

SEED AND POLLEN TRANSMISSION OF PLANT VIRUSES AND VIROIDS



Objectives:

- Understand the different types of classical seed transmission of viruses
- Be able to distinguish seed transmission from seed-borne transmission
- Understand the biological and economic significance of seed transmission of viruses
- Know the means by which detection and disease management respond to seed transmission of viruses
- Recognize variations in classical seed transmission of plant viruses:
Amalgaviridae, Endornaviridae, Partitiviridae
Caulimoviridae

Classical Seed and Pollen Transmission:

Vertical transmission of a plant virus through seed

Seed transmission = infection of progeny through seed

Seed infection can result from infected mother plants
(maternal)

OR

through fertilization by virus-infected pollen (paternal)

Significance of Seed Transmission of Viruses :

- Seed transmission is of economic significance for viruses in >26 genera
- Seed transmission is an important means of survival for viruses with narrow host ranges, hosts that are all annual species, and/or vectors with limited mobility
- Important means of introduction of a virus to a new location
Ex. MCMV 0.04% transmission rate was enough for introduction of the virus to new cropping areas
- Rates of seed transmission are not related to its epidemiological or economic significance

Distribution of Seed-Borne or Seed–Transmitted Plant Viruses

Family	Genus	No. of species known to be seed-transmitted
<i>Bromoviridae</i>	<i>Alfamovirus</i>	1
	<i>Bromovirus</i>	2
	<i>Cucumovirus</i>	4
	<i>Ilarvirus</i>	8
<i>Bunyaviridae</i>	<i>Tospovirus</i>	1
<i>Caulimoviridae</i>	<i>Caulimovirus</i> *	1*
<i>Comoviridae</i>	<i>Comovirus</i>	7
	<i>Fabavirus</i>	1
	<i>Nepovirus</i>	18
	<i>Umbravirus</i>	1
<i>Flexiviridae</i>	<i>Capillovirus</i>	1
	<i>Potexvirus</i>	3
<i>Potyviridae</i>	<i>Potyvirus</i>	20
	<i>Bymovirus</i>	1
	<i>Rymovirus</i>	1

**From: Mink
1993 Ann. Rev.
Phytopath.**

Ability to be seed transmitted is widespread among plant viruses:

As of 1993 seed transmission reported from:
109 species
in 26 genera
in 11+ virus families

Distribution of Seed-Borne or Seed –Transmitted Plant Viruses

Family	Genus	No. of species known to be seed-transmitted
<i>Rhabdoviridae</i>	<i>Cytorhabdovirus</i> <i>Nucleorhabdovirus</i>	4
<i>Secoviridae</i>	<i>Waikavirus</i>	1
<i>Solemoviridae</i>	<i>Sobemovirus</i>	4
<i>Tombusviridae</i>	<i>Carmovirus</i>	3
	<i>Tombusvirus</i>	1
<i>Tymoviridae</i>	<i>Tymovirus</i>	3
<i>Virgaviridae</i>	<i>Furovirus</i>	2
	<i>Hordeivirus</i>	2
	<i>Tobamovirus</i>	3
	<i>Tobravirus</i>	2
11+	26	109

Seed transmission is not a conserved characteristic of a genus: Some or all of the species within a genus can be seed transmitted

Dominant factors determining whether seed transmission occurs and at what frequency:

Interactions of the following:

Timing, Environment

Genetic Components of the Virus/Viroid

Maternal/Paternal Host

Timing and Environment:

- Seed transmissibility originating through the mother plant depends upon the ability of a virus to infect floral parts early in their development.
- The efficacy of seed transmission is environmentally influenced (which is why variations in rates of seed transmission are often presented)
- Temperature can influence transmission frequencies but to a lesser extent than timing.
- Co-infection of parent plant with other viruses can affect seed transmission

Symptoms of *Soybean mosaic virus* (*Potyvirus*) in soybean



Genetic Components of the Virus/Viroid:

- Rate of seed transmission is reported to vary between almost 0 to 100% (but rarely exceeds 50%)
- About 18% of described plant viruses have been demonstrated to be seed transmitted in at least one host (estimated that up to 33% will be found to be transmitted in at least one host)
- Seed transmission rates can vary across different isolates of the same virus in the same host cultivar

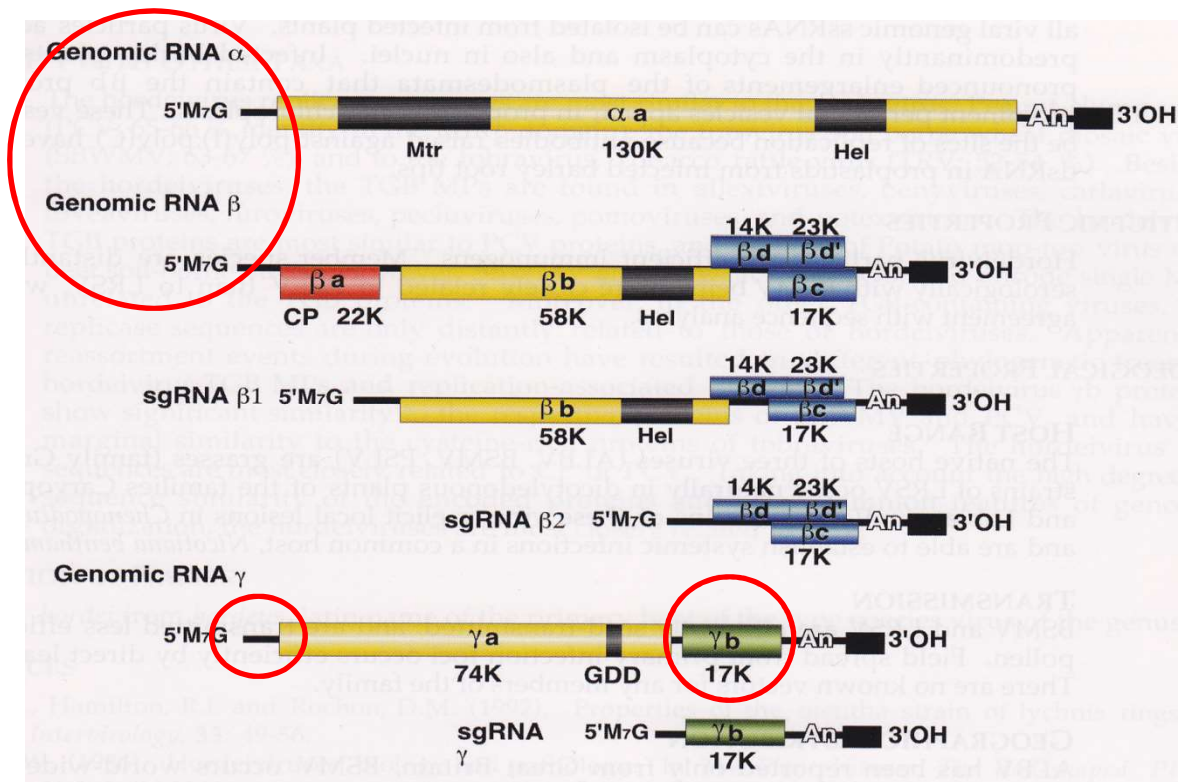


Squash mosaic virus in
cantaloupe seedlings

What viral proteins control seed transmission? Genetic Components of the Virus/Viroid:

