

Chapter 11

Viral Diseases in Potato



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Abstract Viruses are among the most significant biotic constraints in potato production. In the century since the discovery of the first potato viruses we have learned more and more about these pathogens, and this has accelerated over the last decade with the advent of high-throughput sequencing in the study of plant virology. Most reviews of potato viruses have focused on temperate potato production systems of Europe and North America. However, potato production is rapidly expanding in tropical and subtropical agro-ecologies of the world in Asia and Africa, which present a unique set of problems for the crop and affect the way viruses can be managed. In this chapter we review the latest discoveries in potato virology as well as the changes in virus populations that have occurred over the last 50 years, with a particular focus on countries in the (sub-)tropics. We also review the different management approaches including use of resistance, seed systems, and cultural approaches that have been employed in different countries and reflect on what can be learnt from past research on potato viruses, and what can be expected in the future facing climate change.

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11.1 Introduction

In terms of human consumption, potato (*Solanum tuberosum*) is currently the third most important food crop globally after rice and wheat, and over half of its production currently occurs in developing countries (Devaux et al. 2014). Worldwide, over the last few decades, potato production has increased at a much higher rate compared to other major staple crops. This increase has occurred principally in developing countries located in largely tropical and subtropical regions. Due to its ability to produce high amounts of digestible energy per unit time and unit area for home consumption, but at the same time provide income as a cash crop, planting potato tends to be popular with farmers wherever they are able to grow them. In the future, development of new heat tolerant and early maturing potato cultivars will likely lead to further expansion of its production into warmer areas of the tropics. However, as temperatures increase virus vectors often become more abundant and the incidence of virus epidemics increases. This increase in insect vectors and virus disease incidence, combined with the fact that virus-tested seed systems are weak or entirely absent, explains why potato virus diseases are of particular importance in the developing world and estimated to account for 50% or more of the potential total yield being lost (Harahagazwe et al. 2018). In addition, the presence of year-round potato cultivation in some tropical regions and the lack of cool upland areas where insect vector pressure is low enough to produce high-quality seed potatoes, both exacerbate potato virus disease problems in these regions. Several global or regional reviews and intercontinentally focused research papers on potato virus diseases have been written during the last decade, devoted to many different aspect or particular viruses, including economic losses, detection methods, molecular variability, resistance genes, and evolution (Valkonen 2007; Gray et al. 2010; Karasev and Gray 2013; Jones 2014; Gibbs et al. 2017; Lacomme et al. 2017; Santillan et al. 2018) and we refer to them for details on those specific aspects. In this chapter we will review potato viruses with a focus on developing world regions and changes that have occurred over the past 50 years. The reason for this is that they have traditionally received less attention in the literature, but also are generally located in places with warmer climates, and with global temperatures rising, may be representative for what the future holds also for the currently more temperate regions. We will start with a general overview of potato infecting viruses of global importance, the damages they cause to potato production, and where they occur. Next, we describe the viruses found in the center of origin of wild and cultivated potatoes, the Andes. Then we describe the situation in two emerging economies in (sub-)tropics with functional seed systems, one, Brazil which is largely based on imported basic seed tubers and one, India, which largely produces its own potato cultivars and seed. This is followed by a brief review of the situation in Africa, and a description of the situation in two contrasting developed economies, Australia and Europe. Finally, we consider the main control methods for potato viruses, how they are being applied in the different agro-ecologies, and how they might be affected by changing climates.

11.2 Viruses of Potato

Whereas more than 50 different viruses and one viroid have been reported infecting potatoes worldwide (Table 11.1, Fig. 11.1), only a handful of them cause major losses globally. However, some are locally and/or temporarily relevant, while others

Table 11.1 List of viruses of potato worldwide

Virus ^a	Genus, family	Transmission	Distribution
<i>Potato virus Y</i> (PVY)	<i>Potyvirus</i> , <i>Potyviridae</i>	Aphids	Worldwide
<i>Potato virus A</i> (PVA)			Worldwide
<i>Potato virus V</i> (PVV)			Europe, South America
<i>Wild potato mosaic virus</i> (WPMV)			Andes, only reported in wild potatoes
<i>Potato virus X</i> (PVX)	<i>Potexvirus</i> , <i>Alphaflexiviridae</i>	Contact	Worldwide
<i>Potato aucuba mosaic virus</i> (PAMV)			Worldwide, very rare
<i>Potato leaf roll virus</i> (PLRV)	<i>Polerovirus</i>	Aphids	Worldwide
<i>Potato virus S</i> (PVS)	<i>Carlavirus</i> , <i>Betaflexiviridae</i>	Contact, aphids	Worldwide
<i>Potato latent virus</i> (PotLV)		Aphids	North America, rare
<i>Potato virus M</i> (PVM)		Aphids	Worldwide
<i>Potato virus H</i> (PVH)		unknown	China
<i>Potato virus P</i> (PVP syn. Potato rough dwarf virus: PRDV)		unknown	Brazil & Argentina
<i>Potato virus T</i> (PVT)	<i>Tepovirus</i> , <i>Betaflexiviridae</i>	Contact, seed	Southern Andean region
<i>Andean potato mottle virus</i> (APMoV)	<i>Comovirus</i> , <i>Secoviridae</i>	Beetles	Andean region, Brazil
<i>Potato black ringspot virus</i> (PBRV = TRSV-Ca)	<i>Nepovirus</i> , <i>Secoviridae</i>	true seed, nematodes	Peru
<i>Potato virus U</i> (PVU)		nematodes	Peru, only reported once
<i>Potato virus B</i> (PVB)		nematodes?	Peru, recently reported, relatively common
<i>Cherry leaf roll virus</i> (CLRV)		Nematodes, TPS, pollen?	Europe, North & South America
<i>Lucerne Australian latent virus</i> (LALV)		Unknown	Australia and New Zealand, rare in potato
<i>Tomato black ring virus</i> (TBRV)		Nematodes	Europe, rare
<i>Cherry rasp leaf virus</i> (CRLV)			North America, only reported once
<i>Arracacha virus B</i> (AVB)	<i>Cheravirus</i> , <i>Secoviridae</i>	TPS, pollen	Andes

(continued)

Table 11.1 (continued)

Virus ^a	Genus, family	Transmission	Distribution
<i>Tomato spotted wilt virus</i> (TSWV)	<i>Tospovirus</i> , <i>Bunyaviridae</i>	Thrips	Worldwide
<i>Tomato chlorotic spot virus</i> (TCSV)			South America
<i>Groundnut bud necrosis virus</i> (GBNV)			India
<i>Groundnut ringspot virus</i> (GRSV)			Americas
“Tomato yellow fruit ring virus” (TYFRV)			Reported from potato in Iran
<i>Impatiens necrotic spot virus</i> (INSV)			Worldwide, reported in greenhouse grown potatoes in USA
<i>Andean potato latent virus</i> (APLV)	<i>Tymovirus</i> , <i>Tymoviridae</i>	Beetles	Andean region
<i>Andean potato mild mottle virus</i> (APMMV)			Andean region
<i>Potato yellow vein virus</i> (PYVV)	<i>Crinivirus</i> , <i>Closteroviridae</i>	Whiteflies	Northern Andean region, Panama
<i>Tomato chlorosis virus</i> (ToCV)			Brazil, Spain, India
“Potato yellowing virus” (PYV)	<i>Ilarvirus</i> , <i>Bromoviridae</i>	Unknown	Andean region
<i>Tobacco streak virus</i> (TSV)		Pollen, thrips	Worldwide, reported in potato in Brazil
<i>Cucumber mosaic virus</i> (CMV)	<i>Cucumovirus</i> , <i>Bromoviridae</i>	Aphids	Worldwide, sporadic in potato
<i>Alfalfa mosaic virus</i> (AIMV)	<i>Alfamovirus</i> , <i>Bromoviridae</i>	Aphids	Worldwide, sporadic in potato
<i>Tomato leaf curl New Delhi virus</i> (ToLCNDV)	<i>Begomovirus</i> , <i>Geminiviridae</i>	Whiteflies	India
<i>Tomato severe rugose virus</i> (ToSRV)			Brazil
<i>Tomato yellow vein streak virus</i> (ToYVSV=PDMV)			Brazil, Argentina
<i>Tomato mottle Taino virus</i> (ToMoTV)			Cuba
“ <i>Solanum</i> apical leaf curl virus” (SALCV)			Peru, only reported once
<i>Potato yellow mosaic virus</i> (PYMV)			Carribean
<i>Beet curly top virus</i> (BCtV)	<i>Curtovirus</i> , <i>Geminiviridae</i>	Leaf hopper	Americas, Europe, Asia under dry conditions

(continued)

Table 11.1 (continued)

Virus ^a	Genus, family	Transmission	Distribution
<i>Potato mop-top virus</i> (PMTV)	<i>Pomovirus</i> , <i>Virgaviridae</i>	Spongospora	Americas, Europe, Asia in cool and humid environments
“Colombian potato soil-borne virus” (CPSbV)		Spongospora?	Colombia, isolated from potato soils;
“Soil-borne virus 2” (SbV2)		Spongospora?	CPSbV could infect potatoes symptomless
<i>Tobacco rattle virus</i> (TRV)	<i>Tobravirus</i> , <i>Virgaviridae</i>	Nematodes	Worldwide, common in cool climates, or Australia
<i>Tobacco mosaic virus</i> (TMV)	<i>Tobamovirus</i> , <i>Virgaviridae</i>	Contact	Worldwide, rare on potato
<i>Tomato mosaic virus</i> (ToMV)			Europe, Andes, rare on potato
<i>Tobacco necrosis virus</i> (TNV)	<i>Necrovirus</i> , <i>Tombusviridae</i>	Fungus	Worldwide, rare on potato
<i>Sowbane mosaic virus</i> (SbMV)	<i>Sobemovirus</i> , unassigned	Contact	Worldwide, rare on potato
SB26/29 “potato rugose stunting virus”	Torradorvirus-like, <i>Secoviridae</i>	Psyllids	Southern Peru
<i>Potato yellow dwarf virus</i> (PYDV)	<i>Nucleorhabdovirus</i> , <i>Rhabdoviridae</i>	Leafhoppers	North America, has become rare
<i>Eggplant mottle dwarf virus</i> (EMDV)		Aphids	Europe, Africa, Asia, occasionally infects potatoes
<i>Cauliflower mosaic virus</i> (CaMV)	<i>Caulimovirus</i> , <i>Caulimoviridae</i>	Aphids	Intercepted once in potato from South America
<i>Potato spindle tuber viroid</i> (PSTVd)	<i>Pospiviroid</i> , <i>Pospiviroidae</i>	Contact, aphids (when co infecting with PLRV)	Worldwide
“Potato stunt virus” (PStV)	?	?	Europe

^aOfficially accepted virus species names italicized, whereas unofficial names are between quotation marks and not in italics

are currently only of minor importance anywhere in the world. PVY (see Table 11.1 for virus acronyms) and PLRV are now the most damaging viruses of potato worldwide, with PVY having overtaken PLRV as the most important. Tuber yield losses are caused by either of them in single infections and can reach more than 80% in combination with other viruses. PVX occurs commonly worldwide and causes losses of 10–40% in single infections and is particularly damaging in combination with PVY or PVA. This is due to its synergism with both potyviruses leading to tuber yield losses of up to 80%. PVS also occurs commonly worldwide but generally causes only minor tuber yield losses unless severe strains are present or it occurs in mixed infection with PVX. PVA can cause yield losses of up to 40% by itself but is far less prevalent than PVY, PVS, or PLRV. PVM is relatively uncommon in most

