Discrimination Among Luteoviruses and Their Strains by Monoclonal Antibodies and Identification of Common Epitopes

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ABSTRACT

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Twenty-seven monoclonal antibodies to four luteoviruses were tested for their ability to detect 17 strains of seven luteoviruses in triple-antibody-sandwich enzyme-linked immunosorbent assay. Monoclonal antibodies (produced in Canada, the United Kingdom, and the United States) were to barley yellow dwarf virus (BYDV)-PAV (PAV) (3), BYDV-MAV (MAV) (3), BYDV-RPV (RPV) (5), beet western yellows virus (BWYV) (6), potato leafroll virus (PLRV) (6), and soybean dwarf virus (SDV) (4). Virus-specific monoclonal antibodies were identified for each virus to which antibodies had been produced. Many heterologous reactions, some as strong as the homologous reactions, were detected. The minimum number of epitopes identified on each virus varied from one to five. Common epitopes were identified for MAV-PAV, PAV-PLRV, PAV-PLRV-BWYV (beet mild yellowing strain), RPV-bean leafroll virus (BLRV), RPV-PLRV, RPV-BLRV-BWYV, BWYV-PLRV, BWYV-SDV, PLRV-groundnut rosette assistor virus, and PLRV-SDV. The serological relationships between PAV and PLRV and between RPV and BLRV have not been reported previously. None of the antibodies tested detected BYDV-RMV, carrot red leaf virus, or strawberry mild yellow edge virus, a possible luteovirus.

Luteoviruses are plant viruses with small, icosahedral particles that are transmitted in a persistent manner by aphids (4). Diseases caused by these viruses have been diagnosed historically first by visual assessments, later by insect transmission tests, and most recently by serodiagnosis by enzyme-linked immunosorbent assay (ELISA). Because luteoviruses are phloem-limited, mechanical transmission to indicator hosts and serological techniques that are less sensitive than ELISA are not useful diagnostic tools. With ELISA, luteovirus diagnosis has become routine and can be done on a large scale. However, this assay is currently based on a supply of polyclonal antisera to luteoviruses that is limited worldwide, and the antisera differ in quality and specificity. Also, many cross-reactions are recorded between polyclonal sera and heterologous luteoviruses (20). The application of monoclonal antibody technology to luteovirus detection and diagnosis is one solution to these problems.

Monoclonal antibodies to luteoviruses have been produced in several laboratories around the world (6,8–10,13,18). These monoclonal antibodies have been used, most often locally but sometimes on a worldwide scale, for the detection and diagnosis of their homologous antigens (3,13). The available information on the usefulness of these monoclonal antibodies for the detection and diagnosis of heterologous luteoviruses is more limited (10,11,13,14).

In this study we gathered 27 monoclonal antibodies to four luteoviruses in two locations (North America and the United Kingdom) to test their ability to detect homologous and heterologous luteovirus strains. The results indicate new possibilities for the detection of some luteoviruses and indicate other viruses for which monoclonal antibody technology remains to be developed.

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MATERIALS AND METHODS

Virus strains. The strains of barley yellow dwarf virus (BYDV) used were vector-nonspecific strains from Illinois (BYDV-PAV-IL) and the United Kingdom (BYDV-PAV-G), strains transmitted specifically by *Rhopalosiphum padi* from the same locations (BYDV-RPV-IL and BYDV-RPV-R), strains transmitted specifically by *Sitobion avenae* from Pennsylvania from F. E. Gildow and from the United Kingdom (BYDV-MAV-PA and BYDV-MAV-F), and a strain transmitted specifically by *R. maidis* from New York (BYDV-RMV-NY). All North American BYDV strains were propagated in oats (*Avena byzantina* C. Koch 'Coast Black' or *A. sativa* L. 'California Red' or 'Rodney'). Leaf tissue of Avalanche oats infected with BYDV strains from the United Kingdom was provided by R. T. Plumb and E. A. Lennon (Rothamsted Experimental Station, Harpenden, Herts., United Kingdom).

