

Resistance to phloem transport of potato leafroll virus in potato plants

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A 'double-graft sandwich' technique in which sections of potato stem from different potato cultivars were grafted between a susceptible healthy stock plant and a potato leafroll virus (PLRV)-infected scion was used to study the rate of phloem transport of PLRV in cultivars differing in resistance to PLRV infection (I^R) and accumulation (A^R). Resistance to phloem transport (i.e. delayed PLRV systemic movement) was found in Bismark cultivar (I^R A^S). This was independent of I^R and A^R as the rate of movement in Bismark cultivar was markedly slower than that in Omega and Spunta (I^R A^R), Delaware (I^S A^R), and Desiree and Renova (I^S A^S) cultivars. It operated in Bismark cultivar stems of

two different ages, but did not operate against potato virus X (PVX) and was not influenced by previous infection with this virus. Aphid vector (*Myzus persicae*) feeding preferences and colonization rates differed between cultivars, but the cultivar characteristics responsible were unrelated to I^R, A^R or resistance to phloem transport. Delayed systemic movement of PLRV out of leaves inoculated with viruliferous aphids was independent of A^R and resistance to phloem transport, and remained unaffected by previous infection with PVX. It was also independent of cultivar factors causing different aphid feeding preferences and colonization rates, but may be linked to I^R.

Introduction

Virus-specific resistance that decreases or prevents infection, replication, symptom expression and/or systemic movement is of obvious value in the control of economically important plant viruses such as potato leafroll luteovirus (PLRV) in potato. Two main types of virus-specific resistance to PLRV have been studied: resistance to initial infection by viruliferous aphids (Cockerham, 1945; Ross, 1958) and resistance to virus accumulation in infected plants (Jones, 1979; Barker & Harrison, 1985, 1986), which operate independently (Barker, 1989). Resistance to infection (I^R) is overcome if the inoculum dose is sufficient, and this is polygenically controlled (Ross, 1958; Davidson, 1973, 1980), whereas resistance to accumulation (A^R), which decreases but does not prevent virus multiplication, may be determined by a single gene (Barker & Solomon, 1990). A third component of virus-specific resistance is recognized, decreased PLRV movement from infected foliage to tubers (McKay & Clinch, 1951; Hutton & Brock, 1953). This is independent of the non-specific 'mature plant resistance' which increases as potato plants age (Beemster, 1987). Barker (1987) has found decreased movement to tubers in cultivars with both I^R and A^R.

Systemic movement of most plant viruses (including PLRV) takes place in two steps. These are first, slow cell-to-cell movement from initially infected cells to adjacent cells, or into the sieve elements and second, more rapid long distance transport through the phloem (Samuel, 1934; Atabekov & Dorokhov, 1984; Beemster, 1987; Meshi & Okada, 1987; Hull, 1989; Atabekov & Taliansky, 1990; Maule, 1991). This paper describes the results of an investigation of the rate of systemic movement of PLRV in a selection of potato cultivars with differing combinations of I^R and A^R and reports resistance to phloem transport independent of I^R and A^R in one cultivar. Aphid vector feeding preferences and colonization rates in cultivars with and without I^R and A^R, and in the cultivar with resistance to phloem transport were also investigated.

Methods

Virus isolates and antiserum. PLRV isolate KK and potato virus X (PVX) isolate XK from Western Australia were both obtained from and maintained in cv. Kennebec plants. These plants were used as sources of virus for infected scions in top-grafts and for infected positive controls in ELISA. For PLRV, they were also used to culture viruliferous *Myzus persicae*. The polyclonal antisera to PLRV and PVX were supplied by Boehringer Mannheim.