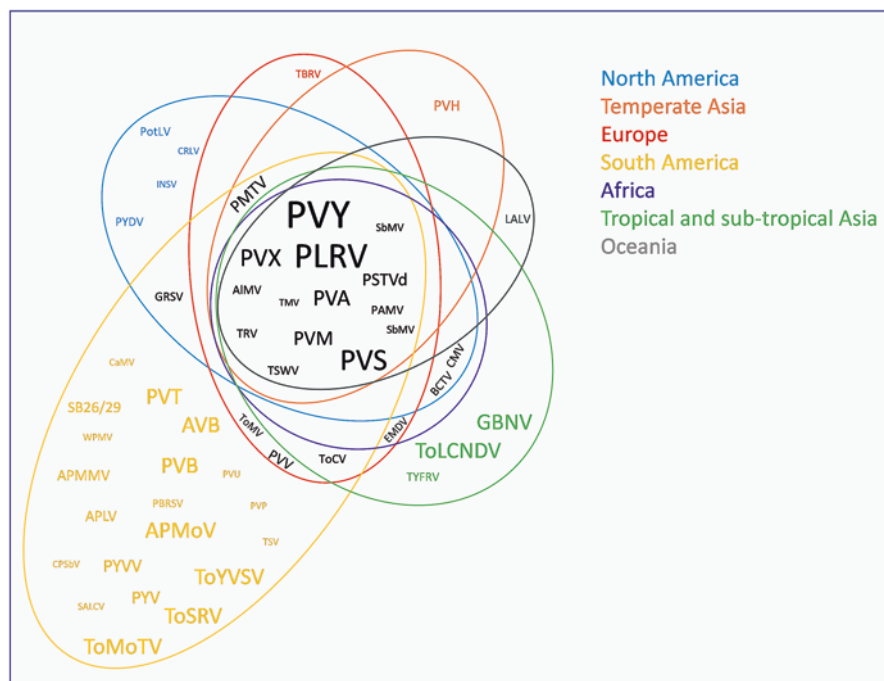


Fig. 11.1 VENN diagram of geographic occurrence of commoner potato viruses worldwide. Their relative importance/incidence globally, or regionally in case they are geographically restricted, is illustrated by the size of the virus acronym. See Table 11.1 for virus acronyms

countries and, like PVS, mostly causes only minor tuber yield losses, except in mixed infection with PVX or other viruses.

Besides yield reduction, several viruses cause economic losses by affecting potato quality, particularly by inducing internal and surface tuber necrosis. PLRV sometimes causes necrosis of the tuber vascular system known as “net necrosis.” Tuber necrosis, consisting of necrotic rings or arcs in the flesh, sometimes develop with the thrips-transmitted virus TSWV, and with soil-borne viruses like nematode vectored TRV (Sahi et al. 2016) and protist-transmitted PMTV (Abbas and Madadi 2016). TSWV generally infects potato in warmer regions but TRV and PMTV both occur globally in cooler regions where their vectors are established. Certain phylogenetically defined recombinant strains of PVY cause similar necrotic symptoms known as “potato tuber ringspot disease.” Over the last three decades, these have caused particularly heavy economic losses to potato industries in Europe and North America as well as in many developing countries in Asia and South America but have not yet reached all parts of the world, e.g. south-west Australia (Kehoe and Jones 2016) or Peru (Fuentes et al. 2019a). Therefore, PVY “strains” have been heavily studied worldwide over the past two decades revealing an exceptional amount of variation and a plethora of genotypes, many of them recombinants. PVY “strains” separate into at least 13 different subgroups defined either biologically or by phylogenetics (Karasev and Gray 2013; Kehoe and Jones 2016; Glais et al. 2017; Gibbs et al. 2017).

Biological strains of PVY are differentiated by the phenotypes they develop when different strain-specific hypersensitive HR resistance genes are present in potato cultivar differentials and whether they introduce necrotic symptoms in tobacco. Strain groups PVY^C, PVY^O and PVY^Z elicit HR phenotypes with hypersensitivity genes *Nc*, *Ny*, or *Nz*, respectively. Strain groups PVY^N and PVY^E overcome all three hypersensitivity genes, but differ in the phenotypes they induce in tobacco, only PVY^N eliciting veinal necrosis (Chikh-Ali et al. 2014; Karasev and Gray 2013; Rowley et al. 2015; Kehoe and Jones 2016; Jones and Vincent 2018). Such biological strains do not necessarily coincide with the phylogenetic lineages named after them. For example, previously potato biological strain groups PVY^C and PVY^O were thought to coincide with major lineages PVY^C and PVY^O, respectively. However, this proved incorrect as isolates within biological strain group PVY^D fitted within phylogroup PVY^C and those in PVY^Z within phylogroup PVY^O (Kehoe and Jones 2016; Jones and Vincent 2018). As the number of complete PVY genome sequences from different world regions grows, phylogenetic nomenclature based on biological, geographical, and sequence names is becoming increasingly unsustainable so substituting Latinised numerals for current PVY subgroup names was suggested (Jones 2014; Kehoe and Jones 2016; Jones and Kehoe 2016). Biological strains of PVA and PVV are also differentiated by the phenotypes they develop with strain-specific hypersensitive resistance genes present in potato cultivar differentials, but their phylogenetics is little studied. PLRV strains are differentiated biologically based on the severity of symptom expression in potato, but are phylogenetically very homogenous with limited sequence variation between isolates worldwide.

Potato spindle tuber disease caused by a viroid, PSTVd also impairs tuber quality in addition to direct yield loss. Although it led to several disease outbreaks in potato in different parts of the world in the past, through implementation molecular detection and eradication programs its presence in potato has now been significantly diminished in North America and Europe. By contrast, PSTVd is still prevalent in Central-Asia (CIP, unpublished) and China (Qiu et al. 2016). Although PSTVd presence in potato has declined recently globally, the opposite is the case for tomato where outbreaks have been increasing due to its worldwide spread in tomato seed via the international seed trade (Constable et al. 2019). This is of concern for global potato production as tomato PSTVd can cause severe yield and tuber quality losses in potato (Mackie et al. 2019). Additional collateral damage can be caused by virus infections as was demonstrated for PVY infection, which compromises plant defense responses rendering them more vulnerable to Colorado potato beetle (*Leptinotarsa decemlineata*) attack (Petek et al. 2014). Similarly, Lin et al. (2014) found that PVS infection rendered late blight (*Phytophthora infestans*) resistant cultivars more susceptible to late blight.

Among the most important viruses PVY, PLRV, PVA, PVS, and PVM are all aphid-transmitted. All of these except PLRV are transmitted nonpersistently by aphids, whereas PLRV is persistently transmitted. Insecticides have long been known to be effective only against persistently transmitted viruses, which likely explains the decline in prevalence observed in PLRV over the last 50 years in devel-

oped and emerging economies. Thrips- and whitefly-transmitted viruses continue to cause outbreaks in potato in warmer climatic regions. These outbreaks are usually only occasional, but TSWV is found commonly infecting potatoes in some countries, e.g. Australia and Argentina such that it is among the common viruses tested for in seed potato production schemes. Such outbreaks of thrips and whitefly-transmitted viruses are becoming steadily more frequent due to a warming climate, and at least one of these viruses, ToLCNDV has recently become a major potato pathogen in India (Jeevalatha et al. 2017a).

Recent phylogenetic studies, that use dating programs to compare the complete genomic sequences of common potato virus isolates, obtained at different times, are providing new insights into their evolution. So far, this has only been done with PVY and PVS (Gibbs et al. 2017; Santillan et al. 2018). Gibbs et al. (2017) inferred the phylogeny of the genomic sequences of 240 PVY isolates collected since 1938, 42% of which were nonrecombinants; sequences from the Andean region were lacking. The nonrecombinants all fitted into major lineages C, O, and N, and recombinants all into lineages R-1 and R-2. The main parents of R-1 and R-2 were PVY^N or PVY^O, respectively, and vice versa for their minor parents. The minor phylogroups within these major lineages [roman numerals in parentheses are from PVY classification system of Kehoe and Jones 2016] were: C with C1(II) and C2(III); O with O (=I) and O5 (=X); N with Eu-N (=IV), XIII and NA-N (=IX); R-1 with NTN-NW + SYR-I (XII), NTN-B (VI), NTN-NW + SYR-II (XI), N-Wi (VII), and N:O (VIII); and R-2 with NTN-A (V). Analysis of the nonrecombinant genomes found the estimated “time to most recent common ancestor” (TMCRA) for PVY to be around 1000 CE which corresponds with the end of the Tiahuanaco and start of the Inca civilizations in the Andes. A more comprehensive study including Andean PVY sequences recently found that PVY-N (=III) could be divided into three phylogroups (N1, N2 and N3), and two of them were unique to the Andes, suggesting PVY-N originated from the Andean region in contrast to PVY-O for which no such evidence could be found (Fuentes et al. 2019a).

Santillan et al. (2018) studied the phylogenetics of PVS genomic sequences collected since 1976, including Andean region sequences. The nonrecombinant genomes belonged to three major PVS lineages, two evenly branched and predominantly South American and a non-South American one with a long basal branch and many distal subdivisions. The South American lineages contained isolate sequences from three cultivated potato species, pepino (*Solanum muricatum*) and arracacha (*Arracacia xanthorrhiza*), whereas only isolates from a single cultivated potato species (*Solanum tuberosum*) were present in the other lineage. The two nodes of the basal PVS trifurcation were dated at 1079 and 1055 CE corresponding with the end of the Tiahuanaco and well before the start of the Inca civilizations, and the basal node to the non-SA lineage at 1837 CE corresponding roughly with the start of the European potato famine caused by late blight (*Phytophthora infestans*). The PRDV/PVP cluster diverged from PVS 5–7000 years ago. This suggests a potato-infecting proto-PVS/PRDV/PVP emerged in South America, and spread into a range of local *Solanum* and other species, one early lineage spreading worldwide in potato.

Kutnjak et al. (2014) studied the phylogeny of PVX genomic sequences from the Andes. What they found was similar to the PVS situation with three major lineages, two of which were South American and one non-South American. However, an earlier study with PVX coat protein gene sequences had found several European and North American sequences in the single major South American lineage known at that time, and their presence was confirmed by Kutnjak et al. (2014).

At least 37 of the known potato viruses are found in South America and this number is set to increase further with the application of high-throughput sequencing (HTS) techniques to screen for virus infections (Kreuze 2014; Fuentes et al. 2019b; CIP, <http://potpathodiv.org/>). Only the above-mentioned viruses and PAMV have so far established themselves globally as potato infecting viruses, whereas most of the other global viruses may be the result of generalist viruses that have managed to become established in potatoes, or more recent newcomers from related crops that have achieved a foothold in potato due to increasing vector populations, principally whiteflies (crini- and begomoviruses) and thrips (tospoviruses). At least 20 potato viruses remain restricted to South America and most of these represent viruses that evolved together with wild and/or cultivated potatoes in the Andean region.

