



Department
for Environment
Food & Rural Affairs

Pest specific plant health response plan:

Outbreaks of *Potato spindle tuber viroid* on potato
crops



Figure 1. Healthy potato tuber (left), and spindle shaped tubers (right) that have been affected by PSTVd. © Dr. J. W. Roenhorst

We are the Department for Environment, Food and Rural Affairs. We're responsible for improving and protecting the environment, growing the green economy, sustaining thriving rural communities and supporting our world-class food, farming and fishing industries.

We work closely with our 33 agencies and arm's length bodies on our ambition to make our air purer, our water cleaner, our land greener and our food more sustainable. Our mission is to restore and enhance the environment for the next generation, and to leave the environment in a better state than we found it.



© Crown copyright 2022

This information is licensed under the Open Government Licence v3.0. To view this licence, visit www.nationalarchives.gov.uk/doc/open-government-licence/

This publication is available at

<https://planthealthportal.defra.gov.uk/pests-and-diseases/contingency-planning/>

Any enquiries regarding this document should be sent to us at:

The UK Chief Plant Health Officer

Department for Environment, Food and Rural Affairs

Room 11G32

York Biotech Campus

Sand Hutton

York

YO41 1LZ

Email: plantpestrisks@defra.gov.uk

www.gov.uk/defra

Executive summary

Background	
Regulation	GB Regulated Non-Quarantine pest
Key Hosts	Potato, tomato, pepper
Distribution	Africa, North America, South America, Asia, Europe, Oceania
Key pathways	Seed and ware potatoes, produce, plants for planting and seed
Industries at risk	Potato, tomato and pepper growers and packers
Symptoms	Stunting, chlorosis, distortion, purpling or reddening of leaves, reduction in fruiting and smaller spindle-shaped potato tubers
Surveillance	
Demarcated zones (5.24)	Infected fields, neighbouring fields, other fields which staff/growers have visited or worked in, including those fields where machinery used was the same as that for the infested field, stores, grading lines, premises in which stock has been sent or received, and/or any other premises where there is a perceived risk.
Surveillance activities (5.22-5.23)	<ul style="list-style-type: none"> • Visual surveys will be carried out in the infested fields • Sampling of symptomatic plants
Response	
Interceptions (5.1-5.4)	<ul style="list-style-type: none"> • Consignment should be destroyed or re-exported if dead larvae or feeding damage is seen. • Tracing exercises carried out where required • UKPHINs notification to be made.
Outbreaks (5.27-5.34)	<ul style="list-style-type: none"> • Destruction of infested crop and any other fields where the same machinery has been used • In some situations the harvested tubers may be allowed to move off site for processing/retail • Removal and destruction of volunteers • Two year crop/volunteer free period before planting with potatoes
Key control measures	
Biological	N/A
Chemical	Herbicide applications
Cultural	Cleaning of equipment and machinery, removal and destruction of waste and infested tubers, working on infested crop at the end of the day
Declaration of eradication	
Eradication can be declared if no PSTVd is detected during annual surveys for two years after the infested material was destroyed if no volunteers have been identified.	

Contents

Executive summary	3
1.Introduction and scope.....	5
2.Summary of threat	5
3.Risk Assessments.....	6
4.Actions to prevent outbreaks	6
5.Response.....	7
Official action to be taken following the suspicion or confirmation of PSTVd on imported plants, including seeds	7
Official action to be taken following the suspicion of PSTVd inland	7
Confirming a new outbreak	10
Criteria for determining an outbreak.....	11
Official Action to be taken following the confirmation of an outbreak	11
Review measures in the case of prolonged official action.....	14
6.Criteria for declaring eradication / change of policy	15
7.Evaluation and review of the contingency plan	15
8.Appendix.....	16
Data sheet for Potato spindle tuber viroid	16
9.References	7
10.Author and reviewers	21

1. Introduction and scope

- 1.1. This pest specific response plan has been prepared by the Defra Risk and Horizon Scanning Team. It describes how the Plant Health Service for England will respond if infection by *Potato spindle tuber viroid* (PSTVd) is discovered on potato (*Solanum tuberosum*).
- 1.2. The plant health authorities in Northern Ireland, Scotland, Wales and the Crown Dependencies have been consulted on this plan and will use it as the basis for the action they will take in the event of PSTVd being detected in their territories.
- 1.3. This document will be used in conjunction with the Defra Generic Contingency Plan for Plant Health in England (<https://planthealthportal.defra.gov.uk/assets/uploads/Generic-Contingency-Plan-for-Plant-Health-in-England-FINAL-2.pdf>), which gives details of the teams and organisations involved in pest response in England, and their responsibilities and governance. It also describes how these teams and organisations work together in the event of an outbreak of a plant health pest.
- 1.4. The aim of this response plan is to facilitate the containment and eradication of PSTVd.
- 1.5. This document can also be used as a basis for responding to outbreaks in potato of related pospiviroids. A datasheet containing background information on PSTVd is included in the appendix.

2. Summary of threat

- 2.1. *Potato spindle tuber viroid* (PSTVd) probably originates from Central America, but it was first identified in New Jersey, USA, in 1922 (Martin, 1922). It is now also present in South America, Europe, Africa, Asia and Oceania (EPPO, 2014). Within Europe, the viroid is widespread in Belarus and is present or occasionally present in Austria, Belgium, Croatia, Czech Republic, Georgia, Germany, Italy, Malta, Montenegro, Netherlands, Poland, Russia, Slovenia, Spain, Turkey and the Ukraine. The viroid is also reported as being under eradication in Greece, Hungary and Switzerland (EPPO, 2014).
- 2.2. The viroid causes growth reduction and other damaging symptoms in potato (*Solanum tuberosum*), tomato (*Solanum lycopersicum*) and pepper (*Capsicum annum*). Other *Solanum* spp. and some ornamental species in the family *Solanaceae* can also be infected, but the viroid is generally asymptomatic in these species. Yield losses of ~ 65% in potato have been recorded (Hunter and Rich,

1964), and potential yield losses of almost 100% may occur for tomato plants that are infected early (EFSA Panel on Plant Health, 2011).

- 2.3. In the UK, there have been two outbreaks of PSTVd, both on tomato, one in 2003 and one in 2011, and the viroid was eradicated on each occasion in the same year. There have also been several interceptions of the viroid in ornamental plants which have originated within the EU and multiple interceptions of the viroid on tomato and pepper seeds.

3. Risk Assessments

- 3.1. The viroid currently has an unmitigated and mitigated UK plant health risk register score of 75 and 45 respectively. Overall scores range from 1 (very low risk) to 125 (very high risk). These scores are reviewed as and when new information becomes available (<https://planthealthportal.defra.gov.uk/pests-and-diseases/uk-plant-health-risk-register/viewPestRisks.cfm?cslref=11980>).
- 3.2. The European Food Safety Authority (EFSA) published a scientific opinion on the risk of solanaceous pospiviroids for the EU territory in 2011.

4. Actions to prevent outbreaks

- 4.1. *Potato spindle tuber viroid* is a GB Regulated Non-Quarantine Pest (RNQP) when associated with ornamental plants for planting of pepper (*Capsicum annuum*), vegetable propagating and planting material (other than seeds) of pepper and tomato (*Solanum lycopersicum*), pepper and tomato seed, seed potatoes (*Solanum tuberosum*) and potato seeds as listed in Parts C, E, F, H and J of [Schedule 4 of The Plant Health \(Phytosanitary Conditions\) \(Amendment\) \(EU Exit\) Regulations 2020](#). There is a 0% threshold for findings of PSTVd on consignments of the listed commodities in GB, and measures to prevent their presence can be found in [Schedule 5](#) of the above regulations.
- 4.2. *Potato spindle tuber viroid* is an EU RNQP when associated with ornamental plants for planting of pepper (*Capsicum annuum*), vegetable propagating and planting material (other than seeds) of pepper and tomato (*Solanum lycopersicum*), pepper and tomato seed, seed potatoes (*Solanum tuberosum*) and potato seeds as listed in Parts D, F, G, I and K of Annex IV of Commission Implementing Regulation (EU) 2016/2031. There is a 0% threshold for findings of PSTVd on consignments of the listed commodities in EU.
- 4.3. *Potato spindle tuber viroid* is an A2 listed pest for the EPPO region and is therefore recommended for regulation by EPPO member countries.

- 4.4. The Plant Health Service (including the Animal and Plant Health Agency, Defra and Fera Science Ltd.) should be aware of the measures described in this plan and be trained in responding to an outbreak of PSTVd in potato crops. It is important that capabilities in detection, diagnosis and risk management are available.

5. Response

Official action to be taken following the suspicion or confirmation of PSTVd on imported plants, including seeds

Holding consignments at ports of entry

- 5.1. If PSTVd is suspected by the Plant Health and Seeds Inspectorate (PHSI) to be on a consignment moving in trade, the PHSI should hold the consignment until a diagnosis is made. Samples should be sent in by the PHSI to Plant Clinic, Fera Science Ltd., York Biotech Campus, Sand Hutton, York, YO41 1LZ (01904 462000), in a sealed bag or container, within at least two other layers of containment which are not liable to be crushed during transit.
- 5.2. If PSTVd is confirmed, the PHSI should advise the client of the action that needs to be taken by way of an official notice. The consignment should be destroyed by either incineration or deep burial.
- 5.3. If PSTVd is confirmed, a UKPHINS (UK Plant Health Interception Notification System) notification should be made. UKPHINS is the IT system for recording findings and non-compliance in order to maintain records and notify other National Plant Protection Organisations (NPPO) of plant health issues.
- 5.4. If all or part of the consignment has been distributed to other premises prior to diagnosis, trace forward inspections should take place upon suspicion or confirmation of PSTVd.

Official action to be taken following the suspicion of PSTVd inland

- 5.5. Suspected outbreaks will be assessed on a case by case basis. An Outbreak Triage Group (OTG), chaired by the Chief Plant Health Officer (CPHO) or their deputy and including specialists from APHA, Defra and other organisations, should be set up to assess the risk and decide on a suitable response. . Where appropriate, the OTG will also decide who will be the control authority, and the control authority will then nominate an incident commander. An Incident Management Team (IMT) meeting,

chaired by the Incident Commander, will subsequently convene to produce an Incident Action Plan (IAP). See the [Defra Generic Contingency Plan for Plant Health in England](#) for full details.

- 5.6. The OTG will determine the alert status, which will consider the specific nature of the outbreak. These alert levels, in order of increasing severity, are white, black, amber and red (more detail on these levels can be found in table 2 of the *Defra Generic Contingency Plan for Plant and Health in England*). Due to the potential for spread, a suspected finding of PSTVd in a potato field is likely to be given an amber alert status. An amber alert status refers to a serious plant pest/disease with potential for relatively slow but extensive geographical spread leading to host death and/or major economic, food security or environmental impacts.
- 5.7. If PSTVd is suspected (or confirmed) in an allotment or garden then this will be dealt with on a case by case basis.

Restrictions on movement of material, equipment and machinery to and from the place of production

- 5.8. *Potato spindle tuber viroid* can be transmitted mechanically, on gloves and hands (van Brunshot *et al.*, 2014), on machinery (Merriam and Bonde, 1954) and on tools (Verhoeven *et al.*, 2010b). The viroid can also remain infective on the outside of plants for at least 8 weeks (Mumford *et al.*, 2004b). Movement of material, equipment and machinery between infected and non-infected areas should therefore be restricted. However, if movement is necessary, the material, equipment and machinery should be thoroughly cleaned and disinfected (see 5.25).

