

## Characterization of Evolutionary Potential of the Viruses Analyzed

### ACMV (*African cassava mosaic virus*)

**Host range.** Narrow; cassava is the main source of inoculum for infection of cassava crops

**Transmission.** Persistent nonpropagative, by the whitefly *Bemisia tabaci*

**Seed transmission.** None, but transmission occurs through plant cuttings

**Survival at site.** Medium to high, depending on cropping systems (overlapping crops)

**Population size.** Host frequent, vector active, survival high, population large: risk category 3

**Gene flow.** Medium, in tens of kilometers: risk category 2

**Genetic exchange.** Reassortment and recombination are frequent: risk category 3

**Risk.** 8

### BCMV (*Bean common mosaic virus*)

**Host range.** Narrow, species in the Fabaceae; main inoculum source is contaminated seed; except in East Africa, weeds are not a source of inoculum

**Transmission.** Nonpersistent, by several species of aphids

**Seed transmission.** About 30%

**Survival at site.** Low

**Population size.** Host range narrow, vectors periodical, survival low: risk category 1

**Gene flow.** High, with long-distance dispersal through seed: risk category 3

**Genetic exchange.** Recombinants are frequent: risk category 3

**Risk.** 7

### BCTV (*Beet curly top virus*)

**Host range.** Very large, more than 300 species in 44 dicot families

**Transmission.** Persistent nonpropagative, by the leafhopper *Circulifer tenellus*

**Seed transmission.** None

**Survival at site.** High, different strains favored in weeds and in crops

**Population size.** Risk category 3

**Gene flow.** Medium, dispersal over tens of kilometers: risk category 2

**Genetic exchange.** Recombinants occur but are not frequent: risk category 2

**Risk.** 7

### BLRV (*Bean leafroll virus*)

**Host range.** Narrow, species in the Fabaceae only

**Transmission.** Persistent nonpropagative, by 12 aphid species

**Seed transmission.** None

**Survival at site.** High in perennial legumes; alfalfa and clovers are sources of inoculum for infection of pea

**Population size.** Narrow host range, high survival: risk category 2

**Gene flow.** Unknown, but only one strain has been found worldwide: risk category 3

**Genetic exchange.** Not analyzed, but only one strain has been reported worldwide: risk category 1

**Risk.** 6

### BNYVV (*Beet necrotic yellow vein virus*)

**Host range.** Narrow, species in the Chenopodiaceae

**Transmission.** In cystosori of the soil fungus *Polymyxa betae*

**Seed transmission.** None, but transmission occurs through soil contaminating roots, water, or fruits

**Survival at site.** High

**Population size.** Narrow host range, high survival: risk category 2

**Gene flow.** Low naturally, but with a high potential through human-mediated movement on contaminated machinery; regulations in Europe limit movement: risk category 1

**Genetic exchange.** Acquisition of genomic segments is rare; no recombination reported: risk category 1

**Risk.** 4

### BYDV (*Barley yellow dwarf virus*)

**Host range.** Moderate, many species in the Poaceae

**Transmission.** Persistent nonpropagative, by several aphid species

**Seed transmission.** None

**Survival at site.** High in perennial grasses and volunteer barley

**Population size.** Moderate: risk category 2

**Gene flow.** High; barley-adapted strains are similar around the world: risk category 3

**Genetic exchange.** No recombination reported: risk category 1

**Risk.** 6

### CLCuV (*Cotton leaf curl virus*)

**Host range.** Broad, species in several dicot families

**Transmission.** Persistent nonpropagative, by *B. tabaci*

**Seed transmission.** None

**Survival at site.** High, frequently in weeds and volunteer cotton

**Population size.** Host frequent all year round, vector active, survival high: risk category 3

**Gene flow.** Medium, 10–100 km: risk category 2

**Genetic exchange.** Recombinants are frequent: risk category 3

**Risk.** 8

### CMV (*Cucumber mosaic virus*)

**Host range.** Very broad, species in more than 80 mono- and dicot families

**Transmission.** Nonpersistent, by more than 70 aphid species

**Seed transmission.** In some hosts, but not in cucumber cultivars

**Survival at site.** Low, severe bottlenecks in winter

**Population size.** Large host range, low survival at site: risk category 2

**Gene flow.** Long-range; Asian strains invaded Europe in the 1980s: risk category 3

**Genetic exchange.** Recombinants and reassortants described: risk category 3

**Risk.** 8

### GRV (*Groundnut rosette virus*)

**Host range.** Narrow, *Arachis* spp. only

**Transmission.** More or less circulative, by a few aphid species

**Seed transmission.** None

**Survival at site.** Low

**Population size.** Low: risk category 1  
**Gene flow.** At regional level: risk category 2  
**Genetic exchange.** Recombinants not reported: risk category 1  
**Risk.** 4