11.2.1 Viruses in the Andean Region

Cultivated potatoes were first domesticated in the Andean region of South America where they show the highest level of genetic diversity including four cultivated potato species with various ploidy levels and many native cultivar groups and wild potato relatives. Their viruses evolved with them and it is therefore not surprising that more viruses are found infecting potatoes in this region than elsewhere in the world (Fig. 11.1). Besides the usual viruses associated with potato production throughout the world and which were distributed globally through infected tubers, the Andean region hosts several unique viruses that do not seem to have established themselves beyond their geographical region of origin. These include the nepoviruses PBRSV, PVU, and PVB, the tymoviruses APLV, APMMV, the Ilarvirus PYV, the crinivirus PYVV, the cheravirus AVB, and the tepovirus PVT. HTS-based approaches have recently also detected the presence of new viruses corresponding to at least 14 different genera (Fuentes et al. 2019b; CIP, <http://potpathodiv.org/>). Many of the Andean potato viruses have also been reported infecting other root and tuber crops that are grown in the same environments as potatoes, such as Ulluco (PVS, PVT, PLRV, AVA, APLV/APMMV), Oca (PBRSV, PVT, AVB), Mashua (PVT), Aracacha (PVS, AVA, AVB, PBRSV) & Maca (APLV/APMMV), and in the solanaceous bush fruit pepino (PVS). These are crops from such diverse species that it is likely many wild hosts may also be infected constituting a continual environmental reservoir for these viruses present in the absence of cultivated plant hosts. In addition, the viruses commonly found in other parts of the world often show much higher level of variability in the Andean region (Gil et al. 2016a, b; Kalyandurg

et al. 2017; Santillan et al. 2018; Gutierrez et al. 2013; Gibbs et al. 2017; Henao-Díaz et al. 2013).

In the pre-ELISA era, surveys to establish the occurrence of potato viruses in Andean countries mostly involved potato germplasm collections, but in the 1970s Peruvian potato crops were widely sampled. They were undertaken using older serological detection assays and inoculation to indicator hosts complemented by electron microscopy. The viruses found in that era included nine also found in Europe and North America (PLRV, PVX, PVY, PVV, PVS, PVA, PVM, PMTV, PAMV) and eight others only found in Andean countries (APLV, APMoV, PVT, AVB, PBRV, PVU, PYVV, WPMV) (Jones 1981, references therein). Since the 1980s, surveys have been conducted using ELISA to detect the most common potato viruses (PVY, PVX, PVS, PLRV, APMoV, APLV) in potatoes growing at higher altitude (>3000 m) in the Peruvian highlands. The most frequently detected viruses have consistently been contact-transmitted with PVX (30–82% incidence) and PVS (20–50%) being the commonest followed by APMoV (4–15%) and APLV (2–6%). Similar viruses and incidences were found in higher altitude plantings in Ecuador where PYVV was also found occurring at low frequency (0–3% incidence). In contrast, PLRV and PVY were usually only detected at 0–5% in these materials and, when included, PMTV was uncommon (Pérez Barrera et al. 2015). When similar surveys were undertaken at lower altitudes in the Andean region (<3000 m), the findings resembled those in other areas of the world, with PVY and PLRV dominating. The differences in PVY and PLRV incidences between potato crops growing at different altitudes likely reflects the greater abundance of their aphid vectors below 3000 m.

Whereas the potyviruses PVY, PVA, and, to a lesser extent, PVV are established worldwide, another potato potyvirus, WPMV has never been reported infecting cultivated potato even in the Andean region. So far, it has only been reported from a wild potato species growing in an isolated Lomas ecosystem and the cultivated bush fruit crop pepino both in the coastal desert in Peru (Fribourg et al. 2019). In earlier studies, when Andean potato cultivars were inoculated with PVY isolates belonging to biological strain groups PVY^C, PVY^O, PVY^Z, and PVY^N, one developed HR phenotypes consistent with presence of genes *Nc* and *Ny*, one an HR phenotype consistent with gene *Nc* alone, and 1 with neither, so both genes were easily found in commercial cultivars in potato's original center of domestication. With European potato cultivars inoculated at the same time, the corresponding figures were six with *Nc*, six with *Ny* and one with neither. An HR phenotype consistent with *Nz* presence and an ER phenotype consistent with *Ry* presence developed in two cultivars each. There is still a need to determine how common resistance genes *Ry*, *Nc*, *Nz*, *Ny*, and putative *Nd* are among Andean potato cultivars and the degree of protection they provide against PVY in Andean potato crops. This applies not only to commercial plantings grown with or without access to healthy seed programs but also to Andean native potato landraces belonging to the four potato species that grow in Andean subsistence plantings (Jones 1981; Jones and Vincent 2018).

The potexvirus PVX consists of four biological strains differentiated by their phenotypic reactions when they infect potato cultivars with strain-specific hyper-

sensitive resistance genes *Nx* and *Nb*. Group 1 strains fail to overcome either gene, group 2 strains overcome *Nx*, group 3 strains overcome *Nb*, and group 4 strains overcome both genes. All four strain groups occur in the Andean region, along with an additional strain (HB) that has not been reported elsewhere in the world, which overcomes not only these two genes but also extreme PVX resistance gene *Rx*. PVX^{HB} caused a mild or symptomless infection in eight native potato landraces, systemic necrotic symptoms in cultivar “Mi Peru,” and bright yellow leaf markings in “Renacimiento.” Phylogenetic analysis of coat protein gene sequences placed HB in the major PVX lineage that contained group 2 and 4 isolates from South America, North America, or Europe, whereas strain group 1, 3, and 4 sequences, none of which were from South America, were in the main lineage that lacked any South American sequences. Thus, only strain group 4 sequences were in both lineages (Kutnjak et al. 2014).

Three carlaviruses have been reported infecting potatoes in South America (PVS, PVM, and PRDV). Early PVS isolates from the Andean region caused systemic infection in *Chenopodium quinoa*, but isolates from elsewhere only infected its inoculated leaves. The former were therefore called Andean strain (PVS^A) and the latter ordinary strain (PVS^O). However, PVS^A was found subsequently in many countries (Jones 2014, references therein), and, more recently, PVS^O was found in the Andean region (Santillan et al. 2018). These biological defined strains are not coincident with phylogenetically defined PVS strains as PVS^O occurs in both South American and non-South American lineages (Santillan et al. 2018). A new strain of PVS was recently found infecting Arracacha (Santillan et al. 2018; de Souza et al. 2018). The carlavirus PVM has been reported from Bolivia, Chile, and Peru and in the Andean region of northern Argentina, but in recent surveys is conspicuously absent from Peru. The carlavirus PRDV on the other hand has been reported only from Argentina and Brazil (PVP isolate) and probably infected potato from indigenous hosts as they have not been reported from the Andean region, although in evolutionary terms PRDV and PVP are considered likely ancestral parents of PVS from this region (Santillan et al. 2018).

Several nepoviruses infect potatoes in the Andes all of which were originally isolated from potato plants showing calico symptoms (Fig. 11.2), although none of them have been linked to this syndrome by reproducing the symptoms in experimentally infected potato plants. The first was discovered simultaneously by two research groups who separately named it PBRV and the calico strain of TRSV. Subsequently, however, the virus was shown not to be TRSV (Souza Richards et al. 2013) so only the name PBRV remains in use. PVB was recently reported infecting potatoes in Peru (de Souza et al. 2017) where it is now known to be relatively common (Fuentes et al. 2019b; CIP, <http://potpathodiv.org/>). Although PVB was first identified from plants showing calico symptoms, these symptoms were not necessarily caused by it as other viruses, such as PVX, were also present. The virus has not yet been characterized biologically and its impact on tuber yield is unknown. Another subgroup C nepovirus, PVU, was isolated previously from potatoes with calico symptoms in central Peru, but sequence comparison distinguished it from PVB (de Souza et al. 2017).



Fig. 11.2 Field with typical calico and yellowing symptoms, typically associated with nepoviruses, in the highlands of Peru. Photo credits: CIP

The comovirus APMoV (family *Secoviridae*) was identified infecting potato in Peru, Argentina, and in Brazil where it was also found infecting eggplants. In Peru, it was relatively common and widespread in the past based on ELISA results, but in a recent survey using HTS, was not commonly encountered (Fuentes et al. 2019b; <http://potpathodiv.org/>); it is transmitted by beetles of the genus *Diabrotica*, as well as by seed and contact. It also occurs outside South America having been found infecting tabasco peppers in Honduras in Central America.

The tymoviruses APLV and APMMV (family *Tymoviridae*), which was recently separated from APLV (Kreuze et al. 2013; Koenig and Ziebell 2013), have been identified in potato germplasm from Colombia, Ecuador, Peru, and Bolivia. Nevertheless, they seem to be becoming less common in field grown potatoes in the Andean region than when they were first found in the 1970s.

PVT is the only known member of the genus *Tepovirus* (family *Betaflexiviridae*). It has been detected not only in Peruvian, Bolivian, and Chilean potato germplasm, but also ulluco (*Ullucus tuberosus*), oca (*Oxalis tuberosa*), and mashua (*Tropaeolum tuberosum*) plants growing in the field in these countries. It is transmitted through contact and potato true seed, but causes only mild mosaic or no symptoms in potato plants and seems relatively uncommon (Lizárraga et al. 2000).

Two ilarviruses (Family *Bromoviridae*), AIMV and PYV, both sometimes infect potatoes in the Andean region. Whereas AMV is found worldwide and normally causes calico symptoms, including in the highlands of Peru, PYV is largely symp-

tomless and restricted to the Andean region where it has been identified in germplasm from Ecuador, Peru, Bolivia, and Chile.

PYVV (genus *Crinivirus*, family *Closteroviridae*) causes obvious veinal yellowing symptoms, which were first seen in an early Andean potato germplasm collection in Europe. It has been known in Colombia for many years (Jones 1981, references therein; Franco-Lara et al. 2013). PYVV is thought to have originated from the Andean region of Northern Ecuador and Central West Colombia and causes up to 50% yield losses. It is transmitted in a semi-persistent manner by the greenhouse whitefly (*Trialeurodes vaporariorum* Westwood; *Hemiptera: Aleyrodidae*) (Salazar et al. 2000), through tuber seed and underground stem-grafts. It also infects tomatoes and various weed species. The virus also occurs in potato-producing areas of Northern Peru, and in the Venezuelan Andes, and recently spread to Panama in Central America (CIP, unpublished). Its whitefly vector occurs globally so it could spread to other continents. Its prevalence in plantings at lower altitudes in the Andes reflects the restriction of its whitefly vector to warmer conditions (Jones 2016, references therein).

A begomovirus PALCV was reported infecting potatoes and wild solanaceous hosts from the highland jungle region of central Peru in the late 1980s (Hooker and Salazar 1983). Although apparently relatively common at the time, the original isolates were lost and the virus was never found again in the same region. On the other hand, during the late 90s a novel virus coded SB-26/29 and transmitted by brown leafhoppers (*Russelliana solanicola*) was associated with a novel and rapidly spreading rugose stunting disease in Southern Peru. The disease caused yield reductions of 20–90% (Tenorio et al. 2003). The disease has now become rare, likely due to changes in cropping patterns that led to reduction in leafhopper populations. Partial sequence determination identified this virus as related to torradoviruses (CIP, unpublished), and recent surveys (Fuentes et al. 2019b; <http://potpathodiv.org/>) in Peru indicate it, and related viruses, can still be found with some frequency in potatoes. In Colombia, two new Pomoviruses related to PMTV were identified in soil samples from potato fields (Gil et al. 2016b). At least one of them (CPSbV) was shown to infect potatoes and transmitted through tubers, but the virus could only be detected in roots, and the plants were without symptoms.