General biosecurity advice and advisory measures for growers

- 5.9. Hygiene best practice should be followed (adapted from EFSA Panel on Plant Health, 2011). This includes:
 - Training staff to identify symptoms of PSTVd, and to follow best practice procedures.
 - Prohibiting the sorting/packing of tubers produced from other companies/locations. If the tuber is infected, machinery, equipment and people could become contaminated and infect other crops on the premises.
 - Using clothes (including overshoes), which will either be destroyed (via incineration or deep burial) or washed following work on a particular field. This prevents spread between fields.
 - Using disposable gloves that will be destroyed (via incineration or deep burial) following work on a particular crop, between different areas within a crop or between plants (reducing spread).
 - Washing hands with soap before and after entering a new field (reducing spread).

- Restricting the use of equipment, particularly knives, to one location, to prevent the viroid spreading to other locations (via mechanical transmission).
- Chemical disinfection of knives and pruning instruments (between crops, areas within a crop or plants to reduce spread) (see 5.25).
- Cleaning and disinfection of machinery between crops. As with handheld equipment, machinery is another means of mechanical transmission. Disinfection and cleaning of machinery with high water pressure, steam cleaners or other methods may therefore reduce spread. Records of this should be maintained.
- Maintaining the working direction. If human-assisted spread of a pathogen occurs, it will occur in the direction that the human is working. Working in the same direction reduces the extent of the spread and allows measures to be carried out in a more concentrated way.
- Restricting access to the working area. The fewer people entering a particular field, the less chance there is that PSTVd will be introduced. Wherever possible, employees should work in the same areas each day rather than swapping around work areas.

5.10. Volunteer plants and weeds, particularly perennials, act as reservoirs for PSTVd (EFSA Panel on Plant Health, 2011). Controlling these plants reduces the chance of the crop becoming infected. Volunteer plants and weeds arising in potato cultivations can be controlled mechanically (e.g. by hoeing, roguing, flame weeding), chemically (e.g. using herbicides) and by cultural practices (e.g. lifting of potatoes). It is important there is no 'carry over' into the next crop by self-sown seedlings arising from seed of squashed fruit from the previous season. Any disposal required should be as in point 5.35-38.

5.11. Transmission of PSTVd by aphids has occasionally been reported in potato within and between species but transmission is at a very low level. Research suggests that higher levels of transmission have been observed when the viroid has been acquired from potato plants co-infected with Potato leafroll virus (PLRV) (e.g. for *Myzus persicae*, Syller *et al.*, 1997). Controlling aphids in crops, particularly those crops that are also hosts of PLRV, is therefore recommended.

Preliminary trace forward / trace backward

5.12. If an infested consignment is considered as being the source of the suspect outbreak, investigations regarding the origins of infested consignments will be undertaken to locate other related and therefore potentially infested consignments moving to and from the site. If applicable the relevant NPPO should be contacted. This process is particularly important for propagation or seed stock.

5.13. In addition to tracing investigations relating to consignments, trace forward/back investigations linked to equipment, vehicles and machinery used in the infected field or production site should also be carried out.

Confirming a new outbreak

How to survey to determine whether there is an outbreak

- 5.14. Information to be gathered on the suspicion of PSTVd by the PHSI, in accordance with ISPM 6; guidelines for surveillance (<https://www.ippc.int/en/publications/615/>):
- The origin of the potatoes and seed lot numbers etc.
 - Details of other premises or destinations where the potatoes have been grown or sent, where the viroid may be present.
 - The layout of the premises and surrounding area, including a map of the cultivations/buildings, at risk growers, any other host plants, including susceptible ornamentals etc.
 - Details of the host plant: the species, variety, growth stage and any other relevant information.
 - Description of the surrounding habitat and climate.
 - Level of infection, including a description of symptoms (could take photos).
 - The date and time the sample was taken, how it was identified and by whom.
 - Current controls in place e.g. chemical treatments (These cannot be used against the internal viroid infection, but may be used for insect control. Chemicals may also distort the appearance of symptoms, reducing the effectiveness of visual survey).
 - Details on the movement of people, equipment, machinery etc. to and from the infected area.
 - Cultural and working practices.
 - History of PSTVd on the site and nearby, if any.
 - The presence of aphids and PLRV.
- 5.15. Further to information gathering, samples of other symptomatic host plants should be taken to confirm the extent of infection e.g. in surrounding lots or fields. This initial survey will be used to determine if it is an isolated case or an established outbreak.
- 5.16. Finance for the surveys will depend on the individual circumstances of the outbreak and will be subject to discussion.

Sampling

- 5.17. Following the identification of a suspect plant, symptomatic parts of the plant (e.g. leaves, fruit and stems) should be sent to Fera Science Ltd. as in 5.1. Plants should be handled with gloves. Gloves should be destroyed (via incineration or deep burial) following use. Hygiene best practice should be followed while sampling. Each sample should be labelled with full details of sample number, location, variety etc.

Diagnostic procedures

5.18. The principal means of detecting pospiviroids is through reverse transcription-polymerase chain reaction (RT-PCR) (Shamloul *et al.*, 1997; Bostan *et al.*, 2004; Verhoeven *et al.*, 2004; Verhoeven *et al.*, 2011). At Fera, TaqMan is used. This method is generally non-specific and will not allow identification down to species level (e.g. Singh *et al.*, 1999; Verhoeven *et al.*, 2011). Real-time RT-PCR is also often run in tandem, which narrows down the viroid species to either PSTVd or TCDVd (Boonham *et al.*, 2004). Identification to species level and separation from similar viroids such as TCDVd requires sequencing of the RT-PCR products and BLAST analysis (Boonham *et al.*, 2005; Verhoeven, 2010a). This is in accordance with ISPM 8 (<https://www.ippc.int/en/publications/612/>) and ISPM 27 Annex 7 (<https://www.ippc.int/en/publications/593/>).

Criteria for determining an outbreak

5.19. If PSTVd is detected at a location other than at a port or confined to a particular consignment with no risk of spread, then an outbreak should be declared.

Official Action to be taken following the confirmation of an outbreak

5.20. The scale of the outbreak will determine the size and nature of the management team and action.

Communication

5.21. The IMT will assess the risks and communicate details to the IPPC, EU and EPPO, in accordance with ISPM 17: pest reporting (<https://www.ippc.int/en/publications/606/>), as well as within Government to Ministers, senior officials, devolved administrations and other government departments and agencies (e.g., the Environment Agency) on a regular basis as appropriate; and to other relevant stakeholders.

Surveillance

5.22. Host plants in the affected field should be visually inspected at a surveying rate determined by the IMT. This should focus on potato in particular, and symptomatic plants should be tested.

5.23. Locations to survey:

- neighbouring potato fields

- fields which staff/growers have visited or worked in
- fields where machinery used was the same as that for the infected field and
- other fields where there is a perceived risk such as those linked by a footpath

Demarcated zones

5.24. The affected field, neighbouring fields, other fields which staff/growers have visited or worked in, including those fields where machinery used was the same as that for the infected field, stores, grading lines, premises in which stock has been sent or received, and/or any other premises where there is a perceived risk, should be demarcated for surveillance.

Decontamination procedures

5.25. Thorough cleaning and application of disinfectants should be used for all non-disposable material, equipment and machinery. Virkon S (2%, containing potassium peroxymonosulfate) and sodium hypochlorite (e.g. 10% Clorox regular bleach) are recommended disinfectants (Li *et al.*, 2015). Any waste (plant or other potentially infected material) should be removed and destroyed (via deep burial, incineration or other appropriate methods prescribed in 5.36 - 5.38).

Tracing forwards / backwards

5.26. Once other sites that are potentially infected by PSTVd have been identified, these should be inspected as per surveillance highlighted in paragraphs 5.22 - 5.23. Information, which is aimed at raising awareness of the disease and its symptoms, should be sent to affected and at risk growers.

Pest Management procedures

5.27. Host plants should not be moved off site, with exception of potato tubers which may be moved off site for retail/processing if agreed by the IMT.

5.28. There are no chemical or biological methods for controlling PSTVd. Therefore, the only effective method of eradication is destruction. If an outbreak is found within a breeding stock or in seed potatoes, there should be no further propagation from the infected stock or other stocks on the same production unit and all plants should be destroyed. Likewise, if infection is detected in ware potatoes, normally, all potatoes within the field should be destroyed. However, restricted movement of seed and ware potatoes may be allowed under particular circumstances (to be agreed by the IMT).

- 5.29. Fields which are not known to be infected, but have used the same machinery as an infected field or have been exposed to PSTVd in another way, should be treated as if they are infected.
- 5.30. Work on known infected fields should be completed at the end of the day to avoid spreading the viroid to other areas. Machinery should be cleaned and disinfected using water and detergent to remove soil and plants and then treated with an appropriate disinfectant as in 5.25.
- 5.31. Once all susceptible crops have been harvested, the field should be inspected for known hosts of PSTVd and other solanaceous weeds, and subsequently destroyed. This would involve the removal of any weeds and volunteer plants, thereby reducing the likelihood of PSTVd carrying over into any following susceptible crops. Weeds should be removed from the field and in hedgerows around the field.
- 5.32. Before potatoes can be planted in the infected field again, it should have been free from host volunteer plants for a minimum of two consecutive years (EPPO, 2011). Volunteer potato plants and weed hosts found should be tested for PSTVd.
- 5.33. During the two years following an outbreak, several measures have been prescribed in EPPO (2011) for other fields on the same premises or those being used by the same grower, if potatoes are being grown, including:
- Potato production, handling and storage should be carried out under official supervision of the PHSI.
 - Harvested seed- and ware-potato stocks should be kept separate, or cleaning and disinfection should be carried out between the handling of the stocks.
 - Only certified seed potatoes should be planted.
 - Official monitoring should be conducted using laboratory testing at a sampling rate established by the NPPO.
- 5.34. Following this period, only ware potatoes should be produced for at least one rotation cycle, with harvested tubers and leaf material inspected and tested for PSTVd (sampling rate to be determined by the IMT). If found free of PSTVd, either seed or ware potatoes may then be produced on the field (EPPO, 2011).

Disposal plan

- 5.35. The primary means of destruction of potato plants in a field is through herbicide application. The Defra Risk and Horizon Scanning Team should be consulted for appropriate treatments.
- Any applications should be made following the advice on the product label and be in accordance with HSE guidance. In some cases there may be a requirement to carry out a Local Environment Risk Assessment for

Pesticides (LERAP) depending on the product used and the situation of the finding.

- If the crop is organic, pesticides will still have to be used if the situation demands it.
- Growers will be placed under notice to apply the recommended pesticides and make the applications using their own or contractor's equipment. Records of applications will be kept, including details of the amount of product and water use.

5.36. Tubers that remain in herbicide treated fields/areas should be harvested and destroyed by incineration (licensed) or deep burial. These destruction methods may also be preferred for small batches of infected plants outside of fields. Deep burial may be done at an approved landfill site, or on the site or nearby farm, if practical and in agreement with the local Environment Agency. Incineration must comply with appropriate waste management regulations, Environment Agency in England, Scottish Environment Protection Agency and Natural Resources Wales. If the material has to be moved off the premises, it should be contained within at least two sealed layers, if possible.

