This strong RNA-silencing-inducing ability of plant viruses is used in virus-induced gene silencing (VIGS). VIGS is an RNA-silencing-based technique used to reduce the level of expression of a gene of interest and study the function of the knocked-down gene. Full-length viral clones can be modified to carry a fragment of an endogenous gene of interest and these are known as VIGS vectors. DsRNA of the inserted fragment is generated during viral replication and mediates the silencing of the target gene. Both RNA and DNA viral genomes have been successfully developed into VIGS vectors and have been used in reverse genetics studies in many different plants. The most widely used VIGS vectors are based on TRV, TMV, and cabbage leaf curl geminivirus (CbLCV).

See also: Plant Resistance to Viruses: Engineered Resistance; Virus Induced Gene Silencing (VIGS); Viral Suppressors of Gene Silencing.

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Relevant Website

http://microrna.sanger.ac.uk – miRBase::Sequences.

Plant Reoviruses

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Glossary

Open reading frame A sequence of nucleotides in DNA that can potentially translate as a polypeptide chain.
Icosahedral Having twenty equal sides or faces.
Capsid The protein shell that surrounds a virus particle.
Monocotyledon A flowering plant that has only one cotyledon or seed leaf in the seed.
Dicotyledon A flowering plant that has two cotyledons or seed leaves in the seed.
Transovarial Transmission from one generation to another through eggs.

Introduction

The family *Reoviridae* comprises a diverse group of viruses which can infect vertebrates, invertebrates, and plants. Despite their large host range, all members of the family *Reoviridae* share common properties including an icosahedral shaped virion and segmented double-stranded RNA (dsRNA) genome. The family *Reoviridae* consists of nine genera of which three genera, *Fijivirus*, *Oryzavirus,* and *Phytoreovirus* are plant-infecting reoviruses. These reoviruses generally replicate in both plant hosts and insect vectors. Infection of the insect vector is non-cytopathic and persists often throughout the life of the insect. Infection of the host plant is tissue specific and can cause severe disease. Fiji leaf gall disease, caused by Fiji disease

virus (FDV), has caused yield losses of up to 90% in susceptible varieties of sugarcane in Australia. Rice ragged stunt virus (RRSV) is reported to reduce yield of rice by up to 100% in severe infections (generally 10–20%). Rice dwarf disease, caused by rice dwarf virus (RDV), can also cause significant losses as infected plants often fail to bear seeds. The genera of plant-infecting reoviruses are differentiated according to the number of genomic dsRNA segments and their electrophoretic profile, hosts, serological relationships, and capsid morphology (**Table 1**).

Taxonomy and Classification

Currently there are three genera of the family *Reoviridae* which are classed as plant-infecting reoviruses, *Fijivirus*, *Oryzavirus*, and *Phytoreovirus*. These reoviruses replicate both in plant hosts (except for one fijivirus: *Nilaparvata lugens* reovirus) and in their insect vectors (**Table 1**). Infection of the host plant is species specific, although the host range can often be extended under experimental conditions, and can produce various symptoms, including severe disease. The complete genome sequence has been obtained for a number of viruses and at least partial sequence information is now available for all plant reoviruses. This has allowed detailed comparisons within these genera and across all of the *Reoviridae*, thus providing a basis for the classification of these viruses into species and genera.

Within the genus *Fijivirus*, individual species have considerable similarities to the type species, Fiji disease virus. Classification into separate species is based on unique characteristics such as capacity to exchange genome segments, relatively high amino acid sequence similarity, serological cross-reaction, cross-hybridization of RNA or cDNA probes, host species, and insect vector species. In addition to these commonly used identifiers, analysis of the available genome sequences has assisted in identification of *Fijivirus* species. Gross genome characteristics for fijivirus members include a genome size of approximately 29 kbp and a characteristically low G+C content of 34–36%. Unique, and highly conserved, 5′ and 3′ terminal sequences are present in different plant reovirus species; in all RNA segments, the 3′ terminal trinucleotide is conserved across all species within the genus *Fijivirus* (**Table 2**). Inverted repeats are found adjacent to the terminal sequences and these differ from those of other plant reoviruses.