Potato plants. Healthy seed potato tubers of cv. Bismark were obtained from B. M. Beattie (Department of Primary Industry, Fisheries and Energy, Tasmania) and healthy seed tubers of the other

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cultivars were supplied by P. D. Dawson (Western Australian Department of Agriculture). Plants were grown in steam-sterilized potting compost (mix of soil, sand and peat) in insect-proof glasshouses. In experiments, plants were grown from eyecores. Virus inoculations were top-grafts (PLRV and PVX) or were done using viruliferous aphids enclosed in small clip cages (PLRV). For grafts, the stock cultivar was Renova whereas the infecting scions were of cv. Kennebec. Except with aphid feeding preference work in which trays were used, in each experiment pots were arranged in a randomized block design. The occurrence of I^R and A^R in the cultivars used is shown in Table 1.

ELISA. Leaf samples were extracted using a leaf press (Pollahne) in PBS (0.01 M-potassium phosphate, 0.15 M-sodium chloride) pH 7.4 containing 5 ml/l Tween 20 and 20 g/l polyvinyl pyrrolidone. Extracts were tested by ELISA as described by Clark & Adams (1977) using 0.5 mg/ml *p*-nitrophenyl phosphate in 10 ml/l diethanolamine pH 9.8 as substrate. Absorbance (A_{405}) was measured in a Titertek photometer (Flow Laboratories). Samples were tested in duplicate wells and control samples from infected and healthy potato were included on each plate.

Rate of phloem transport of PLRV. A 'double-graft sandwich' technique was used. In Expt. 1, stock plants, infecting plants and test cv. Bismark, Desiree, Omega and Renova were grown for 7 weeks until they were approximately 25 to 30 cm tall. Stock plants were top-grafted with an apical 20 to 25 cm portion of a plant from one of the test cultivars and 3 weeks later an infecting scion was grafted onto the top of each of the first scions. This resulted in a stem section approximately 15 cm long containing two to four nodes, sandwiched between infected scion and healthy stock. Five double grafts (one/plant) were done with each test cultivar; graft failure resulted in only four successfully double-grafted Bismark and Omega plants. Virus movement to the stock was followed by periodically removing and testing the youngest leaf of the axillary shoot produced at the node within the stock nearest to the lower graft union. Terminal leaflets were removed from each plant 8, 12, 15, 18, 21 and 25 days after the second grafting. The time taken until PLRV was first detected by ELISA in the stock was recorded.

In Expt. 2, test cv. Bismark, Delaware, Omega and Spunta, stock and infecting plants were grown as in Expt. 1, but only four plants of each test cultivar were used. The first graft was done 6 weeks after planting, and the second after a further 2 weeks; there were only three successfully double-grafted Bismark and Delaware plants. Terminal leaflets from the topmost axillary shoot of the stock from each plant were removed and tested at 3 to 4 day intervals from 8 to 36 days after the second grafting.

In Expt. 3, test cv. Bismark and Desiree were planted in two batches 2 weeks apart; stock and infecting plants were planted with the first batch. Grafting of stem sections to stocks and of infected scions onto stem sections was done simultaneously 3 weeks after the second planting (5 to 6 plants successfully grafted/batch/cultivar). Terminal leaflet samples were taken for testing by ELISA at 2 to 3 day intervals 10 to 35 days after grafting.

In Expt. 4, five stem sections from healthy 4-week-old plants of cv. Bismark and Desiree were sandwiched between healthy stocks and PVX-infected scions using simultaneous double grafting. In Expt. 5, 4-week-old healthy or PVX-infected stem sections of cv. Omega (seven plants/treatment) and Bismark (10 plants/treatment) were sandwiched between healthy stock plants and PLRV-infected scions in simultaneous double grafts. These grafts were done without touching any leaves so as to avoid any chance of contact transmission of PVX to stem piece or stock. Also, the scalpel blade used was discarded after each graft involving a PVX-infected scion or stem section. In both experiments, sampling of terminal leaflets in the stock and testing for PVX (Expt. 4) or PLRV (Expt. 5) by ELISA was as before, and was done at 2 to 3 day intervals 8 to 31 days after grafting.