5.37. Aside from herbicide application, incineration and deep burial, other viable methods of destruction, at least for potato tubers, include heat sterilization, industrial processing (subject to adequate disposal of waste water), fermentation and composting, steaming and feeding to animals, and anaerobic digestion. Alternatively, tubers can be fed directly to cattle in a contained area. This is on the basis that manure and debris is collected and composted for at least 2 months in a contained area and is not returned to arable land likely to be used for host crops. Fermentation of contaminated potatoes during silage production provides a pre-treatment to direct feeding.

Review measures in the case of prolonged official action

5.38. Following an outbreak in potatoes, the infected field should be surveyed for the presence of volunteer potato plants and weed hosts of PSTVd. No potato crop should be grown in the infected field until there have been two years during which no volunteers have been found. Monitoring should involve visual inspection and testing of volunteer plants and/or weeds. Other demarcated fields should also be visually surveyed. In addition, it is advised that potatoes from these fields are inspected following harvest.

5.39. The EPPO protocol states that if continuing official action is required within the demarcated area over a prolonged period, a review of eradication and containment measures should be undertaken regularly to determine the success and cost-

effectiveness of measures in the longer term. This review will involve consultation with stakeholders and should include:

- Evaluation of the effectiveness of current measures
- Evaluation of the economic impact and cost-effectiveness of continuing existing measures
- Consideration of further measures to strengthen containment and eradication actions
- Consideration of statutory obligations and impact on import and export procedures
- Consideration of alternative approaches, including pursuing measures to contain the pest rather than eradication or even the cessation of statutory action.

In circumstances where it is considered that the pest cannot be eradicated or contained and official action is no longer considered appropriate, stakeholders should be consulted and a timetable and mechanism for the removal of official measures, and for the dissemination of pest management information, should be agreed with the EU commission.

6. Criteria for declaring eradication / change of policy

- 6.1. *Potato spindle tuber viroid* can be declared eradicated (by the Chief Plant Health Officer Unit) in potato after at least two years during which no volunteers have been identified in the field due to the persistence of volunteer plants and no weeds have been found to be infected with PSTVd (EPPO, 2011).

7. Evaluation and review of the contingency plan

- 7.1. This pest specific contingency plan should be reviewed regularly to consider any changes in legislation, control procedures, sampling and diagnosis methods, and any other relevant amendments.
- 7.2. Lessons should be identified during and after any PSTVd or non-PSTVd outbreak, including what went well and what did not. These should be included in any review of the contingency plan leading to continuous improvement of the plan and response to outbreaks.

8. Appendix

Data sheet for Potato spindle tuber viroid

Identity

PREFERRED SCIENTIFIC NAME	AUTHOR (taxonomic authority)
<i>Potato spindle tuber viroid</i>	Diener (1971)

SUPERKINGDOM: Viroids

FAMILY: Pospiviroidae

GENUS: Pospiviroid

NON- PREFERRED SCIENTIFIC NAME (EPPO, 2014)	AUTHOR (taxonomic authority)
<i>Potato gothic virus</i>	-
<i>Potato spindle tuber pospiviroid</i>	-
<i>Potato spindle tuber virus</i>	-
<i>Tomato bunchy top viroid</i>	-

INTERNATIONALLY USED COMMON NAME(S) AND INTERNATIONAL LANGUAGE (EPPO, 2014):

Spindelknollenkrnakheit (German)

Bunchy top of tomato (English)

Spindle tuber of potato (English)

Notes on taxonomy and nomenclature

There are two viroid families; Avsunviroidae and Pospiviroidae. They are distinguished based on the presence or absence of a Central Conserved Region (CCR) and hammerhead ribozymes. The family Pospiviroidae has a CCR and does not form hammerhead ribozymes. This family is composed of five genera, including the genus Pospiviroid. *Potato spindle tuber viroid* (PSTVd) is the type species of the Pospiviroid genus (CABI, 2015; Flores *et al.*, 2009).

Species are discriminated from one another based on their level of sequence similarity across the whole genome; if their sequences differ by more than 10%, they are classified as separate species (Flores *et al.*, 2005). However, some genetically similar viroids are also separated because of differences in host range and symptoms. This is the case for PSTVd and *Tomato chlorotic dwarf viroid*.

Biology and ecology

Once the viroid has been transmitted into a host plant cell, it replicates within the nuclei via a rolling circle mechanism (Flores *et al.*, 2009).

Hosts/crops affected

The main host of PSTVd is considered to be potato (*Solanum tuberosum*), primarily because of the severity of symptoms that are seen on the plant following infection. Other hosts which suffer symptoms are *Solanum lycopersicum* (tomato), *Capsicum annuum* (pepper) and *Physalis peruviana* (Cape gooseberry) (Mackie *et al.*, 2002; Lebas *et al.*, 2005; Ward *et al.*, 2010). Symptomless infections have also been reported from , *Brugmansia* spp., *Chrysanthemum* sp., *Calibrachoa* sp., *Cestrum* spp., *Dahlia* sp., *Datura* sp. *Ipomoea batatas* (sweet potato), *Lycianthes rantonnei*, *Persea americana* (avocado), *Petunia* sp., *Solanum pseudocapsicum*, *Streptosolen jamesonii*, *Solanum jasminoides*, *Solanum muricatum* and wild *Solanum* spp. (Salazar, 1989; Owens *et al.*, 1992; Querci *et al.*, 1995; Behjatnia *et al.*, 1996; Di Serio, 2007; Verhoeven *et al.*, 2008a, b, 2009, 2010; Lemmetty *et al.*, 2011; Luigi *et al.*, 2011; Mertelik *et al.*, 2010; Verhoeven, 2010b; Tsushima *et al.*, 2011). The experimental host range of the viroid is even wider, numbering over 130 species, including several solanaceous plants (e.g. *Solanum melongena* (aubergine)) and species from Amaranthaceae, Asteraceae, Boraginaceae, Campanulaceae, Caryophyllaceae, Compositae, Convolvulaceae, Dipsacaceae, Orobanchaceae, Sapindaceae, Scrophulariaceae and Valerianaceae (Singh, 1973; Matoušek *et al.*, 2007; Vachev *et al.*, 2010; Matsushita and Tsuda, 2015).

Plant stages affected

Potato spindle tuber viroid affects the flowering stage, fruiting stage and the vegetative growing stage.

Plant parts affected

Potato spindle tuber viroid affects the leaves, roots, fruits and tubers, as well as the size of the plant.

Symptoms/signs – description

Potato

Growth is often reduced, but impacts range from very mild (barely noticeable) to severe (CABI, 2015). There is an accumulation of pigment at the top of stems, which is generally associated with the rolling of terminal leaflets. If viewed from above, an infected potato plant is considered to exhibit clockwise phyllotaxy (= arrangement of leaves on the plant stem) (EPPO data sheet). Vines may be smaller, more spindly and upright. Leaves may also be smaller, as well as darker and more crinkled (CABI, 2015). Axillary buds

sometimes proliferate to give the impression of Witches' Broom (EPPO data sheet). Further down the plant, tubers lose their shape, some becoming thinner and smaller, while others become bigger ('giant hill') (Gilbert, 1925; CABI, 2015; EPPO data sheet). The tubers also exhibit a cracked appearance (CABI, 2015). The eyes of the tubers are sometimes more pronounced, increase in number and may be borne on 'knob-like protuberances' (Martin, 1922, 1924; CABI, 2015). Sprouting might also be slower than normal (EPPO data sheet).

The type and severity of symptoms vary depending on the strain of PSTVd and the cultivar of potato (Singh *et al.*, 1971; Pfannenstiel and Slack, 1980; Kowalska-Noordam *et al.*, 1987; Nakahara *et al.*, 1997). For example, Macleod (1927) found symptoms to be more obvious on Irish Cobbler than on Oreen Mountain Potatoes. Environmental conditions have also been shown to impact on symptoms, with higher soil moisture and temperature resulting in more serious damage of tubers (Goss, 1930).

Tomato

The first signs of PSTVd are growth reduction, epinasty (drooping of the leaf, caused by greater growth on the upper surface), chlorosis and crinkling at the top of the plant (Fig. 2; CABI, 2015; EPPO data sheet). This is followed by more severe chlorosis lower down the plant, which eventually results in reddening and purpling, and/or necrosis, and the leaves becoming brittle (Fig. 3; CABI, 2015). The growth reduction at the top of the plant may also lead to stunting of the whole plant (CABI, 2015). This is coupled with the cessation of flower and fruit initiation (CABI, 2015). In the worst case, stunting is followed by the death of the plant.

Pepper

Outside of the laboratory, the only symptoms observed on pepper have been the distortion of the leaf margins at the top of the plant (Lebas *et al.*, 2005). Artificial inoculation of the viroid has also resulted in a reduction of fruit size (Verhoeven *et al.*, 2009a).

Other fruit and vegetable crops, and ornamentals

Infection outside of potato, tomato and pepper is generally asymptomatic, though there is a record of symptom expression in Cape gooseberry plants (Ward *et al.*, 2010). Symptoms have also been displayed in aubergine and *Petunia x hybrida* following experimental inoculation (Matsushita and Tsuda, 2015).

Morphology

Potato spindle tuber viroid is a small, circular, single stranded RNA (Gross *et al.*, 1978). Depending on the strain, the number of nucleotides can total between 356 and 363 (Puchta *et al.*, 1990; Lakshman and Tavantzis, 1993; Behjatnia *et al.*, 1996; Verhoeven *et al.*, 2010a).



Figure 2. Epinasty, chlorosis and leaf crinkling of tomato plant.
© Sharon van Brunschot



Figure 3. Purpling of tomato leaves.
© Sharon van Brunschot

Similarities to other species/diseases/plant damages

The host range and symptom expression of other pospiviroids is similar to PSTVd (CABI, 2015). At least seven pospiviroids outside of PSTVd have been recorded naturally infecting tomato, and *Pepper chat fruit viroid* (PCFVd) has been recorded naturally infecting pepper (EFSA Panel on Plant Health, 2011). However, only PSTVd has been confirmed to infect potato in nature. All other pospiviroid infections of potato have been the result of experimental transmission (EFSA Panel on Plant Health, 2011).

Detection and inspection methods

Visual inspection of potato and tomato allows for the detection of pospiviroids if symptoms are present. However, because symptoms are similar between pospiviroids, it is difficult to distinguish PSTVd from other species. Depending on the severity of the strain, the environmental conditions and the host, symptoms may also not be evident. Laboratory tests are therefore required.

The principal means of detecting pospiviroids is through reverse transcription-polymerase chain reaction (RT-PCR) (Shamloul *et al.*, 1997; Bostan *et al.*, 2004; Verhoeven *et al.*,

2011). This method is generally non-specific and will not allow identification down to species level (e.g. Singh *et al.*, 1999; Verhoeven *et al.*, 2011). Identification to species level requires sequencing of the RT-PCR products and BLAST analysis (Boonham *et al.*, 2005; Verhoeven, 2010a).