Bean leafroll virus (BLRV) from Oregon (BLRV-OR) was obtained from R. O. Hampton and was propagated in pea (*Pisum sativum* L. 'Galaxy') and transmitted by *Acyrthosiphon pisum.*

Beet western yellows virus (BWYV) strains used were a strain from sugar beet (*Beta vulgaris* L.) in British Columbia, Canada (BWYV-BC), a strain from oilseed rape (*Brassica napus* L. subsp. *oleifera*) in the United Kingdom (BWYV-UK), and a beet mild yellowing strain from sugar beet in the United Kingdom (BWYV-BMY-UK). BWYV-BC was propagated in ground-cherry (*Physalis pubescens* L.); BWYV-UK and BWYV-BMY-UK were propagated in *Nicotiana clevelandii* Gray. All BWYV strains were transmitted by *Myzus persicae.*

Carrot red leaf virus (CRLV) from the United Kingdom (CRLV-UK) was obtained from A. F. Murant (Scottish Crop Research Institute, Invergowrie, Dundee, United Kingdom) and was propagated in chervil (*Anthriscus cerefolium* (L.) Hoffm.) and transmitted by *Cavariella aegopodii.*

Groundnut rosette assistor virus (GRAV)-infected groundnut (*Arachis hypogaea* L.) tissue originally from Nigeria was obtained

from A. F. Murant.

Potato leafroll virus (PLRV) strains were from British Columbia (PLRV-BC) and the United Kingdom (PLRV-UK). PLRV-BC was propagated in *P. pubescens* and transmitted by *M. persicae.* PLRV-UK-infected potato (*Solanum tuberosum* L. 'Maris Piper') was obtained from H. Barker (Scottish Crop Research Institute).

Soybean dwarf virus (SDV), dwarfing (SDV-D), and yellowing (SDV-Y) strains, originally from Japan, were obtained in dried soybean (*Glycine max* (L.) Merrill 'Wayne') leaves from V. D. Damsteegt (Frederick, MD).

Strawberry mild yellow edge virus (SMYEV), listed by the International Committee on Taxonomy of Viruses (ICTV) as a possible luteovirus (12), was propagated in strawberry (*Fragaria* × *ananassa* Duch.) and transmitted by *Chaetosiphon fragaefolii.*

Monoclonal antibodies. The sources and designations of the monoclonal antibodies used are given in Table 1. Monoclonal antibodies to SDV were produced by injecting mice with a mixture of SDV-D and SDV-Y.

Polyclonal antisera. Polyclonal antisera used in North American tests were BYDV-PAV-IL and BYDV-RPV-IL (C. J. D'Arcy), BYDV-MAV-NY and BYDV-RMV-NY (W. F. Rochow), BWYV-BC (P. Ellis), BLRV-OR (R. O. Hampton), CRLV-UK (A. F. Murant), PLRV-BC (R. R. Martin), SDV-D and SDV-Y (A. D. Hewings), and SMYEV (R. R. Martin). Polyclonal antisera used in the United Kingdom were BYDV-PAV-G and BYDV-MAV-F (Bioreba Ag, Basel, Switzerland), BYDV-RPV-IL (C. J. D'Arcy), BWYV-UK (D. A. Govier), GRAV (A. F. Murant), and PLRV-UK (B. D. Harrison).

Triple-antibody-sandwich ELISA (TAS-ELISA). The homologous and heterologous detection capabilities of all 27 monoclonal antibodies were tested in TAS-ELISA. The monoclonal antibodies were compared in tests done simultaneously on the same sap samples, and each monoclonal antibody was tested at least twice in single wells in each location. All reagents were used at 100 μl per well in Linbro flat-bottom microtiter plates (Flow Laboratories, McLean, VA), except for the blocking step, which was 200 μl per well. Plates were coated for 1 hr at 37 C with polyclonal immunoglobulin homologous to the antigen to be tested diluted in carbonate buffer, pH 9.6. BWYV-UK, GRAV, and PLRV-UK immunoglobulins were used at 2 $\mu g/ml$; all others were at 1 $\mu g/ml$. Plates were blocked with 0.1% nonfat dried milk in phosphate-buffered saline (PBS) for 1 hr at room temperature.

