Neth. J. Pl. Path. 98 (1992) Supplement 2: 47–54

Virus transmission by aphids in potato crops

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Accepted 30 October 1991

Abstract

This paper reviews the contribution of vector activity and plant age to virus spread in potato crops. Determining which aphid species are vectors is particularly important for timing haulm destruction to minimize tuber infection by potato virus Y (PVY). Alate aphids of more than 30 species transmit PVY, and aphids such as *Rhopalosiphum padi*, that migrate in large numbers before flights of the more efficient vector, *Myzus persicae*, appear to be important vectors. Differences in methodology, aphid biotypes and virus strains prevent direct comparisons between estimates of vector efficiencies obtained for aphids in different countries in north western Europe.

M. persicae is also the most efficient vector of potato leafroll virus (PLRV), but some clones of *Macrosiphum euphorbiae* transmit PLRV efficiently to *Nicotiana clevelandii* and potato test plants. The removal of infected plants early in the season prevents the spread of PLRV in cool regions with limited vector activity. The proportion of aphids acquiring PLRV from infected potato plants decreases with plant age, and healthy potato plants are more resistant to infection later in the season. Severe symptoms of secondary leafroll developed on progeny plants of cv. Maris Piper derived from mother plants inoculated with PLRV in June or July of the previous year. Progeny plants derived from mother plants inoculated in August showed only mild symptoms, but the concentration of PLRV in these plants was as high as that in the plants with severe symptoms.

Additional keywords: potyvirus, PVY, luteovirus, PLRV, *Myzus persicae*, *Rhopalosiphum padi*, *Macrosiphum euphorbiae*, Maris Piper, *Nicotiana clevelandii*

Introduction

Although the basic principles determining the epidemiology of aphid-transmitted potato viruses are well established, recent breakdowns in control measures in Northern Europe have exposed gaps in our knowledge. To improve control we need more information on the ecological interactions between three components: potato viruses, their host plants and aphid vectors. Virus spread in potato crops depends on the number and maturity of virus source plants, and the number of aphid vectors and their movements and seasonal phenology in relation to the susceptibility of potato cultivars. This paper reviews two aspects of these interactions: assessments of aphid species and biotypes as virus vectors, their activity in potato crops, and effects of the date of infection on virus spread.

Vector Activity

Potato virus Y (PVY) and potato leafroll virus (PLRV) cause the most important aphid-borne virus diseases in potato crops. Differences in the transmission characteristics and number of vector species affect their spread and methods of control. PVY is transmitted in the non-persistent manner and is acquired and inoculated during brief probes by aphids,

including alatae of many species that do not colonize potatoes. Most insecticides are relatively ineffective in controlling the spread of PVY, probably because they fail to affect aphids fast enough (Gibson et al., 1982; Peters, 1987). PLRV is transmitted in a persistent manner. In the plant the virus is confined to phloem tissues, and only those aphids that feed long enough to penetrate the phloem acquire PLRV. Also, feeds of several hours are needed for efficient inoculation by virus-carrying aphids. Apterae of potato-colonizing species transmit PLRV from infected plants within crops and insecticides prevent spread, particularly from virus sources within treated crops (Burt et al., 1960; Woodford et al., 1983).

Potato virus Y. Determining which aphid species are vectors is particularly important for control of the spread of PVY. This virus, especially the tobacco veinal necrosis strain, PVY^N, has caused serious problems in Northern Europe in recent years (Van Hoof, 1977; Robert, 1978; Sigvald, 1987), but virus transport from the foliage into developing tubers can be minimized by early haulm destruction. In the Netherlands, haulm destruction dates were formerly related to the detection of alate *Myzus persicae* in yellow traps (Hille Ris Lambers, 1972), but in some years during the 1970s PVY^N spread before the main flights of *M. persicae* (Van Hoof, 1977; Van Harten, 1983). In assessing the importance of other vectors it is useful to distinguish between experiments designed to assess whether a particular species is capable of transmitting PVY, usually under closely defined conditions (vector efficiency), and those that try to assess the role of these species in transmitting the virus in the field. This latter measure, which Irwin and Ruesink (1986) called 'vector propensity', allows for transmission by aphids that alight on an infected potato plant, probe and then move to an uninfected plant.

