# Transmission of Plant Viruses



l'm a lot smarter than I look.











# Outline

Overview of the transmission of plant viruses

Hemiptera and plant virus transmission

Three types of plant virus transmission by Homoptera

Focus: Aphids and plant virus transmission

Focus: Whiteflies and plant virus transmission

**Tritrophic interactions** 

### **Plant Virus Transmission:**

Interface of the biology and molecular biology of three types of entities: Virus Host(s) Vector With the environment

Viruses are not passive passengers on the vector 'bus'



Types of
Virus
Transmission

Mode of Transmission	Host	
	Plant	Animals and Humans
Passive transmission among environments (soil, water)	x	x
Passive mechanical transmission among hosts	x	x
Receptor-site-mediated non- persistent transmission	x	
Receptor-site-mediated semi- persistent transmission	х	
Receptor-site-mediated circulative, non-propagative	x	
Amplifying (circulative, propagative)	х	х
Vectors as reservoirs	X	x



# Vectors of Plant Viruses

The majority of plant viruses are vector-borne.

Arthropods and nematodes transmit 76% of plant viruses

Most important group of vectors are sap-sucking insects which transmit 55% of all described plant viruses.

http://www.personal.psu.edu/ncj111/Evolution%20and%20Phylogeny.htm

#### **Taxonomy of Insect Vectors of Plant Viruses**

Phylum: Arthropoda Class: Hexapoda Orders:

Archaeognatha Blattodea (Cockroaches) Coleoptera (Beetles) Dermaptera (Earwigs) Diptera (Flies) Embioptera (Webspinners) Ephemeroptera (Mayflies) Hemiptera (Bugs)

*Hymenoptera Isoptera* (Termites) Lepidoptera Mantodea (Mantises) Mecoptera Megaloptera Neuroptera Notoptera Odonata Orthoptera Phasmatodea (Sticks)

*Phthiraptera* (Lice)

Plecoptera Psocoptera Raphidioptera (Snakeflies) Siphonaptera (Fleas) Strepsiptera Thysanoptera (Thrips) Trichoptera (Caddisflies) Zoraptera Zygentoma (Thysanura)

# **Taxonomy of Insect Vectors of Plant Viruses**

Phylum: Class: Orders: Arthropoda Hexapoda Passive transmission: mostly by
immature insects AND by mechanical inoculation. Viruses are VERY stable.

Archaeognatha Blattodea (Cockroaches) Coleoptera (Beetles) Dermaptera (Earwigs) Diptera (Flies) Embioptera (Webspinners) Ephemeroptera (Mayflies) Hemiptera (Bugs) Hymenoptera

*Isoptera* (Termites)

Lepidoptera Mantodea (Mantises) Mecoptera Megaloptera Neuroptera Notoptera Odonata Orthoptera

*Phasmatodea* (Sticks) *Phthiraptera* (Lice) Plecoptera Psocoptera Raphidioptera (Snakeflies) Siphonaptera (Fleas) Strepsiptera Thysanoptera (Thrips) Trichoptera (Caddisflies) Zoraptera Zygentoma (Thysanura)

#### **Taxonomy of Insect Vectors of Plant Viruses**

Phylum: Class: Orders: Arthropoda Hexapoda

Transmission is by a highly evolved relationship between virus and vector

*Archaeognatha Blattodea* (Cockroaches)

Coleoptera (Beetles) Dermaptera (Earwigs) Diptera (Flies) Embioptera (Webspinners) Ephemeroptera (Mayflies)

Hemiptera (Bugs)

*Hymenoptera Isoptera* (Termites) Lepidoptera Mantodea (Mantises) Mecoptera Megaloptera Neuroptera Notoptera Odonata Orthoptera Phasmatodea (Sticks)

*Phthiraptera* (Lice)

Plecoptera
Psocoptera
Raphidioptera (Snakeflies)
Siphonaptera (Fleas)
Strepsiptera
Thysanoptera (Thrips)
Trichoptera (Caddisflies)
Zoraptera
Zygentoma (Thysanura)

#### **ORDER: HEMIPTERA**

# Suborder: Homoptera

- Aleyrodidae (15) whiteflies
- Aphididae (192) aphids
- •Cercopidae
- Cicadellidae (49) leafhoppers
- Cicadidae
- *Cixiidae* (1) planthoppers
- Coccidae (3) scales
- Delphacidae (18) planthoppers
- Diaspididae

