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Effective management of viruses in pulse crops in south eastern Australia should include management of weeds

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Abstract This study addressed the role of weeds in the epidemiology of the six most important pulse viruses in the production areas of south eastern Australia- *Alfalfa mosaic virus-Bean yellow mosaic virus-cucumber mosaic virus-pea seedborne mosaic virus-bean leafroll virus-beet western yellows virus-pulse viruses-legume viruses-weeds*. We found that the weed host range of these viruses was greater than previously reported and that not only were weeds a potential source of virus during the cropping season, but many persisted over hot, dry summers providing a "green bridge" for the viruses and their aphid vectors between cropping seasons. Weed surveys were conducted for the six pulse viruses in and around pulse crops during the 2000–2001 growing seasons. Virus was detected in 55 of 180 weed samples (selected as representative of 1416 samples), which included 15 species in 12 genera of seven families, including six allegedly new host-virus records. A weed survey was conducted between pulse growing seasons, over the summer of 2002 to determine the survival of weed hosts. It was found that even under severe drought conditions most weed species survived in a range of locations, providing a potential reservoir for viruses and allowing aphid vectors to over-summer on green hosts. Inoculation of 36 weed species common to the area resulted in additional potential weed hosts. As a result, weed control would seem to be an important element in controlling viruses in pulse crops in south eastern Australia.

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Introduction

The pulse industry has rapidly expanded in Australia since 1980. Victoria, in south eastern Australia, is now a major producer of lentils, field peas, faba beans, chickpeas, and, to a lesser extent, lupins, with these crops being grown in areas previously devoted to cereal and sheep production. Such changes in farming systems often result in changes in pathogen pressure, making disease predictions difficult. Thirteen viruses are reported to infect these crops in Australia (Latham and Jones 2001a; Schwinghamer and Schilg 2003; Thomas et al. 2004). Of these, the non-persistently aphid-transmitted viruses *Alfalfa mosaic virus* (*Bromoviridae*, genus *Alfamovirus*) (AMV), *Cucumber mosaic virus*, (*Bromoviridae*, genus *Cucumovirus*) (CMV), *Bean yellow mosaic virus* and *Pea seedborne mosaic virus* (*Potyviridae*, genus *Potyvirus*) (BYMV and PSbMV) occur most commonly and have been found to be seed-transmitted in one or more of these pulses in Australia (Jones and Coutts 1996). In recent years, crop surveys in New South Wales, Victoria, South Australia and Western Australia have also established the presence of the persistently aphid-transmitted (but not seedborne) viruses *Bean leaf roll virus* (*Luteoviridae*) (BLRV) and *Beet western yellows virus* (*Luteoviridae*, genus *Polerovirus*) (BWYV) in pulse crops in all four states (Schwinghamer et al. 1999; Latham and Jones 2001a; Freeman and Aftab 2001; Freeman et al. 2003; Van Leur et al. 2003; Aftab et al. 2005; Aftab et al. 2007)). To properly manage these viruses in south eastern Australia, an understanding of virus ecology and disease epidemiology is important.

Many studies on plant virus epidemiology, particularly studies on non-persistently transmitted viruses, focus on the crop host plant, the virus and the vector (Irwin et al. 2000) and the role of weeds and other virus hosts is not included. However, in many situations other hosts play an integral part in virus transmission to crop plants, and the epidemiology of a virus disease in an area may be a highly complex phenomenon involving a number of wild hosts, commercial crops and different insect species (Duffus 1971). Carry-over on non-crop hosts between cropping seasons is the only means of survival of the persistently transmitted viruses, such as BLRV and BWYV, which are not seedborne and has been demonstrated for BWYV in Western Australia (Latham et al. 2003; Coutts et al. 2006). The non-crop hosts may also be important for survival of non-persistently transmitted viruses, particularly if their rate of speed transmission is low, as has been found with AMV, CMV, BYMV and PSbMV in some legume species and varieties (Makkouk et al. 1993; Jones and Coutts 1996; McKirdy et al. 2000; Latham et al. 2001; Latham and Jones 2001b).