11.2.2 Brazil

In Brazil, the potato is grown throughout the year, in three successive crops: rainy season, with harvest from December to March, with more than 50% of the total production; dry season, with harvest from April to August, representing about 30% of production, and winter season, with harvest from September to November, with lower production volume (IBGE 2017). The positive aspect of three harvesting seasons is a supply of fresh potatoes on the market throughout the year. However, this year-long field production also means a greater opportunity for uninterrupted spread of insect-transmitted viruses. This is a major factor why Brazil imports virus-tested

seed-potato stocks from abroad annually, especially from Netherlands, Germany, France, Canada and Chile. This frequent importation has, historically, allowed the introduction of new pathogens into the country.

A first report of potato cultivation in Brazil dates from the 1920s in São Paulo, and since extended to other neighboring states of the South and Southeast, and later further expanded to the Northeast and Central-West regions. However, the largest production still occurs in the South and Southeast regions, with the State of Minas Gerais ranking as the first, with about 1.3 million tons/year (Agrianual 2016). Since the beginning of potato cultivation in Brazil, *Potato leafroll virus* (PLRV) had always been the most important viral agent associated with seed-potato tuber degeneration (Souza-Dias et al. 2013). The predominance of PLRV among seed-potato viruses in Brazil lasted until the mid-1990s, when two new strains of PVY were introduced, nearly simultaneously, through seeds imported from countries where their incidence was already known. After their introduction, this virus became a major cause of rapid seed-potato degeneration, overtaking the historical importance of PLRV as main cause for rejecting early field generations (G-1 or G-2), based on tolerance limits for viruses of the Federal Brazilian seed-potato tuber production-certification program.

As mentioned, PLRV has shown high incidences in Brazilian potato fields in the past. Until the mid 1990s it was normal for qualified and traditional seed-potato producers to face high incidences of PLRV (over 20%) in the very first (G-1) field multiplication of imported seed-potato stocks, which are officially considered, in Brazil, as G-0 (Souza-Dias et al. 2016a). This traditional and prevalent virus problem started to decline, coincidentally in space and time with the introduction and fast outbreak of new PVY strains detailed below.

A possible reason for the shifting from PLRV to PVY was that seed-potato producers had over the years become more conscious regarding PLRV infected plants, learning to recognize its symptoms such as interveinal yellowing and rolled leaves, but did not recognize or understand the relevance of new symptoms such as mosaic, chlorosis and leaf deformation characteristic of PVY. As PVY expanded in association with the introduction of imported potato seeds, this virus soon became the major cause of seed-potato tuber degeneration (Barrocas et al. 2000). To counter this, a more intensive and efficient action toward controlling aphids, including the use of new insecticides such as neonicotinoids, took place. The vector transmission mechanism of PLRV (persistent circulatory, requiring significant time for acquisition and transmission) and PVY (nonpersistent, almost immediate transmission) would be more affected by the insecticidal effect, which could explain the noticeable reduction in the field incidence and spread of PLRV, whereas it is well known that insecticides have limited effect on nonpersistently transmitted viruses such as PVY. Nowadays, the detection of PLRV in seeds within official certification programs is extremely rare. In the State of Minas Gerais, as well as in most of the potato producing states, PLRV has not been associated with the rejection of seed lots since the beginning of the new millennium. However, imported seed potatoes are a big concern; Villela et al. (2017), testing national and imported potato seeds, found virus incidences as high as 10% in seed potatoes imported by Brazil.

The probable first report of PVY necrotic strain (PVY^N) in South America was in the beginning of 1940s (Nóbrega and Silberschmidt 1944). They studied some PVY isolates from Peru, inducing vein necrosis in leaves of tobacco. It took 20 years before a first official scientific report on PVY in Brazil was published in Sao Paulo State (Kitajima et al. 1962) where the authors describe the virus particle morphology and the histological symptoms. During the following years, although PVY was not considered a major problem for Brazilian potato producers, attempts to discover new methods to avoid PVY infection and to find new indicator plants were carried out in Brazil.

Surveying for PVY isolates in experimental fields, Andrade and Figueira (1992) detected five different strains, based on the reactions induced in the tobacco cultivar “Turkish NN.” Although PVY^N was present, the PVY^O strain had a much higher incidence and was identified in almost all cultivars planted during 1980–1990. The investigation of PVY strains, done between 1983 and 1988, showed the presence of PVY^O in 80% of samples infected with PVY collected in experimental fields, planted with “Achat,” “Baraka,” “Baronesa,” “Bintje,” “Granola,” and “Mona Lisa” cultivars. On the other hand, the incidence of PVY^N ranged from 0 to 12.4%. Even if present, PVY was never found in high incidences in fields of either ware or seed potatoes. Possibly the strains present in the country at that time were not as easily spread as the PVY strains introduced in Brazil in mid-1990s.

It is considered that the first significant introduction of a new PVY strain into Brazil came with seed potatoes of the cultivars “Achat” and “Baraka” imported from Germany, where it encountered optimal conditions for dissemination. This strain was later recognized as being the Wilga strain of PVY (PVY-N^{wi}; Galvino-Costa et al. 2012). All over the country, where seeds of these cultivars were used, large outbreaks of PVY were soon observed, reaching incidence rates above 70% in plants produced from infected seeds. A second introduction is suggested to have occurred through imported seed-potato of cv. Atlantic from Canada. It was later confirmed to be PVY^{NTN}, which causes necrotic rings in tubers of susceptible cultivars, such as “Monalisa”. This strain also adapted itself very well to the Brazilian conditions, spreading rapidly to all potato growing regions (Galvino Costa et al. 2012). The introduction of these two strains brought a major problem to the potato growers who were used to plant cvs “Achat”, “Baraka”, and “Bintje”, and easily recognized PLRV infected plants as showing, symptoms of leaf roll and yellowing of the lower leaves, but not chlorosis and mosaic that started appear as new PVY strains expanded. In 1995, in Minas Gerais, the seed-potato areas under certification were covered by more than 50% with cvs “Achat” and “Baraka,” and a little less than 18% with “Bintje”. Due to the increasing incidence of new PVY strains, these cultivars were abandoned, and only 3 years later, in 1998, little more than 15% of the potato seed production area was planted with those three potato cultivars. Conversely, where “Monalisa”, a ware potato, used to occupy only around 5% of the certified area, it rose to about 29%. By 2000, “Monalisa” reached more than 50% of the production area, after which PVY^{NTN} began to spread rapidly, mainly associated to regions where “Atlantic” was grown, implicating it as the source of introduction of PVY^{NTN}. Due to a high susceptibility to PVY^{NTN} and sensitivity to the typical super-

ficial tuber necrotic rings, “Monalisa” rapidly became unmarketable. Soon after in 2001, the Dutch cv “Agata” began to be tested and gained broad acceptance among the producers due to its high productivity, marketable phenotype, soil adaptability, and resistance to different PVY strains (Ramalho et al. 2012). The lack of expression of PVY^{NTN} symptoms in tubers of “Agata”, in striking contrast to “Monalisa”, contributed much to the fast replacement of “Monalisa” by “Agata”. Thus, 4 years later, “Agata” was occupying over 30% of the area planted in Minas Gerais and nowadays is the main cultivar planted in Brazil (Silva et al. 2015).

Early characterization of PVY strains in Brazil was based on host symptoms, and the serological tests employed were DAS-ELISA which did not identify specific strains. The first serological tests using monoclonal antibodies and molecular studies started in the 1990s, confirming the presence of PVY^{N-Wi} and PVY^{NTN} strains in Brazil. Based on the reaction of PVY isolates to monoclonal antibodies, and on the symptoms shown by host plants, a great variability among them became evident (Galvino-Costa et al. 2012). More recent investigations (authors, unpublished data) have shown that there is a large abundance of PVY isolates with uncommon serology and that apparently N and O strains have disappeared from the Brazilian fields. Galvino-Costa et al. (2014) found that the incidence of PVY^{N:O/N-Wi} was either equal to or greater than that of PVY^{NTN}, depending on the region in which the tubers have been produced and that mixed infections with both strains occur often, although this is sometimes only detectable with more sensitive techniques, such as RT-qPCR.

“Agata” has reached about 80% of the potato producing areas in Brazil and being a symptomless carrier of PVY, it acts as an efficient silent disseminator of the virus, particularly among “home saved” (not certified) seed-potato producers. This scenario has been a serious sanitary problem for potato production in Brazil, as it is strongly correlated with the successive increase of PVY reservoir, favoring spread of this virus into certified seed-potato fields.

Two other viruses that have been monitored in the field by the official certification programs are PVS and PVX. The incidence of these viruses in the field is sporadic and has never been associated with crop losses in Brazil. However, their monitoring is because some countries that export seed potatoes to Brazil have high incidences of these two viruses in the field (Souza-Dias et al. 2016a). If potato seeds with high PVS/PVX incidence reach Brazil, where high incidence of PVY usually occurs, the consequences could be disastrous. Recent surveys have shown incidences as high as 10% of PVX and 20% of PVS in imported potato seeds (Villela et al. 2017).

An increasing number of potato fields showing over 50% of typical PLRV-like symptoms, brought concerns about a possible PLRV outbreak, associated with whitefly instead of with aphids as virus vector. However, later on it was identified as ToCV (Souza-Dias et al. 2013; Lima 2016). The field symptoms of ToCV are characterized by internervial chlorosis and slight curling of the leaf edges, which begin in the apical leaves. ToCV can be transmitted by at least five species of whitefly (Orfanidou et al. 2016). In recent years an outbreak of the whitefly *Bemisia tabaci*, has been noticed in potato crops in Brazil (Moraes et al. 2017), favoring the spread of ToCV, probably from infected tomato plants in the vicinity. Despite of

continued reports of whitefly infestation in Brazilian potato fields over the past 5 years, high occurrences of ToCV have been associated with tomato but not with potato crops (Orfanidou et al. 2016). Some outbreaks in potato have been reported in certain areas such as in the states of Goiás and São Paulo (Souza-Dias et al. 2013). However, at least for the time being, it does not appear to be a recurring problem for this crop. Thus, special care is being taken to monitor this disease in the field, as well as other whitefly-transmitted viruses, also reported in commercial Brazilian potato fields (see below).

The overlapping cropping cycles of tomato and potato, combined with favorable climatic conditions and the frequent proximity between the areas where they are planted, has caused other tomato viruses to occasionally migrate into potato crops. Two species of *Begomovirus* (family *Geminiviridae*) have been described in potato in Brazil: *Tomato yellow vein streak virus* (ToYVSV) and *Tomato severe rugose virus* (ToRSV). ToYVSV and ToRSV, the latter which has been prevailing in tomato crops, seems to be also prevalent in potato fields and both inducing similar deforming yellow mosaic symptoms (Souza-Dias et al. 2016a). The vector of both viruses is also the whitefly *Bemisia tabaci* (Pantoja et al. 2014). In contrast to what has been normal for tomato producing areas in Brazil, so far, there has not been any record of widespread begomovirus outbreaks in Brazilian potato producing areas. However, considering they are whitefly-transmitted viruses, and the high populations of whiteflies observed in potato crops in recent times (Moraes et al. 2017), careful monitoring of begomoviruses in potato should take place, as recommended for ToCV.