- Flatidae
- •*Kermesidae*
- Kermesidae
- •*Kerriidae*
- •Lygaeidae
- •Margarodidae
- Membracidae (1) Treehopper
- Phylloxeridae
- *Pseudococcidae* (19) mealybugs
- •Psyllidae











(X) = no. of plant virus vector species



#### **Transmission of Plant Viruses by Homoptera**

- Most plant viruses do not replicate in their *Homopteran* vector, which is the opposite of the case for animal viruses, where almost all of the viruses replicate in the vector
- All of these *Homopteran* vector virus relationships have evolved over millions of years

#### All of these Homopteran vector virus relationships have evolved over millions of



Insects evolved first (300-400 million yrs ago)

then plants and insects that feed on plants (aprox. 100 million years ago)

All vector virus relationships have evolved over millions of years

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Phanerozoic Eon

Evolution of plant and vertebrate RNA viromes appears to be driven by horizontal virus transfer from vast RNA virome of invertebrates (marine and terrestrial).



"It is not clear why invertebrates grew into such a fertile niches for incubating an enormous variety of the RNA viruses.

Many invertebrates are excellent agents of horizontal virus transfer because they form tight associations with vertebrates and plants, often serving as vectors that shuttle viruses between these organisms.

Dolja and Koonin 2018, Virus Res 244:36



#### **Evolution of (+)ss RNA viruses**

(A) Schematic dendrogram based on phylogenetic tree for RNA-dependent RNA polymerases (RdRp) of the Picorna-Calici clade.

Major clusters of the related viruses are shown as triangles colored in accord with virus host ranges: red, vertebrates; blue, invertebrates; green, plants; plum, protists.

Approximate diagrams of typical virus genomes for each cluster showing encoded proteins and their functions (rectangles; homologous proteins are in the same color)

(B) Hypothetical scenario for the evolution of picornavirus-like viruses. Vertical arrows denote virus transmission that follows host evolution, whereas horizontal arrows show presumed horizontal virus transfer (HVT) events between distinct host organisms.

#### Earliest association of Homoptera and plant viruses (> 270 million years ago)





After http://vishnu.glg.nau.edu/rcb/globaltext.html

#### **Homopteran Mouthparts**



 Mouthparts are highly specialized, consisting of a pair of interlocking maxillary stylets and an outer pair of mandibular stylets sheathed by the labium.

Fig. 4.3.1. Cross section of the stylet bundle of aphids

- Food and salivary canals are formed by the interlocking maxillary stylets.
- One of two behaviors are important for virus transmission:
  - Probing or feeding
  - Usually one or the other is responsible for transmission, but not both



Exterior view of labium and stylet





Generalized model of hemipteran stylet penetration of a plant leaf

Proteinaceous stylet sheaths are formed from saliva



# <image>

Stylets extend from leaf surface to phloem tissue. (2) Whitefly nymph stylets (S) and stylet tracks (St) in young leaf. In many places the stylets had probed cells, retracted, and proceeded in different direction, leaving behind stylet tracks. W = whitefly body, s -stylets, st = stylet tracks, p = phloem tissue.

#### **Transmission of Plant Viruses by Homoptera**

Viruses can be transmitted by Homopteran vectors by one of four ways:

Receptor-site-mediated Non-persistent Receptor-site-mediated Semi-persistent Receptor-site-mediated Persistent, Circulative Amplifying (circulative, propagative)

#### Terms used in the process of transmission:

- Acquisition -- process by which vector takes up virus particles from an infected plant
- Retention -- length of time the virus particles are carried in the vector
- Latent period -- length of time after acquisition until virus particles can be transmitted
- Inoculation -- release of virus particles into susceptible plant in a way that leads to an infection

# **Receptor-site-mediated <u>Non-persistent</u>**

**Non-persistent (old term: stylet-borne)** -- entire transmission cycle takes a few minutes, virus is not usually retained in the vector for more than a few minutes

Characterized by:

- Very brief periods (a few minutes) required for acquisition and inoculation
- No latent period
- Retention period is short (a few minutes usually)

# **Receptor-site-mediated <u>Non-persistent</u>**

#### **Examples:**

Aphid	Alphaflexiviridae: Potexvirus (few) Betaflexiviridae: Carlavirus Bromoviridae: Alfamovirus, Cucumovirus Potyviridae: Potyvirus; Secoviridae: Fabavirus
Whitefly	Betaflexiviridae: Carlavirus