Table 1. Resistance to PLRV infection and accumulation, and symptom severity in cultivars used*

Cultivar	Infection	Accumulation	Symptom severity
Omega	R†	R	Moderate-severe
Spunta	R	R	Mild-moderate
Bismark	R	S	Moderate-severe
Delaware‡	S	R	Moderate
Desiree	S	S	Mild-moderate
Kennebec	S	S	Moderate-severe
Renova	S	S	Mild-moderate

* Data from Wilson (1991) and Wilson & Jones (1993).

† R, Resistant; S, susceptible.

‡ Delaware is called White Rose in North America (Wilson & Jones, 1990).

PLRV movement out of inoculated leaves. In Expt. 1, 30 plants each of cv. Bismark, Delaware, Desiree and Omega were grown for 4 weeks until approximately 10 to 15 cm tall. Then approximately 25 viruliferous aphids were caged for 4 days on the underside of the terminal leaflet of the fourth leaf from the plant apex, the cages removed and the aphids killed with a pyrethrin-based insecticide (Slayafe; Hortico). All but the inoculated leaflet and the youngest two leaves were then removed from each plant. Inoculated terminal leaflets were removed from six or seven plants/cultivar 10, 13, 16 and 22 days after inoculation and destroyed. A further four plants/cultivar were left as intact controls. Young apical leaf tissue was tested for PLRV by ELISA 4 and 6 weeks after inoculation. In addition, one tuber from each test plant was harvested 10 weeks after inoculation and leaf tissue produced by progeny plants was tested by ELISA.

In Expt. 2, 20 healthy and 20 PVX-infected plants of cv. Omega were inoculated with PLRV using approximately 25 caged viruliferous aphids each. Inoculated leaflets were removed from four plants/treatment 14, 16, 18 and 20 days after inoculation. Young leaf tissue sampled 4 weeks after inoculation was tested by ELISA. Tissue from progeny plants grown from tubers (one/plant) harvested 11 weeks after inoculation was also tested.

Determination of aphid feeding preferences. In Expt. 1, four trays were planted with two tuber eyecores from each of test cv. Bismark, Delaware, Desiree, Omega, Renova and Spunta. The eyecores were planted in a 20 cm diameter circle such that no two plants of a single cultivar were next to one another and each adjacent pair consisting of the same two cultivars was represented only once in each tray. The plants were grown until approximately 10 cm tall and the trays were then transferred to controlled environment cabinets at 20 °C, 2000 lux and 16 h day length. Alates were starved for 2 to 4 h, transferred to a plastic beaker (approx. 56/beaker) and the beaker was placed in the centre of the ring of plants. There was no leaf contact between the beaker and the plants. The number of alates found feeding on each plant was counted 1 to 4 days later. All aphids were then removed using a suction device and the tests repeated immediately for three of the trays, giving seven tests in all. Within each test, the proportion of the alates present on the two plants of each cultivar was determined and the overall results were expressed as a percentage.

In Expt. 2, eyecores of test cv. Spunta and Desiree were planted alternately in a ring of eight plants/tray. Alates (approx. 40/beaker) were released as in Expt. 1. The number of alates/cultivar was recorded as before. Six tests were done.

Determination of aphid colonization rate. Four plants each of test cv. Bismark, Delaware, Desiree, Omega and Spunta were grown until approximately 20 cm tall. Large adult apterae that had been starved for

2 to 3 h were then transferred to the fifth leaf from the plant apex (four/plant). Pots were arranged in a randomized block design, well separated from each other so that leaves did not touch, and stood in shallow trays of water so aphids could not walk from plant to plant. The numbers of nymphs and large aphids present on each plant were recorded separately at 2 to 3 day intervals.

Statistical analyses. Differences in times taken for initial virus detection in stocks in double-graft sandwich tests were subjected to analyses of variance. Where double-grafts failed, these plants were treated as missing data. For the aphid colonization rate experiment, numbers of aphids/plant/day data were analysed. With the aphid feeding preference experiments, each identical test was treated as a replicate and percentage preference data were subjected to angular transformation prior to analysis.

