nucleoprotein (nucleic acid and protein). The study of plant viruses is so important because they cause diseases to the economically important crops. They cause a great loss to the quality and quantity of the crops. Plant viruses show various types of symptoms such as colour breaking, chlorosis, mottling, vein clearing, vein bending, leaf curl, decrease in size, distorted growth, etc. The plant viruses are very simple and are very host specific.

Keywords

History • Plant virus • Taxonomy • Nomenclature • ICTV

1.1 Introduction

Viruses are very small (submicroscopic) pathogenic particles (virions) composed of a protein which forms covering (coat) and a nucleic acid core. The nucleic acid, which is DNA or RNA, carries all genetic information required for sustaining. All viruses are obligate parasites and require cellular machinery of hosts for the multiplication. Replication and transcription of viruses to produce more nucleic acid and formation of proteins takes place within the host cell using some of the host's machinery by reprogramming hosts gene expression (Hanley-Bowdoin et al. 2004). Viruses are not functional outside their host. Therefore all the viruses are obligate parasites. All types of living organisms are hosts for viruses, but most of the viruses are host specific and infect only one type of host. Viruses are usually named on the basis of their host, for example, viruses that infect bacteria are known as bacteriophages, whereas others, those that infect algae, are phycoviruses, protozoa, fungi that are known as mycoviruses.

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1.2 Definition

'Viruses are obligate intracellular parasites that are capable of infecting eukaryotes, bacteria and archaea, as well as other organisms' (Desnues and Raoult 2012; Desnues et al. 2012; Raoult and Forterre 2008)

According to Roger Hull (2009), a virus is a set of one or more nucleic acid template molecules normally encased in a protective coat or coats of protein or lipoproteins that is able to organise its own replication only within suitable host cells. Within such cells, virus replication is (1) dependent on the host's protein-synthesising machinery, (2) organised from pools of the required materials rather than by binary fission and (3) located at sites that are not separated from the host cell contents by a lipoprotein bilayer membrane and (4) continually gives rise to variants through several kinds of change in the viral nucleic acid.

1.3 Plant Viruses

Plant viruses are also obligate intracellular parasites as the other viruses that use the molecular machinery of the host for their replication (Ahlquist et al. 2003). These viruses are widely distributed and economically important (Wren et al. 2006). The plant viruses cause many harmful plant diseases and they are responsible for a tremendous loss in crop production and crop quality worldwide. Virus-infected plants show several kinds of symptoms depending on the disease type and host but leaf yellowing is common. Some of the other symptoms of virus infection are whole leaf or in a pattern of stripes or blotches; leaf distortion, like leaf curling, mottling and other growth distortions like stunting of the whole plant; and abnormalities in flower or fruit formation (Giampetruzzi et al. 2012).

1.4 History

Tobacco mosaic virus (TMV) was the first virus to be discovered and studied, which causes mosaic disease in tobacco plants (Soosaar et al. 2005). In 1882, Adolf Mayer (1843–1942) while studying tobacco plant described a condition, which he called 'mosaic disease' (Mosaaikkrankheit), and now it is well known to be caused by the tobacco mosaic virus (TMV). The diseased plants had variegated leaves that were mottled (Mayer 1882). He excluded the possibility of a fungal infection and could not detect any bacterium and speculated that a 'soluble, enzyme-like infectious principle was involved' (van der Want and Dijkstra 2006). He did not pursue his idea any further and a major observation was made in 1892 by Iwanowski who showed that sap from tobacco plants displaying the disease described by Mayer was still infective after it had been passed through a bacteria-proof filter candle (Roger Hull 2009). However, based on previous studies, it was thought that this agent was a toxin. Iwanowski's experiment was repeated in 1898 by Beijerinck, who showed that the agent multiplied in infected tissue and called it contagium vivum fluidum (Latin for 'contagious living fluid') to distinguish it from contagious corpuscular agents (Beijerinck 1898). Beijerinck and other scientists used the term virus to describe the causative agents of such transmissible diseases to contrast them with bacteria (Roger Hull 2009). Earlier workers used the term 'virus' for both bacteria and viruses, but later on with more discoveries, the term 'filterable viruses' was used (Roger Hull 2009). With further discoveries the word filterable was dropped and term virus was adopted (Roger Hull 2009).

In the history of plant viruses, the importance of tobacco mosaic virus cannot be underestimated. TMV was the first virus to be studied and also to be crystallised. It was the very first virus to be studied in detail. In 1941 the first X-ray diffraction pictures of TMV was obtained by Bernal and Fankuchen. On the basis of her pictures, Rosalind Franklin discovered the full structure of the virus in 1955 (Creager and Morgan 2008). In the year 1941, Heinz Fraenkel-Conrat and Robley Williams showed that purified tobacco mosaic virus RNA and its coat protein can assemble by themselves to form functional viruses, suggesting that this simple mechanism was probably the means through which viruses were created within their host cells. Replication of TMV involves -sRNA using + strand RNA as template (Buck 1999; Ishikawa and Okada 2004).