#### **Receptor-site-mediated <u>Non-persistent</u>**

- Most of our understanding comes from studies of non-persistent transmission by aphids
- Acquisition and inoculation is by **probing** (not by feeding)
- Vector specificity varies: Some cases one species transmits one virus, in others some insect species can transmit several viruses, and some viruses can be transmitted by several insect species.
- Some of these viruses are known to require a viral-encoded protein for successful non-persistent transmission

Ex. Potyvirus: HC-PRO

#### **Receptor-site-mediated <u>Non-persistent</u>: Acquisition**

- Virions are ingested along with viral proteins (ex. HC-PRO) and cell contents from virus-infected host plants.
- Aphids require relatively few virus particles to successfully transmit (Ex. potyviruses, 1 x 10<sup>(-15)</sup> virus particles could initiate an infection (Pirone & Thornbury, 1988)
- Therefore for potyviruses, the probability of transmission does not depend on the number of particles acquired





From: Martin et al. 1997

#### **Receptor-site-mediated <u>Non-persistent</u>**: **<u>Retention</u>**

- HC-PRO mediates the adherence of virions to the cuticular lining of the stylets.
- The common duct is most likely the functional site of virion retention.



VirionsHC-Pro

Common duct <1% of the length of the aphid stylet.

(Martin et al. 1997; Powell 2005)

#### **Receptor-site-mediated <u>Non-persistent</u>**: Helper protein

- HC-PRO acts as a "bridge" between aphid cuticle and virus particle
- Radioactively-labeled TEV virions with and without addition of HC-Pro.
- Label retained in stylets (common duct) only when HC-PRO present.



#### **Receptor-site-mediated <u>Non-persistent</u>: Latent Period**

- <u>No latent period in non-persistent transmission</u>
- Inoculation occurs immediately or up to 1 hour after acquisition, although most occurs within a few minutes after acquisition
- Transmission occurs as soon as the insect probes.
   Virus leaves the aphid with saliva regardless of what it probes in (or on)



#### **Receptor-site-mediated <u>Non-persistent</u>**: **Inoculation**

- Inoculation occurs when virions are flushed from the food common duct surface during intracellular secretion of watery saliva.
- This watery saliva is different than the gelling saliva that forms a sheath around the stylets during penetration.



VirionsHC-Pro

Martin et al. 1997; Powell 2005

Semi-persistent -- longer access to infected plant needed for efficient transmission. No latent period but longer retention than non-persistent

Acquisition and inoculation is by vector **feeding** (not probing)

Characterized by:

- Usually 15 to 30 min acquisition access periods needed
- Usually 15 to 30 min inoculation access periods needed
- No latent period
- Retention: varies with virus and vector (2-5 days)
   Ex. Aphid cannot transmit CaMV 2 days after acquisition
   Ex. Whitefly cannot transmit *Crinivirus* 3-5 days after acquisition

Examples of viruses transmitted in a semi-persistent manner:

Aphid:	Closteroviridae: Closterovirus Caulimoviridae: Caulimovirus, Badnavirus
Whitefly:	Closteroviridae: Crinivirus Potyviridae: Ipomovirus
Mealybug:	Closteroviridae: Ampelovirus Caulimoviridae: Badnavirus
Leafhopper:	Caulimoviridae: Badnavirus Sequiviridae: Waikivirus

- Virus particles found in vector foregut in Crinivirus transmission
- Location of a *Crinivirus* (*Lettuce infectious yellows virus*) in the head capsule shown in whitefly vector (using immunofluorescence to detect the LIYV coat protein)



Download Movie S01 (AVI)

Chen et al 2011 PNAS www.pnas.org/cgi/doi/10.1073/pnas.1109384108

# LIYV (Crinivirus)

Minor coat protein (mCP) not the coat protein is responsible for binding to the vector Crinivirus



 In others (*Caulimovirus* – CaMV) virus binds to the tips of the aphid stylet, like Potyviruses.

Using various enzymes and reagents, a specific receptor for CaMV transmission was located on the aphid stylet.