**LMV (*Lettuce mosaic virus*)**

**Host range.** Moderate, species in 10 dicot families  
**Transmission.** Nonpersistent, by several aphid species  
**Seed transmission.** 3–10%  
**Survival at site.** Moderate  
**Population size.** Moderate host range and survival: risk category 2  
**Gene flow.** High dispersal through seed: risk category 3  
**Genetic exchange.** Recombinants not found: risk category 1  
**Risk.** 6

**MNSV (*Melon necrotic spot virus*)**

**Host range.** Narrow, a few cucurbit species  
**Transmission.** In resting spores of soil fungi, *Oplidium* spp.  
**Seed transmission.** Yes  
**Survival at site.** High  
**Population size.** Moderate, with narrow host range and high survival: risk category 2  
**Gene flow.** High dispersal through seed: risk category 3  
**Genetic exchange.** Recombination reported in a resistance-breaking (RB) strain: risk category 2  
**Risk.** 7

**MSV (*Maize streak virus*)**

**Host range.** Moderate, species in the Poaceae; weeds can be inoculum sources  
**Transmission.** Persistent (for weeks), by leafhoppers, *Cicadulina* spp.  
**Seed transmission.** None  
**Survival at site.** High in riverine weeds or maize, depending on cropping systems  
**Population size.** Large: risk category 3  
**Gene flow.** Dispersal not long-range: risk category 2  
**Genetic exchange.** Recombinants are frequent: risk category 3  
**Risk.** 8

**PEMV (*Pea enation mosaic virus*)**

**Host range.** Narrow, primarily species in the Fabaceae  
**Transmission.** Persistent nonpropagative, by a few aphid species  
**Seed transmission.** Low, 1.5%  
**Survival at site.** High, in perennial legumes; clovers are the main source of inoculum for infection of pea  
**Population size.** Narrow host range, high survival: risk category 2  
**Gene flow.** Different geographical isolates exist: risk category 2  
**Genetic exchange.** Recombinants not described: risk category 1  
**Risk.** 5

**PMMoV (*Pepper mild mottle virus*)**

**Host range.** Narrow, pepper only  
**Transmission.** Plant-to-plant contact  
**Seed transmission.** Yes  
**Survival at site.** Moderate; crop debris can maintain infective virus for months  
**Population size.** Moderate; population structure does not change with time: risk category 2  
**Gene flow.** Long-range dispersal through seed: risk category 3  
**Genetic exchange.** None: risk category 1  
**Risk.** 6