Members of the genera *Oryzavirus* and *Phytoreovirus* have significant similarity to type members rice ragged stunt virus and wound tumor virus, respectively.

Table 1 Characteristics of plant reoviruses

Genus	*Virus*	*dsRNA genome segments*	*Host*	*Vector/s*
Fijivirus	Fiji disease virus (FDV)	10	Monocot (Gramineae)	Planthoppers: *Perkinsiella saccharicida*, *P. vastatrix*, *P. vitiensis*
	Rice black-streaked dwarf virus (RBSDV)	10	Monocot (Gramineae)	Planthoppers: *Laodelphax striatellus*, *Ribautodelphax albafascia*, *Unkanodes sapporona*
	Maize rough dwarf virus (MRDV)	10	Monocot (Gramineae)	Planthopper: *Ribautodelphax notabilis*
	Pangola stunt virus (PaSV)	10	Monocot (Gramineae)	Planthoppers: *Sogatella furcifera*, *S. kolophon*
	Mal del Rio Cuarto virus (MRCV)	10	Monocot (Gramineae)	Planthopper: *Delphacodes kuscheli*
	Oat sterile dwarf virus (OSDV)	10	Monocot (Gramineae)	Planthoppers: *Javesella pellucidia*, *J. discolour*, *J.dubia*, *J.obscurella*, *Dicranotropis hamata*
	Garlic dwarf virus (GDV)	10	Monocot (Liliaceae)	Planthopper: Unknown
	Nilaparvata lugens reovirus (NLRV)	10	No plant host reported	Planthoppers: *Nilaparvata lugens*, *Laodelphax striatellus*
Oryzavirus	Echinochloa ragged stunt virus (ERSV)	10	Monocot (Gramineae)	Planthoppers: *Sogatella longifurcifera*, *S. vibix*
	Rice ragged stunt virus (RRSV)	10	Monocot (Gramineae)	Planthopper: *Nilaparvata lugens*
Phytoreovirus	Wound tumor virus (WTV)	12	Dicots	Leafhoppers: *Agallia constricta*, *A.quadripunctata*, *Agalliopsis novella*
	Rice dwarf virus (RDV)	12	Monocot (Gramineae)	Leafhoppers: *Nephotettix cincticeps*, *N. nigropictus*, *Recillia dorsalis*
	Rice gall dwarf virus (RGDV)	12	Monocot (Gramineae)	Leafhoppers: *Nephotettix cincticeps*, *N. nigropictus*, *N. virescens*, *N. malayanus*, *Recillia dorsalis*

Demarcation of species within the oryzaviruses and phytoreoviruses are primarily based on the ability to exchange genome segments although other characteristics, as mentioned for fijiviruses above, are also used. When available, genomic sequences are examined to reveal distinguishing features to support the classification. Oryzaviruses have a total genome size of approximately 26 kbp and specific 5′ and 3′ terminal sequences in all RNA segments: $^{5'}$GAUAAA—GUGC$^{3'}$. Phytoreoviruses have a total genome size of approximately 25 kbp, a G+C content between 38% and 48% and specific 5′ and 3′ terminal sequences, ($^{5'}$GG(U/C)A—(U/C)GAU$^{3'}$) in all RNA segments.