Only a few examples: Ex. 1: Seed transmission of *Barley stripe mosaic virus* (*Virgaviridae, Hordeivirus*) was mapped to several genes

- Ability to be seed-transmitted was located on RNA γ
- However, viral genes with known roles in replication and movement played important roles in influencing the ability to be seed transmitted.
[Complex interaction of leader sequence of RNA γ , and the γb gene with RNA α and RNA β]



Edwards (1995) MPMI 8:906-915

Ex 2: Seed transmission of Pea seedborne mosaic virus (*Potyvirus*)

Genetic Components of the Virus/Viroid:

This study showed again that multiple viral proteins were involved in seed transmission.

ie. HC-Pro which affects replication and/or long-distance movement in reproductive tissues influenced the number of embryos which became infected and hence, the final seed transmission frequency.

Infectious recombinants were constructed using PSbMV isolates which had different abilities to be seed transmitted

(a)		(b)					
		Symptoms	Virus acc.	Inf./Tot.	% ST	% Germination	
P-1		Severe	0.66 c	116/464	25 b	94 b,c	
P-4		Mild	0.37 d	1/505	0.2 d	91 c,d	
vP-1		Severe	0.71 b,c	136/366	37 a	96 a,b	
vP-1114		Severe	0.34 d	93/521	18 b	88 d	
vP-4111		Severe	0.93 a	28/614	4.6 c	98 a	
vP-1144		Mild	0.81 a,b	44/626	7.0 c	95 a,b	
vP-4144		Mild	0.34 d	12/729	1.6 d	95 a,b	

Journal of General Virology (1996), 77, 3149-3154. Printed in Great Britain

Multiple viral determinants affect seed transmission of pea seedborne mosaic virus in *Pisum sativum*

I. E. Johansen,¹ W. G. Dougherty,² K. E. Keller,³ D. Wang⁴ and R. O. Hampton³

Maternal/Paternal Hosts:

- Different cultivars of the same host species may vary in their efficiency of seed transmission of a single virus isolate
- Seed-transmitted viruses are mechanically transmissible and extensively infect parenchymatous tissues.
(so phloem-limited viruses are generally not seed-transmitted)
- The frequency of virus transmission to seedlings through pollen is typically less than through ovules.

Maternal/Paternal Hosts:

Plants have strong defense systems to protect the embryo from invasion by viruses from the mother plant

- Physical Barriers
cytoplasmic discontinuity between the generations
- Physiological/Biochemical Barriers – large number known

Maternal/Paternal Hosts:

Plants have multiple lines of defense to prevent transmission of a virus to the progeny:

Seed transmission does not occur when:

- the virus is unable to infect the gametes prior to fertilization
- the virus is unable to enter the embryo during development
- the virus is inactivated in the embryo during seed maturation and storage

Paternal Transmission of Viruses (Pollen)

Table 8 Viruses that appear to spread plant-to-plant through pollen

Genus	Virus	Plant	Reference
<i>Illarvirus</i>	blueberry shock	blueberry	100
	prune dwarf	stone fruit	CMI/AAB No. 19
	prunus necrotic ringspot	stone fruit	CMI/AAB No. 5
	tobacco streak	various	CMI/AAB No. 307
<i>Nepovirus</i>	artichoke yellow ringspot	artichoke	98
	blueberry leaf mottle	blueberry	27
	cherry leafroll	walnut, betula	CMI/AAB No. 306
<i>Sobemovirus</i>	sowbane mosaic	chemopodium	82
<i>Idaeovirus</i>	raspberry bushy dwarf	raspberry	CMI/AAB No. 165

From: Mink 1993 Ann. Rev. Phytopath.

Example of Pollen Transmission of a Virus:

Pelargonium zonate spot virus (PZSV)
(*Bromoviridae, Anulavirus*)

(Lapidot et al (2010) Phytopathology 100:798-804)

Significance:

- Commercial practices - pollen is collected from the male parent, and is transported to the fields of the mother plants, which may be many miles away. This practice may increase the spread of PZSV to new geographical areas.
- The commercial use of insect pollinators, such as bumblebees, is wide spread in many tomato production greenhouses. Pollinators may spread of PZSV to new fields.

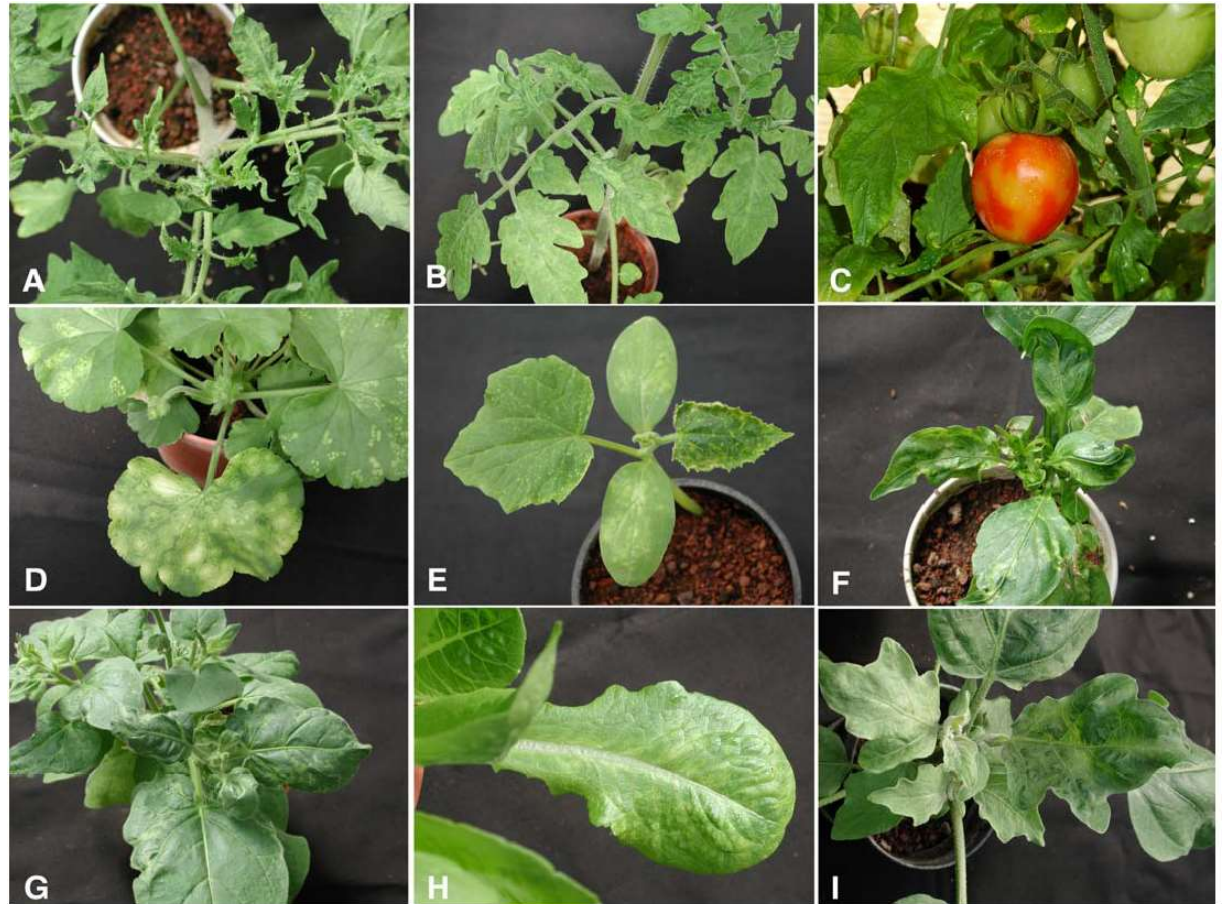
TABLE 4. Seed transmission of *Pelargonium zonate spot virus* following hand pollination of healthy mother plants with pollen collected from infected tomato plants