Infected or healthy leaf tissue was ground in a mortar with a pestle in PBS plus 0.05% Tween 20 (1 g/5 ml), and extracts were incubated in wells overnight at 4 C. SDV strains were extracted from dried leaf tissue by grinding 0.1 g of tissue in 3 ml of PBS-Tween. GRAV was extracted in PBS-Tween (4 ml/g of leaf) containing 0.1 M diethyldithiocarbamate. Homologous or heterologous monoclonal antibodies from ascites were diluted 1:500, 1:1,000, or 1:5,000, and monoclonal antibodies in cell culture supernatants were diluted 1:20 in PBS-Tween plus milk and incubated 2 hr at 37 C. Conjugate (Sigma Chemical Co., St. Louis, MO; A1902 for mouse monoclonal antibodies, A9529 for rat monoclonal antibodies) was diluted 1:1,000 in PBS-Tween plus milk and incubated 2 hr at 37 C. Substrate (*p*-nitrophenyl phosphate, Sigma 104-105) at 0.5 mg/ml in 10% diethanolamine, pH 9.8, was incubated for 1 hr at room temperature, then overnight at 4 C.

Absorbance of each well at 405 nm (A_{405}) was read in an ELISA plate reader (Titertek Multiscan Plus Mark II, Flow Laboratories). Reactions were classified as strong (greater than or equal to 1.0), moderate (between 0.5 and 1.0), weak (between twice background and 0.5), or negative (less than or equal to twice background). Background was the average absorbance of at least two samples from uninoculated plants of the same species.

RESULTS

Of the 27 monoclonal antibodies tested, 24 reacted strongly with their homologous antigen, where available, or with a closely related virus strain in TAS-ELISA (Tables 2 and 3). The exceptions were BYDV monoclonal antibody MAV1A and SDV monoclonal antibodies 52H1 and 14F5 (Table 2). The weakness of the SDV monoclonal antibody reactions may have been the result of a relatively low virus titer in the SDV-infected tissue used for the test; however, SDV monoclonal antibodies 29D15 and 311G19 gave stronger homologous reactions. Reactions of monoclonal antibodies with SDV-D and SDV-Y were usually of the same magnitude, so they are not listed separately. The weakness of the BYDV monoclonal antibody MAV1A reaction may reflect serological differences between the NY strain used as immunogen and the PA strain used in these tests.

We were able to identify virus-specific antibodies for each virus to which monoclonal antibodies had been produced. For BYDV, MAC 91 specifically detected BYDV-PAV strains; MAFF 1, MAFF 2, and MAV1A detected only BYDV-MAV strains; and RPV3 specifically detected BYDV-RPV strains. Four monoclonal antibodies (13CD, 15CB, 31CC, and 43GB) were specific for BWYV; three (41BA, 46H12, and SCR 1) were specific for PLRV; and two (29D15 and 52H1) were specific for SDV.

Many heterologous reactions were detected among the 27 monoclonal antibodies and seven luteoviruses (17 strains) tested. In some instances the heterologous reactions were as strong as the homologous one. For example, PAV-IL-1 reacted as strongly with North American and U.K. PLRV strains and with BWYV-BMY-UK as with BYDV-PAV strains (Tables 2 and 3). Similar results were seen for BYDV-RPV monoclonal antibodies RPV-IL-1 and RPV-IL-5, BWYV monoclonal antibody 510H, PLRV monoclonal antibodies SCR 6 and SCR 10, and SDV monoclonal antibody 311G19 (Tables 2 and 3). Only the PLRV monoclonal antibodies SCR 6 and SCR 10 detected GRAV. Additional weaker heterologous reactions were found for many monoclonal antibodies (Tables 2 and 3). We believe this is the first report of serological relationships between BYDV-PAV and PLRV and between BYDV-RPV and BLRV.

This study revealed minor differences between luteovirus strains in the United Kingdom and in North America. For example, MAC 92 readily detected BYDV-RPV-R (Table 3) and also BYDV-RPV-NY (R. M. Lister, *personal communication*), but