Virion Structure and Genome Organization

Fijivirus

The virions have a complex double icosahedral capsid construction and consist of a capsid, a core, and a nucleoprotein complex. Virions are fragile structures and readily break down *in vitro* to give cores. The outer capsid is 65–70 nm in diameter with 12 'A' type spikes located at the vertices of the icosahedron. The inner core is about 55 nm in diameter, with 12 'B' type spikes located at the vertices. The viral nucleic acid is located at the center of the virus particle, within the inner core capsid. Each virion contains a single full-length copy of the genome. Fijivirus genomes contain ten dsRNA genomic segments varying from approximately 1.8–4.5 kbp (**Figure 1**). The total genome is approximately 29 kbp with a low G + C content of 34–36%. Highly conserved unique 5′ and 3′ terminal sequences are found on all RNA segments (**Table 2**). Segment-specific inverted repeats are found adjacent to these terminal sequences. Segments 1–6, 8, and 10 are monocistronic, containing one open reading frame (ORF), while segments 7 and 9 each contain two ORFs. NLRV is the only fijivirus identified to date which differs from this structure, with one ORF on segment 7. The functions of proteins encoded by most ORFs are still unconfirmed; gene functions of segments 1–4 and 8–10 have been predicted based on protein expression studies or sequence similarities to related reoviruses (**Table 3**).

Oryzavirus

The virions have a double-shelled icosahedral capsid and consist of an outer capsid, an inner capsid, and a core. Virions are fragile and readily break down *in vitro* to give subviral core particles unless pre-treated. The outer capsid is 75–80 nm in diameter with 12 'A' type spikes located at the

Table 2 Conserved 5′ and 3′ sequences identified in fijiviruses

Virus	*5′ conserved sequence*	*3′ conserved sequence*[a]
Fiji disease virus	$^{5'}$AAGUUUUU—$^{3'}$	$^{5'}$—CAGCNNNNG*UC*$^{3'}$
Rice black-streaked dwarf virus	$^{5'}$AAGUUUUU—$^{3'}$	$^{5'}$—AGCUNN(C/U)G*UC*$^{3'}$
Maize rough dwarf virus	$^{5'}$AAGUUUUUU—$^{3'}$	$^{5'}$—U*GUC*$^{3'}$
Mal del Rio Cuarto virus	$^{5'}$AAGUUUUU—$^{3'}$	$^{5'}$—CAGCUNNNG*UC*$^{3'}$
Oat sterile dwarf virus	$^{5'}$AACGAAAAAAA—$^{3'}$	$^{5'}$—UUUUUUUUAG*UC*$^{3'}$
Nilaparvata lugens reovirus	$^{5'}$AGU—$^{3'}$	$^{5'}$—GUU*GUC*$^{3'}$

[a]Italicized trinucleotide is conserved in all fijivirus sequences reported to date.

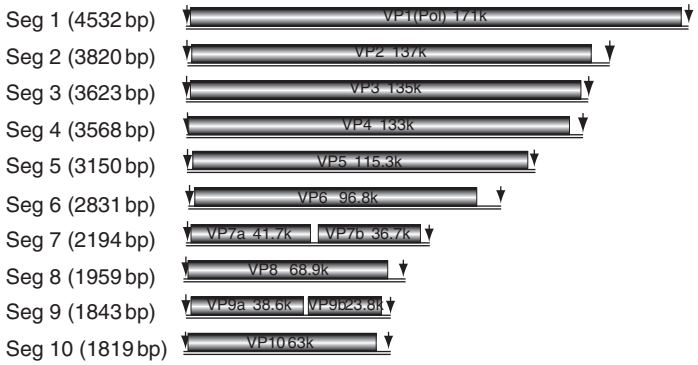

Figure 1 Genome organization of Fiji disease virus (FDV) containing 10 dsRNA segments. Each segment contains one ORF except for Seg 7 and Seg 9 which contain two ORFs. The arrows indicate the location of the 5′ and 3′ conserved sequences, respectively. Reproduced from Fauquet CM, Mayo MA, Maniloff J, Desselberger U, and Ball LA (2005) *Virus Taxonomy – Classification and Nomenclature of Viruses: Eighth Report of the International Committee on the Taxonomy of Viruses*. San Diego, CA: Elsevier Academic Press, with permission from Elsevier.