Results

Rate of phloem transport of PLRV

In Expt. 1 and 2, the rate of PLRV movement through stem sections of cv. Bismark was significantly slower than that through stem sections of the other six cultivars (Table 2). The slower rate of PLRV movement in cv. Bismark was independent of I^R and A^R as cv. Omega and Spunta had both, and cv. Delaware had only the latter. In Expt. 3, the rate of movement through cv. Bismark stem sections was significantly slower than that through those of cv. Desiree, and a 2 week difference in age affected rate of movement; 5-week-old stem sections of both cultivars allowed PLRV to pass less rapidly than did 3-week-old sections.

In Expt. 4, a mean delay of 14.8 and 16.2 days for cv. Bismark and Desiree respectively was found between grafting with PVX-infected scions and detection of PVX in the stock plants. The difference between these means was not statistically significant. Also, in Exp. 5 no significant difference was found between the mean rates of PLRV movement through PVX-infected and healthy stem sections of either cv. Omega or Bismark, although significant differences in the rate of PLRV movement were again found between the two cultivars. Following grafting of PLRV-infected scions, PLRV was detected after mean delays of 17.6 (PVX-infected) and 17.9 (healthy) days with cv. Omega and 26.6 (PVX-infected) and 25.8 (healthy) days with cv. Bismark.

PLRV movement out of inoculated leaves

In Expt. 1, systemic infection was readily detected in PLRV-inoculated plants of cv. Delaware and Desiree after 10 days (Table 3). By contrast, infection was markedly slower to move out of inoculated leaves in plants of cv. Bismark and Omega. In Expt. 2, PLRV infection was detected after 16 days in cv. Omega, both in plants infected with PVX and in those healthy when

Table 2. *Rate of PLRV movement through stem sections of resistant and susceptible potato cultivars*

Test cultivar	Time (days) until virus was detected in stock	Significance
Expt. 1		
Desiree (I ^S A ^S)	13.6	A*
Renova (I ^S A ^S)	14.4	A
Omega (I ^R A ^R)	15.2	A
Bismark (I ^R A ^S)	22.5	B
<i>P</i>	<0.001	
D.F.	10	
S.E.D.	1.22	
Expt. 2		
Omega (I ^R A ^R)	16.0	A*
Spunta (I ^R A ^R)	17.0	A
Delaware (I ^S A ^R)	19.8	A
Bismark (I ^R A ^S)	28.7	B
<i>P</i>	0.012	
D.F.	7	
S.E.D.	2.88	
Expt. 3		
	Time (days) until virus was detected in stock	Age of stem section (weeks)
Desiree (I ^S A ^S)	14.1	3
Bismark (I ^R A ^S)	20.7	3
Desiree (I ^S A ^S)	22.0	5
Bismark (I ^R A ^S)	33.7	5
Significance (S.E.D.)		
Cultivar	<0.001 (1.79)	
Age	<0.001 (1.79)	
Cultivar × age	NS†	
D.F.	12	

* Values followed by the same letter are not significantly different at *P* 0.05.

† NS, Not significant.

Table 3. *The rate of systemic movement of PLRV out of inoculated leaves of resistant and susceptible potato cultivars**

Cultivar	Removal of inoculated leaflet (days after inoculation)				Control
	10	13	16	22	
Omega (I ^R A ^R)	0/7†	0/7	3/7	2/6	2/4
Bismark (I ^R A ^S)	0/7	1/7	3/7	3/6	3/4
Delaware (I ^S A ^R)	5/6	7/7	7/7	6/6	4/4
Desiree (I ^S A ^S)	6/6	7/7	6/6	6/6	4/4

* Viruliferous aphids (approx. 25) were caged for 4 days on the terminal leaflet of the fourth leaf from the apex of each plant. All but the inoculated leaflet and the youngest two leaves were then removed. Inoculated leaflets were subsequently removed at different times and apical leaf tissue was tested for PLRV by ELISA 4 and 6 weeks after inoculation.

† Figures are the number of plants of each cultivar in which systemic infection was detected by ELISA following removal of the inoculated leaflet/total number of plants tested.