TABLE 1. Sources of monoclonal antibodies

Homologous antigen	Monoclonal antibody	Supplier or reference
BYDV-PAV-G	MAC 91[a]	Torrance et al (1986)
	MAC 94[a]	Torrance et al (1986)
BYDV-PAV-IL	PAV-IL-1	C. J. D'Arcy, University of Illinois
BYDV-MAV-F	MAFF 1[a]	Pead and Torrance (1988)
	MAFF 2[a]	Pead and Torrance (1988)
BYDV-MAV-NY	MAV1A	H.-T. Hsu, formerly American Type Culture Collection
BYDV-RPV-R	MAC 92[a]	Torrance et al (1986)
BYDV-RPV-IL	RPV-IL-1	C. J. D'Arcy
	RPV-IL-5	C. J. D'Arcy
BYDV-RPV-NY	RPV1	Hsu et al (1984)
	RPV3	Hsu et al (1984)
BWYV-BC	13CD	P. Ellis, Agriculture Canada Research Station, Vancouver
	15CB	
	31CC	P. Ellis
	43GB	P. Ellis
	510H	P. Ellis
	43BC	P. Ellis
PLRV-BC	41BA	Martin and Stace-Smith (1984)
	46H12	Martin and Stace-Smith (1984)
	371A	Martin and Stace-Smith (1984)
PLRV-UK	SCR 1	Massalski and Harrison (1987)
	SCR 6	Massalski and Harrison (1987)
	SCR 10	Massalski and Harrison (1987)
SDV-D+Y	29D15	R. R. Martin, Agriculture Canada Research Station, Vancouver
	52H1	
	311G19	R. R. Martin
	14F5	R. R. Martin

[a] Monoclonal antibodies produced from immunized rats; all others from mice.

its reaction with BYDV-RPV-IL was weak (Table 2). Also, it did not react with PLRV-UK, although a weak cross-reaction was found with PLRV-BC. The anti-PLRV-BC monoclonal antibody 371A did not detect BYDV-RPV-R but gave a weak reaction with BYDV-RPV-IL.

The results can be used to determine the minimum number of epitopes we were able to detect on each luteovirus (Table 4). Minimum numbers are given because we do not know whether similar reactions with different monoclonal antibodies represent only one epitope, for example, the RPV-BLRV-BWYV epitope detected by RPV-IL-1 and RPV1. Herein, we have considered them to be the same. Data are given separately for the experiments done in the two locations (Table 4) because different virus strains were used.

The minimum number of epitopes identified for each virus in either location varied from one to five (Table 4), with the greatest number identified on PLRV. Epitopes identified were either unique to a single virus or were shared by two or three of the viruses tested.

None of the 25 monoclonal antibodies tested in the North American experiments detected BYDV-RMV-NY, CRLV-UK, or SMYEV (results not presented).

DISCUSSION

We compared 27 monoclonal antibodies to four luteoviruses for their ability to detect and diagnose 17 strains of seven luteoviruses and one possible luteovirus. The monoclonal antibodies detected six of the viruses tested—the four to which they were made (BYDV, BWYV, PLRV, and SDV) and two others (BLRV and GRAV). Monoclonal antibodies that reacted only with BYDV-PAV, BYDV-MAV, BYDV-RPV, BWYV, PLRV, or SDV were identified. These monoclonal antibodies will aid the diagnosis of luteovirus strains and isolates because of their increased specificity compared to polyclonal antisera.

When polyclonal antisera to different luteoviruses are used, many serological cross-reactions occur, some of them very close (1–3 SDIs [20]). This study demonstrates that monoclonal

TABLE 2. Homologous (underscored) and heterologous reactions[a] obtained in triple-antibody-sandwich ELISA with luteovirus monoclonal antibodies in North America

Monoclonal antibody	Antigen[b]						
	BYDV-PAV-IL	BYDV-MAV-PA	BYDV-RPV-IL	BWYV-BC	BLRV-OR	PLRV-BC	SDV
MAC 91	S	—	—	—	—	—	—
MAC 94	S	W	—	—	—	—	—
PAV-IL-1	S̲	—	—	—	—	S	
MAFF 1	—	M	—	—	—	—	—
MAFF 2	—	W	—	—	—	—	—
MAV1 A	—	W	—	—	—	—	—
RPV-IL-1	—	—	S̲	S	S		—
RPV-IL-5	—	—	S̲	—	S	—	—
MAC 92	—	—	W	—	—	W	—
RPV1	—	—	S	W	M	—	—
RPV3	—	—	S	—	—	—	—
13CD	—	—	—	S̲	—	—	—
15CB	—	—	—	S̲	—		—
31CC	—	—	—	S̲	—	—	—
43GB	—	—	—	S̲	—		—
510H	—	—	M	S̲	W	—	
43BC	—	—	—	S̲	—	W	
41BA	—	—	—	—	—	S̲	
46H12	—	—	—	—	—	S̲	—
SCR 1	—	—	—	—	—	S	—
371A	—	—	W	—	—	S̲	
29D15	—	—	—	—	—	—	S̲
52H1	—	—	—	—	—	—	W̲
311G19	—	—	—	S	—	—	S̲
14F5	—	—	—	—	—	S	M̲