**PSbMV (*Pea seed-borne mosaic virus*)**

**Host range.** Narrow, a few pulse crops; weeds are not important sources of inoculum

**Transmission.** Nonpersistent, by several aphid species

**Seed transmission.** 30–50%

**Survival at site.** Low

**Population size.** Narrow host range, low survival: risk category 1

**Gene flow.** Long-range dispersal through seed: risk category 3

**Genetic exchange.** Not analyzed, but generally high in potyviruses: risk category 3

**Risk.** 7

**PVX (*Potato virus X*)**

**Host range.** Moderate, solanaceous crops and weeds

**Transmission.** Primarily plant-to-plant contact

**Seed transmission.** Through tubers

**Survival at site.** Moderate

**Population size.** Low (with good sanitation): risk category 1

**Gene flow.** High in tubers, but regulated in Europe for many years: risk category 2

**Genetic exchange.** None: risk category 1

**Risk.** 4

**PVY (*Potato virus Y*)**

**Host range.** Moderate, solanaceous crops and weeds

**Transmission.** Nonpersistent, by many aphid species

**Seed transmission.** In potato tubers, but not in pepper or tobacco

**Survival at site.** Moderate

**Population size.** In potato, risk category 2; in tobacco and pepper, risk category 1

**Gene flow.** Effective dispersal through tubers, movement regulated in Europe: risk category 2

**Genetic exchange.** Recombinants are frequent: risk category 3

**Risk.** 7 (potato), 6 (pepper and tobacco)

**RpRSV (*Raspberry ring spot virus*)**

**Host range.** Very large, hosts in many mono- and dicot families

**Transmission.** By nematodes, *Longidorus* spp., in which the virus persists for up to 9 months

**Seed transmission.** In many hosts; transmission also occurs in vegetative propagation of raspberry

**Survival at site.** High

**Population size.** Large: risk category 3

**Gene flow.** Low dispersal: risk category 1

**Genetic exchange.** Recombinants not described, reassortants selected against: risk category 1

**Risk.** 5

**RGSV (*Rice grassy stunt virus*)**

**Host range.** Narrow, rice only

**Transmission.** Propagative, not transovarial, by the planthopper *Nilaparvata lugens*

**Seed transmission.** None

**Survival at site.** Low to high, according to cropping systems

**Population size.** Large in southern and southeastern Asia: risk category 3

**Gene flow.** Long-range dispersal of viruliferous vectors by monsoons: risk category 3

**Genetic exchange.** Reassortants reported: risk category 2

**Risk.** 8

**RSV (*Rice stripe virus*)**

**Host range.** Moderate, about 40 species in the Poaceae

**Transmission.** Propagative transovarial, by the planthopper *Laodelphax striatellus*

**Seed transmission.** None

**Survival at site.** Moderate to high, depending on cropping systems

**Population size.** Moderate, in Japan: risk category 2

**Gene flow.** High, long-range dispersal: risk category 3  
**Genetic exchange.** Probably: risk category 2  
**Risk.** 7

#### RTSV (*Rice tungro spherical virus*)

**Host range.** Narrow, species in the Poaceae; weeds are not inoculum sources  
**Transmission.** Semipersistent (for 5 days), by the leafhopper *Nephotettix virescens*  
**Seed transmission.** None  
**Survival at site.** High in continuous rice crops  
**Population size.** Large in southeast Asia (mainland and archipelagos): risk category 3  
**Gene flow.** Not long-distance, in the range of 100 km: risk category 2  
**Genetic exchange.** Recombinants reported: risk category 3  
**Risk.** 8

#### SBWMV (*Soil-borne wheat mosaic virus*)

**Host range.** Narrow, very few graminaceous crops and weeds  
**Transmission.** By the soil fungus *Polymyxa graminis*, with long-term survival in cystosori  
**Seed transmission.** None  
**Survival at site.** High  
**Population size.** High survival, narrow host range, but large host populations: risk category 2  
**Gene flow.** Short-range dispersal: risk category 1  
**Genetic exchange.** Recombinants not reported, but defective RNAs of RNA2 occur, and reassortants can be formed: risk category 2  
**Risk.** 5

#### SMV (*Soybean mosaic virus*)

**Host range.** Narrow; soybean is the only inoculum source  
**Transmission.** Nonpersistent, by a few aphid species  
**Seed transmission.** About 30%  
**Survival at site.** Low  
**Population size.** Small: risk category 1  
**Gene flow.** High dispersal through seed: risk category 3  
**Genetic exchange.** Not analyzed, but exchange is frequent in potyviruses: risk category 3  
**Risk.** 7

#### TBRV (*Tomato black ring virus*)

**Host range.** Very large, species in many mono- and dicot families and in the Coniferae  
**Transmission.** By nematodes, *Longidorus* spp.  
**Seed transmission.** Very efficient in many species  
**Survival at site.** High  
**Population size.** Large: risk category 3  
**Gene flow.** Low: risk category 1  
**Genetic exchange.** Not reported: risk category 1  
**Risk.** 5

#### TMV (*Tobacco mosaic virus*)

**Host range.** Narrow, mostly tobacco  
**Transmission.** Plant-to-plant contact  
**Seed transmission.** None  
**Survival at site.** High, in plant debris (2–3 years)  
**Population size.** Moderate: risk category 2  
**Gene flow.** High dispersal in processed tobacco: risk category 3  
**Genetic exchange.** None: risk category 1  
**Risk.** 6

#### ToMV (*Tomato mosaic virus*)

**Host range.** Narrow, including tomato, pepper, and eggplant  
**Transmission.** Plant-to-plant contact  
**Seed transmission.** Yes  
**Survival at site.** Moderate, in plant debris  
**Population size.** Moderate: risk category 2  
**Gene flow.** Long-range dispersal through seed: risk category 3  
**Genetic exchange.** None: risk category 1  
**Risk.** 6