Nowadays at least 3705 viruses are known of which about 1000 are plant viruses. The plant viruses are studied because they have negative impact on crop production. The viruses were considered as a health threat to humans, livestock and crop plants. In recent few decades, research and development in virology has made it possible in understanding virus-host interactions and has transformed viruses into important tools of biomedicine and biotechnology (Rajamaki et al. 2004). For example, many plant viruses are used to produce proteins useful for plants and animals (Pogue et al. 2002), and many animal viruses are used for the development of vaccines against human and animal viruses such as chicken pox, rabies, foot and mouth disease, measles, etc. (Walmsley and Arntzen 2000).

The development of plant virology can be categorised into five major (overlapping) ages as follows according to Roger Hull 2009.

Prehistory age	752 AD Plant virus in Japanese
• •	poem written by the Empress Koken
	and translated by T. Inouye:
	In this village
	It looks as if frosting continuously
	For, the plant I saw
	In the field of summer
	The colour of the leaves were yellowing
	1600–1637 Tulipomania
Recognition of	1886 Mayer transmission of TMV
viral entity	1892 Iwanowski filterability of TMV
	1898 Beijerink viruses as an entity
Biological age	1900–1935 Descriptions of many viruses
Biochemical/	1935 Purification of TMV
Physical age	1936 TMV contains pentose nucleic acid
	1939 EM TMV rod-shaped particles
	1951 TYMV RNA in protein shell
	1956 Virus particles made of
	identical protein subunit
	1955/56 Infectious nature of TMV
	RNA
	1962 Structure of isometric particles
	1983 Structure of TBSV to 2.9 Å

Molecular age	1960 Sequence of TMV coat protein
	1980 Sequence of CaMV DNA
	genome
	1982 Sequence of TMV RNA
	genome
	1984 Infectious transcripts of
	multicomponent BMV
	1986 Transgenic protection of plants
	against TMV
	1996 Recognition of RNA silencing
	1997 Recognition of virus
	suppressors of silencing

The transmissions of animal and plant viruses use different strategies to move from one host to other host and from one cell to other. The movements of plant viruses from one plant to the other need some vector, i.e., means of transmission such as insects, mites, flies, etc. The movement of viruses from one plant cell to other occurs through the plasmodesmata because viruses cannot pass through the thick cell wall. Plants probably have specialised mechanisms for transporting mRNAs through plasmodesmata, and these mechanisms are thought to be used by RNA viruses to spread from one cell to another (Ivanovski 1892).

1.5 Classification and Nomenclature of Viruses

The arrangement of different living organisms into different taxonomic categories (taxa) on the basis of their similarities and/ or relationships is called as *classification*, while assigning a particular name to them is called as *nomenclature*. The classification and nomenclature are studied under broader terminology known as taxonomy. The taxonomy of viruses is somewhat recent exercise. Johnson (1927) was the first virologist for emphasising the importance of the viral taxonomy. The earliest classification of virus was based on only few properties which include ecological and biological properties, basically the pathological property which was given greater emphasis. In 1939, Holmes published his system of classification of viruses, which was based on interaction of host with its pathogen using binomial and

trinomial system of nomenclature. With the discovery of electron microscope and biochemical studies, the classification of viruses as a group was done by different virologists such as herpesvirus group, myxovirus group, poxvirus group, etc. During this period several attempts were made to classify viruses but none were perfect. There was a need to develop a universal system of viral classification.

Earlier viruses were classified on the basis of the two developed system, the Linnaean system and Adansonian system (Roger Hull 2009). The Linnaean system was based on monothetic hierarchical system which was developed by Linnaeus for plant and animal taxonomy. The classification based on Linnaean system was not suitable for the classification of viruses due to several shortcomings. The second system, i.e., Adansonian system, was more suitable for the viral classification because this system considers several criteria at once. The Adansonian system used in viral taxonomy is polythetic hierarchical classification system published by Adanson in 1763. A polythetic class can be defined as the class in which all the members share the several properties in common (Adanson 1763). According to this system, the virus species are defined by several common properties which they share. In other words the members of a virus species are defined collectively by a consensus group of properties. Earlier this system was not so feasible due to its complexity of several characters. The problems of Adansonian system were sort out by use of computers and now it is used universally. At present more than sixty characters are used for classifying viruses. Various discoveries in cell and molecular biology have provided many tools and techniques, which helped in comparing nucleic acid sequences. The sequencing of DNA or RNA has helped in creating phylogenetic trees for the viruses (Hull 2009).