Table 3 Genome organization of FDV and predicted gene function

Segment	*Size (bp)*	*Protein nomenclature*	*MW (kDa)*	*Predicted function (location)*
S1	4532	VP1	170.6	RdRp (core)
S2	3820	VP2	137.0	Possible core protein (core)
S3	3623	VP3	135.5	Possible B spike (capsid)
S4	3568	VP4	133.2	Possible core protein (core)
S5	3150	VP5	115.3	Unknown
S6	2831	VP6	96.8	Unknown
S7	2194	VP7a	41.7	Unknown
		VP7b	36.7	Unknown
S8	1959	VP8	68.9	Possible NTP-binding (core)
S9	1843	VP9a	38.6	Structural protein (unknown)
		VP9b	23.8	Nonstructural
S10	1819	VP10	63.0	Outer capsid protein (capsid)

Reproduced from Fauquet CM, Mayo MA, Maniloff J, Desselberger U, and Ball LA (2005) *Virus Taxonomy – Classification and Nomenclature of Viruses*: *Eighth Report of the International Committee on the Taxonomy of Viruses*. San Diego, CA: Elsevier Academic Press, with permission from Elsevier.

five fold axis of the icosahedron. The core capsid is about 57–65 nm in diameter, with 12 'B' type spikes. The viral nucleic acid is located at the center of the viral particle, within the core capsid. The virus genome consists of ten dsRNA segments ranging in size from 1162–3849 bp (RRSV) with a total length of 26 kbp (**Figure 2**). Genome segments 1–3, 5, 7–10 of RRSV each contain a single ORF, while segment 4 contains two ORFs. Segment 8 encodes a polyprotein which is cleaved into two proteins. **Table 4** summarizes the organization of the RRSV dsRNA segments and the predicted function of the encoded proteins.

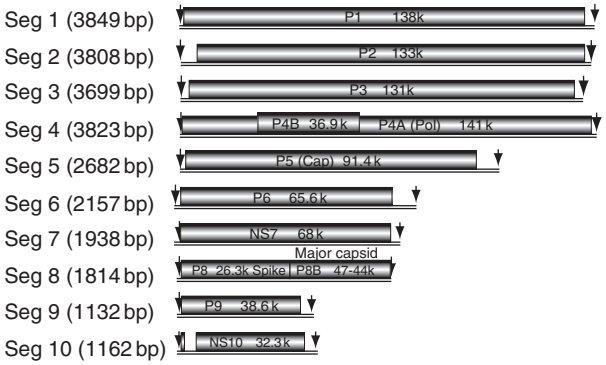

Figure 2 Genome organization of rice ragged stunt virus (RRSV) containing 10 dsRNA segments. Each segment contains one ORF except for Seg 4 which contains two ORFs. The arrows indicate the location of the 5′ and 3′ conserved sequences, respectively. Reproduced from Fauquet CM, Mayo MA, Maniloff J, Desselberger U, and Ball LA (2005) *Virus Taxonomy – Classification and Nomenclature of Viruses*: *Eighth Report of the International Committee on the Taxonomy of Viruses*. San Diego, CA: Elsevier Academic Press, with permission from Elsevier.

Phytoreovirus

The virions have a double-shelled icosahedral capsid construction and consist of an outer capsid, a core capsid, and a smooth core. Virions are approximately 70 nm in diameter with 12 spikes located at the fivefold vertices of the icosahedron and generally remain intact when purified. WTV, the type member, possesses three protein shells: an outer amorphous layer made up of two proteins, an inner capsid made up of two proteins, and a smooth core made up of three proteins that is about 50 nm in diameter. Each virion contains a single full-length copy of the genome. Phytoreoviruses have 12 segments of dsRNA which range in size from approximately 1–4.5 kbp with a total genome length of approximately 25 kbp (**Figure 3**) and a G+C content of 38–44%. Each segment of RDV contains a single ORF except for segment 12, which contains two ORFs. **Table 5** summarizes the organization of the RDV dsRNA segments and the putative function of the encoded proteins.