Other methods that allow for the detection of pospiviroids include the use of indicator plants (Raymer *et al.*, 1964; Fernow *et al.*, 1969; Singh, 1984; Grasmick and Slack, 1987), gel electrophoresis (Morris and Wright, 1975; Schumann *et al.*, 1978; Schumacher *et al.*, 1986), nucleic acid hybridization (Owens and Diener 1981; Salazar *et al.*, 1983, 1988a, Lakshman *et al.*, 1986; Roy *et al.*, 1989; Candresse *et al.*, 1990; Podleckis *et al.*, 1993; Singh *et al.*, 1994; Khan *et al.*, 2009; Monger and Jeffries, 2015), real-time RT-PCR (Boonham *et al.*, 2004; Roenhorst *et al.*, 2005), reverse transcription loop-mediated isothermal amplification (RT-LAMP) (Tsutsumi *et al.*, 2010), real-time RT-LAMP (Lenarcic *et al.*, 2012) and macro/microarrays (Agindotan and Perry, 2008; Tiberini and Barba, 2012).

Distribution

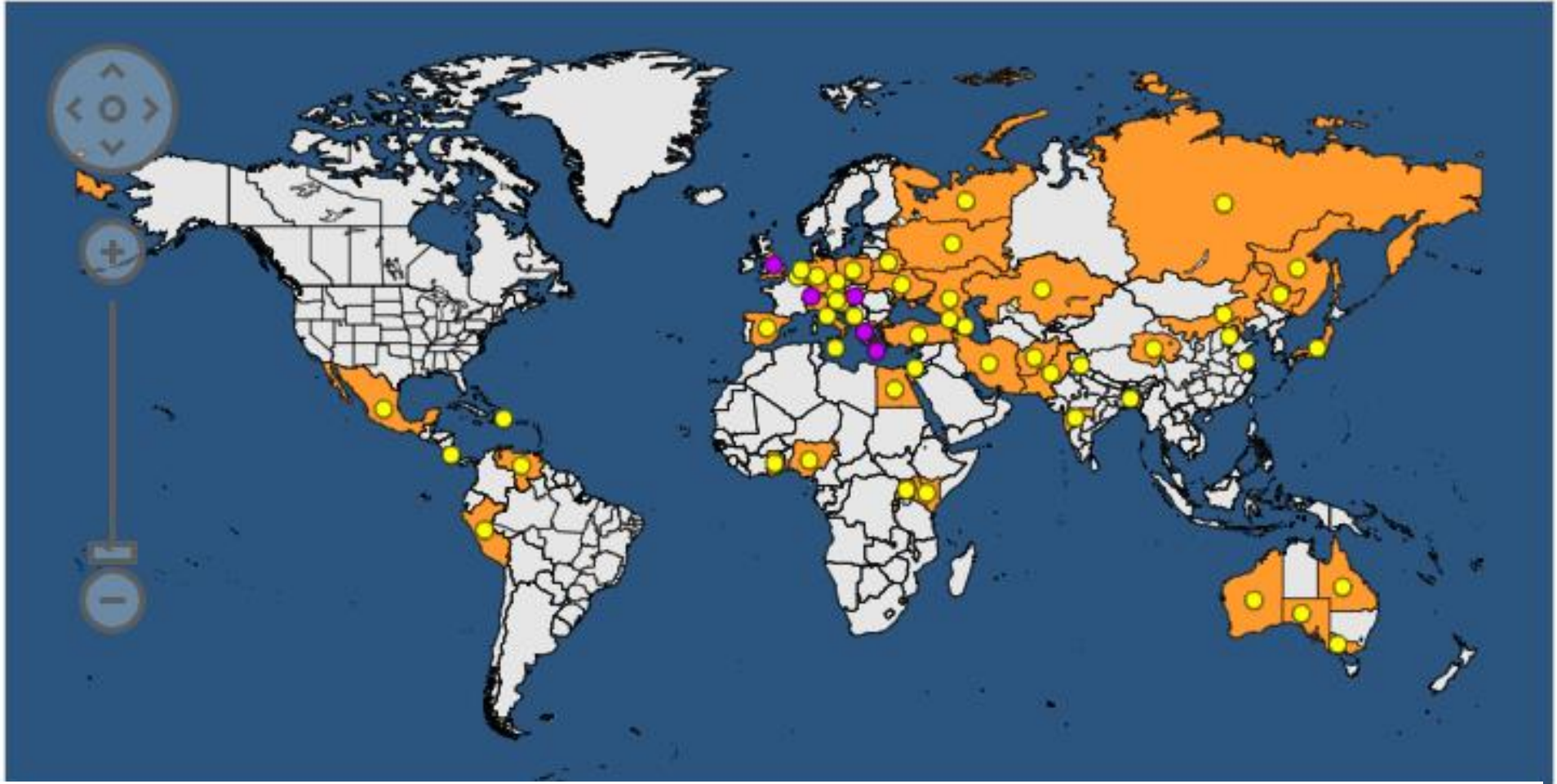


Figure 2. Distribution of PSTVd (yellow = present, purple = transient) (Source EPPO Global database). Up to date distribution data can be found using the link below.

<https://gd.eppo.int/taxon/PSTVD0/distribution>

History of introduction and spread

It has been suggested that PSTVd, along with *Mexican papita viroid* and *Tomato plancho macho viroid*, descends from a common ancestor originating in Mexico, on a wild *Solanum cardiophyllum* plant (Hoop *et al.*, 2008). However, spindle tuber disease was first identified in New Jersey, USA, in 1922 (Martin, 1922), and soon after in Maine (Martin 1922; Schulz and Folsom 1923). The viroid has since spread to a number of countries across various continents (Fig. 2). Reports of the viroid in potato fields have come from the USA, Canada, China, Russia and Turkey (Singh *et al.*, 1970, 1991, 1993b; Tien, 1985; He *et al.*, 1987; Güner *et al.*, 2012). The USA and Canada have since eradicated PSTVd (Sun *et al.*, 2004; De Boer *et al.*, 2005). The viroid has also been recorded in potato collections and breeding material in the UK, Australia, Argentina, Peru, the Netherlands, Venezuela and Brazil (Cammack and Richardson, 1963; Scottish Plant Breeding Station, 1976; Schwinghamer *et al.*, 1983; Cartwright, 1984; Fernandez-Valiela, 1965; Singh, 1983; Netherlands NPPO, 2014), but has been eradicated in the UK and Argentina. In tomato, reports of PSTVd have come from Australia, Belgium, Italy, Japan, New Zealand, the Netherlands, UK and the USA (Puchta *et al.*, 1990; Elliott *et al.*, 2001; Mackie *et al.*, 2002; Hailstones *et al.*, 2003; Mumford *et al.*, 2004a; Verhoeven *et al.*, 2004, 2007; Matshushita *et al.*, 2008; Navarro *et al.*, 2009; Ling and Sfetcu, 2010). Further, there have been a number of reports of PSTVd in other crops, such as ornamentals and peppers, in other countries (e.g. EFSA Panel on Plant Health, 2011; Lebas *et al.*, 2005).

Phytosanitary status

Potato spindle tuber viroid is a GB Regulated Non-Quarantine Pest (RNQP) when associated with ornamental plants for planting of pepper (*Capsicum annuum*), vegetable propagating and planting material (other than seeds) of pepper and tomato (*Solanum lycopersicum*), pepper and tomato seed, seed potatoes (*Solanum tuberosum*) and potato seeds as listed in Parts C, E, F, H and J of Schedule 4 of The Plant Health (Phytosanitary Conditions) (Amendment) (EU Exit) Regulations 2020. There is a 0% threshold for findings of PSTVd on consignments of the listed commodities in GB.

It is also present on several other phytosanitary lists.

Table 1. Global phytosanitary categorisation of PSTVd.

Country/NPPO/RPPO	List	Year of addition
AFRICA		
East Africa	A1 list	2001
Egypt	A1 list	2018
Morocco	Quarantine pest	2018

Country/NPPO/RPPO	List	Year of addition
Tunisia	Quarantine pest	2012
AMERICA		
Argentina	A1 list	2019
Brazil	A1 list	2018
Canada	Quarantine pest	2019
Chile	A1 list	2019
Mexico	Quarantine pest	2018
USA	Quarantine pest	1989
Uruguay	A1 list	1995
ASIA		
Bahrain	A1 list	2003
Israel	Quarantine pest	2009
Jordan	A1 list	2013
Kazakhstan	A1 list	2017
EUROPE		
GB	RNQP	2020
Georgia	A1 list	2018
Moldova	Quarantine pest	2017
Norway	Quarantine pest	2012
Russia	A2 list	2014
Turkey	A2 list	2016
Ukraine	RNQP	2019
RPPO		
COSAVE	A2 list	2018
EAEU	A2 list	2016
EPPO	A2 list	1975
EU	RNQP	2019

Means of movement and dispersal

There is a high transmission rate of PSTVd from mother plants to their vegetatively propagated progeny (Owens and Verhoeven, 2009). This vegetative propagation material can be moved over long distances in trade, and is thought to be a major source of spread in potato and ornamental plants, especially in the absence of symptoms (Singh *et al.*, 1993b; Di Serio, 2007; Owens *et al.*, 2009).

A further form of human assisted transmission is mechanical spread. The spread of PSTVd has been shown between plants of the same and different species, via foliage and tuber contact (Bonde and Merriam, 1951; Merriam and Bonde, 1954), gloves and hands (Siegener *et al.*, 2008; Verhoeven *et al.*, 2010b; Fujiwara *et al.*, 2013; van Brunschot *et al.*, 2014 [fruit sap]), machinery (Merriam and Bonde, 1954; Manzer and Merriam, 1961), and tools (Verhoeven *et al.*, 2010b; Fujiwara *et al.*, 2013). PSTVd remains infective for hours outside of plants, as is shown on hands and gloves (Verhoeven *et al.*, 2010b; van Brunschot *et al.*, 2014). In addition, transmission efficiency varies depending on the recipient host and the source of inoculum (Verhoeven *et al.*, 2010b). For example, PSTVd was more readily transmitted to tomato and potato from *Solanum jasminoides* than from *Brugmansia suaveolens*. Verhoeven *et al.* (2010b) has also shown that temperature is a factor, with 25°C favouring transmission of PSTVd and 15°C being inhibitory.

Transmission by seed and pollen results in spread within a species. This method of transmission for PSTVd has been reported for potato (Hunter *et al.*, 1969; Singh, 1970; Singh *et al.*, 1992), tomato (Benson and Singh, 1964; Singh, 1970; Kryczynski *et al.*, 1988; van Brunschot *et al.*, 2014), and *Scopolia sinensis*, a wild solanaceous plant (Singh and Finnie, 1973), as well as experimentally by Kryczynski *et al.* (1992) and van Brunschot *et al.* (2014). The rates of transmission in potato vary between collections (Fernow *et al.*, 1970; Singh *et al.*, 1993b). EUPHRESCO (2011) have also shown that the viroid accumulates within the tissues of tomato seeds, which might leave it protected (either fully or partially) from disinfection techniques.

Transmission by insect vectors also allows for spread within and between species. Early experiments by Kennedy *et al.* (1962) and Smith (1972) showed that the aphids *Macrosiphum euphorbiae* and *Myzus persicae* transmitted PSTVd in potato. However, a later study by Schumann *et al.* (1980) did not corroborate these findings. Further, in a study by De Bokx and Piron (1981), PSTVd was not transmitted by *M. persicae* or *A. solani*, and was only transmitted by *M. euphorbiae* to tomato with very low efficiency. More recent research has shown that PSTVd is readily transmitted by *M. persicae* in the presence of *Potato leafroll virus* (PLRV) in potato (Salazar *et al.*, 1995). The presence of the virus might even be a necessity for *M. persicae*, with PSTVd failing to be transmitted in the absence of the virus in both potato and tomato (Querci *et al.*, 1997; Singh and Kurz, 1997; Syller *et al.*, 1997 [from *P. floridana*]). Syller *et al.* (1997) also showed that PSTVd was encapsidated by (enclosed within the protein shell of) PLRV, rather than simply being adsorbed onto the outside, and that this might explain the successful aphid transmission.