Several criteria are used for the classification of viruses. Some of the criterians are virion properties, which include shape, size, presence or absence of envelope and peplomers, molecular mass, buoyant density, sedimentation coefficient, pH stability, thermal stability, cation stability (Mg²⁺, Mn²⁺), solvent stability, detergent stability, radiation stability, properties of proteins, genome organisation and replication such as type of nucleic acid, DNA or RNA, single or double stranded, linear or circular, positive or negative sense or ambisense, number of segments, size of genome or genome sequence, presence or absence of 5D terminal cap, presence or absence of 5D terminal polypeptide, presence or absence of 3D terminal poly A tract; nucleotide sequence comparison; number of proteins, size of proteins, functional activities of proteins, presence or absence of lipid nature of lipids, presence or absence of carbohydrate, nature of carbohydrate, genome organisation, strategy of replication of nucleic acids, characteristics of translation and post-translational processing, site of accumulation of virion protein, site of assembly, site of maturation and release, cytopathology, inclusion body formation, antigenic properties such as serological relationship, mapping epitopes and biological properties; host range, natural and experimental, pathogenicity, association with disease, tissue tropisms, pathology, histopathology, mode of transmission in nature, vector relationship, geographic distribution (Roger Hull 2009; Leppard et al. 2007).

The nature (molecular and genetic composition) of the virus genome packaged into the virion particle is one of the major factors in classification of viruses. Possible genome types are:

- dsDNA
- ssDNA
- ssDNA(-)
- ssDNA(+)
- ssDNA(+/-)
- dsDNA-RT
- ssRNA-RT
- dsRNA
- ssRNA(-)
- ssRNA(+)
- ssRNA(+/-)
- Viroid

1.6 Baltimore System of Virus Classification

Developed by David Baltimore (1971). The Baltimore classification has + RNA as its central point. This system of virus classification is based upon the relationship between viral genome and messenger RNA. All viruses must produce mRNA, or (+) sense RNA and a complementary strand of mRNA, or nucleic acid is called (-) sense (strand) (Voyles 2002). According to Baltimore viruses can be grouped into seven classes on the basis of mRNA synthesis:

- 1. Class 1: dsDNA viruses; mRNA is synthesised normally using negative strand as template.
- 2. Class 2: ssDNA viruses ; mRNA is synthesised by double stranded DNA intermediate.
- Class 3: dsRNA viruses; mRNA is synthesised by complementary strand(template strand).
- 4. Class 4: ssRNA viruses; RNA directly functions as mRNA.
- 5. Class 5: (-) sense ssRNA viruses; mRNA is synthesised by synthesis of positive strand.
- 6. Class 6: genome (+) strand RNA viruses; genome is synthesised by reverse transcription.
- 7. Class 7: DNA reverse transcribing viruses with RNA intermediates.

The international committee on nomenclature of virus was established by a group of 43 virologists from all over the world in 1966 at International Congress for Microbiology held in Moscow to develop a uniform system of classification and nomenclature (Fauquet et al. 2005). The name of ICNV was changed to International Committee on Taxonomy of Viruses in 1974. The ICTV is the main governing body for all matters related to viral taxonomy. At present, International Committee on Taxonomy of Viruses (ICTV) is a committee of the Virology Division of the International Union of Microbiological Societies. The ICTV is made up of an executive committee (EC) with officers of the ICTV, subcommittee chairs and elected members. The officers manage ICTV activities, while the subcommittee chairs are responsible for managing a series of study

groups that assess the current virus taxonomy and recommend updates. Elected members assist the subcommittee chairs in managing the process of making taxonomic assignments.

At present the ICTV is composed of six subcommittees. The responsibilities of subcommittee are to classify fungal and algal viruses, plant viruses, invertebrate viruses, prokaryotic viruses and vertebrate viruses. These subcommittees discuss the classification of newly discovered viruses and manage rules accordingly. The last committee, i.e., the sixth subcommittee, is responsible for managing ICTV data and maintaining the ICTV database and websites. There are 76 international study groups (SGs) functioning under ICTV for the study of families and genera. Each SGs is headed by the chairman. The chairman is appointed by the relevant subcommittee chair. Chairman of the SGs is responsible for (1) organising discussions among SG members of emerging taxonomic issues in their field, (2) for overseeing the submission of proposals for new taxonomy and (3) for the preparation, or revision, of relevant chapter(s) in ICTV Reports. Since its inception ICTV has published nine reports. The first report was published in 1971, 2nd in 1976, 3rd in 1979, 4th in 1982, 5th in 1991, 6th in 1995, 7th in 2000, 8th in 2005 and 9th in 2011. In 2015 ICTV has published its virus taxonomy release. According to this taxonomic release, viruses are divided into seven orders, 111 families, 30 subfamilies, 610 genera and 3705 species.

ICTV activities are governed by statutes agreed with the virology division. The statutes define the objectives of the ICTV. These are:

- To develop an internationally agreed taxonomy for viruses;
- 2. To develop internationally agreed names for virus taxa
- To communicate taxonomic decisions to the international community of virologists;
- 4. To maintain an index of agreed names of virus taxa.