The stylet receptor is a nonglycosylated protein deeply embedded in the chitin matrix

CaMV requires helper proteins (P2, P3, P4) which bind to the virion as well as to vector stylets



Uzest et al 2007. PNAS 104:17959-17964

#### **CaMV: Perceptive Behavior**

- Detailed microscopic examination of CaMV-infected plant cells shows that P2, P3, and P4 proteins are not colocalized.
- When aphids explore cells via probing they produce minute wounds. CaMV "senses" cell wounding and almost immediately respond by dissociating from inclusion bodies and redistributing P2 onto cellular microtubules. Re-localization of P2 is temporary and reversible.
- CaMV virions from viroplasms also relocalize, probably to be able to interact with P2 and be transmitted by aphid vectors.
- This active response <u>increases</u> the probability of CaMV acquisition by aphid vectors



P5 - R

P4 - CP

- <u>Greater host plant-vector specificity</u> than that of non-persistent transmission because vector must feed.
- Longer acquisition access periods (up to 24 h) and longer inoculation access periods (up to 4-6 h) increase transmission rates.
- <u>No latent period</u> means the vector can transmit immediately after acquisition
- A viral encoded <u>helper protein</u> has been found to be essential for transmission of some viruses (ex. Species in *Caulimovirus* genus)
## **Receptor-site-mediated** <u>circulative</u>, <u>non-propagative</u>

- Characterized by:
  - Circulative: virus replicates in plants, and moves through the vector
  - Acquisition and inoculation require feeding not probing
  - A latent period of 8 hours or more between acquisition and inoculation.
  - Vector may retain virus for the rest of its life (up to many days), but transmission efficiency usually decreases over time.
  - Virus retention not affected by molting.

#### **Receptor-site-mediated** <u>circulative</u>, <u>non-propagative</u>

- Virus exits the digestive system at the midgut into the haemolymph of the vector
- Virus migrates across the membranes of the salivary gland cells
- Virus exits the vector with the saliva through the salivary canal



http://www.apsnet.org/education/lessonsPlantPath/Barle yYelDwarf/Images/fig12.htm (courtesy of L. L. Domier)

## Examples of viruses transmitted in a persistent, circulative manner:

Aphids:	Luteoviridae: Luteovirus
Whiteflies:	Geminiviridae: Begomovirus
Leafhoppers:	Geminiviridae: Curtovirus, Mastrevirus,
Treehoppers:	Geminiviridae: Topocuvirus

#### **Close-up of internal abdomen of a whitefly**



From Weber 1935

Right half of

Aleyrodes

brassicae

(female)

#### **Circulative**, non-propagative

Viruses can pass the gut cellular barrier in the midgut or hindgut (depending upon vector/virus combination) within membranous vesicles. And a similar mechanism operates across cells of the salivary glands:

- (a) Virions first attach to the apical plasmalemma (apl) of cells in the gut lumen,
- (b) they are then internalized into diverse types of spherical vesicles (mvb, mlv, vs)



(c-d) transported into tubular vesicles(tv), and(e) finally delivered to the basal lamina (bl).

Viruses are protected from cell cytoplasm

This study used a *Luteovirus* and aphid)

Something similar is presumed for other hemipteran vectors and viruses



## Amplifying (circulative, propagative)

Virus replicates in the vector and in the plant

Characterized by:

- Virus acquisition and inoculation are by feeding rather than probing
- High level of vector specificity (most viruses transmitted by only one or a few closely related species)
- Longest latent period of all the types of transmission (measured in days).
- Virus replicates in insect, appears to decrease longevity in some cases.
- Often replicate in many cell types of the vector.
- Virus is retained through a molt
- This type of transmission is more efficient than other types of transmission
- In some cases, virus is passed through the egg to progeny Known as <u>transovarial</u> <u>transmission</u>

#### **Persistent, Propagative Transmission**

Aphids:

Rhabdoviridae: Cytorhabdovirus, Nucleorhabdovirus

Leafhoppers:

Reoviridae: Phytoreoviridae Rhabdoviridae: Cytorhabdovirus, Nucleorhabdovirus Tenuivirus: (not assigned to family) Tymoviridae: Marafivirus

Planthoppers:

Rhabdoviridae: Cytorhabdovirus, Nucleorhabdovirus

Best studied model: Rice dwarf virus (RDV) (*Reoviridae, Phytoreovirus*) and leafhopper vector (*Nephotettix cincticeps*)

А

- RDV is first detected in epithelial cells of ٠ the filter chamber of the leafhopper within 2 days after acquisition on diseased plants. It then spreads to the anterior midgut, and then into the nervous system, and the muscles surrounding the anterior midgut.
- Later, RDV accumulates in other parts of ٠ the alimentary canal, salivary glands and the follicular cells of the ovarioles.
- RDV uses muscle or neural tissues for viral dissemination from the infected vector's midgut into other tissues.