Table 4. Preference shown by *M. persicae* alates toward PLRV-resistant and -susceptible potato cultivars

Cultivar	Proportion of colonizing aphids		
	Angular transformation		Detransformed means (%)
Expt. 1			
Desiree (I ^S A ^S)	29.6*	A†	24.4
Bismark (I ^R A ^S)	25.2	A	18.0
Delaware (I ^S A ^R)	25.1	A	18.0
Renova (I ^S A ^S)	24.5	A, B	17.2
Omega (I ^R A ^R)	21.7	A, B	13.7
Spunta (I ^R A ^R)	17.2	B	8.7
<i>P</i>	0.04		
S.E.D.	3.67		
D.F.	30		
Expt. 2			
Desiree	58.7*	A	73.0
Spunta	31.3	B	27.0
<i>P</i>	0.001		
S.E.D.	2.00		
D.F.	5		

* Figures are the means of angular transformed percentages on which the statistical analysis was done.

† Values followed by the same letter are not significantly different at *P* 0.05.

Table 5. Colonization efficiency of *M. persicae* on PLRV-resistant and -susceptible potato cultivars

Cultivar	Colony growth* (aphids/day/plant)	Ratio of aphids (small:large)	
		Day 6	Day 9
Omega (I ^R A ^R)	6.1 A†	3.8:1	5.4:1
Desiree (I ^S A ^S)	3.6 B	1.7:1	3.3:1
Delaware (I ^S A ^R)	3.4 B	1.0:1	2.1:1
Bismark (I ^R A ^S)	3.2 B	2.0:1	2.3:1
Spunta (I ^R A ^R)	2.0 C	1.3:1	3.9:1
<i>P</i>	<0.001		
S.E.D.	0.56		
D.F.	23		

* The mean colonization rate for each cultivar was determined from counts of the number of aphids feeding on each plant at days 6 and 9.

† Values followed by the same letter are not significantly different at *P* 0.05.

inoculated. In both experiments, the tests on leaf tissue from progeny plants confirmed results from tests on inoculated plants.

Aphid feeding preferences and colonization rates

In preference Expt. 1, cv. Spunta was significantly less attractive to alates than were cv. Bismark, Desiree or Delaware (Table 4). In preference Expt. 2, cv. Spunta was again significantly less attractive than cv. Desiree. The factors responsible for choice of different cultivars

by alates were independent of I^R and A^R as cv. Bismark and Delaware had I^R and A^R only, respectively, whereas cv. Spunta had both.

In the colonization experiment, significant differences in aphid colonization rate were found between cultivars (Table 5). Omega plants were colonized most readily and plants of cv. Spunta least readily, whereas cv. Bismark, Delaware and Desiree plants fell into an intermediate grouping. Except with cv. Omega, in which the greater colonization rate was reflected in an increase in the proportion of smaller aphids, the ratio of small to large aphids did not vary greatly. Aphids colonizing cv. Spunta plants were often found on the stem. This did not occur with the other cultivars and may indicate some less attractive property of cv. Spunta leaves. As with feeding preference, the cultivar characteristic(s) responsible for different rates of colonization was independent of I^R and A^R.

Discussion

Hutton & Brock (1953) found that many progeny tubers from PLRV-infected plants of cv. Bismark were healthy. Use of standard stock and scion cultivars in our double-graft sandwich experiments removed any variability between cultivars that might arise due to differing efficiencies of PLRV 'sources' and 'sinks', and in detection of PLRV. Also, no differences between cultivars in rate or stability of graft union formation were observed, and subsequent growth was always vigorous whichever was present. This suggests that the numbers of phloem connections made on grafting were similar regardless of cultivar. The double-graft sandwich therefore provided a simple way of investigating the rate of virus movement through stems of cv. Bismark plants and of other cultivars with different combinations of I^R and A^R. The double graft experiments showed that a significantly slower rate of PLRV movement occurs through stems of cv. Bismark plants than through stems of the five other cultivars tested. A specific resistance to phloem transport of PLRV in this cultivar was suggested which was independent of I^R or A^R and was not influenced by previous infection with PVX. Also, it was independent of cultivar properties responsible for differences in aphid feeding preferences and colonization rates, and operated in stems of different ages. The rate of passage of PVX through stem sections of cv. Bismark plants was the same as that through stem sections of a cultivar with a normal rate of PLRV phloem transport. This distinguishes the resistance to PLRV phloem transport in cv. Bismark from mature plant resistance, which is non-specific and would be expected to operate against PVX as well as PLRV (Beemster, 1958, 1961,