The present universal system of viral taxonomy given by ICTV follows the hierarchical system which includes order, family, subfamily in some, genus and species. Lower hierarchical system is also developed by ICTV. According to ICTV the hierarchical system is as follows:

- **Order**: An 'order' is the highest taxonomic level of virus classification into which virus species can be categorised. In the present taxonomic system, use of order is optional. Some of the viruses are unassigned during classification. If 'unassigned' has been entered, the taxon has not been assigned to an order. The first order to be established was Mononegavirales in 1990. This order comprises non-segmented ssRNA negative-sense viruses, namely the families Filoviridae, Paramyxoviridae and Rhabdoviridae (Fauquet et al. 2005). According to current taxonomic release of ICTV (2015), seven orders have been assigned, while 78 virus families have not been assigned to any orders. The orders are Caudovirales (3 families), Herpesvirales (3 families), Ligamenvirales (2 families), Mononegavirales (5 families), *Nidovirales* (4 families), Picornavirales (5 families) and Tymovirales (4 families), and 78 virus families have not been assigned to orders.
- **Family**: A 'family' is a level in the taxonomic hierarchy into which virus species can be classified. If marked 'unassigned' (which is rare), the lower taxonomic level of 'genus' has not been assigned to a family. A total of 104 families have been described by ICTV 2015.
- **Subfamily**: A 'subfamily' is a level in the taxonomic hierarchy into which virus species can be classified. Use of the taxonomic level subfamily is optional. If left blank, the lower taxonomic levels of genus and/or species have not been assigned to a subfamily
- **Genus:** A 'genus' is a level in the taxonomic hierarchy into which virus species can be classified. Viral genus may be defined as 'a population of virus species that share common characteristics and are different from other population of species' (Fauquet et al. 2005). If 'unassigned' (which is rare), that species has not been assigned to a genus.
- **Species:** The 7th ICTV Report formalised for the first time the concept of the virus species as the lowest taxon (group) in a branching hierarchy of viral taxa. As defined therein, 'a virus

species is a polythetic class of viruses that constitute a replicating lineage and occupy a particular ecological niche' (Van Regenmortel 1990). A polythetic class can be defined as the class in which all the members share the several properties in common. According to this system, the virus species are defined by several common properties which they share. In other words the members of a virus species are defined collectively by a consensus group of properties. Virus species thus differ from the higher viral taxa, which are 'universal' classes and as such are defined by properties that are necessary for membership.

One 'type of species' is chosen for each genus to serve as an example of a well-characterised species for that genus. If the value in this column is '1', this indicates that this species has been chosen as the type species for its genus.

1.7 Nomenclature of Viruses

The guide line for naming of viruses by ICTV (9th Report) are as follows:

The genus name ends in '-virus', subfamily name ends in '-virinae', family name ends with '-viridae' and order name ends with '-virales' universally in formal taxonomy. In viral taxonomy, the finalised names of virus orders (e.g., Caudovirales), families (e.g., Myoviridae), subfamilies (e.g., Pseudovirineae Peduovirineae) and genera (e.g., Hpunalikevirus) are printed in italics, and the first letters of the names are written in capitals. The names of species are printed in italics with first letter of first word in capital (e.g., Mumps virus). The rest of the words is not capitalised unless they are proper nouns (e.g., West Nile virus), parts of proper nouns (Enterobacteria phage MS2) or alphabetical identifiers (e.g., Enterovirus A). Names of virus strains, on the other hand, are not italicised. The first letter of the first word is not capitalised (e.g., herpes simplex virus) unless it is a proper noun, typically based on the binomial name of the species it infects (Van Regenmortel 1999; Mayo 2000).

The outline of present, (ICTV taxonomic release, 2014) taxonomy of viruses is as follows:

		Family	Genus	Subfamily	Genus
Caudovirales		Myoviridae	Bcep78likevirus	Eucampyvirinae	Cp220likevirus
			Bcepmulikevirus		Cp8unalikevirus
			Felixounalikevirus	Peduovirinae	Hpunalikevirus
			Hapunalikevirus		P2likevirus
			I3likevirus	Spounavirinae	Spounalikevirus
			Mulikevirus		Twortlikevirus
			Pbunalikevirus		Unassigned
			Phicd119likevirus	Tevenvirinae	Schizot4likevirus
			Phihlikevirus		T4likevirus
	-		Phikzlikevirus		Unassigned
			Punalikevirus		
			Viunalikevirus		
			Unassigned		
	7	Podoviridae	Bcep22likevirus	Autographivirinae	Phikmvlikevirus
			Bppunalikevirus		Sp6likevirus
			Epsilon15likevirus		T7likevirus
			F1 16likevirus		Unassigned
			Luz24likevirus	Picovirinae	Ahjdlikevirus
			N4likevirus		Phi29likevirus
			P22likevirus		Unassigned
			Phieco32likevirus		
			Unassigned		
	б	Siphoviridae	3alikevirus		
			77likevirus		
			Andromedalikevirus		
			Barnyardlikevirus		
			Bignuzlikevirus		
			Bronlikevirus		
			C2likevirus		
			C5likevirus		
			Charlielikevirus		

(continued)