Tospoviruses, whose type member is *Tomato Spotted wilt virus* (TSWV), are transmitted by several species of thrips in a persistent manner. The viruses are acquired only at larvae stage, replicate in the insect vector and persist through the several stages of its life cycle (Rotenberg et al. 2015). They have always had a sporadic occurrence in potato crops in Brazil; but, in general, they are recorded as current season infection, and not as seed-tuber perpetuated virus. Therefore, they were never considered important as causing damage to this crop. However, from 2010 to 2015 there was a long period of drought in the Southeast of Brazil, with a significant increase in temperature, contributing to the increase of viral diseases in several crops, including potato, clearly associated to the same favorable conditions for increase in vector population. Field surveys by Souza-Dias (data not published) showed a high virus incidence of tospoviruses with a rare and isolated observation of virus perpetuation between 2010 and 2015. The more common species are *Tomato spotted wilt virus* (TSWV), *Groundnut ringspot virus* (GRSV) and *Tomato chlorotic spot virus* (TCSV) (Lima and Michereff 2016). Similar outbreaks have been described elsewhere, such as in Argentina (Salvalaggio et al. 2017) and United States of America (Abad et al. 2005).

As a norm, usually not all stems of a plant-hill show tospovirus symptoms: potato tubers are not only symptomless but also tospovirus-free, even when produced from infected plants. However, as a rare event for potato tospoviruses in Brazil, necrotic rings, both on the surface and penetrating the tuber flesh were observed in some of the tuber progeny of a tospovirus-infected plant (cv “Agata”) (Souza-Dias et al. 2016b).

The plants that emerged from these tospovirus symptomatic tubers were however free of the virus. In other countries, there has been evidences of tospovirus species perpetuating via tubers produced by infected plants. These observations cause concern for seed-potato production (Abad et al. 2005; Salvalaggio et al. 2017). Therefore, a close monitoring of the incidence of tospoviruses in Brazilian potato fields is recommended in order to control not only its dissemination in the current season but also its perpetuation by tuber seed transmission.

11.2.3 *India*

PLRV, PVY, PVX, PVA, PVS, PVM, GBNV, and PAMV are known to occur in India. ToLCNDV-[potato], a begomovirus is reported to infect potato only in India. Mosaics and leafroll are the most common and severe symptoms in the subtropical and tropical climates of India. PLRV is important and occurs widely in almost all varieties. The mosaic causing viruses, PVY, PVA, and PVM as well as severe strains of PVX occur either singly and/or in different combinations. PVA and PVM are not common. PVY^N is almost not known in India, but recent study indicates the possible presence of PVY^N and PVY^{NTN}. ToLCNDV-[potato] has emerged as a serious threat to potato production during recent times. Its incidence is reported in almost all major potato growing states (Jeevalatha et al. 2017a). GBNV is reported in the early planted crop in the central and western parts of India (Jain et al. 2004). However, its occurrence in Pant nagar (Pundhir et al. 2012) and northwestern hills of India (Raigond et al. 2017) indicates the adaptation and spread of the virus to new areas. Recently, mixed infection of CMV with other potato viruses was reported (Sharma et al. 2016). It was found mostly in association with PVX, PVYⁿ followed by PVA, PVY^{o/c}, and PVM. Rarely, it was found associated with PAMV (Ghorai et al. 2017).

PVY is an important potato virus, which occurs widely in almost all the potato cultivars in India. Severe strains of PVY have the potential to reduce yield up to 80%. In India, PVY^O is most common and PVY^C strain has also been reported earlier based on the reactions on biological indicator host. Recently, based on host reactions, serology with monoclonal antibodies and complete genome sequence, the evidence of occurrence of a recombinant strain (N:O type) of PVY (isolate PVY-Del-66) was provided for the first time (Jailani et al. 2017). Isolate PVY-Del-66 shared closest sequences identity of 97.7–99.9% and a close phylogenetic relatedness with the N:O strains reported from USA and Germany. Del-66 isolate caused necrosis in tobacco and reacted positively with the MAb to common strain PVY^O but not with necrotic or chlorotic strains of PVY (Jailani et al. 2017). PCR analysis with strain-specific primers showed the possible presence of PVY^N and PVY^{NTN} in India and is being further confirmed by biological assays (CPRI, unpublished). PVA causes mild mosaic symptoms and not common in India. It reduces yield up to 30–40% and higher in combination with PVY or PVX.

PLRV is one of the most prevalent viral diseases of potato in India. All Indian potato varieties are susceptible to this virus. Yield loss normally ranges from 20 to

50% in India but in extreme cases may be as high as 50–80%, and infected plants produce only a few, small to medium tubers in severe secondary infections. At genome level, Indian isolates are closer to European and Canadian isolates than to an Australian isolate (Jeevalatha et al. 2013a).

PVX is one of the mosaic-causing viruses in almost all varieties of potato. In India, PVX infection may depress yield up to 10–30% and in the presence of PVA or PVY reduces yield up to 40% in potato. Indian PVX isolates were characterized for their biological properties, host range and transmission. Molecular analysis of complete and partial genomes of PVX found that all Indian isolates cluster in clade 1 with isolates from Europe and Asia, and none of them with clade II from south America (Jeevalatha et al. 2016c). Amino acid analysis suggested that these isolates cannot overcome *Rx1* gene or *Nx* gene mediated resistance (Jeevalatha et al. 2016c).

Like most parts of the world, PVS and PVM also infect potato in India. The Andean strain of PVS is reported in India (Garg and Hegde 2000). Complete genome sequence of one isolate of PVM, PVM-Del-144 has been sequenced. PVM isolates from northern plains showed considerable diversity in coat protein gene region (Jebasingh and Makesh Kumar 2017).

Tomato leaf curl New Delhi virus-[potato] (ToLCNDV), a species of the genus begomovirus (family *Geminiviridae*) causes apical leaf curl disease of potato in India (Fig. 11.3). Infection leads to severe seed degeneration particularly in susceptible varieties. Primary symptoms appear as curling/crinkling of apical leaves with distinct mosaic symptoms and in case of secondary infection, the entire plant shows severe leaf curling and stunting symptoms (Jeevalatha et al. 2013b; Sohrab et al. 2013). The association of a geminivirus with potato apical leaf curl disease was first reported in northern India and the virus was named tentatively as Potato apical leaf curl virus. However, later it was confirmed that this virus is a strain of

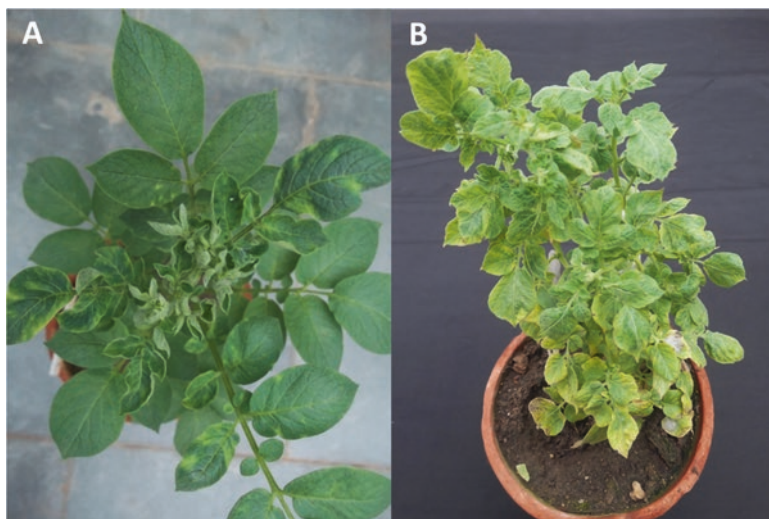


Fig. 11.3 Symptoms of primary (a) and secondary (b) infection by ToLCNDV in potato. Photo credits: CIP

ToLCNDV. ToLCNDV-[potato] is a bipartite begomovirus with two genomic components referred as DNA-A and DNA-B. The DNA A components of the ToLCNDV-[potato] isolates shared more than 90.0% similarity to ToLCNDV isolates from vegetable crops such as tomato and okra, 89.0–90.0% to papaya isolates and 70.4–74.0% to other ToLCVs (Jeevalatha et al. 2017a).

Initially, sporadic incidence of the disease was reported in 1996 at Hisar in Haryana, later severe infections were observed in western Uthar Pradesh and other parts of northern India (Saha et al. 2014). It now occurs in almost all the major potato growing states in India and is reported in all cultivated varieties with varying severity levels (Jeevalatha et al. 2013b, 2017a). All the Indian potato varieties are susceptible to this disease except Kufri Bahar, which shows lowest seed degeneration and no/mild leaf curl symptoms even under favorable field (Kumar et al. 2015) and glass house conditions (Jeevalatha et al. 2017b). The virus is transmitted by whiteflies and the infection is more common in crops planted during October than in November because of the large whitefly population. Between 40 and 75% of incidence was recorded in the cultivars grown in Indo-Gangetic plains of India, up to 100% of incidence from the Hisar (Haryana) in susceptible varieties and recently, up to 40% incidence is reported from West Bengal (Saha et al. 2014). Infection results in significant decrease in size and number of tubers. Losses in marketable yield were reported to be as high as 50% in early planted susceptible cultivars. Currently, it is one of the most important viral diseases of potato in India. Repeated use of the same seed stock for 5 years led to 44.83–60.78% yield reduction in susceptible cultivar in Hisar and seed tubers of these cultivars cannot be reused profitably for more than 2 years. Since the virus spreads through seed tubers, it is critical to ensure quality of seed tubers through effective diagnostic tools. Diagnostic protocols like nucleic acid spot hybridization (NASH), polymerase chain reaction (Jeevalatha et al. 2013b), RCA-PCR (Jeevalatha et al. 2014), qPCR (Jeevalatha et al. 2016a) and LAMP assays (Jeevalatha et al. 2018) are available for the detection of ToLCNDV-[potato] in potato. PCR is being used to screen mother plants meant for tissue culture based seed production and also stage I plants in healthy potato seed production. So far, the infection of potato by ToLCNDV is known to occur only in India.

A tospovirus, GBV causing severe stem/leaf necrosis disease in plains/plateaux of central/western India heavily infects the early crop of potato. It was first reported through morphological and serological studies by Jain et al. (2004). Stem necrosis incidence was recorded up to 90% in some parts of Madhya Pradesh and Rajasthan and up to 50% in Pant nagar. Its occurrence in northwestern hills of India despite of unfavorable conditions indicates possible adaption of the pathogen to new climatic conditions (Raigond et al. 2017).

In northwestern India leaf samples from potato plants with yellow mosaic or flecking symptoms showed positive reaction with PVX and CMV subgroup II in DAS-ELISA and the mixed infection with these viruses was further confirmed by PCR assay using specific primers and sequencing (Sharma et al. 2016). Ghorai et al. (2017) reported above 10% incidence of CMV in potato grown in Punjab. CMV infection in potato occurred mostly in association with PVX (60%), PVYⁿ (60%)

followed by PVA (40%), PVY^{o/c} (30%), and PVM (30%). Rarely, it was found associated with PAMV (10%). Severe symptoms like malformation of leaves, blistering, stunting and reduced leaf size of potato were observed when CMV was present in potato in association with other potato viruses like PVX, PVYⁿ, PVY^{o/c}, PVA, PAMV, and PVM (Ghorai et al. 2017). Since the cropping pattern in Punjab corresponds to potato during October to February followed by cucurbits from February to May, the potato serves as an over wintering host of CMV when preferred host plants are not available and CMV is transmitted from potato to cucurbits through aphids (Ghorai et al. 2017).