Most studies of the transmission of non-persistent viruses have been made with apterous aphids allowed a brief acquisition access period on a leaf from an infected plant (Irwin and Ruesink, 1986). Using this method, Van Hoof (1990) found that apterae of 13 out of 24 aphid species transmitted PVY. More recent studies have tested alatae because they are more important than apterae in transmitting PVY in potato fields. In total, alatae of more than 30 aphid species or species groups have now been shown to transmit PVY in England (Harrington and Gibson, 1989) and the Netherlands (De Bokx and Piron, 1990). There are large differences in the transmission efficiencies reported by these and other authors (Kostiw, 1979; Ryden, 1979; Van Hoof, 1980; Sigvald, 1984; Singh and Boiteau, 1986) resulting from the use of different test plants, aphid biotypes and virus strains, and also the objectives of the experiments. Table 1 gives examples for the transmission rates of PVY obtained by several authors for some aphids that are widespread in Northern Europe. Whereas Van Hoof (1980) tested the ability of a few clones of apterae to transmit the virus to tobacco test plants, De Bokx and Piron (1990) trapped large numbers of alate aphids in potato fields and gave them controlled acquisition access and inoculation feeds on young healthy potato test plants. Provided observations can be carried out for several years, this method appears to give the most reliable measure of the potential ability of aphids to transmit PVY. However, it does not determine the probability of aphids landing on infected and healthy potato plants. Harrington and Gibson (1989) attempted to do this by trapping alatae downwind of PVY-infected potato plants and then transferring them rapidly to tobacco test plants. They found rather low transmission rates, except for some species caught in small numbers, but calculated that most of the trapped aphids had not previously probed the infected potato plants. In addition, tobacco may be a less suitable test plant than potato for

Table 1. Percentage of tobacco or potato test plants infected with potato virus Y (PVY) by some aphid species in reports from the Netherlands, England and Sweden.

Aphid species	The Netherlands		England Tobacco (Harrington and Gibson, 1989)	Sweden Potato (Sigvald, 1984)
	Tobacco[1] (Van Hoof, 1980)	Potato (De Bokx and Piron, 1990)		
Acyrthosiphon pisum	14	5.6	3.8	25.0
Aphis fabae group	24	3.8	7.6	1.0
A. nasturtii group	_	21.4	50.0+	7.1
Brachycaudus helichrysi	0	10.5	5.9	_
Macrosiphum euphorbiae	29	3.5	7.7	_
Myzus persicae	50	50.8	8.4	26.0
Rhopalosiphum padi	2	7.2	2.4	1.5
Sitobion avenae	0	1.2	0.1	0.0

[1] Test plant and author; _ = not tested; + = only eight individuals trapped

some aphid species, such as *Rhopalosiphum padi* (Ryden, 1979). Although the results obtained by Sigvald (1984) are not directly comparable with the Dutch and English experiments, because he used PVY^{O}, his method of allowing alate aphids free movement in cages containing infected and healthy potato plants gives a good measure of vector propensity, but the experiments were laborious and involved only a few clones of aphids reared in the laboratory.

No single method for assessing aphid vectors in the field gives an adequate measure of aphid behavior and mobility. Nevertheless, the concept of vector pressure (Van Harten, 1983), in which the numbers of selected species are scaled by their 'relative efficiency factors (REF)', has been found to give a better estimate of the spread of PVY than unmodified numbers of aphids. This approach has been used to examine annual variations in the incidence of PVY in the Netherlands (Van Harten, 1983), Sweden (Sigvald, 1984) and Scotland (Turl and MacDonald, 1987). However, it is still not clear how well numbers of aphids caught in suction traps, nets or yellow water traps indicate their activity in potato crops. Doubts also remain over how many, and which, aphid species to include in the estimate of vector pressure, and what REF values to give them. Although methodology may account for some of the differences found by various authors, the relative importance ascribed to particular species also reflects their abundance and phenology in different areas. For example, *Brachycaudus helichrysi* was both a more efficient vector than *M. persicae* and was caught in larger numbers in 1984 at Harpenden in southern England (Harrington et al., 1986). *Rhopalosiphum padi* is an important vector in Sweden (Sigvald, 1987) and the Netherlands (De Bokx and Piron, 1990) because it migrates in large numbers, and earlier than *M. persicae*, when potato plants are very susceptible to PVY. In contrast, Turl and MacDonald (1987) found that catches of *M. persicae* alone accounted for most of the variance in the annual incidence of PVY in southeast Scotland. However, recent large increases in the area of winter cereals grown in Scotland may provide additional overwintering host plants for anholocyclic populations of *R. padi* and *Sitobion avenae* or 'green bridges' in the spring. These changes in crop practice could indirectly increase the importance of cereal aphids as PVY vectors and may partly account for the