Although bumblebees have shown transmission of *Tomato apical stunt viroid* (TASVd) and *Tomato chlorotic dwarf viroid* (TCDVd) (Antignus *et al.*, 2007; Matsuura *et al.*, 2010), a study by Nielsen *et al.* (2012) did not demonstrate transmission of PSTVd in this way. Nielsen *et al.* (2012) also did not show transmission of the viroid in adult thrips, though encapsidation was not explored, and nor was feeding by nymphs.

Mehle *et al.* (2014) has recently shown that PSTVd can remain infective within water for up to 7 weeks, and that infected water can lead to the infection of tomato roots and later the infection of the green parts of the plant. Potato tubers developed from plants grown in PSTVd infected water were also shown to be sources of the viroid. In hydroponic systems, where water is recycled, tomato and pepper plants are grown for several months, and sometimes a year. There is therefore time for the viroid to accumulate in or on roots. Although, it should be noted that infection efficiency was low, and that if infection did occur, movement into the rest of the plant was delayed and unevenly distributed.

Control

Chemical and biological control

There are currently no effective chemical or biological control options for PSTVd itself (CABI, 2015). However, its aphid vectors can be controlled through traditional means (EFSA Panel on Plant Health, 2011).

Resistant crop cultivars

There are currently no naturally occurring plant cultivars that offer full resistance to PSTVd. *Solanum acaule* offers partial resistance and is impervious to mechanical inoculation by PSTVd, but is vulnerable to infection when cDNAs containing the viroid are used in agroinfection (Salazar *et al.*, 1988b). Partial resistance has also been reported for other plants, including *Solanum guerreroens* and *Solanum berthaultii* (Harris *et al.*, 1979; Pfannenstiel and Slack, 1980; Singh, 1985; Palukaitis, 2012). Experimentally, resistance to PSTVd has been shown by Yang *et al.* (1997), Sano *et al.* (1997) and Schwind *et al.* (2009).

Cultural controls and sanitary methods during cultivation

Hygiene best practice

Principles of hygiene best practice for pospiviroids, including PSTVd, are outlined in the EFSA Panel on Plant Health (2011) and are briefly described in the contingency plan (Precautionary measures section).

Cleaning and disinfectants

Thorough cleaning of a glasshouse using a steam cleaner, and a scrub brush for less easily accessible structures, together with detergent is advised. An acid treatment for watering tubes and drippers has also been suggested by Owens and Verhoeven (2009).

Both Virkon and Virkon S (Li *et al.*, 2015; Olivier *et al.*, 2015), and sodium hypochlorite (e.g. Clorox regular bleach, Singh *et al.*, 1989; Roenhorst *et al.*, 2005; Li *et al.*, 2015) have been shown to be particularly effective as disinfectants of PSTVd. Nonfat dry milk, Lysol all-purpose cleaner, Viroid, Hyprelva SL and Jet S have also been shown to have a marked effect on PSTVd (Li *et al.*, 2015; Olivier *et al.*, 2015). Although Menno Florades and MENNO clean are mentioned in EPPO (2011) as suitable disinfectants for PSTVd, they were not demonstrated to be that effective by Li *et al.* (2015) or Olivier *et al.* (2015), respectively. It should be noted that disinfectants were less effective when applied to dried sap droplets infected with PSTVd (Olivier *et al.*, 2015). This was attributed to thick halos of sap forming at the periphery of the droplets, allowing the viroid to avoid the disinfectants. It is therefore important that appropriate contact is made between the viroid and the disinfectant if there is to be an effect.

Monitoring and testing

Regular monitoring of a crop allows for the early identification of symptoms. Testing also provides a means of detecting PSTVd in symptomatic, but also asymptomatic, plants, such as ornamentals.

Recovery

Potato spindle tuber viroid-free plants can be recovered from the infected plants by first exposing them to low temperatures (5-8°C) and then producing a meristem culture from these plants. This resulted in a recovery rate of 18.5-80% (Lizarraga *et al.* 1980; Paduch-Cichal and Kryczyński, 1987). Treatment of plants at high temperature (33-36°C) and producing a culture from the axillary buds also resulted in PSTVd-free plants, though this only produced a recovery rate of 2.4-6% (Stace-Smith and Mellor, 1970).

Phytosanitary measures

Import control measures

At ports, general surveillance is carried out, involving visual inspection for PSTVd symptoms, and subsequent testing if symptoms are found. If PSTVd is confirmed, the consignment is generally destroyed by either incineration or deep burial. Specific surveys are also instigated if there is considered to be sufficient risk of PSTVd spread.

Impacts

Economic impact

Reported yield losses for potato vary between 10 and 74% (Singh *et al.*, 1971; Cui *et al.*, 1992; Leontyeva, 1963; Cammack and Richardson, 1963; Folsom and Schultz, 1924; Bonde *et al.*, 1943; Murphy *et al.*, 1966; Hunter and Rich, 1964; Martin, 1924, 1928; Wedgworth, 1928; McKay and Dykstra, 1932; Burger, 1927; Balashev, 1941). The level of loss is dependent on the cultivar of potato, the strain of PSTVd and the length of time the

crop has been infected with the viroid. For example, in the Saco cultivar, tuber yield was reduced by 24% when infected with the mild strain, but by 64% when infected with the severe strain (Singh *et al.*, 1971).

Tomato also suffers from variable yield losses (Verhoeven *et al.*, 2004, 2007). As well as the factors mentioned for potato, the growth stage at which the plant is infected is also important. Because fruit stops developing once stunting sets in, if tomato plants are infected prior to fruit production, yield losses could be as much as 100%, whereas if they are infected post fruit production, the fruit may still develop to a marketable size. Further, high infection rates in the past have been caused by a delay in identifying PSTVd in the crop and instigating measures. It has recently been found that elevated ozone concentration can reduce the impact of PSTVd in tomato (Abraitene and Girgždiene, 2013).

Soliman (2012) calculated the economic losses of PSTVd in Europe if left unchecked to be 4.4 million euros in potato and 5.7 million euros in tomato, with the bulk of the costs borne by consumers having to pay a higher price for the same product, due to decreases in supply. Owens and Verhoeven (2009) have also calculated yield losses in North America over the period 1922-2009 to be 1% even after attempting to control the viroid.

In peppers, ornamentals, and other plants, no yield losses have been recorded, with only mild symptoms in pepper to date (Lebas *et al.*, 2005).

Environmental impact

No impact has been recorded.

Social impact

No impact has been recorded.

9. References

- Abraitene, A. and Girgždiene, R.** (2013) Impact of the short-term mild and severe ozone treatments on the potato spindle tuber viroid-infected tomato (*Lycopersicon esculentum*). Zemdirbyste-Agriculture. 100, 277-282.
- Agindotan, B. and Perry, K. L.** (2008) Macroarray detection of eleven potato-infecting viruses and Potato spindle tuber viroid. Plant Disease. 92, 730-740.
- Antignus, Y., Lachman, O. and Pearlsman, M.** (2007) Spread of tomato apical stunt viroid (TASVd) in greenhouse tomato crops is associated with seed transmission and bumble bee activity. Plant Disease. 91, 47-50.
- Arezou, Y., Jafarpour, B., Rastegar, M. F. and Javadmanesh, A.** (2008) Molecular detection of Potato Spindle Tuber Viroid in Razavi and Northern Khorasan provinces. Pakistan Journal of Biological Sciences. 11, 1642-1645.
- Balashv, N. N.** (1941) Virus diseases and potato degeneration in Uzbekistan. Doklady Vsesoyuznoi Akademii sel'sko khozyaistvennykh Nauk im, 22-27.
- Behjatnia, S. A. A., Dry, I. B., Krake, L. R., Condé, B. D., Connelly, M. I., Randles, J. W., Rezaian, M. A.** (1996) New potato spindle tuber viroid and tomato leaf curl geminivirus strains from a wild *Solanum* sp. Phytopathology. 86, 880-886.
- Benson, A. P. and Singh, R. P.** (1964) Seed transmission of potato spindle tuber virus in tomato. American Potato Journal. 41, 294.
- Bonde, R. and Merriam, D.** (1951) Studies on the dissemination of the potato spindle tuber virus by mechanical inoculation. American Potato Journal. 28, 558-560.
- Bonde, R., Schultz, E. S. and Raleigh, W. P.** (1943) Rate of spread and effect on yield of potato virus diseases. Bulletin Maine Agricultural Experiment Station. 421, 28.
- Boonham, N., Fisher, T. and Mumford, R. A.** (2005) Investigating the specificity of real-time PCR assays using synthetic oligonucleotides. Journal of Virological Methods. 130, 30-35.
- Boonham, N., González Pérez, L., Mendez, M. S., Peralta, E. L., Blockley, A., Walsh, K., Barker, I., Mumford, R. A.** (2004) Development of a real-time RT-PCR assay for the detection of Potato spindle tuber viroid. Journal of Virological Methods. 116, 139-146.
- Bostan, H., Nie, X. and Singh, R. P.** (2004) An RT-PCR primer pair for the detection of pospiviroids and its application in surveying ornamental plants for viroids. Journal of Virological Methods. 116, 189-193.

- Bostan, H., Gazel, M., Elibuyuk, I. O. and Caglayan, K.** (2010) Occurrence of Pospiviroid in potato, tomato and some ornamental plants in Turkey. *African Journal of Biotechnology*. 9, 2613-2617.
- Brunschot, S. L. van., Verhoeven, J. T. J., Persley, D. M., Geering, A. D. W., Drenth, A. and Thomas, J. E.** (2014) An outbreak of Potato spindle tuber viroid in tomato is linked to imported seed. *European Journal of Plant Pathology*. 139, 1-7.
- Burger, O. F.** (1927) Report of Plant Pathologist. University of Florida, Agricultural Experiment Station, Report for the fiscal year ending June 30 1927. 62R-77R.
- CAB International (Centre for Agricultural Bioscience International)** (2015) Datasheets: Potato spindle tuber viroid (spindle tuber of potato). *Crop Protection Compendium*. Last modified 20 January 2015. Report accessed on 13 March 2015 at <http://www.cabi.org/cpc/>.
- CABI/EPPO** (2012) Potato spindle tuber viroid. [Distribution map]. *Distribution Maps of Plant Diseases*, No. April. Wallingford, UK: CABI, Map 729 (Edition 2).
- CABI/EPPO.** Data sheets on quarantine pests: Potato spindle tuber viroid [Online]. Available from: http://www.eppo.int/QUARANTINE/virus/PSTVd/PSTVD0_ds.pdf. [Accessed: 27/03/2015].
- Cammack, R. H. and Richardson, D. E.** (1963) Suspected potato spindle tuber virus in England. *Plant Pathology*. 12, 23-26.
- Candresse, T., Macquaire, G., Brault, V., Monsion, M. and Dunez, J.** (1990) ³²P- and biotin-labelled *in vitro* transcribed cRNA probes for the detection of potato spindle tuber viroid and chrysanthemum stunt viroid. *Research in Virology*. 141, 97-107.
- Cartwright, D. N.** (1984) Potato spindle tuber viroid survey - South Australia. *Australasian Plant Pathology*. 13, 4-5.
- Cervená, G., Necekalová, J., Mikulková, H., Levkanicová, Z., Mertelík, J., Kloudová, K., Dedic, P. and Ptáček, J.** (2011) Viroids on petunia and other solanaceous crops in the Czech Republic. *Acta Horticulturae* [12th International Symposium on Virus Diseases of Ornamental Plants, Haarlem, Netherlands, 21 April 2008.]. 901, 35-40.
- Cui, R. C., Li, Z. F., Li, X. L. and Wang, G. X.** (1992) Identification of potato spindle tuber viroid (PSTVd) and its control. *Acta Phytologica Sinica*. 19, 263-269.
- De Boer, S. H. and Dehaan, T. L.** (2005) Absence of Potato spindle tuber viroid within the Canadian potato industry. *Plant Disease*. 89, 910.
- De Bokx, J. A. and Piron, P. G. M.** (1981) Transmission of potato spindle tuber viroid by aphids. *Netherlands Journal of Plant Pathology*. 87, 31-34.