11.2.4 Africa

Relatively little has been published regarding the viruses infecting potatoes in Africa and the few studies performed have focused on the globally common viruses using antisera. However the same viruses, most of them commonly found elsewhere in the world, have also been found throughout the continent where surveys have been performed. Thus, in Kenya Gildemacher and coworkers (2009) tested over 1000 tubers from 11 markets in seven districts for PLRV, PVY, PVA, and PVX and found average incidences of 71%, 57%, 75%, and 41%, respectively. Mixed infections were common and only 2.4% of tubers were free of any of these viruses. In Tanzania, Chiunga and Valkonen (2013) surveyed for the occurrence of the same viruses, but also PVM and PVS in plants from 16 fields in the south western highlands and found incidences of 55%, 39%, 14% and 5% for PVS, PLRV, PVX, and PVM whereas PVY and PVM were only detected in two locations. In a survey performed in South-West Uganda during 2014, PVX and PLRV were most frequent, followed by PVY and PVM, whereas PVA was not detected (CIP/IITA, unpublished). AIMV and *Beet curly top virus* (BCTV) were found to be locally frequent in Sudan around Kartoum (Baldo et al. 2010).

Although there have been no reports of whitefly-transmitted viruses, whiteflies can be abundant in potato crops in some locations during some seasons and because potatoes are often grown in close proximity to other vegetables there is a clear risk of transfer and possibly emergence of whitefly-transmitted viruses as has already been observed in India and Brazil.

11.2.5 Europe

There are some ten viruses infecting potatoes and causing significant yield losses in Europe (Table 11.1; Fig. 11.1). The main viral pathogens include PLRV, PVY, PVA, PLRV, PVM, and PVS which are all transmitted by aphids. PVV is also aphid-transmitted but occurs only in a few cultivars. They also include PSTVd and PVX which are solely contact-transmitted, and PMTV and TRV both of which are soil-

borne and mainly cause problems in the northern more cooler countries of the continent. PLRV was formerly the most important potato virus but has been on the decline for many decades. Conversely, PVY has become the most important, especially its new necrogenic strains which often cause mild foliar symptoms that are often difficult to see in field inspections and tend to be more efficiently aphid transmitted. Their importance resides in the necrotic symptoms they induce in tubers.

One of the viruses with potential to become a serious problem in potato production in Europe could be *Tomato spotted wilt virus* (TSWV). This virus has an unusually large host range of over 1000 plant species, including potato (Bulajic et al. 2014). TSWV is transmitted by thrips preferring climates warmer than those typical for potato growing areas in Europe, which may be a reason why damage caused by TSWV in potato crops has remained mostly modest or negligible and the yield losses affect mainly greenhouse production. However, climate change is predicted to increase temperatures in Europe (Lamichhane et al. 2015), which would provide more favorable conditions for thrips to thrive outdoors in more diversified living environments.

Geographical location and climate seem to create the conditions where different potato viruses get established and spread over the years. Therefore, while the potato viruses transmitted persistently by their vectors can spread over long distances, it is not self-evident that the virus gets established in the new area. For example, PVY is found in potato crops in all potato production areas of Europe, whereas PLRV is rare in northern Europe, i.e., in Finland and the northern parts of Sweden and Norway, despite the fact that both viruses are transmitted by aphids, and transmission of PLRV in the vector aphids continues much longer than PVY. Winged viruliferous aphids carrying PLRV cross the Baltic Sea during warm weather and suitable wind, and transfer PLRV from the potato fields in northern Germany and Poland to southern Finland. Nevertheless, PLRV has not become a significant pathogen in Finland and the infection rate of PLRV in potato crops has remained negligible. Why the abundance of potato viruses is different in different parts in Europe is not fully understood, but the climatic conditions are anticipated to play a role.

Another example of differences in geographical distribution of potato viruses in Europe is PMTV. It is common in potato crops in Scotland, Northern Ireland, all Nordic countries including Denmark, and in Czech Republic and Austria, but rare in the other countries at the southern side of Baltic Sea. It was only recently detected in Poland (Santala et al. 2010). The likely means for spread of PMTV over long distances are seed potatoes produced in an area where soils are contaminated with PMTV and its vector. However, PMTV can spread over long distances also in the resting spores of *S. subterranea* adhering to tools, equipment or vehicles, and in traded materials containing soil, e.g., ornamental plants. Taking the seed potato trade between the European countries to consideration, it seems that factors which are not well-known limit establishment of PMTV and/or development of the necrotic symptoms in tubers in many areas in Europe. Learning more about those factors might also help to design means for control of PMTV.

The advanced seed potato producers in Europe base production on multiplication of pathogen-free in vitro plants of potato cultivars. In practice, the propagation material is tested only for selected viruses considered to be the most harmful and included in the phytosanitary regulations. There are new methods to ensure that the plants are free of those viruses that are not among those routinely tested. First, cryotherapy is an efficient approach to ensure that the promising potato cultivars and breeding lines are virus-free and free from phytoplasma before they are introduced to long-term maintenance in vitro (Wang and Valkonen 2009). Secondly, all known plant viruses and also related, unknown viruses can be detected by analyzing the small RNAs generated by RNA silencing, the main antiviral defense mechanism in plants. The small RNAs (21–24 nucleotides) are extracted from plant tissue, sequenced and used to assemble longer sequences (contigs) using methods of bioinformatics. Viruses in the sample are identified by comparing the contigs with sequences available in databases (Kreuze 2014). This new method called small RNA sequencing and assembly (sRSA) is as sensitive for virus detection as the widely used PCR-based methods (Santala and Valkonen 2018). The advantage of sRSA is that it detects all types of plant viruses in the same assay without need for virus-specific primers or probes.

11.2.6 Australia

The viruses so far found infecting potato in the Australian continent are PLRV, PVY, PVA, PVS, PVM, PAMV, AMV, CMV, TSWV, and *Lucerne Australian latent virus* (LALV), and the viroid PSTvD has also been found (Buchen-Osmond et al. 1988). *Beet western yellows* virus was reported infecting potato in Tasmania but later shown to be confused with PLRV. Of the viruses infecting the potato crop, the most prevalent are PLRV, PVY, PVX, PVS, and TSWV, and these five viruses are the ones tested for routinely in Australian seed potato production schemes. For many years, PVM, PAMV, CMV, and LALV have not been recorded infecting Australian potato crops, but ALMV infection typified by bright yellow calico symptoms still occurs sporadically. Soil-borne viruses, such as TRV and PMTV, that cause problems in other world regions have not yet been recorded infecting potato in Australia, although the PMTV vector *Spongospora subterranea* and TRV vectors *Trichodorus* and *Paratrichodorus* are present.

The most important potato viruses in Australia are PLRV and PVY. The PVY recombinant PVY^{NTN} has been found infecting potato crops in four eastern Australian states (Queensland, New South Wales, Victoria, South Australia) where it is causing similar problems in seed potato production to the ones it causes in Europe. However, it has not, as yet, been found infecting potatoes in Tasmania or Western Australia (Kehoe and Jones 2016). PLRV remains the most prevalent and important potato virus in south-west Australia. PVX and PVS are common contaminants detected during Australian seed potato production but their incidence is now much lower than in the past when roguing was focused on PLRV rather than viruses causing

mild foliar symptoms and no routine virus testing was done. TSWV is another common contaminant detected during seed potato production and tuber necrosis due to TSWV infection (Wilson 2001) continues to be found in ware potatoes in some states due to the common occurrence of this virus in weed hosts growing in or near to potato fields and its spread to potato plants by its thrips vector. In the last decade (2000–2010) relaxation of seed potato regulations concerning isolation from commercial potato crops in two Australian states (Victoria, Tasmania) led to a temporary upsurge in the incidence of common potato viruses in high grade seed potatoes. More thorough seed production regulations had to be reintroduced to counteract this situation.

Recent studies on potato viruses in Australia have focused mainly on PVX, PVS, PLRV and PVY. Nyalugwe et al. (2012) inoculated PVX isolates belonging to two strain groups to 38 cultivars grown in Australia to identify phenotypic responses and presence or absence of different PVX resistance genes. They also found that infection with PVX and PVS increased the titer of PVS and enhanced expression of foliar symptoms in potato plants. In a similar study with PVY, Jones and Vincent (2018) inoculated PVY^O and PVY^D to 39 cultivars to identify phenotypic responses and presence or absence of different PVY resistance genes. Coutts and Jones (2015) investigated PVY^O's contact transmissibility, stability on surfaces, and inactivation with disinfectants. It was contact-transmitted to potato foliage but not to tubers, remained infective for up to 24 h on some surfaces, and both bleach and the less caustic nonfat milk were useful PVY disinfectants.

When Cox and Jones (2010a) studied the CP nucleotide sequences of 13 PVS isolates from mainland Australia, all isolates were in phylogroup PVS^O. None of them invaded *C. quinoa* systemically so they were all in biological strain PVS^O. However, when Lambert et al. (2012) studied 42 PVS isolates from the Island of Tasmania, based on ability to invade *C. quinoa* systemically three of them belonged to PVS^A, while the others belonged to PVS^O. When their CP genes were sequenced, they all belonged to phylogroup PVS^O. Santillan et al. (2018) included two complete PVS genomes from Australia in their evolutionary study on PVS, and both belonged to the main non-South American grouping, i.e. PVS^O. When Cox and Jones (2010b) studied the CP nucleotide sequences of 11 PVX isolates from Australia, all 11 belonged to the main non-South American grouping, i.e. phylogroup I. There was no relationship between biological strain and phylogroup as phylogroup I contained PVX isolates in biological strain groups 1, 3 and 4, whereas minor phylogroups II-1 and II-2 both contained isolates in strain groups 2 and 4. Kehoe and Jones (2014) compared the biological and genomic properties of eight historical European (1943–1984) and five Australian (2003–2012) PVY isolates from potato. Based on eliciting hypersensitivity genes *Nc*, *Ny*, or *Nz*, the European isolates belonged to biological strain groups PVY^C, PVY^O or PVY^Z, whereas the Australian isolates belonged to PVY^O, PVY^Z or new strain group PVY^D which elicited putative hypersensitivity gene *Nd*. The Australian and historical European isolates all fitted in phylogroups Y^O or Y^C. Moreover, biologically defined PVY^O and PVY^Z isolates were both within phylogroup Y^O while biologically defined Y^C and Y^D isolates were

both phylogroup Y^C revealing disagreement between the current biological and phylogenetic PVY nomenclature systems.

11.3 Control of Potato Viruses

Potato is clonally propagated by planting tubers, which increases the risk of virus accumulation in the next crop and tuber generations. Apart from semi-persistently or persistently vector-transmitted viruses, such as PLRV, for which insecticide application as seed tuber dressings or foliar sprays are effective during seed potato production, such treatments are generally ineffective at controlling nonpersistently vector-borne viruses like PVY (Jones 2014). Thus, most potato viruses are controlled by three principal methods: host plant resistance, clean seed systems and cultural practices. Nowadays, in developed countries potato viruses are by and large controlled through formal certified clean seed production systems and to some extent through virus resistance. On the other hand, despite many years of intensive investment, formal certified seed systems have had only very limited, if any, penetration in many developing countries, where farmers mostly obtain their seed from their previous crop or through informal trade involving low-quality planting material. High cost of seed production, lack of adequate infrastructure and economic resources of small scale family farms are some of the reasons contributing to this situation.