Genus																															
Subfamily																															
Genus	Che8likevirus	Che9clikevirus	Chilikevirus	Cjwunalikevirus	Corndoglikevirus	D3112likevirus	D3likevirus	Halolikevirus	Hk578likevirus	Iebhlikevirus	Jerseylikevirus	L5likevirus	Lambdalikevirus	N15likevirus	Omegalikevirus	P23likevirus	Pbiunalikevirus	Pgonelikevirus	Phic3unalikevirus	Phicbklikevirus	Phie125likevirus	Phietalikevirus	Phifilikevirus	Phijlunalikevirus	Psimunalikevirus	Reylikevirus	Sap6likevirus	Sfi1 unalikevirus	Sfi21dtunalikevirus	Skunalikevirus	Spbetalikevirus
Family																															
Order																															

				T5likevirus		
				Tm4likevirus		
				Tp2unalikevirus		
				Tunalikevirus		
				Wbetalikevirus		
				Xp 10likevirus		
				Yualikevirus		
7	Herpesvirales		Alloherpesviridae	Batrachovirus		
				Cyprinivirus		
				Ictalurivirus		
				Salmonivirus		
		2	Herpesviridae	1	Alphaherpesvirinae	Iltovirus
						Mardivirus
						Scutavirus
						Simplexvirus
						Unassigned
						Varicellovirus
					Betaherpesvirinae	Cytomegalovirus
						Muromegalovirus
						Proboscivirus
						Roseolovirus
						Unassigned
					Gammaherpesvirinae	Lymphocryptovirus
						Macavirus
						Percavirus
						Rhadinovirus
						Unassigned
						Unassigned
		ю	Malacoherpesviridae	Aurivirus		
				Ostreavirus		
						(continued)