Plant no.	No. of fruit	No. of germinated seedlings		Infection rate (%)
		Infected	Total	
1	1	3	9	33.3
2	7	30	75	40.0
3	4	15	57	26.3
4	9	83	280	29.6
5	10	35	120	29.2
6	4	37	131	28.2
7	4	25	98	25.5
8	4	14	56	25.0
9	7	74	270	27.4
10	2	12	28	42.9
11	4	22	86	25.6
12	5	41	165	24.8
13	2	13	79	16.5
Total	...	404	1,454	...
Average	...	...	...	28.8

Significance:

- PZSV infection results in blemished tomato fruit
- PZSV has a host range not limited to tomato, also can infect: pepper, lettuce, eggplant, cucumber, and a number of ornamental species

[What does that say about
How PZSV can be
transmitted?]



Seed Transmission of Viroids

Pollen and seed transmission of viroids has been known for a long time.

But little is known of the mechanisms of:

- how viroids infect pollen grains,
- how they are introduced into the seed,
- how they escape gametophytic tissues to invade maternal plants
- how these modes of transmission might contribute to natural spread of viroids

Paternal Transmission of Viroids (Pollen)

Table 9 Reports of transmission of viroids through pollen to seed and mother plants

Viroid	Host	Viroid detected in			
		Pollen	Seed	Seedling	Plant
Apple scar skin	apple	no	yes	.	.
Apple dapple apple	apple	no	yes	.	.
Avocado sun blotch	avocado	.	.	yes	.
Avocado sun blotch	avocado	yes	.	yes	no
Chrysanthemum stunt	chrysanthemum	.	.	no	.
Chrysanthemum stunt	chrysanthemum	.	.	yes	.
Chrysanthemum stunt	tomato	yes	yes	yes	yes
Citrus exocortis	citrus	.	.	no	.
Citrus exocortis	tomato	.	.	yes	.
Citrus xyloporosis					
Coconut cadang-cadang	coconut	.	.	yes	.
Coleus viroid	coleus	.	yes	yes	yes
Grapevine yellow speckle	grapevine	.	.	no	.
Hop stunt-cucumber strain	cucumber	.	.	no	.
Hop stunt-cucumber strain	tomato	yes	yes	yes	yes
Hop stunt-grapevine strain	grapevine	.	.	no	.
Hop stunt-hop strain	hop	.	.	no	.
Hop stunt-hop strain	tomato	.	.	no	.
Potato spindle tuber	tomato	.	.	yes	.
Potato spindle tuber	tomato	yes	yes	yes	yes
Potato spindle tuber	potato	yes	yes	yes	.
Potato spindle tuber	potato	yes	yes	yes	yes

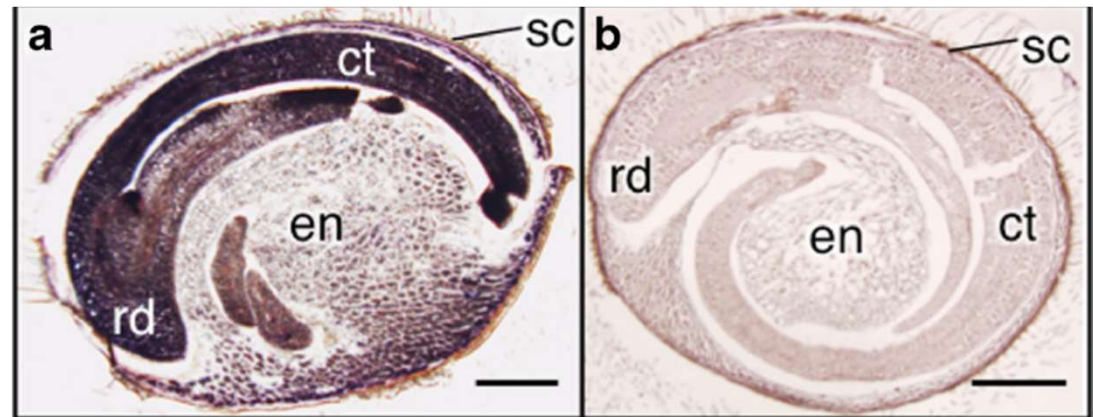
From: Mink 1993 Ann. Rev. Phytopath.

- Pollen transmission is an ability common among many viroids.
- Viroid may be seed transmitted but not detected in the pollen
- Viroid-infected pollen can initiate an infection in the mother plant

Direct evidence for pollen transmission of a viroid

Distribution of PSTVd in Flowers and Seed

Viroid is shown by the dark purple color (in situ hybridization of a DIG-labelled minus-stranded PSTVd riboprobe (RNA) to PStVd RNA)

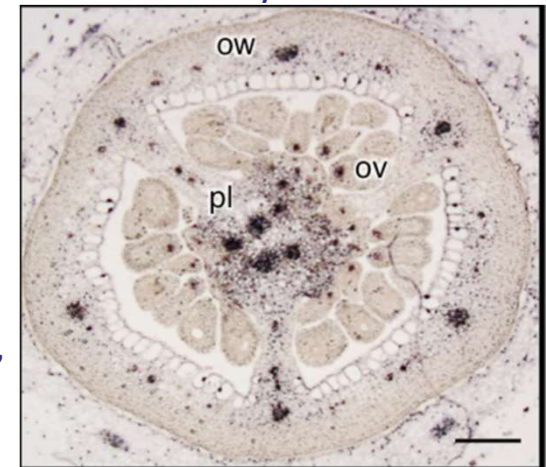


PSTVd-infected tomato seed

Healthy tomato seed

Above: PSTVd was widely distributed throughout the tomato seed (including the embryo)