Replication and Gene Expression

The replication and gene expression of plant-infecting reoviruses is thought to be similar to that of other reoviruses. The best described of these is bluetongue virus (BTV), type member of the genus *Orbivirus*. If the BTV model is accurate for the plant-infecting reoviruses, replication occurs after virions (or viral cores) are delivered into the host cell. Replication is initiated when the viral capsid layer is removed and the core enters the cytoplasm of the cell. The viral genome (10–12 segments) remains packaged in the central cavity of the viral core to ensure host cell defense responses to dsRNA are not activated. The core is biochemically active with RNA-dependent RNA polymerase (RdRp), capping enzyme, and helicase enzyme. The viral core contains a number of channels, the largest of which is at the fivefold axis of the icosahedral structure. Smaller channels allow the entry of nucleotides into the core which are required for transcription. The large channel is located adjacent to the

Table 4 Genome organization of RRSV and predicted gene function

Segment	*Size (bp)*	*Protein nomenclature*	*MW (kDa)*	*Predicted function (Location)*
S1	3849	P1	137.7	Virion associated (B spike)
S2	3810	P2	133.1	Inner core capsid (core capsid)
S3	3699	P3	130.8	Major core capsid (core capsid)
S4	3823	P4a	141.4	RdRp
		P4b	36.9	(unknown)
S5	2682	P5	91.4	Capping enzyme
S6	2517	P6	65.6	Unknown
S7	1938	NS7	68	Nonstructural protein (unknown)
S8	1814	P8	67.3	Precursor polyprotein/protease
		P8a	25.6	Spike
		P8b	41.7	Major capsid protein
S9	1132	P9	38.6	Vector transmission (spike)
S10	1162	NS10	32.3	Nonstructural protein

Reproduced from Fauquet CM, Mayo MA, Maniloff J, Desselberger U, and Ball LA (2005) *Virus Taxonomy – Classification and Nomenclature of Viruses*: *Eighth Report of the International Committee on the Taxonomy of Viruses*. San Diego, CA: Elsevier Academic Press, with permission from Elsevier.

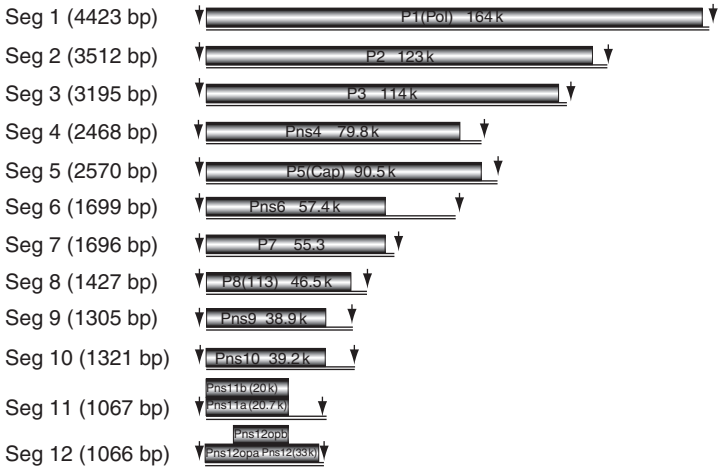

Figure 3 Genome organization of rice dwarf virus (RDV) containing 12 dsRNA segments. Each segment contains one ORF except for Seg 11 and Seg 12 which contain two ORFs. The arrows indicate the location of the 5′ and 3′ conserved sequences, respectively. Reproduced from Fauquet CM, Mayo MA, Maniloff J, Desselberger U, and Ball LA (2005) *Virus Taxonomy – Classification and Nomenclature of viruses*: *Eighth Report of the International Committee on the Taxonomy of Viruses*. San Diego, CA: Elsevier Academic Press, with permission from Elsevier.

replicase/transcriptase complex which has helicase activity for the unwinding and rewinding of the dsRNA genome during transcription of negative RNA strand. The newly formed positive strand mRNA molecules are modified to form a Cap1 structure by the guanylyltransferase, nucleotide phosphohydrolase, and transmethylase activity of the capping enzyme prior to the extrusion of mRNA, from the major pore, into the cytoplasm. These mRNA molecules released into the cytoplasm can be translated to produce viral proteins. Nonstructural viral proteins aggregate to form inclusion bodies or viroplasms. The viroplasm is the site of most of the mRNA production and assembly of core proteins. The mRNA molecules, one of each segment, are assembled with these viral proteins to form new virus core particles. Once a copy of the mRNA is inside a new viral core, the negative strand is synthesized completing the replication of the dsRNA genome. The complete viral core containing dsRNA then moves to the periphery of the viroplasm where capsid proteins are assembled to form the complete new viral particle.