Weeds are of known economic importance in Australian farming ecosystems due to the costs they impose on producers through crop yield and quality reduction and their role as reservoirs for viruses and vectors has been generally established (McClement and Richards 1956; Duffus 1971). Although a number of weed hosts of common pulse viruses have been reported in Australia and elsewhere, their significance in pulse virus epidemiology is poorly understood.

Infected crop seed and perennial weeds are the most likely primary sources of virus inoculum infecting pulse crops in south eastern Australia. The role of annual weeds and weed seed is less clear. Seed transmission of AMV, CMV, BYMV and PSbMV in a number of pulse crops is well established (Abraham and Makkouk 2002; Makkouk et al. 1993; Jones and Coutts 1996; McKirdy et al. 2000; Latham et al. 2001; Latham and Jones 2001b; Parry and Freeman 2001) and infected pulse seed often provides the primary inoculum for aphids to spread virus within crops (Latham and Jones 2001a; Latham and Jones 2001b; Jones et al. 2008; Coutts et al. 2009). A survey of chickpea, fababean, field pea and lentil seed used on farm in 1997 in the Wimmera and Mallee regions of Victoria showed that *Malva parviflora*, *Medicago spp., Raphanus raphanistrum*, *Sonchus spp*., and *Vicia sativa* seeds were common as contaminants in pulse grains (Moerkerk 2002). All five species are known hosts of common pulse viruses and BYMV is reported as transmitted through *Medicago indica* and *M. polymorpha* seeds (McKirdy and Jones 1995). BLRV and BWYV are not seed transmitted, as they are phloem-limited viruses (Johnstone and Duffus 1984). Both viruses have been reported widely in pulse crops in NSW, South Australia, Victoria and WA in recent surveys, which suggests that weeds probably play an important role as BLRV and BWYV reservoirs between cropping seasons and are the primary inoculum source. In Western Australia, a number of weeds have been identified as hosts of BWYV, including wild radish (*R. raphinistrum*), bitter melon (*Citrullus lanatus*), fleabane (*Conzya spp*.), stinkweed (*Naverretia squarrosa*) and blackberry nightshade (*Solanum nigrum*), all of which have been found over summer infected with BWYV (Coutts and Jones 2000; Latham et al. 2003; Coutts et al. 2006).

Methods

Weed field surveys during the cropping season

Weed surveys were conducted in the major pulse production areas of western Victoria during the cropping seasons of 2000 and 2001 and on the Yorke Peninsula, South Australia, in 2001. The surveys included 117 and 115 pulse crops in Victoria in 2000 and 2001 respectively and 23 pulse crops in South Australia in 2001 and surrounding areas. The sampling points were recorded using GPS. Weed species collected, any virus symptoms observed, details of the site and presence of aphids were all recorded. One thousand four hundred and sixteen weed samples were collected and sorted and 180 representative weeds were placed in plastic bags and stored at −20°C until testing for AMV, CMV, BYMV, PSbMV, BLRV and BWYV using ELISA. Any positive results were confirmed using tissue-blot immunoassay (TBIA) and/or PCR and all new host records were confirmed by PCR and where possible, mechanical or aphid transmission.

Summer “green bridge” weed survey

Due to the fact that a number of weed hosts of the six viruses under study were identified during the growing seasons of 2000 and 2001, a summer “green bridge” weed survey was conducted in the major pulse production areas of western Victoria and the Victorian border area of South Australia over summer (January–March, 2002). The survey was conducted when there were no pulse crops in paddocks, with the aim of determining the presence and distribution of weed hosts and their potential as reservoirs for viruses and aphids. Two hundred and twenty five sites in the pulse production areas were inspected and the species of weeds present were identified. Locations included fallow paddocks, fence lines, roadsides, waterways and undisturbed lands. Sampling points were recorded using GPS. Weed species and any virus symptoms, details of the site and presence of aphids were recorded.

Aphid monitoring

To determine the importance of weeds as reservoirs for aphids that potentially vector viruses, aphid species colonising weeds and other non-crop hosts were monitored and identified during both the cropping and summer seasons of 2000–2002.