Di Serio, F. (2007) Identification and characterization of potato spindle tuber viroid infecting *Solanum jasminoides* and *S. rantonnetii* in Italy. *Journal of Plant Pathology*. 89, 297-300.

EFSA Panel on Plant Health (PLH) (2011) Scientific Opinion on the assessment of the risk of solanaceous pospiviroids for the EU territory and the identification and evaluation of risk management options. *EFSA Journal*. 9, 2330. Available from: <http://www.efsa.europa.eu/en/efsajournal/pub/2330.htm>.

Elliott, D. R., Alexander, B. J. R., Smales, T. E., Tang, Z. and Clover, G. R. G. (2001) First report of Potato spindle tuber viroid in tomato in New Zealand. *Plant Disease*. 85, 1027.

EPPO (2011) EPPO Reporting Service. EPPO Reporting Service. Paris, France: EPPO. http://archives.eppo.org/EPPOReporting/Reporting_Archives.htm.

EPPO (2011) Potato spindle tuber viroid on potato. *EPPO Bulletin*. 41, 394-399.

EPPO (2014) Global database. Paris, France: European and Mediterranean Plant Protection Organization. <https://gd.eppo.int/taxon/PSTVDO>.

EUPHRESKO (2011) Detection and epidemiology of pospiviroids (DEP) [Online]. Available: <https://secure.fera.defra.gov.uk/euphresco/downloadFile.cfm?id=536> [Accessed: 11/05/2015].

Fernow, K. H., Peterson, L. C. and Plaisted, R. L. (1969) The tomato test for eliminating spindle tuber from potato planting stock. *American Potato Journal*. 46, 424-429.

Fernow, K. H., Peterson, L. C. and Plaisted, R. L. (1970) Spindle tuber virus in seeds and pollen of infected potato plants. *American Potato Journal*. 47, 75-80.

Fernandez-Valiela, M. V. and Calderoni, A. V. (1965) The search for potato growing areas in the Argentine Republic. *Actas Inst. Micol.* 2, 60.

Flores, R., Randles, J. W., Owens, R. A., Bar-Joseph, M. and Diener, T. O. (2005) Viroidae. In: *Virus Taxonomy, Eighth Report of the International Committee on Taxonomy of Viruses* (Eds. C. M. Fauquet, M. A. Mayo, J. Maniloff, U. Desselberger & A. L. Ball). London. Elsevier Academic Press, 1145-1159.

Flores, R., Gas, M-E., Molina-Serrano, D., Nohales, M-Á., Carbonell, A., Gago, S., Peña, M. D. and Daròs, J-A. (2009) Viroid replication: rolling-circles, enzymes and ribozymes. *Viruses*. 1, 317-334.

Folsom, D. and Schultz, E. S. (1924) The importance and natural spread of potato degeneration diseases. *Bulletin Maine Agricultural Experiment Station*. 316, 28.

Fujiwara, Y., Nomura, Y., Hiwatashi, S., Shiki, Y., Itto, T., Hamanaka, D. and Saito, N. (2013) Pathogenicity of *Potato spindle tuber viroid* isolated from dahlia and its

transmissibility in dahlia. Research Bulletin of the plant Protection Service, Japan. 49, 41-46.

Gilbert, A. H. (1925) 'Giant hill' potatoes a dangerous source of seed. A new phase of spindle-tuber. Bulletin Vermont Agricultural Experiment Station. 245, 16.

Goss, B. W. (1930) The symptoms of spindle tuber and unmottled curly dwarf of the potato. Nebraska Agricultural Experiment Station Research Bulletin. 47, 39.

Grasmick, M. E. and Slack, S. A. (1987) Detection of potato spindle tuber viroid in true potato seed by bioassay on Rutgers tomato. American Potato Journal, 64, 235-244.

Gross, H. J., Domdey, H., Lossow, D., Jank, P., Raba, M., Alberty, H. and Sanger, H. L. (1978) Nucleotide sequence and secondary structure of potato spindle tuber viroid. Nature. 273, 203-208.

Guner, ., Sipahioglu, H. M. and Usta, M. (2012) Incidence and genetic stability of Potato spindle tuber pospiviroid in potato in Turkey. Turkish Journal of Agriculture and Forestry. 36, 353-363.

Hailstones, D. L., Tesoriero, L. A., Terras, M. A. and Dephoff, C. (2003) Disease Notes or New Records. Detection and eradication of Potato spindle tuber viroid in tomatoes in commercial production in New South Wales, Australia. Australasian Plant Pathology. 32, 317-318.

Harris, P. S., Miller-Jones, D. N. and Howell, P. J. (1979) Control of potato spindle tuber viroid: The special problems of a disease in plant breeder's material. In: Plant Health: The Scientific Basis for Administrative Control of Plant Parasites (eds. D. L. Ebbels and J. E. King). Oxford, UK: Blackwells Scientific Publications, pp. 231-237.

He, L. Y., Zhang, H. L. and Huang, H. (1987) Potato diseases in Asia: recent and expected developments. Acta Horticulturae. 213, 129-142.

Hoop, M. B. de, Verhoeven, J. T. J. and Roenhorst, J. W. (2008) Phytosanitary measures in the European Union: a call for more dynamic risk management allowing more focus on real pest risks. Case study: *Potato spindle tuber viroid* (PSTVd) on ornamental Solanaceae in Europe. 38, 510-515.

Hunter, D. E., Darling, D. H., Beale, W. L. (1969) Seed transmission of potato spindle tuber virus. American Potato Journal. 46, 247-250.

Hunter, J. E. and Rich, A. E. (1964) The effect of potato spindle tuber virus on growth and yield of Saco Potatoes. American Potato Journal. 41, 113-116.

IPPC (2011) Potato spindle tuber viroid. IPPC Official Pest Report, No. GBR-26/1. Rome, Italy: FAO. <https://www.ippc.int/>.

- IPPC (2014a)** Finding of Potato spindle tuber viroid (PSTVd) in breeding material of *Solanum tuberosum* (potato) - no links with commercial cultivars of potato. IPPC Official Pest Report, No. NLD-30/1. Rome, Italy: FAO. <https://www.ippc.int/>.
- IPPC (2014b)** First finding of Potato Spindle Tuber Viroid (PSTVd) in *Dahlia* sp. corm production in the Netherlands. IPPC Official Pest Report, No. NLD-21/1. Rome, Italy: FAO. <https://www.ippc.int/>.
- Kennedy, J. S., Day, M. F. and Eastop, V. F.** (1962) A conspectus of aphids as vectors of plant viruses. Commonwealth Institute of Entomology, London, pp. 114.
- Khan, M. S., Timmermann, C., Hoque, M. I., Sarker, R. H. and Mühlbach, H. P.** (2009) Detection of potato spindle tuber viroid (PSTVd) in minute amounts of potato (*Solanum tuberosum* L.) leaf tissue by hybridization techniques and, together with potato viruses, by multiplex RT-PCR. Journal of Plant Diseases and Protection. 116, 97-105.
- Kowalska-Noordam, A., Chrzanowska, M. and Skrzeczkowski, S.** (1987) Reaction of ten Polish potato cultivars to severe and mild strains of *potato spindle tuber viroid*. Ziemiak. 87, 71-92.
- Kryczynski, S. Paduch-Cichal, E. and Skrzeczkowska, S.** (1988) Transmission of three viroids through seed and pollen of tomato plants. Journal of Phytopathology. 121, 51-57.
- Kryczynski, S., Stawiszynska, A. and Skrzeczkowska, S.** (1992) Pollen transmission of potato spindle tuber viroid (PSTV) to pollinated potato plants. Annals of Warsaw Agricultural University SGGW-AR, Horticulture. 16, 59-64.
- Lakshman, D. K. and Tavantzis, S. M.** (1993) Primary and secondary structure of a 360-nucleotide isolate of potato spindle tuber viroid. Archives of Virology. 128, 319-331.
- Lakshman, D. K., Hiruki, C., Wu, X. N. and Leung, W. C.** (1986) Use of [³²P] RNA probes for the dot-hybridization detection of potato spindle tuber viroid. Journal of Virological Methods. 14, 309-319.
- Lebas, B. S. M., Clover, G. R. G., Ochoa-Corona, F. M., Elliott, D. R., Tang, Z. and Alexander, B. J. R.** (2005) Distribution of potato spindle tuber viroid in New Zealand glasshouse crops of capsicum and tomato. Australasian Plant Pathology, 34, 129-133.
- Lemmetty, A., Laamanen, J., Soukainen, M., Tegel, J.** (2011) Emerging virus and viroid pathogen species identified for the first time in horticultural plants in Finland in 1997-2010. Agricultural and Food Science. 20, 29-41.
- Lenarcic, R., Morisset, D., Mehle, N. and Ravnikar, M.** (2012) Fast real-time detection of Potato spindle tuber viroid by RT-LAMP. Plant Pathology. 62, 1147-1156.

- Leontyeva, J. A.** (1963) Distribution and harmfulness of spindle tuber (gothic) of potato. Seed breeding and measures for combating potato degeneration diseases in the Far East. 33-55.
- Ling, K. S. and Sfetcu, D.** (2010) First report of natural infection of greenhouse tomatoes by Potato spindle tuber viroid in the United States. *Plant Disease*. 94, 1376.
- Ling, K. S., Li, R., Groth-Helms, D. and Assis Filho, F. M.** (2014) First report of Potato spindle tuber viroid naturally infecting field tomatoes in the Dominican Republic. *Plant Disease*. 98, 701.
- Li, R., B-G, F., Abdo, Z., Miller, S. A. and Ling, K-S.** (2015) Evaluation of disinfectants to prevent mechanical transmission of viruses and a viroid in greenhouse tomato production. *Virology Journal*. 12, 5.
- Lizarraga, R. E., Salazar, L. F., Roca, W. M. and Schilde-Rentschler, L.** (1980) Elimination of Potato spindle tuber viroid by low temperature and meristem culture. *Phytopathology*, 70, 754-755.
- Luigi, M., Luison, D., Tomassoli, L., Faggioli, F.** (2011) First report of Potato spindle tuber and Citrus exocortis viroids in *Cestrum* spp. in Italy. *New Disease Reports*. 23.
- Mackie, A. E., McKirdy, S. J., Rodoni, B. and Kumar, S.** (2002) Potato spindle tuber viroid eradicated in Western Australia. *Australasian Plant Pathology*. 31, 311-312.
- Manzer, F. E. and Merriam, D.** (1961) Field transmission of potato spindle tuber virus and virus X by cultivating and hilling equipment. *American Potato Journal*. 38, 346-352.
- Martin, W. H.** (1922) "Spindle tuber", a new potato trouble. Hints to potato growers, New Jersey State Potato Association. 3, 8.
- Martin, W. H.** (1924) Spindle tuber – a disease of potatoes. Forty-fourth Annual Report New Jersey Agriculture Experiment Station for the year ending June 30, 1923, pp. 345-347.
- Martin, W. H.** (1928) Report of the Department of Plant Pathology. Forty-eighth Annual Report New Jersey Agriculture Experiment Station for the year ending June 30, 1927, pp. 205-238.
- Marn, M. V. and Plesko, I. M.** (2012) First report of Potato spindle tuber viroid in cape gooseberry in Slovenia. *Plant Disease*. 96, 150.
- Matoušek, J., Orctová, L., Ptáček, J., Patzak, J., Dědič, Steger, G. and Riesner, D.** (2007) Experimental transmission of Pospiviroid populations to weed species characteristic of potato and hop fields. *Journal of Virology*. 81, 11891-11899.