1987). Moreover, the effect of mature plant resistance was apparent in Expt. 3 (Table 2) and was independent of the PLRV resistance shown by cv. Bismark. In similar double-graft experiments, stem sections of resistant lines of *Lycopersicon peruvianum* showed inhibited transport of PLRV and tomato yellow top virus (Hassan & Thomas, 1988). Moreover, phloem transport of tobacco mosaic virus (TMV) is delayed when stem sections of tobacco engineered to express the TMV coat protein gene are sandwiched between a virus source and a susceptible scion (Register *et al.*, 1989). Previous work on PLRV transport in potato has involved inoculations with viruliferous aphids (e.g. Beemster, 1958, 1961; Barker, 1987) rather than graft inoculation and therefore did not separate out aphid feeding preferences, colonization rates or virus inoculation differences from virus movement in the phloem.

The slow systemic movement of PLRV out of aphid-inoculated leaves found in two cultivars was independent of resistance to PLRV phloem transport or A^R and was not influenced by previous infection with PVX. It may be linked to I^R as it occurred in cv. Omega and Bismark, but not in cv. Delaware and Desiree which lack this property. Moreover, there were no significant differences in aphid feeding preference between the four cultivars, whereas the aphid colonization rate on cv. Omega was significantly greater than that on the other three. Thus differences between cultivars in rate of PLRV movement out of inoculated leaves are unlikely to be due to differences between PLRV inoculation and placement by caged viruliferous aphids. Possibly, they were due to decreased numbers of primary PLRV infection foci forming in inoculated leaves of cultivars with I^R despite the large inoculum (approx. 25 viruliferous aphids/leaf) applied. With aphid inoculation, no differences in rate of systemic movement of PLRV were revealed between cv. Omega and Bismark. Presumably, the initial effect of I^R in inoculated leaves overwhelmed the subsequent effect of resistance to phloem transport in cv. Bismark such that occurrence of the latter was not evident with the experimental design used.

Barker (1987) found that the proportion of virus-free progeny tubers produced by PLRV-infected plants is greater in potato cultivars with both I^R and A^R than that in susceptible cultivars. This trend was most pronounced in clone G7445(1), in which PLRV failed to move from infected foliage to tubers in some plants in glasshouse tests. However, the general tendency of cultivars with I^R and A^R to transmit PLRV to fewer tubers was not reflected in slower PLRV movement through stems in our double-graft tests on two cultivars (Omega and Spunta) with these attributes. Possibly G7445(1) also has the specific resistance to phloem transport found in cv. Bismark in addition to the other two resistance types.

Barker & Harrison (1986) have suggested that the mechanism which restricts PLRV accumulation in potato cultivars with A^R may operate by retarding PLRV movement within the phloem rather than by inhibiting virus replication within individual cells. However, cv. Bismark lacks A^R so the mechanism causing it is unlikely to be the same as that causing resistance to phloem transport in stem sections of this cultivar. Also, as mentioned above, we did not find resistance to phloem transport in stem sections of three other cultivars with A^R. The study of fundamental features of virus transport was not an objective of this investigation. However, Hutton & Brock (1953) had previously suggested that cv. Bismark 'has a PLRV inactivating mechanism which is continually localising the virus and reducing its concentration so that even infected plants with severe symptoms produce varying percentages of progeny free of symptoms'. A possible candidate for this mechanism was the severe phloem necrosis associated with PLRV infection in cv. Bismark (Hutton, 1949; Hutton & Brock, 1953). Future studies should examine stems for both PLRV accumulation and phloem abnormalities at different times after grafting.

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