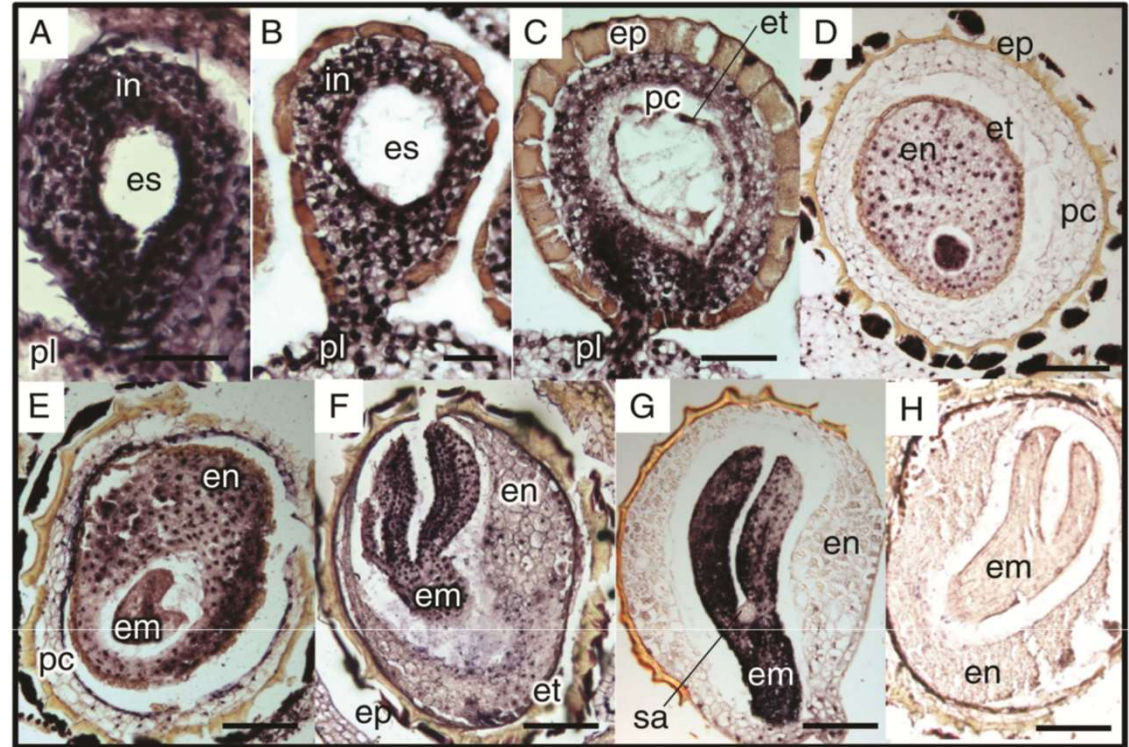
Right: Pepper flower: PSTVd can be seen in the ovary wall (ow) and placenta (pl) but is not present in the ovule. [ct cotyledon, rd radical, en endosperm, sc seed coat, ow ovary wall, ov ovary, pl placenta]



PSTVd-infected pepper flower

PStVd-infected Mother Plant Viroid-free Pollen Donor

Distribution of PSTVd in developing ovules from a PSTVd-infected petunia plant fertilized with pollen from a healthy plant



A: before fertilization; **B to G,** after fertilization from the ovule to the mature seed. **H,** healthy mature seed.

Abbreviations: es = embryo sac; em = embryo; en = endosperm; ep = epidermis of the seed coat; et = endothelium; in = integuments; pl = placenta; pc = parenchyma cells; sa = shoot apical meristem.

Matsushita & Tsuda 2014.
Phytopathology 104:964-969.

Three Basic Types of Classical Seed Transmission:

- A. Outside the embryo**
- B. Indirect embryo invasion**
- C. Direct embryo invasion**

Distinction may be important as each type may require different management techniques

Type of seed transmission not established for every plant virus

A. Outside the embryo (aka “seed-borne”)

seed transmission that does not involve the embryo:

I. Virus is a contaminant on the seed surface

Seedling infection occurs by mechanical transmission especially during handling of the seeds

Only occurs with very stable viruses, like tobamoviruses



Tomato brown
rugose fruit virus

II. Virus is present in seed parts of maternal origin

Only one example known of infectious virus in the seed coat resulting in seed transmission:

Southern bean mosaic virus in bean (SBMV - *Sobemovirus*)

B. Indirect embryo invasion

- Virus invades the embryo indirectly by infection of reproduction tissues (Ovule) before embryogenesis
- Evidenced by visualization of virus in megaspore mother cell and egg, or in the pollen mother cells and pollen
- Shown for a number of viruses
- Viruses transmitted through pollen are in this category

Seed Transmission and Small dsRNA Viruses

Amalgaviridae

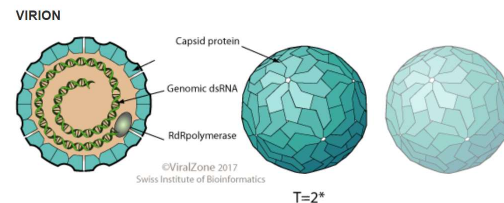
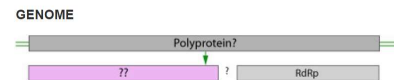
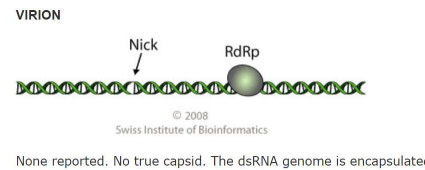
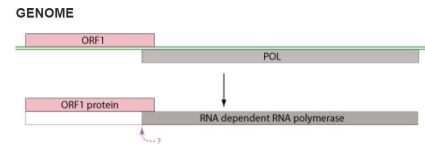
No particles

Endornaviridae

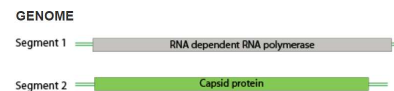
No particles

Partitiviridae

Isometric virions



Non-enveloped icosahedral capsid, about 35-40 nm in diameter with a T=2* icosahedron. The two genomic segments are encapsidated separately.