- Matsuura, S., Matshushita, Y., Kozuka, R., Shimizu, S. and Tsuda, S.** (2010) Transmission of *tomato chlorotic dwarf viroid* by bumblebees (*Bombus ignitus*) in tomato plants. *European Journal of Plant Pathology*. 126, 111-115.
- Matsushita, Y. and Tsuda, S.** (2015) Host ranges of Potato spindle tuber viroid, Tomato chlorotic dwarf viroid, Tomato apical stunt viroid, and Columnea latent viroid in horticultural plants. *European Journal of Plant Pathology*. 141, 193-197.
- Matsushita, Y., Kanda, A., Usugi, T. and Tsuda, S.** (2008) First report of a Tomato chlorotic dwarf viroid disease on tomato plants in Japan. *Journal of General Plant Pathology*. 74, 182-184.
- McKay, M. B. and Dykstra, T. P.** (1932) Potato virus diseases: Oregon investigations 1924-1929. *Bulletin Oregon Agricultural Experiment Station*. 294, 40.
- Mehle, N., Gutiérrez-Aguirre, I., Prezelj, N., Delić, D., Vidic, U. and Ravnikar, M.** (2014) Survival and transmission of Potato virus Y, Pepino mosaic virus, and Potato spindle tuber viroid in water. *Applied and Environmental Microbiology*. 80, 1455-1462.
- Merriam, D. and Bonde, R.** (1954) Dissemination of spindle tuber by contaminated tractor wheels and by foliage contact with diseased plants. *Phytopathology*. 44, 111.
- Mertelik, J., Kloudova, K., Cervena, G., Necekalova, J., Mikulkova, H., Levkanicova, Z., Dedic, P. and Ptacek, J.** (2010) First report of Potato spindle tuber viroid (PSTVd) in *Brugmansia* spp., *Solanum jasminoides*, *Solanum muricatum* and *Petunia* spp. in the Czech Republic. *Plant Pathology*, 59, 392.
- Monger, W. A. and Jeffries, C.** (2015) Detection of Potato spindle tuber viroid and other related viroids by a DIG labelled RNA probe. *Plant Pathology Methods in Molecular Biology*. 1302, 259-271.
- Morris, T. J. and Wright, N. S.** (1975) Detection on polyacrylamide gel of a diagnostic nucleic acid from tissue infected with potato spindle tuber viroid. *American Potato Journal*. 52, 57-63.
- Mumford, R. A., Jarvis, B. and Skelton, A.** (2004a) The first report of potato spindle tuber viroid (PSTVd) in commercial tomatoes in the UK. *Plant Pathology*. 53, 242.
- Mumford, R. A., Skelton, A., O'Neil, T., Ratcliffe, T., Spence, N. and Morley, P.** (2004b) Protected tomato: sources, survival, spread and disinfection of Potato spindle tuber viroid (PSTVd), Final report of the project PC212, December 2004. Horticultural Development Company, Kenilworth (UK), pp. 29.
- Murphy, H. J., Govern, M. J. and Merriam, D. C.** (1966) Effect of three viruses on yield, specific gravity, and chip color of potatoes in Maine. *American Potato Journal*. 43, 393-396.

Nakahara, K., Hataya, T., Kimura, I. and Shikata, E. (1997) Reactions of potato cultivars in Japan to potato spindle tuber viroid and its gene diagnosis. Annual Report of the Society of Plant Protection of North Japan. 48, 69-74.

Navarro, B., Silletti, M. R., Trisciuzzi, V. N. and di Serio, F. (2009) Identification and characterization of Potato spindle tuber viroid infecting tomato in Italy. Journal of Plant Pathology. 91, 723-726.

Netherlands NPPO (2014) March 2014 PEST Report - THE NETHERLANDS [Online]. Available: https://www.nvwa.nl/txmpub/files/?p_file_id=2206234. Accessed: 17/07/2015.

Nielsen, S. L., Enkegaard, A., Nicolaisen, M., Kryger, P., Marn, M. V., Pleško, I. M., Kahrer, A. and Gottsberger, R. A. (2012) No transmission of Potato spindle tuber viroid shown in experiments with thrips (*Frankliniella occidentalis*, *Thrips tabaci*), honey bees (*Apis mellifera*) and bumblebees (*Bombus terrestris*). European Journal of Plant Pathology. 133, 505-509.

Olivier, T., Sveikauskas, V., Grausgruber-Gröger, S., Virscek Marn, M. V., Faggioli, F., Luigi, M., Pitchugina, E., Planchon, V. (2015) Efficacy of five disinfectants against *Potato spindle tuber viroid*. Crop Protection. 67, 257-260.

Owens, R. A. and Diener, T. O. (1981) Sensitive and rapid diagnosis of potato spindle tuber viroid disease by nucleic acid hybridization. Science, USA. 213, 670-672.

Owens, R. A. and Verhoeven, J. T. J. (2009) Potato spindle tuber. The plant health instructor. DOI: 10.1094/PHI-I-2009-0804-01.

Owens, R. A., Khurana, S. M. P., Smith, D. R., Singh, M. N., Garg, I. D. (1992) A new mild strain of potato spindle tuber viroid isolated from wild *Solanum* spp. in India. Plant Disease. 76, 527-529.

Owens, R. A., Girsova, N. V., Kromina, K. A., Lee, I. M. Mozhaeva, K. A. and Kastalyeva, T. B. (2009) Russian isolates of potato spindle tuber viroid exhibit low sequence diversity. Plant Disease. 93, 752-759.

Paduch-Cichal, E. and Kryczyński, S. (1987) A low temperature therapy and meristem-tip culture for eliminating four viroids from infected plants. Journal of Phytopathology. 118, 341-346.

Palukaitis, P. (2012) Resistance to viruses of potato and their vectors. The Plant Pathology Journal. 28, 248-258.

Pfannenstiel, M. A. and Slack, S. A. (1980) Response of potato cultivars to infection by the potato spindle tuber viroid. Phytopathology. 70, 922-926.

- Podleckis, E. V., Hammond, R. W., Hurtt, S. S. and Hadidi, A.** (1993) Chemiluminescent detection of potato and pome fruit viroids by digoxigenin-labeled dot blot and tissue blot hybridization. *Journal of Virological Methods*. 43, 147-158.
- Puchta, H., Herold, T., Verhoeven, K., Roenhorst, A., Ramm, K., Schmidt-Puchta, W. and Sanger, H. L.** (1990) A new strain of potato spindle tuber viroid (PSTVd-N) exhibits major sequence differences as compared to all other PSTVd strains sequenced so far. *Plant Molecular Biology*. 15, 509-511.
- Querci, M. Owens, R. A., Vargas, C., Salazar, L. F.** (1995) Detection of potato spindle tuber viroid in avocado growing in Peru. *Plant Disease*. 79, 196-202.
- Querci, M., Owens, R. A., Bartolini, I., Lazarte, V. and Salazar, L. F.** (1997) Evidence for heterologous encapsidation of potato spindle tuber viroid in particles of potato leafroll virus. *Journal of General Virology*. 78, 1207-1211.
- Raymer, W. B., O'Brien, M. J., Merriam, D.** (1964) Tomato as a source of and indicator plant for the potato spindle tuber virus. *American Potato Journal*. 41, 311-314.
- Roenhorst, J. W., Jansen, C. C. C., Kox, L. F. F., de Haan, E. G., van den Bovenkamp, G. W., Boonham, N., Fisher, T. and Mumford, R. A.** (2005) Application of real-time RT-PCR for large-scale testing of potato for Potato spindle tuber pospiviroid. *Bulletin OEPP*. 35, 133-140.
- Roy, B. P., AbouHaidar, M. G. and Alexander, A.** (1989) Biotinylated RNA probes for the detection of potato spindle tuber viroid (PSTV) in plants. *Journal of Virological Methods*. 23, 149-155.
- Salazar, L. F.** (1989) Potato spindle tuber. In: *Plant Protection and Quarantine. Volume II. Selected Pests and Pathogens of Quarantine Significance* [ed. R. P. Kahn]. Boca Raton, Florida, USA; CRC Press, Inc., 155-167.
- Salazar, L. F., Balbo, I. and Owens, R. A.** (1988a) Comparison of four radioactive probes for the diagnosis of potato spindle tuber viroid by nucleic acid spot hybridization. *Potato Research*. 31, 431-442.
- Salazar, L. F., Owens, R. A., Smith, D. R. and Diener, T. O.** (1983) Detection of potato spindle tuber viroid by nucleic acid spot hybridization: evaluation with tuber sprouts and true potato seed. *American Potato Journal*. 60, 587-597.
- Salazar, L. F., Hammond, R. W., Diener, T. O. and Owens, R. A.** (1988b) Analysis of viroid replication following Agrobacterium-mediated inoculation of non-host species with potato spindle tuber viroid cDNA. *Journal of General Virology*. 69, 879-889.
- Salazar, L. R., Querci, M., Bartolini, I. and Lazarte, V.** (1995) Aphid transmission of potato spindle tuber viroid assisted by potato leafroll virus. *Fitopatologa*. 30, 56-58.