increased incidence of PVY in some potato cultivars in Scotland (Turl, 1987; Woodford, 1988).

Potato leafroll virus. *M. persicae* is the most efficient and important vector of PLRV but several other aphids that feed on potato crops also transmit the virus (Kennedy et al., 1962), and clones of *Aphis gossypii* that transmit PLRV efficiently have been reported from India (Singh et al., 1988). Particular attention has been paid to *M. euphorbiae* as a vector of PLRV in Scotland because infestations of this species on Scottish potato crops are often much larger than those of *M. persicae*. Most of the evidence indicates that *M. euphorbiae* is an inefficient vector of PLRV. Tamada and Harrison (1981) detected high concentrations of PLRV in migrant *M. euphorbiae* collected from PLRV-infected potato plants in June, but these aphids and a laboratory clone of *M. euphorbiae* rarely transmitted the virus to indicator plants. In these and subsequent tests with additional British isolates of PLRV (Tamada et al., 1984), *M. euphorbiae* was only 2–3% as efficient as *M. persicae* in transmitting PLRV. In addition, the low rates of spread of PLRV in field trials with large populations of *M. euphorbiae* but low populations of *M. persicae* suggested that large numbers of *M. euphorbiae* did not substantially increase the risk of PLRV spread in Scotland (Woodford et al., 1983). In contrast, one of five clones of *M. euphorbiae* tested in France (Robert and Maury, 1970) was almost half as efficient as *M. persicae* in transmitting PLRV. In their experiments, Robert and Maury (1970) used sprouting potato tubers as test plants. The use of *Physalis floridana* as the test plant may partly explain the low efficiency of *M. euphorbiae* in transmitting PLRV in tests in Scotland (Tamada and Harrison, 1981; Tamada et al., 1984).

Experiments made with *M. persicae* and *M. euphorbiae* collected from PLRV-infected potato clones in the field, and with other laboratory clones of these aphids (J.A.T. Woodford, unpublished), provide some evidence for more efficient transmission of PLRV by *M. euphorbiae*. In these tests, apterae or fourth instar apterous nymphs were given acquisition access feeds of 4–7 days on PLRV-infected potato foliage, and then caged for 4 or 7 days in groups of 3 or 5 on young *P. floridana* or potato (cv. Maris Piper or Désirée) test plants. The potato plants were trimmed to a single stem and the pruned foliage was used for ELISA to check that they were initially free from infection with PLRV. The results confirmed that *M. persicae* transmitted PLRV efficiently to *P. floridana* whereas *M. euphorbiae* did not, but showed that *M. euphorbiae* transmitted PLRV to 9.5% of the potato test plants (Table 2).

Table 2. Numbers of *Physalis floridana* or potato test plants infected by potato leafroll virus (PLRV) by *Myzus persicae* or *Macrosiphum euphorbiae* transferred from infected potato plants.

Inoculation date	*M. persicae*		*M. euphorbiae*	
	P. floridana	Potato	*P. floridana*	Potato
Early June	28/46[1]	–	–	3/20
Mid June	37/46	–	–	0/30
Late June/early July	27/40	5/12	1/64	7/46
Mid July	17/34	–	0/64	4/43
Late July	48/55	–	1/47	1/19

[1] Number of test plants infected/number of test plants inoculated; 3–5 aphids/plant.

Table 3. Transmission rates of potato leafroll virus (PLRV) by *Macrosiphum euphorbiae* from 22 Scottish clones, and by one clone of *Myzus persicae*.