#### TSWV (*Tomato spotted wilt virus*)

**Host range.** Very broad, species in many mono- and dicot families  
**Transmission.** Persistent propagative, by thrips  
**Seed transmission.** Not important (less than 1%)  
**Survival at site.** High  
**Population size.** Large: risk category 3  
**Gene flow.** Moderate-range dispersal by thrips; populations differ in different areas of the United States: risk category 2  
**Genetic exchange.** Reassortants described: risk category 2  
**Risk.** 7

#### TuMV (*Turnip mosaic virus*)

**Host range.** Very broad, species in 43 dicot families  
**Transmission.** Nonpersistent, by many aphid species  
**Seed transmission.** None  
**Survival at site.** High in wild *Brassica oleracea*  
**Population size.** Broad host range, high survival: risk category 3  
**Gene flow.** World population structured at continental level: risk category 3  
**Genetic exchange.** Recombinants are frequent: risk category 3  
**Risk.** 9

#### TYLCV (*Tomato yellow leaf curl virus*)

**Host range.** Moderate, a few crops and weeds  
**Transmission.** Persistent propagative, by *B. tabaci*  
**Seed transmission.** None  
**Survival at site.** High, because of overlapping crops and weeds  
**Population size.** Large: risk category 3  
**Gene flow.** Long-range dispersal by the vector: risk category 3  
**Genetic exchange.** Recombinants are frequent: risk category 3  
**Risk.** 9

## Characterization of Resistance in Hosts

### ACMV-cassava

#### Resistance from Java varieties

**Genetics.** Polygenic recessive  
**Expression.** Decreased infection  
**Deployed.** Uganda, 1940s  
**Overcome.** Pandemic started in 1988  
**Overcoming strains.** Reassortants and recombinants of *East*

*African cassava mosaic virus* (EACMV) and ACMV (UgV isolates)

#### Resistance from *Manihot glaziovii*

**Genetics.** Polygenic recessive  
**Expression.** Decreased virus accumulation and systemicity  
**Deployed.** Madagascar, 1940; East Africa, 1993; 25% of surface in Uganda in 1998

**Overcome.** Never overcome in Madagascar; in East Africa, resistance is effective against ACMV, EACMV, and UgV

#### BCMV-bean

##### Resistance from *bc* genes

**Genetics.** Monogenic recessive

**Expression.** Immunity

**Deployed.** United States, 1930

**Overcome.** Shortly after deployment; strain US2 reported in 1938; US3 and US4, 1961; US5, 1962; US6, 1964; resistance is durable in dry beans

**Overcoming strains.** US2 to US6 plus necrotic strains

**Properties.** Variants of BCMV with a gene-for-gene relationship with *bc* alleles

##### Resistance from *I* gene

**Genetics.** Monogenic incompletely dominant

**Expression.** Immunity in homozygotes, hypersensitive response (HR) in heterozygotes

**Deployed.** 1935

**Overcome.** Not overcome

**Overcoming strains.** So-called necrotic strains, first reported in 1963; outbreaks in the United States, 1984–90, but RB strains are not prevalent

**Properties.** A different potyvirus (with about 10% sequence divergence) now called *Bean common mosaic necrotic virus* (BCMNV)