envirales 1 Lipothrixviridae Alphalipothrixvirus Rudiviridae Alphalipothrixvirus Rudivirus Betalipothrixvirus Rudivirus Betalipothrixvirus Cammalipothrixvirus Benavirus Budivirus Cammalipothrixvirus Cammalipothrixvirus Benavirus Budivirus Cuevourus A Paramyxoviridae Unassigned 		Order		Family	Genus	Subfamily	Genus
S Rudiviridae Beratipothrixvirus Amonegavirales 1 Bornavirus Breatipothrixvirus Gammalipothrixvirus Amonegavirales 1 Bornavirus 2 Filoviridae Beratipothrixvirus 3 Nyamivirdae Detatipothrixvirus 3 Nyamivirae Marburgvirus 4 Paramyzoviridae Nyavirus 5 Rhabdoviriae Lyssovirus 6 Nyavirus - 7 Nyavirus - 8 Nyavirus - 9 Paramyzoviridae Nyavirus 9 Paramyzoviridae - 9 Paramyzoviridae - 10 Naceprints - 11 Bornovirus - 12 Paramyzoviridae - 13 Nyavirus - 14 Paramyzoviridae - 10 - - 11 Bornovirus - 12 Paramyzoviridae - 13 Noviribae - 14 Paramyzoviridae - 15 Paramyzoviridae - 16 Paramyzoviridae -	6	Lipamenvirales	_	Linothrixviridae	Alphalipothrixvirus		
Mononegavirales Imanipultrixvirus Amonoegavirales 1 Bornavirus 2 Filoviridae Bornavirus 3 Nyamivirdae Bornavirus 3 Nyamivirdae Bornavirus 4 Paramyzoviridae Detaulipothrixvirus 5 Rudivirus Detauvirus 6 Cammolipothrixvirus 7 Nomivirus 8 Nomivirus 9 Nyamivirus 9 Nyamivirus 9 Nyamivirus 9 Nyamivirus 9 Nyamivirus 9 Paramyzoviridae 10 Imasigned 11 Dinasigned 11 Lysavirus 11 Divinius	2	0.000	•				
Mononegavirales Detadiportrixvirus 1 Bornavirulae Eammaliportrixvirus 2 Filoviridae Bornavirus 3 Nyamiviridae Ebolovirus 3 Nyamiviridae Unassigned 4 Paramyxoviridae Optimins 5 Rhabdoviridae Cuevavirus 6 Paramyxoviridae Nyavirus 7 Paramyxoviridae Nyavirus 8 Nyavirus Nyavirus 9 Rhabdoviridae Cytorhabdovirus 9 Rhabdovirias Dovinae 9 Rhabdovirus Sigmovirus 9 Rhabdovirus Dovinae 9 Rhabdovirus Divervirus 9 Rhabdovirus Divervirus 9 Rhabdovirus Divervirus 9 Revervirus Divervirus					Betalipothrixvirus		
Mononegavirates I Bernaulridate Gammalipothrixvirus 1 Bernaviridate Bernavirus Bernavirus 2 Filoviridate Bernavirus Bernavirus 3 Nyamiviridate Bernavirus Bernavirus 3 Nyamiviridate Lunasigned 4 Paramyxoviridate Lunasigned 5 Rhabdoviridate - 6 Paramyxoviridate - 7 Noniviridate Lysavirus 8 Noniviridate Cytoridate 9 Rendovirus Noniviridate 9 Rendovirus Nonivirus 9 Rendovirus Nonivirus 9 Rendovirus Lysavirus 9 Rendovirus Sigmavirus 9 Noniviration Lysavirus 9 Rendovirus Lysavirus 9 Rendovirus Lysavirus 9 Rendovirus Lysavirus 9 Rendovirus Lysavirus					Deltalipothrixvirus		
Mononegavirales I Rudiviridae Rudivirus 1 Bornaviridae Bornavirus 2 Filoviridae Bornavirus 3 Nyamiviridae Lonssigned 4 Paramyxoviridae Unassigned 5 Rhabdoviridae - 6 Anarburgvirus - 7 Nowirhabdovirus - 8 Nowirhabdovirus - 9 Rhabdovirus - 9 Rhabdovirus - 9 Novirhabdovirus - 10 Novirhabdovirus -					Gammalipothrixvirus		
Mononegavirales I Bornavirus 2 Filoviridae Bornavirus 3 Nyamivirdae Ebolavirus 4 Paramyxoviridae - 5 Rhadoviridae - 6 Cytorhabdovirus - 7 Novirus Novirus 8 Novirus - 9 Paramyxoviridae - 9 Novirus -				Rudiviridae	Rudivirus		
Filoviridae Cuevavirus Bolavirus Marburgvirus Nyamiviridae Nyavirus Paramyxoviridae Unassigned Paramyxoviridae - Rhabdovirus - Rhabdovirus Cytorhabdovirus Rhabdovirus Ephenerovirus Novirhabdovirus Novirhabdovirus Ryssigned - Impovirus - Sprivivirus - Impovirus	4	Mononegavirales	1	Bornaviridae	Bornavirus		
Ebolavirus Nyamiviridae Nyamiviridae Paramyxoviridae Paramyxoviridae Paramyxoviridae Cytorhabdovirus Rhabdovirudae Cytorhabdovirus Dissigned Paramyxovirus Paramyxovirus			5	Filoviridae	Cuevavirus		
Marburgwirus Nyamiviridae Marburgwirus Paramyxoviridae Nyavirus Paramyxoviridae - Paramyxoviridae - Rhabdoviridae Cytorhabdovirus Rhabdovirus Ephemerovirus Dyssavirus Novirhabdovirus Sigmavirus Sigmavirus Tibrovirus Vesicutovirus					Ebolavirus		
Nyamiviridae Nyawirus Paramyxoviridae Unassigned Paramyxoviridae - Rhabdoviridae Cytorhabdovirus Rhabdovirus Lyssavirus Rhabdovirus Ephemerovirus Sigmavirus Sigmavirus Tibrovirus Sigmavirus Tibrovirus Sigmavirus Tibrovirus Sigmavirus Tibrovirus Tibrovirus					Marburgvirus		
Paramyxoviridae Unassigned Paramyxoviridae - Rhabdoviridae Cytorhabdovirus Rhabdovirus Ephemerovirus Novirhabdovirus Novirhabdovirus Sigmavirus Sigmavirus Tibrovirus Tibrovirus Tibrovirus Tibrovirus Sigmavirus Tibrovirus Sigmavirus Tibrovirus Tibrovirus Tibrovirus Tibrovirus Tibrovirus			æ	Nyamiviridae	Nyavirus		
Paramyxoviridae - Paramyxoviridae - Rhabdoviridae Cytorhabdovirus Rhabdovirus - Rhabdovirus - Sigmavirus - -th Sigmavirus -					Unassigned		
Rhabdoviridae Cytorhabdovirus Rhabdovirus Cytorhabdovirus Rhabdovirus Ephemerovirus Novirhabdovirus Novirhabdovirus Sigmavirus Sigmavirus Sigmavirus Nucleorhabdovirus Tibrovirus Sigmavirus Tibrovirus Tibrovirus Vesiculovirus Unassigned			4	Paramyxoviridae	1		Aquaparamyxovirus
Rhabdoviridae Cytorhabdovirus Rhabdovirus Cytorhabdovirus Rhabdovirus Ephemerovirus Novirhabdovirus Novirhabdovirus Sigmavirus Sigmavirus Tibrovirus Tibrovirus Yuassigned Unassigned							Avulavirus
Rhabdoviridae Cytorhabdovirus Rhabdoviridae Cytorhabdovirus Rhabdovirus Ephemerovirus Novirhabdovirus Novirhabdovirus Sigmavirus Sigmavirus Tibrovirus Tibrovirus Vasiantus Vasiantus						1	Ferlavirus
Rhabdoviridae Cytorhabdovirus Rhabdoviridae Cytorhabdovirus Ephemerovirus Lyssavirus Novirhabdovirus Novirhabdovirus Sigmavirus Sigmavirus Tibrovirus Tibrovirus Vasiantus Sigmavirus Sigmavirus Tibrovirus Vasiantus Vasiantus						4	Henipavirus
Rhabdoviridae Cytorhabdovirus Rhabdovirus Ephemerovirus Novirhabdovirus Novirhabdovirus Sigmavirus Sigmavirus Tibrovirus Tibrovirus Tibrovirus Tupavirus Vesiculovirus Vesiculovirus							Morbillivirus
Rhabdoviridae Cytorhabdovirus Rhabdoviridae Cytorhabdovirus Ephemerovirus Lyssavirus Novirhabdovirus Novirhabdovirus Sigmavirus Sigmavirus Sigmavirus Sigmavirus Tibrovirus Tupavirus Vesiculovirus Vesiculovirus						1	Respirovirus
Rhabdoviridae Cytorhabdovirus Rhabdovirus Ephemerovirus Lyssavirus Novirhabdovirus Novirhabdovirus Sigmavirus Sigmavirus Sigmavirus Tibrovirus Tibrovirus Tupavirus Unassigned Vesiculovirus Vesiculovirus							Rubulavirus
Rhabdoviridae							Metapneumovirus
Rhabdoviridae						1	Pneumovirus
Ephemerovirus Lyssavirus Lyssavirus Novirhabdovirus Nucleorhabdovirus Sigmavirus Sigmavirus Sigmavirus Tibrovirus Tibrovirus Unassigned Vasiculovirus			S	Rhabdoviridae	Cytorhabdovirus		
Lyssavirus Novirhabdovirus Nucleorhabdovirus Perhabdovirus Sigmavirus Sigmavirus Tibrovirus Tibrovirus Unassigned Vesiculovirus					Ephemerovirus		
Nucleorhabdovirus Nucleorhabdovirus Perhabdovirus Sigmavirus Sprivivirus Throvirus Throvirus Unassigned Vesiculovirus					Lyssavirus		
Nucleorhabdovirus Perhabdovirus Sigmavirus Sigmavirus Tibrovirus Tibrovirus Unassigned Vesiculovirus					Novirhabdovirus		
Perhabdovirus Sigmavirus Sigmavirus Tibrovirus Tupavirus Unassigned Vesiculovirus					Nucleorhabdovirus		
Sigmavirus Sprivirus Sprivirus Tibrovirus Tupavirus Unassigned Vesiculovirus					Perhabdovirus		
Sprivivirus Tibrovirus Tupavirus Unassigned Vesiculovirus					Sigmavirus		
Tibrovirus Tupavirus Unassigned Vesiculovirus					Sprivivirus		
Tupavirus Unassigned Vesiculovirus					Tibrovirus		
Unassigned Vesiculovirus					Tupavirus		
Vesiculovirus					Unassigned		
					Vesiculovirus		