Proportion of individuals transmitting PLRV to *N. clevelandii*	Number of test plants/ clone	Number of clones	
		M. euphorbiae	*M. persicae*
0.00–0.10	18–42	11	
0.11–0.20	14–34	4	
0.21–0.30	22–32	5	
0.31–0.40	29	1	
0.41–0.50	24	1	
0.61–0.70	82		1

Both *M. persicae* and *M. euphorbiae* readily settle on seedlings of *Nicotiana clevelandii*, behavior which makes this species a useful test plant for comparing PLRV transmission efficiencies. In the glasshouse, seedlings of *N. clevelandii* infected with PLRV show symptoms (stunting and interveinal necrosis in older leaves) 2–3 weeks after inoculation (Barker, 1987). I used PLRV-infected *N. clevelandii* as a virus source and *N. clevelandii* seedlings as test plants in a survey of the transmission efficiencies of 22 Scottish clones of *M. euphorbiae* (two clones from rose and 20 clones from potato). The aphids were given 9-day acquisition access feeds and were then caged individually on 3–4 leaf stage *N. clevelandii* seedlings (usually between 18 and 32 test plants per clone). Most of the clones tested were poor vectors (Table 3) but one clone, derived from a pink race collected on potato, was almost 75% as efficient as *M. persicae* in 84 control transmission tests. However, these results are likely to exceed transmission rates in the field, where effects of aphid activity and plant age may limit transmission.

In recent years, *M. euphorbiae* has often colonized Scottish potato crops before *M. persicae*. In 1982 and 1984, PLRV-infected potato plants, cv. Désirée, grown in plots of virus-free cv. Maris Piper at Invergowrie, near Dundee, were artificially infested with small numbers of laboratory-reared *M. persicae* or *M. euphorbiae*. The Désirée plants were inoculated with five apterous *M. persicae* or *M. euphorbiae* in mid-June in 1982, and in mid- or late-June in 1984, and rogued in the first week of July. Virus spread was assessed in the following year in Maris Piper plants grown from tubers harvested from two plants on either side of the inoculated infector plants and from plants in the same positions next to uninoculated infector plants. Very low natural populations of aphids were found in the plots

Table 4. Percentage of daughter tubers infected with potato leafroll virus (PLRV) in plots of cv. Maris Piper with added populations of *Myzus persicae* or *Macrosiphum euphorbiae*.

Added aphid species (5 apterae/infector plant)		% PLRV infection	
		1982 1 wk[1]	1984 2 wk
M. persicae	45	24	12
M. euphorbiae	9	12	1
Nil	20	22	

[1] Period before infector plants with added aphid infestations were rogued.

before the infector plants were removed but 20% of the tubers harvested from uninoculated control plots in 1982 and 8% in 1984 were infected with PLRV (Table 4). Releasing *M. persicae* on the within-plot infector plants increased the spread of PLRV, but adding *M. euphorbiae* had variable effects. In 1982 there was less spread of PLRV in those plots in which *M. euphorbiae* was added to infector plants than in uninoculated control plots. In 1984, there was, unexpectedly, less spread of PLRV from infector plants that had received *M. persicae* or *M. euphorbiae* two weeks before roguing than in plots that had been infested with either species for one week before roguing. It is possible that these small artificial infestations of aphids provided food for predators before natural infestations developed on the other plants, or the condition of the Désirée plants when the later inoculations were done may have made those aphids more restless. These results highlight some of the difficulties of measuring vector activity in field experiments.

Effects of infection date on spread of PLRV

Symptoms of primary (current season) infection with PLRV are rarely seen in potato crops grown in cool areas such as Scotland but in most cultivars the symptoms of secondary leaf roll can be distinguished in June or July. Woodford and Barker (1986) recorded plants showing secondary leaf roll symptoms in experimental crops of cv. Maris Piper potatoes at Invergowrie for six years and found that 95–99% of infected plants showed obvious symptoms by mid-late June. However, more infected plants, and more plants with late-developing leaf roll symptoms were found in stocks derived from crops in which haulm destruction had been delayed until September than in stocks grown from crops burned down 2–3 weeks earlier. As plants with secondary leaf roll provide the main source of PLRV in Scottish potato crops their early removal before vector aphids arrive usually prevents the spread of PLRV (Woodford and Gordon, 1990).