#### BCTV-bean

##### Resistance from bean

**Genetics.** Two dominant epistatic genes

**Expression.** Diminished infection (escape)

**Deployed.** Washington State, 1930s

**Overcome.** Not overcome

**Overcoming strains.** Yes

**Properties.** Infection can occur under glasshouse conditions very favorable for disease

#### BCTV-beet

##### Resistance from beet

**Genetics.** Polygenic, inheritance not clear

**Expression.** Lower accumulation and systemicity

**Deployed.** California, 1933

**Overcome.** Late 1960s

**Overcoming strains.** Differ by up to 20% in nucleotide sequence from milder strains

**Properties.** Different pathogenicity in different hosts; poor competitors in weeds

#### BLRV-pea

##### Resistance from pea

**Genetics.** Monogenic recessive, *lr* gene

**Expression.** Resistance to infection

**Deployed.** Before 1980 (mid-1970s?)

**Overcome.** Not overcome

**Overcoming strains.** Not reported

#### BNYVV-beet

##### Resistance from *Beta vulgaris* subsp. *maritima*

**Genetics.** Monogenic dominant, *Rz* gene

**Expression.** Lower accumulation and systemicity

**Deployed.** Europe, 1982, with large-scale deployment in 1985

**Overcome.** Not overcome

**Overcoming strains.** Strain P

**Properties.** Additional satellite-like RNA (RNA5)

#### BYDV-barley

##### Resistance from Ethiopian varieties

**Genetics.** Incompletely dominant, *Yd2* gene

**Expression.** Lower titer, not expressed in protoplasts; interference with movement

**Deployed.** Since late 1970s

**Overcome.** Not overcome

**Overcoming strains.** Resistance is effective against strains PAV and MAV, but not strain RPV

**Properties.** RPV, formerly considered a strain of BYDV, is a different virus species in a different genus

#### CLCuV-cotton

##### Resistance from Indian cotton accessions

**Genetics.** Monogenic dominant

**Expression.** Immunity

**Deployed.** Punjab, Pakistan, 1994; 75% of the crop in 2001

**Overcome.** 2001

**Overcoming strains.** Present in a few localized areas, but spreading

**Properties.** Unknown

#### CMV-cucumber

##### Resistance from Asian accessions of *Cucumis sativus*

**Genetics.** Three recessive genes

**Expression.** Lower accumulation

**Deployed.** Early 1970s

**Overcome.** Not overcome

**Overcoming strains.** Not overcome, but the degree of protection depends on the strain

#### GRV-groundnut

##### Resistance from Virginia-type groundnut (*Arachis hypogaea* subsp. *hypogaea*)

**Genetics.** Two independent recessive genes

**Expression.** Resistance to GRV only, not to *Groundnut rosette assistor virus* (GRAV); no infection causing either chlorotic rosette or green rosette

**Deployed.** 1970s, mostly since 1980 in West Africa

**Overcome.** Not overcome

**Overcoming strains.** Not reported

#### LMV-lettuce

##### Resistance from lettuce cultivars from Argentina and Egypt

**Genetics.** Monogenic recessive, two alleles at *mol*

**Expression.** Decreased accumulation and systemicity; no seed transmission

**Deployed.** Since 1975, largely used in Europe (more than 70% surface), much less in the United States

**Overcome.** Not overcome

**Overcoming strains.** Reported since the 1980s, but not seed-transmitted; overcoming seed-transmitted strains (LMV-Most) reported 1989

**Properties.** Very different strains (about 5% nucleotide sequence divergence)

#### MNSV-melon

##### Resistance from melon

**Genetics.** Monogenic recessive, *msv* gene

**Expression.** HR-like

**Deployed.** Southeast Spain, 1994

**Overcome.** Not overcome

**Overcoming strains.** Reported in 1999, but not found in later surveys

**Properties.** Nucleotide sequence 93% similar to that of the common strain; recombinant at 3' noncoding region

#### MSV-maize

##### Resistance from TZ yellow

**Genetics.** Polygenic, two or three genes involved

**Expression.** Decreased accumulation and systemicity

**Deployed.** 1982

**Overcome.** Not overcome

**Overcoming strains.** Not reported in Africa, but resistance is not effective in La Réunion

**Properties.** Nucleotide sequence of isolates from La Réunion are about 98% similar to those of strains prevalent in Africa

#### **Resistance from Vaalhart composite**

Similar to resistance from TZ yellow

**Deployed.** South Africa, 1978

#### **Resistance from cultivar Revolution**

**Genetics.** Polygenic

**Expression.** Decreased accumulation and systemicity

**Deployed.** La Réunion, 1960s

**Overcome.** Not overcome

**Overcoming strains.** Not reported; resistance is also effective against African strains

#### **PEMV-pea**

##### **Resistance from pea**

**Genetics.** Monogenic dominant, *En* gene

**Expression.** Decreased accumulation

**Deployed.** Since the late 1960s

**Overcome.** Not overcome

**Overcoming strains.** Not reported; only one strain of PEMV has been reported worldwide

#### **PMMoV-pepper**

##### **Resistance from *Capsicum* spp.**

**Genetics.** Monogenic dominant, *L* locus, alleles *L2* and *L3*

**Expression.** HR

**Deployed.** *L2* and *L3* in Holland, since 1979, and in Spain, since 1985

**Overcome.** In about 5 years

**Overcoming strains.** Pathotype P<sub>1,2</sub> overcomes *L2* and P<sub>1,2,3</sub> overcomes *L3* in a gene-for-gene manner