S	Nidovirales	1	Arteriviridae	Arterivirus		
		2	Coronaviridae	I	Coronavirinae	Alphacoronavirus
						Betacoronavirus
						Deltacoronavirus
						Gammacoronavirus
					Torovirinae	Bafinivirus
						Torovirus
		e	Mesoniviridae	Alphamesonivirus		
		4	Roniviridae	Okavirus		
9	Picomavirales	-	Dicistroviridae	Aparavirus		
				Cripavirus		
		2	Iflaviridae	Iflavirus		
		e	Marnaviridae	Marnavirus		
		4	Picornaviridae	Aphthovirus		
				Aquamavirus		
				Avihepatovirus		
				Avisivirus		
				Cardiovirus		
				Cosavirus		
				Dicipivirus		
				Enterovirus		
				Erbovirus		
				Gallivirus		
				Hepatovirus		
				Hunnivirus		
				Kobuvirus		
				Kunsagivirus		
				Mischivirus		
				Mosavirus		
				Oscivirus		
				Parechovirus		
						(continued)

Order		Family	Genus	Subfamily	Genus
			Pasivirus		
			Passerivirus		
			Rosavirus		
			Sakobuvirus		
			Salivirus		
			Sapelovirus		
			Senecavirus		
			Sicinivirus		
			Teschovirus		
			Tremovirus		
	5	Secoviridae		Comovirinae	Cheravirus
					Sadwavirus
					Sequivirus
					Torradovirus
					Unassigned
					Waikavirus
	9	Unassigned	Bacillarnavirus	1	
			Labvrnavirus		

Alphaflexiviridae Betaflexiviridae Gammaflexiviridae Tymoviridae	1 Alphaflexiviridae 2 Betaflexiviridae 3 Gammaflexiviridae 4 Tymoviridae	Allexivirus	Botrexvirus	Lolavirus	Mandarivirus	Potexvirus	Sclerodarnavirus	Unassigned	Capillovirus	Carlavirus	Citrivirus	Foveavirus	Tepovirus	Trichovirus	Unassigned	Vitivirus	Mycoffexivirus	Unassigned	Maculavirus	Marafivirus	Tymovirus
	0 6 4	Alphaflexiviridae							Betaflexiviridae								Gammaflexiviridae	Tymoviridae			