C) anterior midgut region showing a lattice pattern labeling for RDV of virus antigens in muscle fibers at 12-day acquisition.

D) shows RDV accumulation in the nerves (ne; arrows) associated with muscle cells.

E - G RDV CP in the epithelial cells of the middle midgut (mmg; E), hindgut (hg; F) and Malpighian tubules (mt; G) 12-day acquisition.

#### Chen et al 2011 Virus Research 160 (2011) 389-394

# Virus localization sites in insect vectors

Non-circulative viruses are retained in the insect stylet (A) or foregut (B). Non-propagative circulative (yellow circles) viruses are generally phloem limited and penetrate the insect body via the midgut or hindgut. Circulative viruses use a hemolymph route to reach the salivary glands. The salivary glands are the final destination for circulative transmission.



# Virus localization sites in insect vectors

Propagative viruses may use a hemolymph route and others such as the Rhabdoviruses also use a neurotropic route to reach the salivary glands. Propagative viruses replicate in the midgut cells and other insect tissues. Some propagative viruses are phloem limited while others are widely distributed in plant tissues. The salivary glands are reached via nervous tissue or connective tissues. Reoviruses use tubules to move cell to cell in the midgut (C).



- About 4700 aphid species are known, collected everywhere except Antarctica
- Only a few hundred species have been tested for ability to vector plant viruses
- One estimate reported 192 aphid vector species transmitting 275 viruses

(Nault 1997. Ann. Entomol. Soc. Amer. 90:521-541)





#### **Population Dynamics**

- Aphids are viviparous (live birth of offspring), parthenogenetic (reproducing without mating) during most of life cycle, some species alternate host plants.
- Aphids reproduce rapidly: generation time can be one week. Intrinsic rate of increase can be double that of other insects.
- When crowded or on poor quality host, winged forms develop which then fly (locally or long distance) to new hosts.
- Affected by weather (temperature and rainfall), both directly and indirectly through host plant.
- Thus, winter weather affects virus epidemics in spring.



**Dispersal and Flight Behavior** 

Important factor in plant-to-plant spread of viruses

- Aphids generally cannot take off at wind speeds over 3 m/sec but once airborne, can be carried by wind, even to high altitudes (and over long distances)
- Aphids are weak fliers (poor control)--land on many different plants. [Often they probe and then leave if the host is unsuitable, or if the plant is a host they like, they stay and begin feeding]
- Many move short distances, never leaving surface boundary layer. Often, this leads to a distribution of infected plants near the borders of fields.
- Aphids coming from longer distances and landing in a field will generate a random pattern of infected plants

#### **Dispersal and Flight Behavior**

- After flying for a certain time, aphids become sensitive to long-wave light reflected from soil and plants, and become attracted to yellow and green. They are repelled by short-wave light at this stage: so UV-reflective mulches are effective in reducing virus spread.
- Canopy cover may influence alighting behavior-- some species are attracted to closed canopies, others are attracted to a contrast of bare ground and plants.
- Aphids may alternate settling with probing to find more suitable plants, which may involve further flights to new hosts. Aphid movements contribute to secondary spread of non-persistently transmitted viruses.

#### Host Finding Behavior – several behaviors involved

- Pre-alighting behavior—aphids respond to plant-reflected wavelengths of light.
- Initial plant contact, assessment of surface cues. Waving antennae detect volatiles, chemosensory hairs on tips contact surface.
- Probe the epidermis, regardless of other cues, and at which time some viruses are transmitted.
- Then they either leave or move to lower surface of the leaf.

(Powell, Tosh, and Hardie, 2006, Ann. Rev. Phytopathol.)

## **Whiteflies as Virus Vectors**

*Bemisia tabaci* species complex (Sweet potato whitefly)





Parabemisia myricae (bayberry whitefly)





*Trialeurodes vaporariorum* (Greenhouse whitefly)



*Trialeurodes abutilonea* (Banded wing whitefly)







#### Plant Viruses Transmitted by Bemisia tabaci species complex

Family	Genus	No. Species	Example	
Geminiviridae	Begomovirus	400+	Tomato yellow leaf curl virus	
Closteroviridae	Crinivirus	14	Tomato infectious chlorosis virus	
Potyviridae	Ipomovirus	6	Squash vein yellowing virus	
Betaflexiviridae	Carlavirus	47 (6)	Cowpea mild mottle virus	
Sequiviridae	Torradovirus	3	Tomato torrado virus	