**Properties.** P<sub>1,2</sub> and P<sub>1,2,3</sub> differ in a single amino acid in the coat protein

##### **Resistance from *Capsicum chacoense***

**Genetics.** Monogenic partially dominant, *L* locus, allele *L4*

**Expression.** HR

**Deployed.** Holland and Spain, since 1990

**Overcome.** Not overcome

**Overcoming strains.** Not reported

#### **PSbMV-pea**

##### **Resistance from pea**

**Genetics.** Monogenic recessive, *sbm1* gene

**Expression.** Immunity

**Deployed.** United States, 1978

**Overcome.** Not overcome

**Overcoming strains.** Resistance is effective against strains P<sub>1</sub> and P<sub>2</sub>; the overcoming strain P<sub>4</sub> was reported in 1989

**Properties.** P<sub>4</sub> is 81% homologous to P<sub>1</sub> in nucleotide sequence; avirulent gene is central region of VPg; P<sub>4</sub> is very poorly seed-transmitted and does not compete with P<sub>1</sub> in mixed infections

#### **PVX-potato**

##### **Resistance from *Nb* gene**

**Genetics.** Monogenic dominant

**Expression.** HR to strains 1 and 2, elicited by the 25K movement protein

**Deployed.** Since 1920–1930

**Overcome.** By strain 3, but cultivars with this gene are still widely grown in Europe with good protection

**Overcoming strains.** Strain 3 is the most frequent in Europe; strain 4 is not present in the field

**Properties.** One amino acid change determines the RB phenotype

##### **Resistance from *Nx* gene**

**Genetics.** Monogenic dominant

**Expression.** HR to strains in groups 1 and 3, elicited by the coat protein

**Deployed.** 1920–1930

**Overcome.** Not overcome

**Overcoming strains.** Strain 2 is uncommon in Europe; strain 4 is not present in the field

**Properties.** One or two amino acid changes determine the RB phenotype

##### **Resistance from *Rx* gene**

**Genetics.** Monogenic dominant

**Expression.** Immunity to strains in groups 1–4, elicited by the coat protein

**Deployed.** Since 1950s

**Overcome.** Not overcome

**Overcoming strains.** Strain HB, frequent in Bolivia, not in Europe

**Properties.** A single amino acid change determines the HB phenotype

#### **PVY-pepper**

##### **Resistance from *pvr2* gene**

**Genetics.** Monogenic recessive

**Expression.** Impairment of cell-to-cell movement resulting in lower virus accumulation

**Deployed.** Allele *pvr2<sup>1</sup>*, effective against pathotype P(0), deployed in Europe, 1960–1970

**Overcome.** Not overcome

**Overcoming strains.** Pathotypes P(1) and P(2); P(1) is infrequent in the field, and P(2) is not found in the field

**Properties.** All three pathotypes belong to the same genetic strain, and a few amino acid changes determine the phenotype

##### **Resistance from *Pvr4* gene**

**Genetics.** Monogenic dominant

**Expression.** HR

**Deployed.** Europe, about 1990

**Overcome.** Not overcome

**Overcoming strains.** Not reported; resistance is effective against pathotypes P(0), P(1), and P(2)

#### **PVY-potato**

##### **Resistance from *Nc* gene**

**Genetics.** Monogenic dominant

**Expression.** HR

**Deployed.** Early 20th century

**Overcome.** Dates not known, but overcoming strain PVY<sup>O</sup> was present in Europe before World War II

**Overcoming strains.** *Nc* gene is effective against PVY<sup>C</sup> but overcome by PVY<sup>O</sup> and PVY<sup>N</sup>

**Properties.** Strains C, O, and N are genetically very different (about 10% divergence in nucleotide sequence)

##### **Resistance from *Ny* gene**

**Genetics.** Monogenic dominant

**Expression.** HR to PVY<sup>O</sup>

**Deployed.** Early 20th century

**Overcome.** 1960s

**Overcoming strains.** Strain PVY<sup>N</sup>, prevalent in potato in Europe since 1960s, causes a mild infection in potato; the severe overcoming strain PVY<sup>NTN</sup> spread in the late 1980s

**Properties.** PVY<sup>N</sup> is a different genetic strain from PVY<sup>O</sup>, about 90% similar in nucleotide sequence; PVY<sup>NTN</sup> is a recombinant between PVY<sup>N</sup> and PVY<sup>O</sup>