1 Plant Viruses: History and Taxonomy

	Order		Family	Genus	Subfamily	Genus
×	Virus families not	1	Adenoviridae	5 genera		
	assigned to an order	7	Alphatetraviridae	2 genera		
		б	Alvernaviridae	1 genus		
		4	Amalgaviridae	1 genus		
		5	Ampullaviridae	1 genus		
		9	Anelloviridae	11 genera		
		7	Arenaviridae	2 genera		
		8	Ascoviridae	1 genus		
		6	Asfarviridae	1 genus		
		10	Astroviridae	2 genera		
		11	Avsunviroidae	3 genera	Ι	
		12	Baculoviridae	4 genera		
		13	Barnaviridae	1 genus	Ι	
		14	Benyviridae	1 genus		
		15	Bicaudaviridae	1 genus		
		16	Bidnaviridae	1 genus		
		17	Birnaviridae	4 genera		
		18	Bromoviridae	6 genera		
		19	Bunyaviridae	5 genera		
		20	Caliciviridae	5 genera		
		21	Carmotetraviridae	1 genus		
		22	Caulimoviridae	8 genera		
		23	Chrysoviridae	1 genus		
		24	Circoviridae	2 genera		
		25	Clavaviridae	1 genus		
		26	Closteroviridae	4 genera		
		27	Corticoviridae	1 genus		
		28	Cystoviridae	1 genus		
		29	Endornaviridae	1 genus		
		30	Flaviviridae	4 genera		

														1 subfamily										
2 genera	7 genera	1 genus	2 genera	2 genera	2 genera	1 genus	2 genera	2 genera	5 genera	2 genera	3 genera	1 genus	1 genus	3 genera	1 subfamily	2 genera	2 genera	2 genera	1 genera	2 genera	2 genera	1 genera	6 genera	39 genera
Fuselloviridae	Geminiviridae	Globuloviridae	Guttaviridae	Hepadnaviridae	Hepeviridae	Hypoviridae	Hytrosaviridae	Inoviridae	Iridoviridae	Leviviridae	Luteoviridae	Marseilleviridae	Megabirnaviridae	Metaviridae	Microviridae	Mimiviridae	Nanoviridae	Narnaviridae	Nimaviridae	Nodaviridae	Nudiviridae	Ophioviridae	Orthomyxoviridae	Papillomaviridae
31	32	33	34	35	36	37	38	39	40	41	42	43	4	45	46	47	48	49	50	51	52	53	54	55

(continued)

1 Plant Viruses: History and Taxonomy

Genus																								
Subfamily		2 subfamilies												2 subfamilies	2 subfamilies									
Genus	5 genera		1 genus	6 genera	1 genus	1 genus	2 genera	1 genus	5 genera	8 genera	2 genera	3 genera	1 genera			3 genera	1 genus	1 genus	2 genera	13 genera	5 genera	1 genus	14 genera	6 genera
Family	Partitiviridae	Parvoviridae	Permutotetraviridae	Phycodnaviridae	Picobirnaviridae	Plasmaviridae	Polydnaviridae	Polyomaviridae	Pospiviroidae	Potyviridae	Poxviridae	Pseudoviridae	Quadriviridae	Reoviridae	Retroviridae	Sphaerolipoviridae	Spiraviridae	Tectiviridae	Togaviridae	Tombusviridae	Totiviridae	Turriviridae	Unassigned	Virgaviridae
	56	57	58	59	60	61	62	63	64	65	99	67	68	69	70	71	72	73	74	75	76	LL	78	79
Order																								

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Transmission and Movement of Plant Viruses

2

Nikolay Manchev Petrov

Abstract

Plant viruses are obligate parasites and their survival depend on being able to spread from one susceptible organism to another. Viruses cannot penetrate the intact plant cuticle and the cellulose cell wall. Therefore penetration is made trough wounds in the surface layers, such as in mechanical inoculation and transmission by vectors. There is specificity in the mechanism by which the plant viruses are naturally transmitted. They are important economically only if they can spread from plant to plant rapidly. They are contagious agents that differ in their transmissibility. No transmission of virus occurred when the virus titer in the inoculum was too low and there is no susceptibility between virus, vector, and host. Also the presence of some substances in the inoculum, which inhibited the infection process, hampered the transmission of viruses. Knowledge of the ways in which plant viruses spread is essential for the development of control measures.

Keywords

Transmission • Plant viruses

2.1 Introduction

Plant viruses must go through two stages during their infection cycle. First, they must replicate inside host cells, employing cellular systems;

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they have to move to adjacent cells (shortdistance movement) and, through the vascular system, reach other tissues and organs (longdistance movement). Second, viruses must spread to new hosts; to do that, they have to cross cellular barriers to enter cells. For most plant viruses this process is assisted by vector organisms (Matthews 1991). Transmission from plant to plant is an essential process for virus survival. Plant viruses have developed several strategies to perform this task efficiently, in many cases involving the existence of specific viral gene

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