[a]Reactions (A_{405nm}) obtained after overnight incubation of substrate. S (strong) = 1.0 or more, M (moderate) = 0.5–1.0, W (weak) = less than 0.5, — = negative.
[b]No monoclonal antibodies detected BYDV-RMV-NY, CRLV-UK, or SMYEV.

TABLE 3. Homologous (underscored) and heterologous reactions[a] obtained in triple-antibody-sandwich ELISA with luteovirus monoclonal antibodies in the United Kingdom

Monoclonal antibody	Antigen						
	BYDV-PAV-G	BYDV-MAV-F	BYDV-RPV-R	BWYV-UK	BWYV-BMV-UK	GRAV	PLRV-UK
MAC 91	M̲	—	—	—	—	—	—
MAC 94	W̲	W	—	—	—	—	—
PAV-IL-1	M	—	—	—	S	—	S
MAFF 1	—	S̲	—	—	—	—	—
MAFF 2		S̲	—	—	—	—	
RPV-IL-1	—	—	S	S	W	—	—
RPV-IL-5	—	—	S	—	—	—	—
MAC 92	—	—	S̲	—	—	—	—
510H	—	—	M	S	S	—	—
SCR 1	—	—	—	—	—	—	S̲
SCR 6	—	—	—	—	—	S	S̲
SCR 10	—	—	—	—	—	S	S̲
371A	—	—	—	—	—	—	S

[a]Reactions (A_{405nm}) obtained after overnight incubation of substrate. S (strong) = 1.0 or more, M (moderate) = 0.5–1.0, W (weak) = less than 0.5, — = negative.

TABLE 4. Luteovirus epitopes identified by reactions of monoclonal antibodies in triple-antibody-sandwich ELISA

Virus/strain	Epitopes	
	Number	Description
North America		
BYDV-PAV-IL	3	PAV, PAV-MAV, PAV-PLRV
BYDV-MAV-PA	2	MAV, PAV-MAV
BYDV-RPV-IL	4	RPV, RPV-BLRV, RPV-PLRV, RPV-BLRV-BWYV
BLRV-OR	2	RPV-BLRV, RPV-BLRV-BWYV
BWYV-BC	4	BWYV, BWYV-PLRV, SDV-BWYV, RPV-BLRV-BWYV
PLRV-BC	5	PLRV, PAV-PLRV, RPV-PLRV, BWYV-PLRV, SDV-PLRV
SDV	3	SDV, SDV-BWYV, SDV-PLRV
United Kingdom		
BYDV-PAV-G	3	PAV, PAV-MAV, PAV-PLRV-BWYV(BMY)
BYDV-MAV-F	2	MAV, PAV-MAV
BYDV-RPV-R	2	RPV, RPV-BWYV-BWYV(BMY)
BWYV-UK	1	RPV-BWYV-BWYV(BMY)
BWYV-BMY-UK	2	PAV-PLRV-BWYV(BMY), RPV-BWYV-BWYV(BMY)
PLRV-UK	3	PLRV, PLRV-GRAV, PAV-PLRV-BWYV(BMY)
GRAV	1	PLRV-GRAV

antibodies can be used to identify new serological cross-reactions, for example, the relationship between BYDV-PAV and PLRV found with monoclonal antibody PAV-IL-1. Roberts et al (15) demonstrated a distant relationship between PLRV and BYDV-RPV in immunosorbent electron microscopy tests with polyclonal antisera, a relationship confirmed here with monoclonal antibody MAC 92. Roberts et al (15) detected no relationship between PLRV and BYDV-MAV; BYDV-PAV was not tested. Ashby and Huttinga (1) reported that no reaction occurred between antiserum of a New Zealand BYDV strain and their strain of BLRV (= pea leafroll virus). Tests with monoclonal antibody RPV-IL-1 showed that at least some strains of these viruses share a common epitope.