M. persicae acquires PLRV less often from infected cv. Maris Piper plants in mid-July than in mid-June, and the proportion acquiring PLRV in August is very low (Barker and Harrison, 1986). Healthy potato plants inoculated with viruliferous aphids are more resistant to infection with PLRV later in the season (Beemster, 1972; Barker and Woodford, 1987). Thus, when vector aphids are scarce until late July or August, roguing and early haulm destruction prevent the spread of PLRV. However, problems can result if substantial numbers of plants with secondary leaf roll fail to express obvious symptoms and are not detected during roguing. The date of expression of secondary symptoms is related to the date of primary infection (Knutson and Bishop, 1964; Barker and Woodford, 1987). Severe symptoms developed on cv. Maris Piper progeny plants derived from mother plants inoculated with PLRV in June or July of the previous year. However, progeny plants derived from mother plants inoculated in August showed only mild symptoms, but the concentration of PLRV in these plants was as high as that in the plants with severe symptoms (Barker and Woodford, 1987). Thus, although the probability of aphids transmitting PLRV decreases with plant age within a season, late infections add considerably to the risk of virus spread in the following season because roguing and visual inspections fail to detect plants with mild symptoms.

Recent information on the spread of PLRV therefore highlights several points: (a) aphids other than *M. persicae* should not be neglected as potentially significant vectors; (b) early haulm destruction may prevent late infections of tubers and thus the occurrence of infected plants with abnormally mild symptoms that are easily overlooked during roguing;

and (c) although virus spread has often been related to some measure of vector abundance (numbers trapped, population density or the duration of infestations), we need more information about the effect on aphid movement of such factors as plant development and physiological status, aphid population density on leaves, and predator activity.

References

Barker, H., 1987. Invasion of non-phloem tissue in *Nicotiana clevelandii* by potato leafroll luteovirus is enhanced in plants also infected with potato Y potyvirus. Journal of General Virology 68: 1223–1227.

Barker, H. & Harrison, B.D., 1986. Restricted distribution of potato leafroll virus antigen in resistant potato genotypes and its effect on transmission of the virus by aphids. Annals of Applied Biology 109: 595–604.

Barker, H. & Woodford, J.A.T., 1987. Unusually mild symptoms of potato leafroll virus in the progeny of late-infected mother plants. Potato Research 30: 345–348.

Beemster, A.B.R., 1972. Virus translocation in potato plants and mature plant resistance. In: De Bokx, J.A. (Ed.), Viruses of potatoes and seed potato production. Pudoc, Wageningen. p. 144–151.

Burt, P.E., Broadbent, L. & Heathcote, G.D., 1960. The use of soil insecticides to control potato aphids and virus diseases. Annals of Applied Biology 48: 580–590.

De Bokx, J.A. & Piron, P.G.M., 1990. Relative efficiency of a number of aphid species in the transmission of potato virus Y^N in the Netherlands. Netherlands Journal of Plant Pathology 96: 237–246.

Gibson, R.W., Rice, A.D. & Sawicki, R.M., 1982. Effects of the pyrethroid deltamethrin on the acquisition and inoculation of viruses by *Myzus persicae*. Annals of Applied Biology 100: 49–54.

Harrington, R., Katis, N. & Gibson, R.W., 1986. Field assessment of the relative importance of different aphid species in the transmission of potato virus Y. Potato Research 29: 67–76.

Harrington, R. & Gibson, R.W., 1989. Tranmission of potato virus Y by aphids trapped in potato crops in southern England. Potato Research 32: 167–174.

Hille Ris Lambers, D., 1972. Aphids: their life cycles and their role as vectors. In: De Bokx, J.A. (Ed.), Viruses of potatoes and seed potato production. Pudoc, Wageningen. p. 36–56.

Irwin, M.E. & Ruesink, W.G., 1986. Vector intensity: a product of propensity and activity. In: McLean, G.D., Garrett, R.G. & Ruesink, W.G. (Eds), Plant virus epidemics. Academic Press, Sydney. p. 13–33.

Kennedy, J.S., Day, M.F. & Eastop, V.F., 1962. A conspectus of aphids as vectors of plant viruses, Commonwealth Institute of Entomology, London, 114 pp.

Knutson, K.W. & Bishop, G.W., 1964. Potato leafroll virus – effect of date of inoculation on percentage infection and symptom expression. American Potato Journal 41: 227–238.