Order: Unassigned

Amalgaviridae

Amalgavirus

Birnaviridae

Aquabirnavirus

Avibirnavirus

Bosnavirus

Entomobirnavirus

Chrysoviridae

Chrysovirus

Cystoviridae

Cystovirus

Endornaviridae

Alphaendornavirus

Betaendornavirus

Hypoviridae

Hypovirus

Megabirnaviridae

Megabirnavirus

Partitiviridae

Alphapartitivirus

Betapartitivirus

Cryspovirus

Gammapartitivirus

Deltapartitivirus

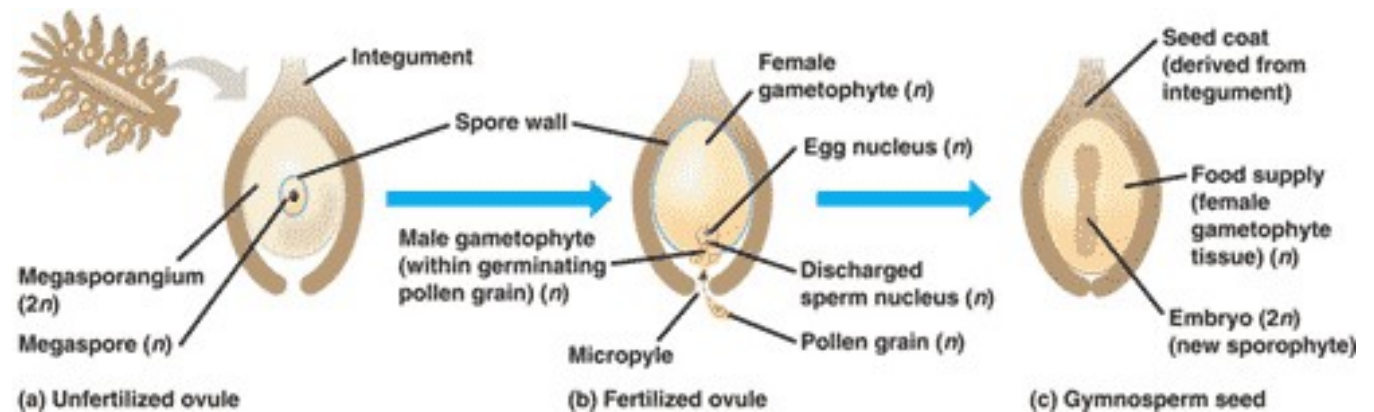
Biological characteristics of *Amalgaviridae*, *Endornaviridae* and *Partitiviridae*

Primary means of movement/survival:

- Virus genome is transmitted vertically from mother to daughter cells
- Horizontal transmission through pollination with virus-infected pollen?
- Transmitted at very high rates by seed (whether pollen or ovule not resolved for most species)
- Not transmitted by any other means

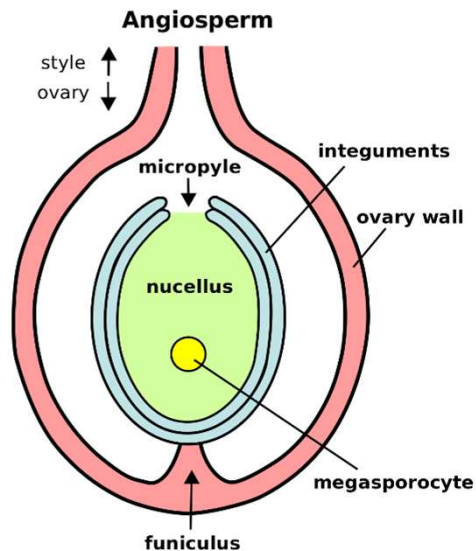
C. Direct embryo invasion

Virus infecting the mother plant invades the developing embryo during embryogenesis



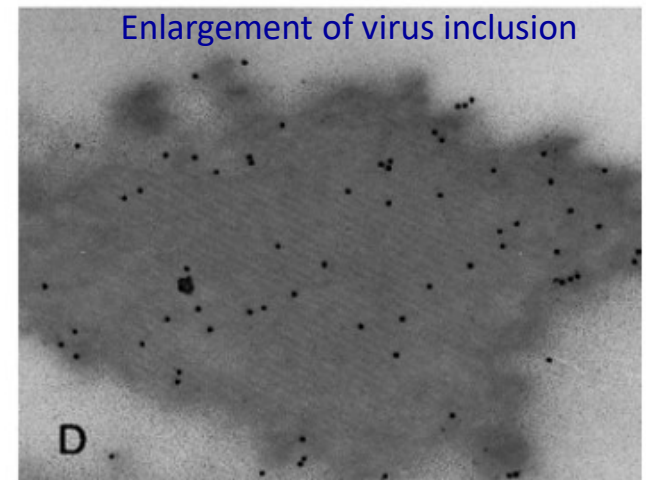
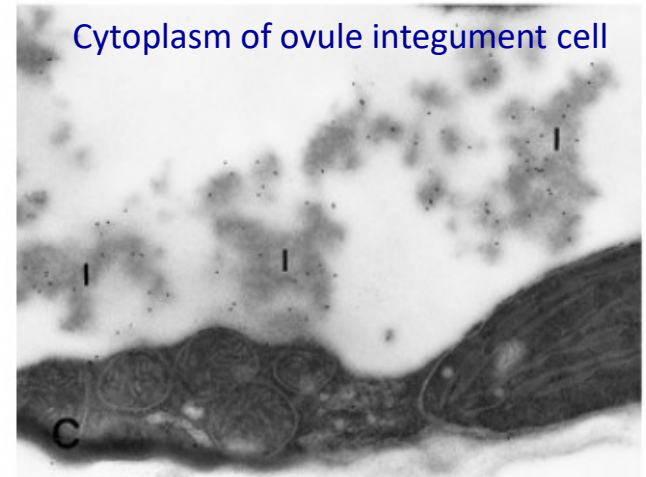
Example: *Cucumber mosaic virus* and spinach
Seed transmission rate of 15-20%

Ultrastructural studies, using immunogold labeling, showed the presence of CMV particles in the cytoplasm of spinach ovary wall cells, ovule integuments and nucellus, anther, and seed-coat cells.



I = Virus inclusions
in the cell vacuole

Example of indirect
embryo invasion
(from either parent)



Yang, Y., Kim, K. S., and Anderson, E. J. 1997. Seed transmission of cucumber mosaic virus in spinach. *Phytopathology* 87:924-931.

C. Direct embryo invasion

Virus infecting the mother plant invades the developing embryo during embryogenesis

An example of seed transmission due to direct embryo invasion:

The Plant Cell, Vol. 6, 777–787, June 1994 © 1994 American Society of Plant Physiologists

RESEARCH ARTICLE

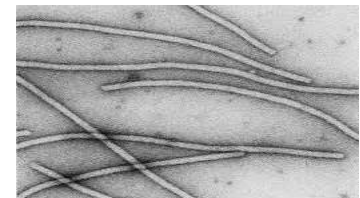
A Model for Seed Transmission of a Plant Virus: Genetic and Structural Analyses of Pea Embryo Invasion by Pea Seed-Borne Mosaic Virus

Daowen Wang and Andrew J. Maule¹

Department of Virus Research, John Innes Institute, John Innes Centre, Colney Lane, Norwich NR4 7UH, United Kingdom

Pea seed-borne mosaic virus (PSbMV), a seed-transmitted virus in pea and other legumes, invades pea embryos early in development. This process is controlled by maternal genes and, in a cultivar that shows no seed transmission, is prevented through the action of multiple host genes segregating as quantitative trait loci. These genes control the ability of PSbMV to spread into and/or multiply in the nonvascular testa tissues, thereby preventing the virus from crossing the boundary between the maternal and progeny tissues. Immunocytochemical and in situ hybridization studies suggested that the virus uses the embryonic suspensor as the route for the direct invasion of the embryo. The programmed degeneration of the suspensor during embryo development may provide a transient window for embryo invasion by the virus and could explain the inverse relationship between the age of the mother plant for virus infection and the extent of virus seed transmission.