ELISA

Initial virus testing was with ELISA using polyclonal antisera to AMV, BYMV, CMV, PSbMV and BWYV, obtained from Sanofi Phytodiagnostics, France. BLRV antisera were obtained from Dr Safaa Kumari (International Centre for Agricultural Research in the Dry Areas, Syria). Local isolates of AMV, BYMV, CMV and PSbMV were used as positive controls. BLRV and BWYV positive controls were supplied by Dr. Mark Schwinghamer (NSW-DPI) and maintained in faba bean and canola respectively in an aphid-proof glasshouse. The samples which were positive in ELISA with the Sanofi antisera were then re-tested by TBIA using polyclonal antisera to these viruses obtained from Loewe, Germany to DSMZ, Germany. BLRV positive samples were re-tested by DSMZ monoclonal antibody. Some positive samples were further reconfirmed by PCR. Only confirmed results are presented unless there is a published reference for the host-virus combination as a number of false positives were found with the Sanofi PSbMV antiserum. Double antibody sandwich ELISA was conducted according to Clark and Adams (1977), with samples diluted 1:5 in buffer for extraction. Absorbance values at 405 nm were measured in a Multiscan plate reader (Labsystems Multiskan RC, Finland) after one and 2 h and values more than twice those of healthy leaves were considered to represent infected plants (Latham and Jones 2001a).

Tissue blot immunoassay (TBIA)

TBIA was performed as described by Makkouk and Kumari (1996). Fresh weed samples and positive and negative controls were blotted in duplicate on multiple Protran® nitrocellulose transfer membranes (Schleicher and Schull Biosience, Germany). Polyclonal antisera to AMV, CMV, BYMV, PSbMV and BWYV (Loewe Biochemica, Germany) and monoclonal antiserum to BLRV (DSMZ, Germany) were used at a dilution of 1:2000. Goat anti-rabbit and goat anti-mouse conjugates (Sigma®) were used at a dilution of 1:2000.

PCR

PCR was conducted to confirm a number of weed hosts for CMV, BLRV and BWYV.

A sample size of 0.3 g tissue was added to 3 ml MacKenzie lysis buffer (MacKenzie et al. 1997) in extraction bags that have an internal membrane (Bioreba®). One percent sodium metabisulfite was used in place of 1% ß-mercaptoethanol in the lysis buffer. Samples were ground with a Homex 6 machine (Bioreba®) and kept on ice while all other samples were prepared. Nine hundred μL of crushed sample was taken and placed in an eppendorf tube with 10 μL of ß -mercaptoethanol and 100 μL of 20% sarkosyl (Sigma®) and shaken to mix. The mixture was incubated at 70°C for 10 min and shaken at 5 min intervals. After incubation, 700 μL of homogenate was used for column extraction using an RNeasy Plant Mini Kit (Qiagen) following manufacturer's instructions. Total RNA was eluted in 50 μL of sterile distilled water and stored at −80°C. One μL of total RNA template was used for each RT-PCR reaction. Bean leaf roll virus was amplified with the specific primers BLRV F Ortiz and BLRV R Ortiz and thermocycling conditions as described by Oritz et al. (2005), yielding a 385 bp product. Beet western yellows virus was amplified with specific primers BWYF and BWYV PCR and thermocycling conditions as described by Miranda et al. (1995), yielding a 428 bp product. Cucumber mosaic virus was amplified with specific primers CMV1 and CMV2 and thermocycling conditions as described by Bariana et al. (1994), yielding a 500 bp product. PCR reactions were set up in 25 μl volumes using the Superscript™ III Platinum® one-step RT-PCR system (Invitrogen®) containing 0.1 μM of each BLRV or BWYV primer or 0.2 μM of each CMV primer and 1 μL total RNA. All thermocycling was conducted in an Eppendorf® mastercycler. PCR experiments were performed with positive, negative and no template controls. Products were separated on 1% agarose gels prepared in 1 × TAE buffer containing 0.1 μL/mL ethidium bromide and visualised under UV light.