Control of gene expression of a multisegmented genome is complex and not fully understood. Each genome segment contained within the viral core is associated with a single replicase/transcription complex, located adjacent to the major pore in the vertices of the icosahedron, and is transcribed separately to make full-length positive sense RNA copies. The location of the replicase/transcription complex also restricts the number of genome segments to a maximum of 12. These 10–12 mRNAs are produced in different molar amounts based largely on segment size

Table 5 Genome organization of RDV and putative gene function

Segment	*Size (bp)*	*Protein nomenclature*	*MW (kDa)*	*Predicted function (location)*
S1	4423	P1	170	RdRp (core)
S2	3512	P2	130	Capsid structural protein (outer capsid)
S3	3195	P3	110	Major core protein (core capsid)
S4	2468	Pns4	83	Nonstructural protein
S5	2570	P5	89	Guanylyltransferase (core)
S6	1699	Pns6	56	Nonstructural protein
S7	1696	P7	58	Nucleic acid binding protein (core)
S8	1427	P8	43	Major outer capsid protein
S9	1305	Pns9	49	Nonstructural protein
S10	1321	Pns10	53	Nonstructural protein
S11	1067	Pns11a	23	Nonstructural protein
		Pns11b	24	
S12	1066	Pns12	34	Nonstructural protein
		Pns12OPa	8	
		Pns12OPb	7	

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resulting in more copies of smaller mRNAs. This interaction between mRNA molecules of varying length and the replicase/transcription complex provides some control over the expression levels of individual virus genes. Translation of mRNA segments is largely independent of mRNA length although some segments are translated more efficiently resulting in a secondary method of control over expression. A third level of control results from the use of multiple or overlapping ORFs on one mRNA strand which are translated at different efficiencies. Lastly, some ORFs encode a polyprotein which must be processed to form functional proteins.

Distribution

Plant-infecting reoviruses are seasonally distributed as a result of plant host/crop cycles and presence of insect vector. Plant reoviruses have been isolated from every continent but some genera are more widespread than others. Fijiviruses are the most widely distributed, which is not surprising given that they are the most numerous. Fijiviruses occur in Africa, Europe, South America, Asia, Australia, and South Pacific Islands. Oryzaviruses have only been isolated from the Indian subcontinent and Asia while phytoreoviruses have been isolated from North America, Asia, and Africa.

Host Range and Virus Transmission

Fijiviruses

The genus *Fijivirus* contains eight species whose members infect a range of monocotyledonous plants of the families Gramineae and Liliacae. Common plant hosts include the Gramineae: *Avena sativa, Oryza sativa*, *Saccharum officinarum, Zea mays,* and the Liliacae: *Allium sativum.* However, this natural host range can be extended significantly by experimental virus infection. Virus is transmitted by delphacid planthoppers (**Table 1**). Virus can be acquired in juvenile stages, replicates in the vector, and, following a two week latent period, is transmitted to plants in a persistent manner. No transovarial transmission of virus has been reported. In addition to transmission by insect vectors, mechanical transmission of the virus to susceptible hosts has been achieved for some members with difficulty.

Oryzaviruses

The genus *Oryzavirus* contains two species whose members infect monocotyledonous plants of the family Gramineae. Common plant hosts include *Oryza sativa* and *Echinochloa crus-galli.* However, this natural host range can be extended by experimental virus infection to include other economically important species such as *Hordeum vulgare, Triticum aestivum,* and *Zea mays.* Virus is transmitted by delphacid planthoppers (**Table 1**). An acquisition period of 3 h is required followed by a 9-day latent period prior to transmission at all life stages in an intermittent manner. No transovarial transmission or mechanical transmission of virus has been reported.