Although the host ranges of BLRV and BWYV overlap, diagnosis of BLRV should be possible if samples are tested with RPV-IL-5 and any of the monoclonal antibodies specific for BWYV. Any dicotyledonous sample testing positive with RPV-IL-5 and negative for BWYV could be scored as a provisional positive for BLRV. Diagnosis of GRAV with the PLRV-UK monoclonal antibodies SCR 6 and SCR 10 (14) is feasible because PLRV does not infect groundnut.

Another potential application of this study may come from the fact that monoclonal antibody PAV-IL-1 detects the BMY strain of BWYV but not the other two BWYV strains tested. BWYV-BMY-UK is serologically very similar to other strains of BWYV but differs significantly in host range (17). Monoclonal antibody PAV-IL-1 may be a useful diagnostic tool for the differentiation of these BWYV strains.

The power to discriminate between these BWYV strains further demonstrates the fine specificity of monoclonal antibodies, because comparisons of coat protein amino acid sequences of BWYV and a strain of BMYV in the German Democratic Republic showed that they differed in only eight amino acid residues (19). The monoclonal antibody PAV-IL-1 does not react with BYDV particles that are disrupted in carbonate buffer at pH 9.6 (C. J. D'Arcy, *unpublished*) and so presumably detects a discontinuous epitope (2). This monoclonal antibody therefore probably recognizes a change in virus structure caused by the substitution of perhaps only one or two amino acids, a difference that is not apparent in tests that use polyclonal antibodies to BWYV. However, a comparison of more strains is desirable to confirm our observations.

Some of the methods we used in this study were selected for their simplicity and low cost. We avoided expensive mechanical extraction equipment and blocking reagents. Mortars and pestles and nonfat dry milk are widely available. Many laboratories in both developing and developed nations therefore should be able to use a similar TAS-ELISA protocol for luteovirus diagnosis if a continuous supply of polyclonal antisera is available.

No monoclonal antibody in this study detected either CRLV-UK or SMYEV, a possible member of the luteovirus group. The RMV-NY strain of BYDV also was not detected. Monoclonal antibodies capable of detecting these viruses and strains need to be produced.

The minimum number of epitopes identified on the luteoviruses tested varied from one to five. The higher number is similar to that reported in studies of epitopes of other plant viruses. Massalski and Harrison (10) found five epitopes on PLRV. It is possible that some of the epitopes found in the North American and U.K. studies are the same. For example, the PAV-PLRV epitope identified in the North American tests may be the same as the PAV-PLRV-BWYV(BMY) epitope found in the United Kingdom.

No conclusions can be drawn from this work as to the closeness of the serological relationships among the viruses studied. The cross-reactions found with the monoclonal antibodies do, however, support the idea that serological relationships among the luteoviruses are numerous and complex (16,20).

Some members of the luteovirus group listed by the ICTV were not included in this study. Indonesian soybean dwarf virus (ISDV) is classified as a luteovirus on the basis of particle morphology and biological properties. No serological relationships to other luteoviruses have been reported. ISDV resembles many of the viruses classified by the ICTV as possible luteoviruses and probably should be so classified (5).

Many virologists consider tomato yellow top virus (TYTV) to be a strain of PLRV (4,7,20), and tests using a panel of 10 monoclonal antibodies to PLRV-UK with nine isolates of TYTV from Australia (11) found only small differences among TYTV, PLRV-UK, and two isolates of PLRV from Australia. PLRV monoclonal antibody 371A also detects TYTV (R. R. Martin, *unpublished*), further supporting the classification of TYTV as a strain of PLRV.

Two other untested viruses, *Solanum* yellows virus (SYV) and tobacco necrotic dwarf virus, may or may not be separate viruses, for both have been reported to be serologically related to PLRV (20). These two viruses may be strains of viruses included in this study and therefore may be detectable by some of the monoclonal antibodies tested. For example, PLRV monoclonal antibody 371A can detect SYV (R. R. Martin, *unpublished*). Further work is necessary to clarify the taxonomic status of these viruses and to test the currently available monoclonal antibodies for their usefulness in detecting these viruses.