Pea seed-borne mosaic virus (*Potyvirus*)



Seed transmission of PSbMV was determined by the maternal genotype

‘Vedetta’ – transmission

‘Progreta’ – no transmission

Table 1. An Assessment of the Role of the Maternal Genotype in Determining PSbMV Seed Transmission

Plant Populations ^a	No. of Seeds Examined ^b	Seed Transmission (%)
Progreta _I , Self-Pollination	120	0
Progreta _{I♀} × Vedette _{H♂}	182	0
Vedette _I , Self-Pollination	87	42
Vedette _{I♀} × Progreta _{H♂}	74	47

^a Subscripts: I, Infected plants; H♂, healthy plants as pollen donor; I♀, infected plants as pollen recipient.

^b Germination rate was 100%.

Seed Transmission Due To Direct Embryo Invasion:

Inheritance of Seed Transmissibility:

Multiple plant genes were involved in determining resistance to PSbMV seed transmission

Other Influencing Factors:

The age of the parent plant at the time of infection was important

Seed Transmission Due To Direct Embryo Invasion:

- PSbMV invasion of the embryo occurred via the suspensor. A prerequisite for embryo infection is therefore, that virus reaches the micropylar region of the testa before disintegration of the suspensor.
- Suspensor is a transient structure in embryo development that serves as a conduit for nutritional support from the material tissues to the growing embryo.
- Mechanism of movement from testa to suspensor is unknown. There are no plasmodesmata that connect the 2 tissues

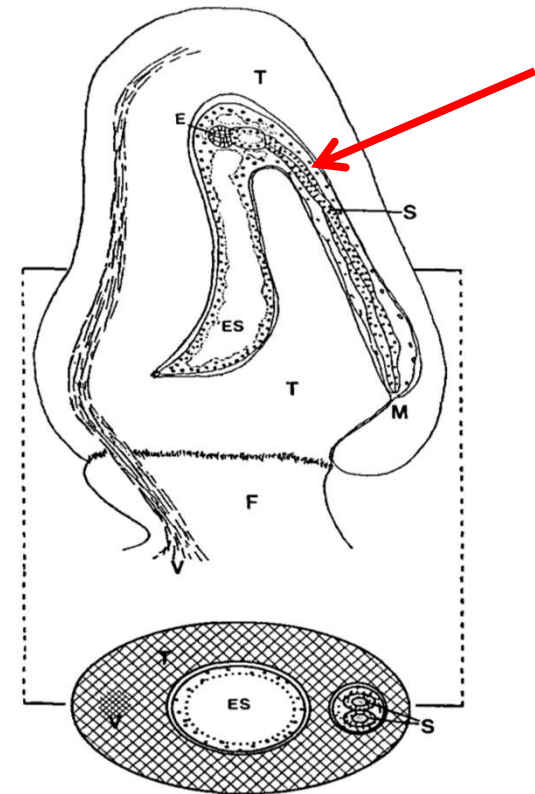


Figure 2. Diagrammatic Representation of an Immature Pea Seed at the Globular Stage of Embryo Development.

The organization of the various tissues of the developing pea seed is shown in longitudinal and cross-sections of the ovule. E, embryo; ES, embryo sac; F, funiculus; M, micropyle; S, suspensor; T, testa; V, vascular strand. Modified from Cooper (1938).

Comparison of the distribution of PSbMV in pea seeds (using a monoclonal antibody to PSbMV) in two cultivars:

‘Vedette’ (PSbMV is seed transmitted) and
‘Progreta’ (PSbMV not seed transmitted)

Immature seed: virus invasion of tissue in ‘Vedette’ is more extensive than that of ‘Progreta’

Older seed:

‘Vedette’- location of virus accumulation has shifted to the testa tissues and where the testa and suspensor contact (arrow).

‘Progreta’- Overall reduced accumulation of virus, only a limited distribution in patches (asterisks) within the testavirus does not reach the suspensor where it contacts the testa.



Detection of viruses transmitted by two different means of seed transmission:

Seedborne vs Embryo Invasion

The effect of mixed infections on seed transmission rates

Virology

Evaluation of Seed Transmission of *Turnip yellow mosaic virus* and *Tobacco mosaic virus* in *Arabidopsis thaliana*

F. M. de Assis Filho and J. L. Sherwood

Department of Plant Pathology, The University of Georgia, Athens 30602.
Accepted for publication 18 July 2000.

ABSTRACT

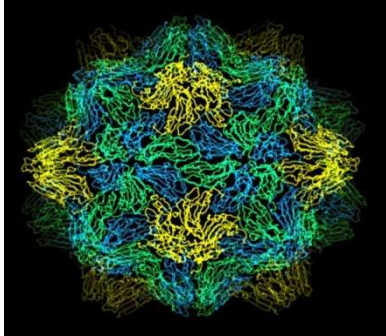
de Assis Filho, F. M., and Sherwood, J. L. 2000. Evaluation of seed transmission of *Turnip yellow mosaic virus* and *Tobacco mosaic virus* in *Arabidopsis thaliana*. *Phytopathology* 90:1233-1238.

The mechanism of virus transmission through seed was studied in *Arabidopsis thaliana* infected with *Turnip yellow mosaic virus* (TYMV) and *Tobacco mosaic virus* (TMV). Serological and biological tests were conducted to identify the route by which the viruses reach the seed and subsequently are located in the seed. Both TYMV and TMV were detected in seed from infected plants, however only TYMV was seed-transmitted. This is the first report of transmission of TYMV in seed of *A. thaliana*. Estimating virus seed transmission by grow-out tests was

more accurate than enzyme-linked immunosorbent assay due to the higher frequency of antigen in the seed coat than in the embryo. Virus in the seed coat did not lead to seedling infection. Thus, embryo invasion is necessary for seed transmission of TYMV in *A. thaliana*. Crosses between healthy and virus-infected plants indicated that TYMV from either the female or the male parent could invade the seed. Conversely, invasion from maternal tissue was the only route for TMV to invade the seed. Pollination of flowers on healthy *A. thaliana* with pollen from TYMV-infected plants did not result in systemic infection of healthy plants, despite TYMV being carried by pollen to the seed.

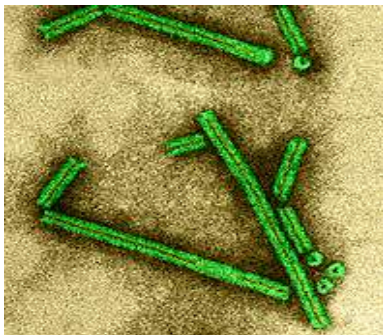
Additional keyword: gamete transmission.