Phytoreoviruses

The genus *Phytoreovirus* contains two species whose members infect monocotyledonous plants of the family Gramineae and one species which infects dicotyledonous plants. Common plant hosts include the Gramineae: *Oryza*

sativa and the dicot – *Melilotus officinalis*. However, the natural host range of the dicot-infecting WTV can be extended significantly by experimental virus infection. Virus is transmitted by cicadellid leafhoppers (**Table 1**). Virus can be acquired after a short feeding period, replicates in the vector, and, following a 10–20 day latent period, is transmitted to plants throughout the life of the vector. Transovarial transmission of virus has been reported. Attempts to transmit the virus to susceptible hosts by mechanical methods have been unsuccessful.

Pathogenicity

The pathogenicity of plant reoviruses is particularly interesting as most viruses replicate in both insects and plant hosts. Most of these viruses do not appear to cause any disease in the insect host and pathogenicity of these viruses is restricted to the plant host. The pathogenicity of fijiviruses varies considerably. Fiji leaf gall disease (caused by FDV) has been reported to cause losses of up to 90% in susceptible sugarcane varieties, while NLRV has no known plant host and, therefore, no pathogenicity. Oryzaviruses can also cause important yield losses. Rice ragged stunt disease (caused by RRSV) has been reported to cause losses of 10–20% but sometimes as high as 100% in severe infections of susceptible varieties. The pathogenicity of phytoreoviruses is much milder although rice dwarf disease (caused by RDV) can be severe as infected plants often fail to bear seeds. There is currently little information on the molecular basis for pathogenicity and it is not known if different isolates of the same virus cause diseases of varying severity.

Diagnosis and Control

Diagnosis of plant reovirus infections can be done on the basis of symptoms or by use of molecular tests. Symptoms vary in different virus/host complexes but symptoms such as plant stunting, increased numbers of side shoots, and tumors or gall formation in phloem tissue are commonly observed. Given the variability in time to symptom expression and symptom severity, alternative tests are often used. Molecular and serological tests have been developed to assist in the diagnosis of viral infection in nonsymptomatic plant material and vector insects. Serological tests are usually in enzyme-linked immunosorbent assay (ELISA) format and rely on polyclonal antisera raised against virions or expressed viral proteins. Recently, molecular tests such as reverse transcriptase-polymerase chain reaction (RT-PCR), which are faster and more specific than serology, have become the most common method of diagnosis. Species-specific primers are now commonly available as increasing numbers of plant reovirus genomes are being sequenced.

Control strategies for plant reoviruses can be focused on either the host plant or insect vector. Plant-based control through breeding to develop resistant plant species is most commonly utilized in combination with removal of susceptible varieties and infected plants which provide a source of inoculum. This approach has provided robust control of RDV in rice and FDV in sugarcane. Genetic engineering of plant hosts has also been explored as an alternative control strategy. Pathogen-derived resistance approaches using either coat protein or other viral genes to control RDV, RRSV, and FDV have not proved as successful as those used to control other RNA plant viruses. However, this may improve in the future as more information on virus infection and replication becomes available providing new resistance targets. Control of insect vector numbers with insecticide has provided some additional disease control. Unfortunately, chemical control appears to be of limited use in cases of high vector pressure. The current combination of diagnosis and control measures is already relatively effective and has resulted in reduced disease incidence and impact.

Future

Although our understanding of plant reoviruses is increasing, many of the molecular and biological properties of these viruses are still unknown. The complete sequence information is now available for a number of these viruses which will allow production of cDNA probes to further elucidate the infection and replication processes in both plant and insect cells. The potential to produce infectious clones also holds promise for detailed studies of both plant and insect host ranges and methods of resistance employed by nonhost species. This information combined with knowledge gained from comparison to animal reoviruses may assist in further development of control strategies for diseases caused by these viruses in plants.

See also: Insect Reoviruses; Reoviruses: General Features; Reoviruses: Molecular Biology.

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