Kostiw, M., 1979. Tranmission of potato virus Y by *Rhopalosiphum padi* L. Potato Research 22: 237–238.

Peters, D., 1987. Control of virus spread. In: De Bokx, J.A. & Van der Want, J.P.H. (Eds), Viruses of potatoes and seed potato production. Pudoc, Wageningen. p. 171–174.

Robert, Y., 1978. Role épidémiologique probable d'espèces de pucerons autre que celles de la pomme de terre dans la dissémination intempestive du virus Y depuis 4 ans dans l'ouest de la France. Abstract E.A.P.R. Conference Papers, Warsaw, Poland. p. 242–243.

Robert, Y. & Maury, Y., 1970. Capacité vectrices comparées de plusieurs souches de *Myzus persicae* Sulz., *Aulacorthum solani* Kltb et *Macrosiphum euphorbiae*. Thomas dans l'étude de la transmission de l'Enroulement de la Pomme de terre. Potato Research 13: 199–209.

Ryden, K., 1979. Havrebladlusen, *Rhopalosiphum padi* kan sprida potatisvirus Y. Vaxtskyddnotiser 43: 51–53.

Sigvald, R., 1984. The relative efficiency of some aphid species as vectors of potato virus Y^0 (PVY^0). Potato Research 27: 285–290.

Sigvald, R., 1987. Aphid migration and the importance of some aphid species as vectors of potato virus Y^0 (PVY^0) in Sweden. Potato Research 30: 267–283.

Singh, M.N., Khurana, S.M.P., Nagaich, B.B. & Agrawal, H.D., 1988. Environmental factors influencing aphid transmission of potato virus Y and potato leafroll virus. Potato Research 31: 501–509.

Singh, R.P. & Boiteau, G., 1986. Reevaluation of the potato aphid *Macrosiphum euphorbiae* (Thomas), as vector of potato virus Y. American Potato Journal 63: 335–340.

Tamada, T. & Harrison, B.D., 1981. Quantitative studies on the uptake and retention of potato leafroll virus by aphids in laboratory and field conditions. Annals of Applied Biology 98: 261–276.

Tamada, T., Harrison, B.D. & Roberts, I.M., 1984. Variation among British isolates of potato leafroll virus. Annals of Applied Biology 104: 107–116.

Turl, L.A.D., 1987. A preliminary analysis of the relationship between aphid abundance and virus spread in Scottish seed potato crops. In: Williams, G.H. (Ed.), Proceedings of a Conference on Crop Protection in Northern Britain, Dundee 1987. p. 159–167.

Turl, L.A.D. & MacDonald, D.M., 1987. The relationship between suction trap catches and the spread of PVY^O in south-east Scotland. In: Cavalloro, R. (Ed.), Proceedings EC Expert Meeting. Aphid migration and forecasting 'Euraphid' systems in European community countries, p. 177–185.

Van Harten, A., 1983. The relation between aphid flights and the spread of potato virus Y^N (PVY^N) in the Netherlands. Potato Research 26: 1–15.

Van Hoof, H.A., 1977. Determination of the infection pressure of potato virus Y^N. Netherlands Journal of Plant Pathology 83: 123–127.

Van Hoof, H.A., 1980. Aphid vectors of potato virus Y^N. Netherlands Journal of Plant Pathology 86: 159–162.

Woodford, J.A.T., 1988. The impact of cropping policy on methods to control potato leafroll virus. Aspects of Applied Biology 17: 163–171.

Woodford, J.A.T. & Barker, H., 1986. Problems of detecting potato leafroll virus following late infection. In: Crop protection of sugar beet and crop protection and quality of potatoes, part II. Aspects of Applied Biology 13: 325–331.

Woodford, J.A.T. & Gordon, S.C., 1990. New approaches for restricting spread of potato leafroll virus by different methods of eradicating infected plants from potato crops. Annals of Applied Biology 116: 477–487.

Woodford, J.A.T., Harrison, B.D., Aveyard, C.S. & Gordon, S.C., 1983. Insecticidal control of aphids and the spread of potato leafroll virus in potato crops in eastern Scotland. Annals of Applied Biology 103: 117–130.