Turnip yellow mosaic virus TYMV
(*Tymoviridae*, *Tymovirus*)



**Embryo
invasion**

Tobacco mosaic virus (TMV)
(*Virgaviridae*, *Tobamovirus*)



Seedborne

Arabidopsis thaliana
Ecotypes: Dijon and La-O



Photo: Dardick et al 2000. MPMI 13 -1139–1144

Presence of TYMV and TMV antigens in embryo, seed coat, whole seed and seedlings of *A. thaliana* as determined by ELISA:

Treatment	Embryo only	Seed coat only	Seed coat and embryo	Whole seed	Seedling ^y
Dijon TYMV	5.4 (184)	58.2 (184)	10.9 (184)	72.6 (274)	2.6 (423)
La-O TYMV	24.5 (184)	12.6 (184)	13.0 (184)	59.5 (274)	20.6 (471)
Dijon TMV	0 (180) ^z	100 (180) ^z	0 (180) ^z	100 (180) ^z	0 (846)
La-O TMV	0 (180)	100 (180)	0 (180)	100 (180)	0 (760)

- TYMV was detected in the embryo and the seed coat of mature seed (embryo invasion)
- TMV was not detected in the embryo but was detected in the seed coat (seed borne)
- Only TYMV was transmitted through seed to infect seedlings

Presence of TYMV and TMV antigens in embryo, seed coat, whole seed and seedlings of *A. thaliana* as determined by ELISA

Treatment	Embryo only	Seed coat only	Seed coat and embryo	Whole seed	Seedling ^y
Dijon TYMV	5.4 (184)	58.2 (184)	10.9 (184)	72.6 (274)	2.6 (423)
La-O TYMV	24.5 (184)	12.6 (184)	13.0 (184)	59.5 (274)	20.6 (471)
Dijon TMV	0 (180) ^z	100 (180) ^z	0 (180) ^z	100 (180) ^z	0 (846)
La-O TMV	0 (180)	100 (180)	0 (180)	100 (180)	0 (760)

- There was a poor correlation between detection of virus in the whole seed and infection of the progeny.
- There was a better correlation between detection in the embryo and infection of the progeny – however while invasion of the embryo by the virus was essential for transmission it was not always sufficient...

Detection of TYMV and TMV in tissues of female parent or seed derived from female parents (in La-O)

Organ	Both parents infected		Female infected		Male infected	
	IF × IM		IF × HM		HF × IM	
	TYMV	TMV	TYMV	TMV	TYMV	TMV
Leaf	+	+	+	+	–	–
Flower	+	+	+	+	+	–
Seed	+	+	+	+	+	–
Silique shell ^z	+	+	+	+	–	–

+ = positive detection

- TYMV was present in tissues derived from either parent
- TMV was only present in tissues derived from the mother plant
- TYMV was capable of being transmitted through either pollen or egg
- TYMV is seed transmitted whereas TMV is seed-borne

This has important implications for seed testing

Detection of TYMV in embryos, seed coats, and seedlings from single and mixed infections with TMV

Treatment	Embryo	Seed coat	Seed coat and embryo	Seedling
TYMV	0	33.3	58.9	31.1 ^x
TYMV + TMV ^y	1.1	22.2	75.5	70.1 ^z

- TMV increased the % seed transmission of TYMV

^wThere was no significant difference in TYMV incidence in (i) embryo only, (ii) seed coat only, and (iii) both seed coat and embryo between treatments. A significant difference was observed in virus incidence in seedlings according to Fisher's exact test ($P = 0.05$). Average of three replications of 30 seeds each. Seeds were dissected into seed coat and embryo. Each part was assayed side by side in the enzyme-linked immunosorbent assay (ELISA) plate to assure the correspondence between them. The occurrence of virus antigen in each seed is represented by three possibilities for TYMV location in seed (columns): embryo invasion but not seed coat invasion; seed coat invasion but not embryo invasion; and seed in which TYMV antigen could be recovered from both the embryo and the seed coat simultaneously.

Virus Detection in the Seed vs Seed Transmission:

- The incidence of TYMV coat protein by ELISA in a seed lot was significantly higher than the incidence of seed transmission of TYMV in that seed lot (as determined by the grow-out tests)
- The detection of virus antigen in seed may not always be a useful indicator of seed transmission.
- In this case, ELISA overestimated % seed transmission
- Grow-out tests were more accurate

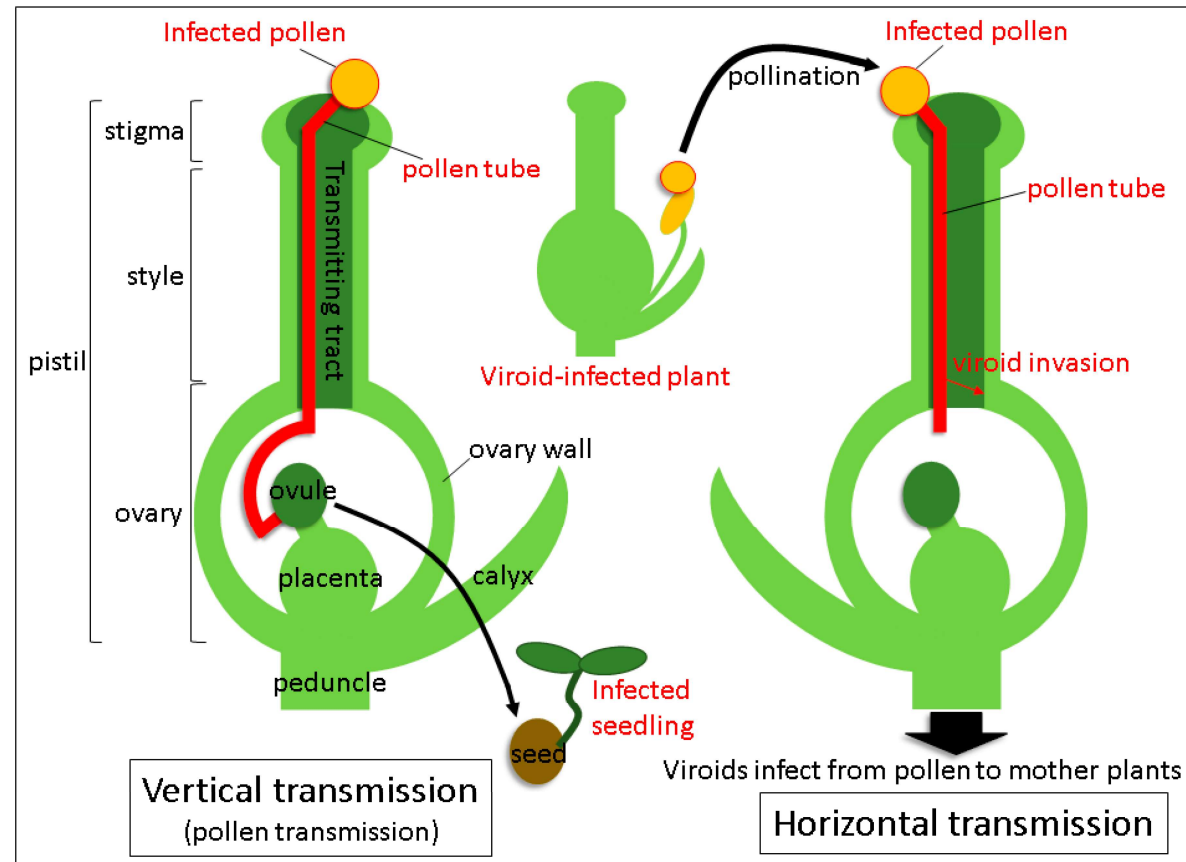
Virus Detection in the Seed vs Seed Transmission:

- The presence of virus in a seed or even in the embryo does not always indicate seedling infection.
- Virus may invade any seed part, but seed transmission most frequently results from embryo infection.
- Embryo invasion depends on virus invasion of the floral meristem and subsequent establishment in the gametophytes and gametes.
- The process of virus seed transmission is environmentally influenced.

Other Considerations:

Sometimes pollination with virus-infected pollen results in the infection of the mother plant

Pollination with virus/viroid infected pollen can result in either or both vertical transmission and horizontal transmission (by infecting the mother plant)

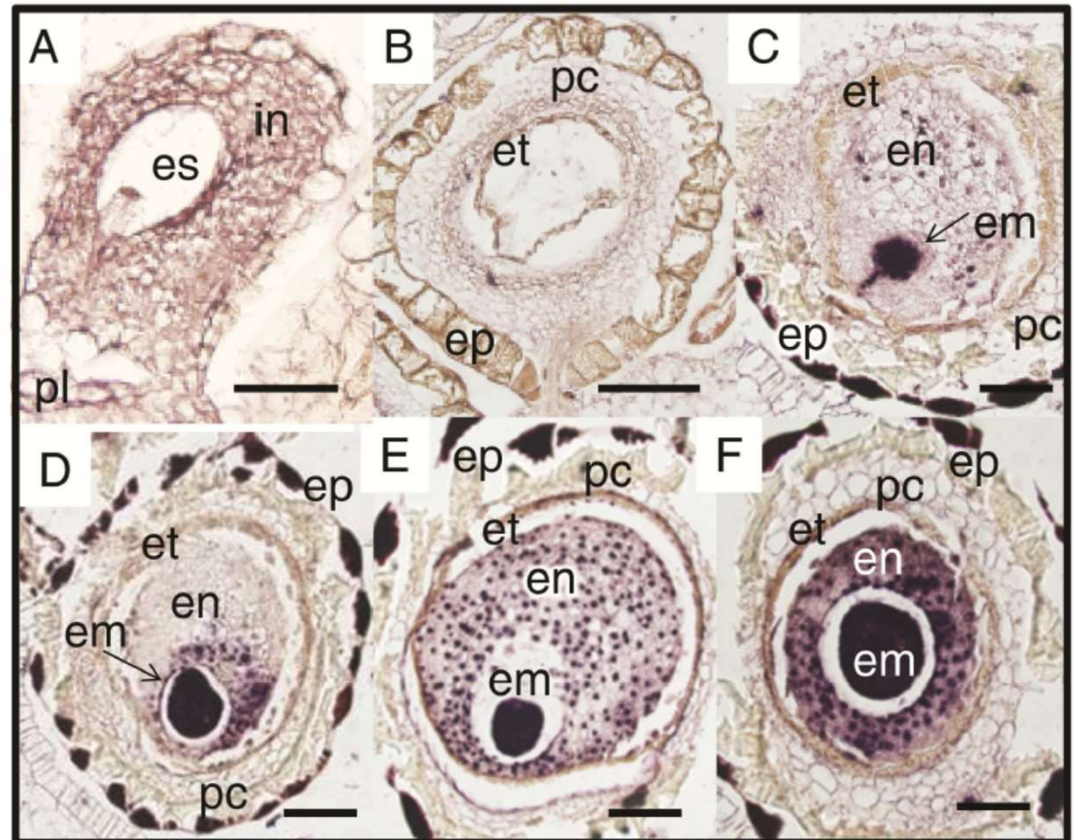


Initially healthy mother plant pollinated with PStVd-infected pollen

Distribution of PSTVd in developing
ovules of healthy petunia fertilized with
pollen from a PSTVd-infected plant

A: before pollination

B to F: after pollination



[es = embryo sac; em = embryo; en = endosperm; ep =
epidermis of the seed coat; et = endothelium; in =
integuments; pl = placenta; pc = parenchyma cells]

Non-traditional Form of Seed Transmission

Seed Transmission and Pararetroviruses

- Species of *Caulimoviridae* integrate into the genome and are passed vertically to the next generation in the genome
- Plant geneticists find integrated viral genomes as they sequence plant genomes and refer to them as Endogenous plant pararetroviruses (EPRVs)
- Not all integrated *Caulimoviridae* sequences have been shown to initiate virus infections (silent vs active)

Seed Transmission and Virus Management:

- **Use as appropriate for the type of seed transmission**

- A. Outside the embryo**

- B. Indirect embryo invasion**

- C. Direct embryo invasion**

- The management techniques used will depend upon:

- importance of the disease,
 - characteristics of the virus,
 - characteristics of the host,
 - the production system

Seed Transmission and Virus Management:

A. Outside the embryo

- Decontaminate seeds using established techniques
 - diluted clorox, HCL, etc...
- Produce seed on mother plants free of virus
- Develop and deploy seed certification program
 - Must establish seed transmission tolerance limits (STTL)
 - Require sensitive and efficient seed testing techniques to determine seed transmission rate in different seed lots.

Seed Transmission and Virus Management:

B. Indirect embryo invasion

- Develop or select for cultivars in which the virus is not seed transmitted
- Produce seed on mother plants free of virus
- Develop and deploy seed certification program

C. Direct embryo invasion

- Develop or select for cultivars in which the virus is not seed transmitted
- Produce seed on mother plants free of virus
- Develop and deploy seed certification program

Extensive (dated but still very useful) reviews of seed transmission:

Annu. Rev. Phytopathol. 1993. 31:375-402
Copyright © 1993 by Annual Reviews Inc. All rights reserved

POLLEN- AND SEED-TRANSMITTED VIRUSES AND VIROIDS

G. I. Mink

Washington State University-Prosser, Irrigated Agriculture Research and
Extension Center, Prosser, Washington 99350

Annu. Rev. Phytopathol. 1994. 32:363-86
Copyright © 1994 by Annual Reviews Inc. All rights reserved

SEED TRANSMISSION OF VIRUSES: Current Perspectives