Experimental weed host range of AMV, CMV, BYMV and PSbMV

Weed seed was obtained from Michael Moerkerk (DPI-Victoria). To determine the experimental host range of AMV, BYMV, CMV and PSbMV, seed from 36 weed species belonging to 27 genera and 16 families was grown for virus inoculation in an aphid-proof glasshouse in steam-sterilised potting mix, at a controlled temperature of 20 C (±5 C). Approximately 25–50 plants of each species were grown in five 10 cm pots, with 5–10 plants per pot. When plants were at the 3–4 leaf stage, four pots were individually and mechanically inoculated using 0.02 M sodium phosphate buffer pH 7 with each of four viruses (AMV, BYMV, CMV and PSbMV) separately. The inoculum (virus-infected sap) was prepared from glasshouse-maintained virus isolates in lucerne (AMV), tobacco (CMV), and faba bean (BYMV, PSbMV). For mechanical inoculations, leaves were first dusted with 180

grit carborundum powder (BDH Chemicals Ltd, England). Two to 3 g of infected leaf tissue were then ground in 0.02 M sodium phosphate buffer, pH 7 and the crude sap rubbed gently onto weed leaves, which were then washed with tap water. The plants of the fifth pot were kept as an uninoculated control. Approximately 3–4 weeks after inoculation 1–2 g of tissue from the inoculated plants to the control plants were collected in plastic bags and tested for these viruses with ELISA or the tissue was blotted on nitrocellulose membranes and tested with TBIA.

Confirmation of BLRV and BWYV weed hosts by aphid transmission

To confirm the host range of BLRV and BWYV, aphid transmissions of these viruses to some of the weed species which had tested positive serologically were carried out. In addition, aphid transmissions of both viruses to a number of potential experimental hosts were conducted. *Bifora testiculata, Galium tricornutum, Medicago truncatula, Myagrum perfoliatum, R. raphanistrum, Rapistrum rugosum*, *Sinapsis alba* and *Trifolium angustifolium* were tested for BWYV transmission by its principal aphid vector *Myzus persicae* (Sulzer). *Helminthotheca echioides, Lactuca serriola, Marrubium vulgare, R. rugosum*, *Salva verbenaca, S. alba*, *Sonchus oleraceus* and *T. angustifolium* were tested for BLRV transmission by its principal aphid vector *Acyrthosiphon pisum* (Harris). Seeds were grown in an aphid-proof glasshouse. Colonies of *M. persicae* and *A. pisum* (BWYV and BLRV vectors respectively) and virus-positive plants of both of these viruses were obtained from Mark Schwinghamer (NSW-DPI). Non-viruliferous colonies of *A. pisum* were reared on faba bean and those of *M. persicae* on canola. When the weed plants were 1 month old, aphids were allowed a 48 h virus acquisition period on the appropriate virus-infected host and then 10–20 aphids were transferred to each test plant in aphid cages and allowed a 48 h transmission feed. After the inoculation period, aphids were sprayed with insecticide and test plants were kept in the greenhouse for observation of symptoms. The plants were tested 3–4 weeks after transmission for the appropriate virus with TBIA.

Results

Detection of AMV, CMV, BYMV, PSbMV, BLRV and BWYV in naturally infected weeds during the cropping season

One or more of the four non-persistently transmitted viruses studied (AMV, CMV, BYMV, PSbMV) were found in nine weed species during the cropping season (Table 1). CMV was found in five weed host species and these included two hosts (*B. testiculata* and *Sisymbrium orientale*) for which we could find no previous record (CABI 2011; Brunt et al. 1996; Edwardson and Christie 1991). The presence of CMV in these weed hosts was confirmed by TBIA, PCR and mechanical inoculation. AMV, BYMV and PSbMV were found in three, one and one host species respectively. None of the hosts were found to have multiple virus infections. In most hosts, the viruses caused yellowing or purpling of leaves or yellow mosaic. None of the four non-persistently transmitted viruses were found in the following 23 species: *Carthamus lanatus*, *Cotula australis*, *H. echioides*, *Xanthium spinosum*, *Buglossoides arvensis*, *Brassica tournefortii*, *Cardaria draba*, *Conringia orientalis*, *Sinapsis arvensis*, *Chenopodium pumilio*, *Cucumis myriocarpus*, *Ecballium elaterium*, *Chrozophora tinctoria*, *Medicago scutellata*, *Fumaria muralis*, *Erodium botrys*, *E. moschatum*, *Oxalis pescapree*, *Papaver hybridum, Acetocella vulgaris*, *Emex australis*, *Rumex crispus* and *Solanum triflorum*.