##### **Resistance from *Ry* gene**

**Genetics.** Monogenic dominant

**Expression.** Immunity

**Deployed.** Europe, 1980  
**Overcome.** Not overcome  
**Overcoming strains.** Not reported

#### PVY-tobacco

##### Resistance from *va* gene

**Genetics.** Monogenic recessive  
**Expression.** Decreased accumulation and systemicity  
**Deployed.** In Europe since the early 20th century in Burley and dark air-cured varieties, and since the 1980s in Virginia types  
**Overcome.** Not overcome  
**Overcoming strains.** Resistance is effective against pathotype P(0) of PVY<sup>N</sup>; PVY<sup>N</sup> has been present in tobacco in Europe since 1952, and the overcoming pathotypes P(1) and P(1,2) have been present since 1990, but P(0) is still prevalent over most of Europe  
**Properties.** All pathotypes belong to PVY<sup>N</sup> and are more than 95% similar in nucleotide sequence

#### RpRSV-red raspberry

##### Resistance from *Rubus idaeus*

**Genetics.** Monogenic dominant, *Irr* gene  
**Expression.** Immunity  
**Deployed.** Scotland, 1940s  
**Overcome.** Not overcome  
**Overcoming strains.** Lloyd George strain, reported in 1963  
**Properties.** Resistance breaking is determined by RNA1, linked to determinants for low virulence, low seed transmission, and poor competitive ability

#### RGSV-rice

##### Resistance from *Oryza nivara*

**Genetics.** Monogenic dominant, *Gs* gene  
**Expression.** Resistance to infection  
**Deployed.** Southeast Asia (continent and archipelagos), 1970s  
**Overcome.** Yes  
**Overcoming strains.** Strain 2, reported in the Philippines in the early 1980s, and similar strains reported in Indonesia, Thailand, and India  
**Properties.** Strains of RGSV differ by up to 10% in nucleotide sequence

#### RSV-rice

##### Resistance from *Oryza sativa indica*

**Genetics.** Monogenic, incompletely dominant, *St2<sup>l</sup>* gene  
**Expression.** Resistance to infection  
**Deployed.** 1972  
**Overcome.** Not overcome  
**Overcoming strains.** Not reported

#### RTSV-rice

##### Resistance from line TKM6

**Genetics.** Monogenic recessive  
**Expression.** Resistance to infection  
**Deployed.** Philippines, since 1972  
**Overcome.** Not overcome  
**Overcoming strains.** Strain Vt6 or III, reported 1992, did not become prevalent  
**Properties.** RTSV strains differ by 5–18% in nucleotide sequence

##### Resistance from cultivar Utri Merah

**Genetics.** Two recessive genes  
**Expression.** Resistance to infection  
**Deployed.** Philippines, 1998; Utri Merah was in use before the etiology of rice tungro was known  
**Overcome.** Not overcome  
**Overcoming strains.** Not reported; resistance is also effective against Vt6

#### SBWMV-wheat

##### Resistance from wheat

**Genetics.** Monogenic dominant, three alleles at a locus,  $R^{mv} > r^m > r^{mv}$   
**Expression.**  $R^{mv}$  confers resistance to mosaic and rosette,  $r^m$  to rosette only, and  $r^{mv}$  to neither; resistance is expressed as decreased accumulation and systemic movement of the virus  
**Deployed.** U.S. Midwest, since the 1920s  
**Overcome.** Not overcome  
**Overcoming strains.** Not reported

#### SMV-soybean

##### Resistance from *Rsv1* gene

**Genetics.** Monogenic incompletely dominant  
**Expression.** Immunity in homozygotes, HR in heterozygotes  
**Deployed.** United States and Korea, since 1960  
**Overcome.** Different alleles of this gene have been overcome by different SMV pathotypes, since 1974 in Korea and since the late 1970s in the United States  
**Overcoming strains.** Strains G1 to G7 according to alleles in a gene-for-gene-like relationship  
**Properties.** HC-Pro-P3 cistrons elicit the gene; a few nucleotide changes determine new phenotype

##### Resistance from *Rsv2* gene

**Genetics.** Monogenic dominant  
**Expression.** Immunity  
**Deployed.** United States, since 1980  
**Overcome.** Not overcome  
**Overcoming strains.** Not reported

#### TBRV-red raspberry

##### Resistance from *Rubus idaeus*

**Genetics.** Monogenic resistant, *Itb* gene  
**Expression.** Immunity  
**Deployed.** Scotland, 1940s  
**Overcome.** Not overcome  
**Overcoming strains.** Not reported until the 1970s, when production was discontinued