LITERATURE CITED

1. Ashby, J. W., and Huttinga, H. 1979. Purification and some properties of pea leafroll virus. Neth. J. Plant Pathol. 85:113-123.
2. Atassi, M. Z., and Smith, J. A. 1978. A proposal for the nomenclature of antigenic sites in peptides and proteins. Immunochemistry 15:609-610.
3. Barker, I., Forde, S., and Plumb, R. T. 1987. Barley yellow dwarf virus. Pages 119-120 in: Report of Rothamsted Experimental Station for 1986. Rothamsted Experimental Station, Harpenden, Herts., England.
4. Casper, R. 1988. Luteoviruses. Pages 235-258 in: The Plant Viruses: Polyhedral Virions with Monopartite RNA Genomes. R. Koenig, ed. Plenum Press, New York.
5. D'Arcy, C. J. 1986. Current problems in the taxonomy of luteoviruses. Micro. Sciences 3:309-313.
6. Diaco, R., Lister, R. M., Hill, J. H., and Durand, D. P. 1986. Demonstration of serological relationships among isolates of barley yellow dwarf virus by using polyclonal and monoclonal antibodies. J. Gen. Virol. 67:353-362.
7. Harrison, B. D. 1984. Potato leafroll virus. Descriptions of Plant Viruses, No. 291. Commonw. Mycol. Inst., Assoc. Appl. Biol., Kew, Surrey, England.
8. Hsu, H.-T., Aebig, J., and Rochow, W. F. 1984. Differences among

monoclonal antibodies to barley yellow dwarf viruses. Phytopathology 74:600-605.
9. Martin, R. R., and Stace-Smith, R. 1984. Production and characterization of monoclonal antibodies specific to potato leaf roll virus. Can. J. Plant Pathol. 6:206-210.
10. Massalski, P. R., and Harrison, B. D. 1987. Properties of monoclonal antibodies to potato leafroll luteovirus and their use to distinguish virus isolates differing in aphid transmissibility. J. Gen. Virol. 68:1813-1821.
11. Massalski, P. R., Thomas, J. E., and Harrison, B. D. 1986. Production and properties of monoclonal antibodies to potato leafroll luteovirus (PLRV). Pages 165-166 in: Report of the Scottish Crop Research Institute for 1985. Scottish Crop Research Institute, Invergowrie, Dundee, United Kingdom.
12. Matthews, R. E. F. 1982. Classification and nomenclature of viruses. Fourth report of the International Committee on Taxonomy of Viruses. Intervirology 17:1-200.
13. Pead, M. T., and Torrance, L. 1988. Some characteristics of monoclonal antibodies to a British MAV-like isolate of barley yellow dwarf virus. Ann. Appl. Biol. 113:639-644.
14. Rajeshwari, R., Murant, A. F., and Massalski, P. R. 1987. Use of monoclonal antibody to potato leafroll virus for detecting groundnut rosette assistor virus by ELISA. Ann. Appl. Biol. 111:353-358.
15. Roberts, I. M., Tamada, T., and Harrison, B. D. 1980. Relationship of potato leafroll virus to luteoviruses: Evidence from electron microscope serological tests. J. Gen. Virol. 47:209-213.
16. Rochow, W. F., and Duffus, J. E. 1981. Luteoviruses and yellows diseases. Pages 147-170 in: Handbook of Plant Virus Infections: Comparative Diagnosis. E. Kurstak, ed. Elsevier/North-Holland Biomedical Press, Amsterdam.
17. Smith, H. G., and Hinckes, J. A. 1985. Studies on beet western yellows virus in oilseed rape (*Brassica napus* ssp. *oleifera*) and sugar beet (*Beta vulgaris*). Ann. Appl. Biol. 107:473-484.
18. Torrance, L., Pead, M. T., Larkins, A. P., and Butcher, G. W. 1986. Characterization of monoclonal antibodies to a U.K. isolate of barley yellow dwarf virus. J. Gen. Virol. 67:549-556.
19. Veidt, I., Lot, H., Leiser, M., Scheidecker, D., Guilley, H., Richards, K., and Jonard, G. 1988. Nucleotide sequence of beet western yellows virus RNA. Nucleic Acids Res. 16:9917-9932.
20. Waterhouse, P. M., Gildow, F. E., and Johnstone, G. R. 1988. Luteovirus group. Descriptions of Plant Viruses, No. 339. Commonw. Mycol. Inst., Assoc. Appl. Biol., Kew, Surrey, England.