In the past, simple seed potato schemes that, for example, relied solely on visual inspection and roguing combined with flooding and livestock to remove any tubers left behind after harvest proved effective at removing PLRV and other viruses causing obvious foliar symptoms, but ineffective at removing viruses causing mild symptoms e.g. PVS and PVX. Formal certified seed systems are expensive to implement in most developing countries as they require rigorous visual inspections and diagnostic testing. Relying solely on visual inspections is cheaper but leads to selection of viral strains that show few foliar symptoms, as occurred with some strains of PVY. Diagnostic testing often requires laboratories. While well-established method such as ELISA (Enzyme Linked Immunosorption Assay) are relatively cheap, they may lack sensitivity. Various PCR (Polymerase Chain Reaction), reverse transcription PCR and real-time PCR, protocols have been developed and multiplexed (e.g. Raigond et al. 2013; Meena et al. 2017; Jeevalatha et al. 2016a) which can provide ultrasensitive detection of viruses in samples. Field diagnostics with viruses is also possible using lateral flow devices that are commercialized by several companies globally but suffer from similar sensitivity issues as regular ELISA and are not available for all viruses. On the other hand, Loop Mediated Isothermal Amplification (LAMP) has recently emerged as a technology that can provide highly sensitive in field detection of potato viruses, with assays developed for PVY (Treder et al. 2018), PLRV (Ahmadi et al. 2013; Almasi et al. 2013), PVX (Jeong et al. 2015), PSTVd (Learcic et al. 2013) and ToLCNDV (Jeevalatha et al. 2018). LAMP assays can rapidly be designed to detect newly identified viruses and can be multiplexed,

making it a flexible technology. LAMP is also compatible with crude nucleic acid extractions, can achieve high sensitivity, and be combined with the availability of relatively cheap battery powered real-time devices, such as Bioranger or real-time Genie series of devices, so may soon see more routine use in determining virus infections.

11.4 Potato Viruses and Seed Systems

Because of the previously mentioned factors, implementation of healthy seed systems in tropical countries is challenging, especially if there is a lack of cool areas or growing seasons with low aphid vector pressure available to reduce rate of reinfection during seed production. Due to this, as well as lack of appropriate infrastructure, investment, and commercial opportunity for smallholders to recover their investment in expensive seed potatoes, the amount of certified seeds used is generally negligible in most developing countries (Thomas-Sharma et al. 2016). Nevertheless, emerging economies, such as India and Brazil, have implemented seed systems with a level of success.

In **India**, a conventional seed tuber production system based on the “seed plot technique (SPT)” has successfully been used for the last five decades. Since its introduction, the SPT revolutionized the indigenous quality seed production system in the subtropical plains of India by extending it from the hills to the plains. The principle of SPT is growing the seed potato crop using healthy seed during a period with low aphid prevalence from October to the first week of January, coupled with IPM, roguing and dehauling the seed crop during January before aphids reach critical threshold numbers. Today, 90% of seeds are being produced in northern (Punjab), north central (Gwalior), northwestern (Modipuram), and eastern plains (Patna) of the country. This seed is being supplied to the north east, Deccan plateau, and southern parts of the country which are not suitable for quality seed production. The seed production system in India includes tuber indexing for all major viruses and clonal multiplication of virus free mother tubers in four cycles for breeders seed production. The breeder seed produced by ICAR-CPRI is supplied to various State Government Organizations for further multiplication in three more cycles, viz. Foundation Seed 1 (FS-1), Foundation Seed 2 (FS-2) and Certified Seed (CS) under strict health standards. However, the current situation of breeder seed multiplication by the State Governments is not following the desired seed multiplication chain and breeder seed supplied by ICAR-CPRI is often being multiplied only up to FS-1 stage. Therefore, there is a shortage of certified seed in the country (ICAR-CPRI, Shimla). Incorporation of hi-tech seed production systems coupled with advanced virus detection techniques is the only way out in fulfilling the very large demand of quality seed potatoes in the country.

Continuous monitoring of aphid vector dynamics revealed that aphids cross critical limits 1 week earlier in Punjab and 1–2 weeks earlier in western UP in the recent past. In general terms, vector pressure has increased many folds as compared to the

1980s which is a cause of concern. Therefore, “SPT” is being refined to cope with the changing climate and vector pressure. There is also an urgent need to explore possibilities of seed production in nontraditional areas using modern techniques (Singh et al. 2014).

The major problem for potato production in **Brazil** is related to the low availability of virus-free seed tubers. As mentioned earlier, Brazil has three potato growing seasons per year in a climate where high population density of virus vectors occurs. Therefore, one of the most important measures that must be taken in Brazil is the use of virus-free seed tubers, because if there is a source of virus inoculum in the field, there will be a rapid spread during the potato production cycle. As a consequence, the tubers produced suffer rapid degeneration during their multiplication in the field. To address this problem, Brazil has adopted and periodically revised a seed certification system that establishes norms for seed-potato production in diverse categories: (1) G-0, which is the first generation derived from in-vitro plants, although imported basic classes can also be considered as G-0; (2) the basic and certified seeds, usually going up to G-4, but having virus incidence thresholds mandatorily respected. This is currently regulated under the Federal MAPA IN-32 (as of 20/11/2012, <http://www.agricultura.gov.br/assuntos/insumos-agropecuarios/insumos-agricolas/sementes-e-mudas/publicacoes-sementes-e-mudas/INN32de20denovembrede2012.pdf>). Producers have a laboratory support system accredited by INMETRO and certified by the Ministry of Agriculture for analysis and diagnosis of viruses in seed material. Currently a small part of the employed seed originates from tissue culture and another part from the production of mini-tubers in the greenhouse.

An effective low cost alternative system to produce high grade, virus-free, mini-tuber/seed-potato lots involves the sprout/seed-potato technology (Virmond et al. 2017; Souza Dias et al. 2018). This may be accomplished either by the seed-potato exporting or importing country, and the research has shown that sprouts are durable, easy to handle and economic, when compared with potato tubers. The sprouts have to be detached from virus-free seed potatoes when they reach at least 3–5 cm tall (0.5–0.8 g), making sure that they will not be removed by cutting or sectioning, but just by hand-removing at the stolon, and with primordial root formation on the base (Fig. 11.4). After removal, they can easily be packaged into sealed polyethylene bags (100 units) for transport. Storage, before or after export and upon arrival in the country has to be done in under proper environmental conditions, avoiding insect vectors, and having favorable conditions for sprout growth, such as a dark room, 20 °C and 70–80% RU. Upon arrival at the final destination, the sprouts can be directly planted under greenhouse conditions, using horticultural soil-substrate or in a hydro- or aeroponics system to produce minituber/seed-potatoes. Details about the methodology can be found in Virmond et al. (2017). The sprout/seed-potato technology is a novel method to increase the multiplication rate of high-grade (G-0, basic classes), national or imported seed-potato stocks. It has been applied by small and large-scale potato producers in Brazil to obtain minitubers/seed-potato, free of viruses and true-to-type. It has been officially accepted as of 20-11-2012 (MAPA IN 32) to use sprouts, originally from G-0 basic seed-potato lots (national laboratory-



Fig. 11.4 Producing potato seed from tuber sprouts in Brazil. Photo credits: J. A. C. Souza-Dias

greenhouse minituber/seed-potato, or the annually imported tuber/seed-potato basic classes), as propagating material to produce certified minituber/seed-potato stocks. If properly handled, under the same conditions as used for minituber production, they can have the same phytosanitary health status. Moreover, minitubers/seed-potatoes obtained from sprouts through successive generations (G-3) are safer when compared to tissue culture, because they do not run the risk of presenting the common mutations seen with that technique (Souza-Dias et al. 2017).

Due to the difficulty of potato seed production in the country, producers often import seeds from European countries, Canada and the United States. This exposes the country to the entry of new pathogens, as happened with strains of PVY, that, once in Brazil, underwent a rapid adaptation and changed the epidemiology of the virus in Brazilian potato crops.

Another problem that has occurred with the production of seed potatoes in Brazil was the start in 2011 of the Brazilian legislation for production of potato seeds for personal use. This released the farmer from testing the seed planted, allowing him to plant them without laboratory analysis. Based on visual evaluation only, the producer is at risk of planting seeds with high incidences of virus, especially when dealing with cv. Agata. Besides compromising the yield, it can act as symptomless PVY carrier, especially of PVY^{NTN} as tuber necrotic rings are rarely visible in cv Agata, thus providing a generous source of virus inoculum for potato and other Solanaceous crops nearby.

11.5 Resistance

Potato is clonally propagated by planting tubers, which increases the risk of accumulation of viruses in the next crop and tuber generations. Apart from semi-persistent or persistently transmitted viruses such as PLRV, viruses cannot be controlled readily with pesticides, so chemical control of virus vectors provides only partial protection at best or is ineffective. On the other hand, production of healthy seed tubers is an expensive process. Therefore, resistance to viruses in potato cultivars is the most efficient and cost-effective means to control virus diseases in potato when effective seed production systems are absent, as in most developing countries. In developed countries with sophisticated and effective seed tuber production schemes, virus resistance becomes less important than other cultivar characteristics, such as high yield, tuber quality, and adaptation to the local environment.

PVY is now the most widespread viral pathogen in potatoes in most countries. Fortunately, breeders have introduced resistance genes that control PVY to many potato cultivars. Many of them, however, recognize only certain PVY strains. These strain-specific resistance genes can act quickly upon recognition of PVY and kill most of the PVY-infected cells at an early stage of infection leading to localized necrotic lesions, although they are sometimes slower acting resulting in systemic movement followed by single shoot or complete plant death. Therefore, they are called “hypersensitivity resistance” (HR) genes and contrast to “extreme resistance” (ER) genes which do not lead to any visible lesions during the resistance reaction. Furthermore, plasmodesmata connecting the plant cells and used by viruses for movement from cell to cell are sometimes blocked, preventing further spread of the virus. However, mutations in the viral genome can overcome resistance. For example, a few mutations in the helper component protein (HCpro) overcome resistance to PVY^O conferred by the resistance gene *Ny* in potato (Tian and Valkonen 2013). Consequently, the mutant of PVY^O can multiply, spread, and cause leaf mosaic and growth reduction in the potato plants carrying *Ny*.

Jones and Vincent (2018) studied strain-specific HR and ER phenotypes elicited in potato plants by PVY isolates in strain groups PVY^O and PVY^D. These isolates were inoculated to 39 Australasian, European, or North American potato cultivars. HR elicited by infection with strain group PVY^D occurred in 34 of the 39 cultivars, including 2 released as early as 1893–1894 in North America. Since PVY^D elicits putative gene *Nd*, this had apparently been present but unrecognized since the earliest epoch of potato breeding in the second half of the nineteenth century. Systemic hypersensitive resistance (SHR) elicited by strain group PVY^O in presence of hypersensitivity gene *Ny* was present in 23 of the same 34 potato cultivars with putative *Nd*, occurring widely amongst cultivars released in each of the three world regions. Two European cultivars always developed ER following sap and graft inoculation so carried comprehensive PVY resistance gene *Ry*, but no Australasian or North American cultivars carried it. One Australasian and two European cultivars always developed susceptible phenotypes so lacked genes *Ry*, *Ny*, and putative *Nd*. When

breeding new PVY-resistant potato cultivars for countries lacking healthy seed potato stocks, or where subsistence farmers cannot afford them, the next best option to gene *Ry* inclusion is incorporating as many strain-specific PVY resistance genes as possible (Jones and Vincent 2018).