- Sano, T., Nagayama, A., Ogawa, T., Ishida, I. and Okada, Y.** (1997) Transgenic potato expressing a double-stranded RNA-specific ribonuclease is resistant to potato spindle tuber viroid. *Nature Biotechnology*. 15, 1290-1294.
- Schultz, E. S. and Folsom, D.** (1923) Transmission, variation, and control of certain degeneration diseases of Irish potatoes. *Journal of Agricultural Research*. 25, 43.
- Schumacher, J., Meyer, N., Riesner, D., Weidemann, H. L.** (1986) Diagnostic procedure for detection of viroids and viruses with circular RNAs by "return"-gel electrophoresis. *Journal of phytopathology*. 115, 332-343.
- Schumann, G. L., Tingley, W. M. and Thurston, H. D.** (1980) Evaluation of six insect pests for transmission of potato spindle tuber viroid. *American Potato Journal*. 57, 205-211.
- Schumann, G. L., Thurston, H. D., Horst, R. K., Kawamoto, S. O. and Nemoto, G. I.** (1978) Comparison of tomato bioassay and slab gel electrophoresis for detection of potato spindle tuber viroid in potato. *Phytopathology*. 68, 1256-1259.
- Schwind, N., Zwiebel, M., Itaya, A., Ding, B., Wang, M. B., Krczal, G. and Wassenegger, M.** (2009) RNA-mediated resistance to Potato spindle tuber viroid in transgenic tomato expressing a viroid hairpin construct. *Molecular Plant Pathology*. 10, 459-469.
- Schwinghamer, M. W., Scott, G. R., Mallinson, F. K., Tesoriero, L. A. and Morrison, W. L.** (1983) Potato spindle tuber viroid: an extensive infection in the New South Wales potato breeding programme. Abstracts of the 4th International Plant Pathology Conference, Melbourne, Australia, 122.
- Scottish Plant Breeding Station**, 76. Report of the Scottish Plant Breeding Station for 1975-1976. Pentlandsfield, Roslin, Midlothian, UK, 86 pp.
- Shamloul, A. M., Hadidi, A., Zhu, S. F., Singh, R. P., Sagredo, B.** (1997) Sensitive detection of Potato spindle tuber viroid using RT-PCR and identification of a viroid variant naturally infecting pepino plants. *Canadian Journal of Plant Pathology*. 19, 89-96.
- Seigner, L., Kappen, M., Huber, C., Kistler, M. and Köhler, D.** (2008) First trials for transmission of Potato spindle tuber viroid from ornamental Solanaceae to tomato using RT-PCR and an mRNA based internal positive control for detection. *Journal of Plant Diseases and Protection*. 115, 97-101.
- Singh, R. P.** (1970) Seed transmission of potato spindle tuber virus in tomato and potato. *American Potato Journal*. 47, 225-227.
- Singh, R. P.** (1973) Experimental host range of the potato spindle tuber 'virus'. *American Potato Journal*. 50, 111-123.

- Singh, R. P.** (1983) Viroids and their potential danger to potatoes in hot climates. Canadian Plant Disease Survey. 63, 13-18.
- Singh, R. P.** (1984) *Solanum X berthaultii*, a sensitive host for indexing potato spindle tuber viroid from dormant tubers. Potato Research. 27, 163-172.
- Singh, R. P.** (1985) Clones of *Solanum berthaultii* resistant to potato spindle tuber viroid. Phytopathology. 75, 1432-1434.
- Singh, R. P. and Finnie, R. E.** (1973) Seed transmission of potato spindle tuber metavirus through the ovule of *Scopolia sinensis*. Canadian Plant Disease Survey. 53, 153-154.
- Singh, R. P. and Kurz, J.** (1997) RT-PCR analysis of PSTVd aphid transmission in association with PLRV. Canadian Journal of plant Pathology. 19, 418-424.
- Singh, R. P., Finnie, R. E. and Bagnall, R. H.** (1970) Relative prevalence of mild and severe strains of potato spindle tuber virus in eastern Canada. American Potato Journal. 47, 289-293.
- Singh, R. P., Finnie, R. E. and Bagnall, R. H.** (1971) Losses due to potato spindle tuber viroid. American Potato Journal. 48, 262-267.
- Singh, R. P., Boucher, A. and Somerville, T. H.** (1989) Evaluation of chemicals for disinfection of laboratory equipment exposed to potato spindle tuber viroid. American Potato Journal. 66, 239-245.
- Singh, R. P., Boucher, A. and Wang, R. G.** (1991) Detection, distribution and long-term persistence of potato spindle tuber viroid in true potato seed from Heilongjiang, China. American Potato Journal. 68, 65-74.
- Singh, R. P., Boucher, A. and Somerville, T. H.** (1992) Detection of potato spindle tuber viroid in the pollen and various parts of potato plant pollinated with viroid-infected pollen. Plant Disease. 76, 951-953.
- Singh, R. P., Boucher, A. and Somerville, T. H.** (1993a) Interactions between a mild and a severe strain of potato spindle tuber viroid in doubly infected potato plants. American Potato Journal. 70, 85-92.
- Singh, R. P., Nie, X. Z. and Singh, M.** (1999) Tomato chlorotic dwarf viroid: an evolutionary link in the origin of pospiviroids. Journal of General Virology. 80, 2823-2828.
- Singh, R. P., Singh, M., Boucher, A. and Owens, R. A.** (1993b) A mild strain of potato spindle tuber viroid from China is similar to North American isolates. Canadian Journal of Plant Pathology. 15, 134-138.
- Singh, R. P., Boucher, A., Lakshman, D. K. and Tavantzis, S. M.** (1994) Multimeric non-radioactive cRNA probes improve detection of potato spindle tuber viroid (PSTVd). Journal of Virological Methods. 49, 221-233.

- Smith, K. M.** (1972) Potato spindle tuber virus In: A textbook of plant virus diseases, pp. 404-407. London: Longman Group Ltd.
- Soliman, T., Mourits, M. C. M., Oude Lansink, A. G. J. M. and van der Werf, W.** (2012) Quantitative economic impact assessment of an invasive plant disease under uncertainty – A case study for potato spindle tuber viroid (PSTVd) invasion into the European Union. *Crop Protection*. 40, 28-35.
- Stace-Smith, R. and Mellor, F. C.** (1970) Eradication of potato spindle tuber virus by thermotherapy and axillary bud culture. *Phytopathology*. 60, 1857-1858.
- Sun, M., Siemsen, S., Campbell, W., Guzman, P., Davidson, R., Whitworth, J. L., Bourgoin, T., Axford, J., Schrage, W., Leever, G., Westra, A., Marquardt, S., El-Nashaar, H., McMorrán, J., Gutbrod, O., Wessels, T. and Coltman, R.** (2004) Survey of potato spindle tuber viroid in seed potato growing areas of the United States. *American Journal of Potato Research*. 81, 227-231.
- Syller, J., Marczewski, W. and Pawlowicz, J.** (1997) Transmission by aphids of potato spindle tuber viroid encapsidated by potato leafroll luteovirus particles. *European Journal of Plant Pathology*. 103, 285-289.
- Takahashi, T.** (1987) Plant viroid diseases occurring in Japan. *Japan Agricultural Research Quarterly*. 21, 184-191.
- Tiberini, A. and Barba, M.** (2012) Optimization and improvement of oligonucleotide microarray-based detection of tomato viruses and pospiviroids. *Journal of Virological Methods*. 185, 43-51.
- Tien, P.** (1985) Viroids and viroid diseases of China. In: *Subviral Pathogens of Plants and Animals; Viroids and Prions* (Maramorosch, K., McKelvey Jr, J. J. eds.). New York, USA: Academic Press, 123-136.
- Tsushima, T., Murakami, S., Ito, H., He, Y. H., Raj, A. P. C. and Sano, T.** (2011) Molecular characterization of Potato spindle tuber viroid in dahlia. *Journal of General Plant Pathology*. 77, 253-256.
- Tsutsumi, N., Yanagisawa, H., Fujiwara, Y. and Ohara, T.** (2010) Detection of Potato spindle tuber viroid by Reverse Transcription Loop-mediated Isothermal Amplification. *Research Bulletin of the Plant Protection Service, Japan*. 46, 61-67.
- Vachev, T., Ivanova, D., Minkov, I., Tsagris, M., Gozmanova, M.** (2010) Trafficking of the *Potato spindle tuber viroid* between tomato and *Orobanche ramosa*. *Virology*. 399, 187-193.
- Verhoeven, J. T. J.** (2010) Identification and epidemiology of pospiviroids. DPhil Thesis. Wageningen, The Netherlands: Wageningen University, 136 pp.

- Verhoeven, J. T. J., Jansen, C. C. C. and Roenhorst, J. W.** (2008a) First report of pospiviroids infecting ornamentals in the Netherlands: Citrus exocortis viroid in *Verbena* sp., Potato spindle tuber viroid in *Brugmansia suaveolens* and *Solanum jasminoides*, and Tomato apical stunt viroid in *Cestrum* sp. *Plant Pathology*. 57, 399.
- Verhoeven, J. T. J., Jansen, C. C. C. and Roenhorst, J. W.** (2008b) *Streptosolen jamesonii* 'Yellow', a new host plant of Potato spindle tuber viroid. *Plant Pathology*. 57, 399.
- Verhoeven, J. T. J., Roenhorst, J. W. and Owens, R. A.** (2011) Mexican papita viroid and Tomato planta macho viroid belong to a single species in the genus Pospiviroid. *Archives of Virology*. 156, 1433-1437.
- Verhoeven, J. T. J., Jansen, C. C. C., Botermans, M., Roenhorst, J. W.** (2010a) Epidemiological evidence that vegetatively propagated, solanaceous plant species act as sources of Potato spindle tuber viroid inoculum for tomato. *Plant Pathology*. 59, 3-12.
- Verhoeven, J. T. J., Jansen, C. C. C., Roenhorst, J. W., Flores, R. and de la Pena, M.** (2009a). Pepper chat fruit viroid: Biological and molecular properties of a proposed new species of the genus Pospiviroid. *Virus Research*. 144, 209-214.
- Verhoeven, J. T. J., Botermans, M., Roenhorst, J. W., Westerhof, J. and Meekes, E. T. M.** (2009b) First report of Potato spindle tuber viroid in cape gooseberry (*Physalis peruviana*) from Turkey and Germany. *Plant Disease*. 93, 316.
- Verhoeven, J. T. J., Hüner, L., Marn, M. V., Plesko, I. M., Roenhorst, J. W.** (2010b) Mechanical transmission of Potato spindle tuber viroid between plants of *Brugmansia suaveoles*, *Solanum jasminoides* and potatoes and tomatoes. *European Journal of Plant Pathology*. 128, 417-421.
- Verhoeven, J. T. J., Jansen, C. C. C., Willemen, T. M., Kox, L. F. F., Owens, R. A. and Roenhorst, J. W.** (2004) Natural infections of tomato by Citrus exocortis viroid, Columnea latent viroid, Potato spindle tuber viroid and Tomato chlorotic dwarf viroid. *European Journal of Plant Pathology*. 110, 823-831.
- Verhoeven, J. T. J., Jansen, C. C. C., Roenhorst, J. W., Steyer, S., Michelante, D. and Bolivarlaan, S.** (2007) First report of Potato spindle tuber viroid in tomato in Belgium. *Plant Disease*. 91, 1055.
- Ward, L. I., Tang, J., Veerakone, S., Quinn, B. D., Harper, S. J., Delmiglio, C. and Clover G. R. G.** (2010) First report of Potato spindle tuber viroid in Cape Gooseberry (*Physalis peruviana*) in New Zealand. *Plant Disease*. 94, 479.
- Wedgworth, H. H.** (1928) Degeneration diseases of the Irish Potato in Mississippi, Mississippi Agriculture Experiment Station Bulletin. 258, pp. 11.

Yang, X., Yie, Y., Zhu, F., Liu, Y., Kang, L., Wang, X. and Tien, Po. (1997) Ribozyme-mediated high resistance against potato spindle tuber viroid in transgenic potatoes. *Proceedings of the National Academy of Sciences of the United States of America.* 94, 4861-4865.

10. Author and reviewers

Author

Original: Matthew Everatt (Defra) (2016)

Revised by: Simon Honey (Defra) (2022)

Reviewers

Adrian Fox (Fera)

Dominic Eyre (Defra)

Janet Dixon (Defra)

Justin Dixon (Defra)

Ian Sanders (APHA)

Melanie Tuffen (Defra)

Peter Reed (Defra)

Sharon Matthews-Berry (Defra)