#### TMV-tobacco

##### Resistance from *Nicotiana glutinosa*

**Genetics.** Monogenic dominant, *N* gene  
**Expression.** HR  
**Deployed.** Worldwide since 1940 in dark air-cured and Burley varieties  
**Overcome.** Not overcome  
**Overcoming strains.** Only the pepper-infecting tobamovirus *Obuda pepper virus*, which is not found in tobacco  
**Properties.** The helicase domain of the viral 183K protein is the elicitor

#### ToMV-pepper

##### Resistance from *Capsicum annuum*

**Genetics.** Monogenic dominant, *L1* allele at *L* locus  
**Expression.** HR  
**Deployed.** Holland, mid-1960s; Spain, late 1970s  
**Overcome.** P1 in Holland, 1974; P1,2 in France, 1978, and Spain, 1983  
**Overcoming strains.** Strains P1, P1,2, and P1,2,3  
**Properties.** P1 is a different tobamovirus, *Paprika mosaic virus*; P1,2 and P1,2,3 are PMMoV; the coat protein is the elicitor

#### ToMV-tomato

##### Resistance from *Tm1* gene

**Genetics.** Monogenic incompletely dominant  
**Expression.** Decreased virus replication and decreased accumulation

**Deployed.** United Kingdom, 1966

**Overcome.** 1968

**Overcoming strains.** P1

**Properties.** 183K protein is the elicitor; a change at nucleotide 979 determines the new phenotype

**Resistance from *Tm2* gene**

**Genetics.** Monogenic dominant

**Expression.** HR

**Deployed.** Europe, about 1970

**Overcome.** In 2–3 years

**Overcoming strains.** Pathotype P2

**Properties.** MP is the elicitor of the gene; two amino acid changes determine the new phenotype

**Resistance from *Tm2<sup>2</sup>* gene**

**Genetics.** Monogenic dominant, allelic with *Tm2*

**Expression.** HR

**Deployed.** Europe, about 1975

**Overcome.** Not overcome

**Overcoming strains.** Pathotype P2<sup>2</sup>

**Properties.** MP is the elicitor; two amino acid changes determine the new phenotype; RB isolates are outcompeted by non-RB isolates

**TSWV-pepper**

**Resistance from *Tsw* gene from *Capsicum chinense***

**Genetics.** Monogenic dominant

**Expression.** HR

**Deployed.** Italy and Spain, 1999

**Overcome.** 2000

**Overcoming strains.** Yes

**Properties.** RB strains are biologically similar to the wild type, and both are transmitted by thrips

**TSWV-tomato**

**Resistance from *Lycopersicon pimpinellifolium***

**Genetics.** Polygenic?

**Expression.** Resistance to infection

**Deployed.** Hawaii, 1946

**Overcome.** Within 10 years

**Overcoming strains.** Many

**Resistance from *L. peruvianum***

**Genetics.** Monogenic dominant, *Sw-5* gene

**Expression.** HR

**Deployed.** Mid-1990s (1996 in Spain)

**Overcome.** 2002

**Overcoming strains.** An overcoming strain was spreading in northeast Spain in 2002

**TuMV-lettuce**

**Resistance from *Lactuca sativa***

**Genetics.** Monogenic dominant, *Tu* gene

**Expression.** Extreme resistance

**Deployed.** Before 1970

**Overcome.** Not overcome

**Overcoming strains.** Resistance is effective against all tested pathotypes of TuMV

**TuMV-rape**

**Resistance from *Brassica napus***

**Genetics.** Monogenic dominant, *TuRB01* gene

**Expression.** Extreme resistance

**Deployed.** Early 1980s

**Overcome.** Not overcome

**Overcoming strains.** *TuRB01* is effective against pathotype 1, the commonest in Europe, but is overcome by P4, the second most common, and by P3, which is infrequent

**Properties.** A single nucleotide change in the CI cistron determines the RB phenotype; however, RB isolates are less fit than P1 in competition experiments

**TYLCV-tomato**

**Resistance from *Lycopersicon chilense***

**Genetics.** Monogenic dominant, *Ty* gene

**Expression.** Decreased accumulation and systemicity, also tolerance

**Deployed.** Spain, since 1996

**Overcome.** Partially; more infectious strains have been reported since 1999, but tolerance still operates

**Overcoming strains.** Recombinant TYLCV and *Tomato yellow leaf curl Sardinia virus*

**Properties.** More infectious to tomato, and with a broader host range