The degree of PVY⁰ resistance conferred by *Ny* varies between potato cultivars depending on the extent of localized hypersensitive resistance (LHR) and/or severe SHR versus weak SHR that develops. With LHR the source of infection for further virus spread is removed. When SHR involves death of all systemically infected shoots or entire plant death, foci of PVY infection are eliminated from within the crop so they are unavailable to become infection sources for secondary spread. By contrast, weak SHR that allows PVY-infected plants to persist means they can act as virus sources for secondary spread (Jones and Vincent 2018). A recent example of its effectiveness against PVY⁰ in the field was provided by an investigation in a potato growing region of North America following widespread planting of cultivars with *Ny*. Over a 5-year period, incidence of PVY⁰ dropped from 63 to 7% of the PVY population (Funke et al. 2017). Another example comes from potato cv. Yukon Gold, which is grown in Australia, Canada, Europe and USA, and carries genes *Ny*, *Nz*, putative *Nd* (Rowley et al. 2015; Kehoe and Jones 2016; Jones and Vincent 2018). The quick elimination of PVY-infected plants by the SHR response is beneficial, since it occurs before any tubers of useful size have developed. For example, in Finland it has been possible to grow Yukon Gold over 10 years from farm-owned seed.

Although the SHR response to PVY or PVX infection is a frequently observed phenotypic reaction in breeding populations (of e.g. CIP), breeders have traditionally ignored them as this reaction usually kills the plants or severely stunts them. As the above example of Yukon Gold exemplifies, this phenotype is nevertheless effective in controlling virus infection under field conditions. Growing cultivars with *Ny* and *Nz* is likely to be most helpful in potato growing regions where the recombinant PVY strains that overcome it are still rare or absent.

Nyalugwe et al. (2012) studied strain-specific HR and ER phenotypes elicited in potato plants by isolates in PVX strain groups 1 and 3. They inoculated these isolates to 38 potato cultivars. Presence of extreme PVX resistance gene *Rx* was identified in four Australian, two European cultivars, and one North American cultivar. PVX hypersensitivity gene *Nx* was identified two Australian, four European, and one North American cultivar. PVX hypersensitivity gene *Nb* was identified in one Australian, five European, and one North American cultivars. When breeding new PVX-resistant potato cultivars for developing countries, incorporation of gene *Rx* is the best option. However, Andean PVX resistance breaking strain XHB not only overcomes *Rx*, but also overcomes *Nx* and *Nb*, so *Rx* is likely to be less effective in potato cultivars growing in the center of origin of the crop.

Breeders have during the past decades focused on the use of ER genes, that are usually strain unspecific and cause no or only microscopic HR reactions in the plants. Thus, the ER genes *Ry_{adg}*, *Ry_{sto}*, and *Ry_{chc}* have been used to introduce resistance for PVY and *Rx₁* and *Rx₂* for resistance to PVX. To facilitate introgression of PVY resistance, molecular markers have been developed and used, e.g. Bhardwaj

et al. (2015) screened potato germplasms and varieties employing SCAR and SSR marker linked to *Ry_{adg}* and *Ry_{sto}* genes and identified some elite parental lines that can be exploited for transferring the virus resistance into new potato cultivars. On the other hand, triplex parental potato lines containing three copies of the *Ry_{adg}* gene have been developed in various breeding programs ensuring 96% of progeny contain at least one copy of the resistance gene (Kaushik et al. 2013; Kneib et al. 2017). High resolution melting markers developed for *Ry_{sto}* (Nie et al. 2016), *Ry_{adg}* (Del Rosario et al. 2018) and *Rx1* and 2 (Nie et al. 2018) can accurately predict allele dosage and significantly aide in developing such parental lines. Nevertheless, even ER genes may be sensitive to changes in environment, as exemplified in recent study showing reduced efficiency of resistance to PVY by *Ry_{chc}* in response to increasing temperatures observed in Japan (Ohki et al. 2018). In contrast to PVY and PVX, a good source of resistance to PLRV has long evaded breeders, but a dominant gene *Rl_{adg}* conferring high levels of resistance was identified about a decade ago in a potato accession LOP-868 and the subsequently developed SCAR marker (Mihovilovich et al. 2014) has enabled rapid introgression into elite germplasm (Carneiro et al. 2017). Markers have also been developed for another dominant resistance gene, *Rlr_{etb}* originating from the non-tuber bearing wild species *S. etuberosum* (Kuhl et al. 2016), but its introgression into advanced breeding populations may still take time due to linkage drag from its wild progenitor. Screening of germplasm lines for ToLCNDV-[potato] resistance in field or glass house conditions showed possible presence of resistance source (Kumar et al. 2015; Maan et al. 2017; Jeevalatha et al. 2016b).

Additional resistance genes to PVA, PVV, PVS and PVM have also been identified (Palukaitis 2012) and mapped in potatoes but have to date not been widely utilized due to the considered limited importance of these viruses. Naderpour and Sadeghi (2018) developed a multiplex PCR assay including markers for resistance to PVY, PVS, and PLRV to facilitate introgression of multiple resistances into new varieties. Nevertheless, due to the complex genetics of potato it has not been easy to combine virus resistance with the myriad of other necessary traits needed for a successful variety. Transgenic approaches can readily incorporate resistance to multiple viruses into specific potato varieties (Chung et al. 2013), but considering current controversies surrounding transgenic crops, such products will not likely be released for cultivation in the near future.

11.6 Cultural Approaches

Landraces that survive for many years tend to be ones that possess multiple virus resistances as evidenced by the frequent occurrence of virus resistance genes in Andean potato landraces in germplasm collections (Jones 1981, and references therein). However, cultural approaches (such as roguing out plants with obvious virus symptoms, removing volunteer potato plants or weeds likely to harbor potato viruses, deploying reflective mulches to deter insect vector landings, manipulating

the planting date to avoid peak flights of insect vectors, and early haulm destruction to avoid late virus infections) are rarely used by developing country farmers unless they are seed producers. In fact, the common habit of small holder farmers of selling and or consuming large tubers and keeping the small ones as seed for a next crop probably maintains virus loads in the seed high, as virus-infected plants often are the ones producing the smallest tubers. Gildemacher et al. (2011) and Schulte-Geldermann et al. (2012) showed how positive selection of healthy looking mother plants to provide seed tubers could reduce virus incidences in subsequent crops by 35–40% and a corresponding yield increase of 30%. Modeling approaches have similarly indicated that the approach of selecting healthy plants for seed production can be as effective as certified seed in maintaining seed quality (Thomas-Sharma et al. 2017). However, this would only apply where viruses causing little or no symptoms are being discounted. Also, the penetration of positive selection techniques among regular farmers has until now been limited.

The seed plot technique as practiced in India (whereas it starts out with certified virus free seed) is largely based on cultural practices to keep tuber seed healthy, growing during seasons and areas with low vector pressure coupled with IPM (Integrated Pest Management), rouging (negative selection), and dehauling the seed crop before vectors reach a critical threshold limit. The use of straw mulch (Kirchner et al. 2014), mineral oil sprays and intercropping has been shown to enable control of PVY infection, particularly when used in combination (Dupuis et al. 2017a, b), although the economics of it would only justify their application for seed potato production (Dupuis 2017). Insecticide application to prevent PLRV spread in seed potato crops is also routinely used where seed potato stocks are multiplied in more aphid vector prone areas, especially in developed countries.

A unique practice is performed in the Andean region (and also the Himalayas) where farmers traditionally grow their potatoes at higher altitudes to reinvigorate them after several years of cultivation at lower altitudes (De Haan and Thiele 2003). Bertschinger et al. (2017) recently demonstrated that growing potatoes at higher altitude significantly reduced the number of virus-infected tubers produced from infected mother plants. Together with the absence of insect vector populations that could reinfest healthy plants at high altitude, this helps explain how this practice can reduce virus infections in the crop and resulting in subsequent higher yields. The mechanism of this phenomenon (reduced infection of tubers of infected mother plants at higher altitude), however, still remains unknown and should be an interesting topic of further study. Possibly RNA silencing mechanisms as affected by environmental conditions may be involved and understanding them may lead to new approaches for cleaning virus-infected plants.

Other mechanisms may also play a role in reducing losses by virus infections in the Andean region. Anecdotal evidence suggest that healthy planting material repatriated to farming communities often rapidly succumbs to new and more severe virus infections than the original material. An explanation for this may be that farmers have over the generations selected for plants which are infected with mild strains of the viruses, causing only limited yield losses, but protecting from more severe virus strains. This protection is lost when plants are cleaned from viruses.

Whereas this has not been researched until now, it may be worthwhile to investigate this phenomenon as it could lead to identification of new methods to control yield losses by viruses in potato using mild strains.

11.7 Final Remarks

Viruses remain a problem for global potato production, even though, over the years, the importance of certain viruses has increased or decreased globally. These changes in relative importance result from a range of factors including not only increased global trade but also regional changes in cultivar usage, cropping patterns, implemented seed systems and diagnostic testing regimes, appearance and evolution of new viruses and virus strains, and vector populations. All of these factors interact with each other and are further affected by climate change, making it difficult to predict what the future will hold. The two examples of potato-infecting geminivirus and torradovirus in Peru represent interesting cases where viruses have rapidly emerged as a significant local problem, only to subsequently disappear again into the background. This may be something that, in the past, has frequently occurred unnoticed in the potato's center of domestication in the Andes, or elsewhere in the world (e.g. PYDV was a devastating virus in the US during the early twentieth century, but has now all but disappeared). Many factors may influence whether a virus eventually manages to get a foothold in a region and become a permanent threat to the potato crop, but it has obviously happened on several occasions during the past 500 years since potato was introduced worldwide, as evidenced by viruses infecting potato uniquely in geographical areas outside of the Andes. The latter represent viruses that the potato did not encounter until it was moved away from the Andean region. Whitefly- and thrips-transmitted viruses should form a particular concern as witnessed by recurrent outbreaks occurring in (sub-)tropical regions, the increasing geographical spread of crinivirus PVV and the establishment of the begomovirus ToYLCNDV as a major potato pathogen in India. Besides in Brazil, ToCV has also been reported from potatoes in Spain (Fortes and Navas-Castillo 2012) and identified in India associated with leaf-roll disease (CIP, unpublished), and thus the virus does seem to have recurring opportunities to infect potatoes worldwide where conditions are appropriate and it may only be a matter of time until an adaptive mutation appears for it to establish as a significant potato pathogen.

With a warming climate, producing high-quality virus-free seed is set to become more difficult, as opportunities to move to cooler areas with low vector pressure have become fewer in warmer countries, especially those that lack mountainous regions. Some cooler countries have the opportunity to move their seed potato production towards more extreme latitudes, though this rarely applies to developing countries. Thus, there is an increased requirement for new technologies for rapid multiplication of healthy plants under controlled conditions to be able to supply high-quality seeds at an affordable level. Despite the availability of effective resistance genes to, for example, PVY, due to the complex genetics of potatoes, it is

difficult to recombine these with other critical traits necessary for a successful cultivar, and as a result only a fraction of potatoes grown globally possess non-strain-specific host resistance. The use of more efficient molecular markers and the promise of diploid potato breeding (Taylor 2018) may change that in the future, but for now, a combined approach for degeneration control adjusted to the local socio-economical and climatic context, as suggested by (Thomas-Sharma et al. 2016), may be the best way to go in developing countries where sophisticated seed production schemes are not currently a viable option.

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