#### *Bemisia tabaci* – A Very Successful Vector of Viruses

- Many have wide host range (feeding and reproduction)
- Adults are mobile, and can live for several weeks
- Able to move short and long distances (wind assisted)
- Haplo-diploid species (females are diploid, males are haploid)

#### **Coat protein determines vector specificity of geminiviruses**

ACMV= African cassava mosaic virus (Begomovirus) BCTV= Beet curly top virus (Curtovirus)

> ACMV (Begomovirus)





BCTV (Curtovirus)







Recombinant





Briddon et al., 1990

## Life Cycle of Whiteflies



#### Bemisia tabaci – African origin

#### There is a lot of diversity in *B. tabaci*

#### Global relationships of *Bemisia tabaci* (Hemiptera: Aleyrodidae) revealed using Bayesian analysis of mitochondrial COI DNA sequences

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> > > Molecular Phylogenetics and Evolution 44 (2007) 1306-1319

#### Concluded: 12 clades of B. tabaci





The term "biotype" is no longer appropriate (based on recent biological and molecular studies)

Biological studies indicate that these clades will become separate species

## Differences in ability to transmit viruses by different clades (cryptic

## species) has consequences Ex. *Lettuce infectious yellows virus* (LIYV)

"New World" clade (native wf in CA) transmitted LIYV for many years in lettuce fields \_\_\_\_\_\_

"New World" clade transmitted LIYV more efficiently than "MEAM1" clade (Cohen et al 1992 Phyto. 82:86-90)





"MEAM1" clade appears and displaces "New World" clade

No more epidemics of LIYV

(Duffus 1995 pp 12-16 in: Cucurbitaceae '94)

## **Tritrophic Interactions**





In any step of a plant virus life cycle the virus can affect both the host plant and the insect vectors in ways that can potentially increase transmission.

1) Insect vectors are attracted to infected plants by visual and olfactory cues.

2) For non-circulative viruses, the quality of the host plant can be decreased by the infection. The insect vectors rapidly acquire the virus from superficial tissues and soon leave in search for a healthy plant (light gray arrow 4).

3) For circulative viruses, the quality of the host plant can be improved by the infection. The insect vectors settle, feed from deep tissues, and ingest the virus. The vector population growth is accelerated, leading to overcrowding and increased emigration in search for new host plants (dark gray arrow 4).



5) Viruliferous insect vectors often move from any host plant. If the vector fails to find a new host, it will die together with the viruses it carries. Viruses could manipulate the motility or survival time of the insect vectors when away from any host (proposed).

6) Contrary to the preference of virus-free vectors for infected plants (1), virus-loaded vectors are sometimes better attracted by healthy plants.

7) Environmental factors could modify this scheme at any steps in unpredictable ways.

Blanc and Michalakis 2016

#### Summary:

Viruses and their associated vectors and transmission strategies.

Taxonomic family	Virus genus	Representative Virus	Type of Vector	Virus- encoded "transmission proteins" <sup>3</sup>	Location of virion retention or initial entry
Potyviridae	Potyvirus	Tobacco etch virus (TEV)	Aphid	CP, HC-Pro	Stylet
Bromoviridae	Cucumovirus	Cucumber mosaic virus (CMV)	Aphid	СР	Stylet
Caulimoviridae	Caulimovirus	Cauliflower mosaic virus (CaMV)	Aphid	CP, P2, P3	Stylet, acrostyle
Closteroviridae	Crinivirus	Lettuce infectious yellows virus (LIYV)	Whitefly	CPm	Foregut
Luteoviridae <sup>1</sup>	Luteovirus	Barley yellow dwarf virus (BYDV)	Aphid	CP-RTP	Midgut, hindgut
Geminiviridae <sup>1</sup>	Begomovirus	Tomato yellow leaf curl virus (TYLCV)	Whitefly	СР	Midgut, filter chamber
Bunyaviridae <sup>2</sup>	Tospovirus	Tomato spotted wilt virus (TSWV)	Thrips	G <sub>N</sub>	Midgut
Reoviridae <sup>2</sup>	Phytoreovirus	Rice dwarf virus (RDV)	Leafhopper	P2*	Midgut, filter chamber
Rhabdoviridae <sup>2</sup>	Nucleorhabdovirus	Maize mosaic virus (MMV)	Planthopper	G	Midgut



Whiteflies



## Leafhoppers



Mealybugs



## Treehoppers



Scales