BWYV was found in seven weed species during the cropping season (Table 2), and these included four hosts (*M. perfoliatum*, *G. tricornutum, M. truncatula* and *B. testiculata*) for which we could find no previous record (CABI 2011; Brunt et al. 1996; Edwardson and Christie 1991). These new hosts were confirmed by PCR and where possible, a second serological method and aphid transmission. BLRV was found in two species, but these were both medic species. The symptoms of BWYV and BLRV typically caused yellowing and cupping of young leaves. BLRV sometimes caused stunting and distortion of the leaves or whole plant. Neither of the persistently-transmitted viruses was found in the following 12 species: *H. echioides*, *Amsinkia intermedia*, *Brassica tournefortii*, *Cardaria draba*, *C. myriocarpus*, *Scabiosa atropurpurea*, *M. scutellata*, *M. vulgare*, *S. verbenaca*, *Oxalis pescapree*, *Acetocella vulgaris* and *R. crispus*.

In total, virus was detected in 55 of 180 weed samples (selected as representative of 1416 samples), which included 15 species in 12 genera of seven families, including six allegedly new host-virus records (Tables 1 and 2).

Summer “green bridge” survey

Forty-one weed species were identified in the survey. The weeds found most commonly were *H. echioides*, *R. crispus*, *L. serriola* and *S. oleraceus*, in 114, 88, 46 and 28 out of 225 locations respectively. Of these four weed species, *R. crispus*, *L. serriola* and *S. oleraceus* have all been found to host one or more of the six viruses under investigation, either in this or other published studies (Table 3). In total, 14 weed species identified in this summer survey were either found infected with one or more of the six viruses

Table 1 Detection of non-persistently transmitted viruses (AMV, CMV, BYMV and PSBMV) in naturally infected weeds during the 2000 and 2001 cropping seasons in south eastern Australia

Family/species	Location	Symptoms	No samples tested	AMV + ve	BYMV + ve	CMV + ve	PSbMV + ve	Testing methods[1]	Reference/new record
Apiaceae									
Bifora testiculata	Paskeville (SA)	Chlorotic leaves	5	0	0	1[N]	0	ELISA, PCR, TBIA, MI	New record
Asteraceae									
Lactuca serriola	Brinkworth (SA)	Chlorotic, hook-shaped tops	16	0	0	2	0	ELISA, MI	Zitter (2001)
Sonchus oleraceus	Horsham (VIC)	Yellow leaf mosaic	5	5	0	0	0	ELISA, MI	Zitter (2001)
Sonchus oleraceus	Bute (SA)	Purple leaves	26	0	0	2	0	ELISA	Zitter (2001)
Brassicaceae									
Sisymbrium orientale	Balaklava (SA)	Chlorotic and purple leaves	19	0	0	4[N]	0	ELISA, PCR, TBIA, MI	New record
Fabaceae									
Medicago polymorpha	Mallaala (SA)	Chlorotic leaves	6	0	0	3	0	ELISA	Pathipanawat et al. (1995)
Medicago sativa	Horsham	Yellow and red leaf mosaic	10	6	0	0	0	ELISA, TBIA	Jones (2004)
Trifolium subterraneum	Talangatuk (VIC)	Yellow leaf mosaic	6	0	4	0	0	ELISA	McKirdy and Jones (1995)
Vicia sativa	Wimmera (VIC)	Symptomless	21	0	0	0	4	ELISA	Latham and Jones (2001b)
Solanaceae									
Solanum nigrum	Horsham (VIC)	Symptomless	5	1	0	0	0	ELISA	Zitter (2001)

SA South Australia; *VIC* Victoria; *N* new record of host; *MI* mechanical inoculation

[1] All samples tested serologically. Additional testing applied to positive samples only

Table 2 Detection of luteoviruses (BLRV and BWYV) in naturally infected weeds during the 2000 and 2001 cropping seasons in south eastern Australia

Family/species	Location	Symptoms	No samples tested	BLRV + ve	BWYV + ve	Testing methods[1]	Reference/new record
Apiaceae							
Bifora testiculata	Balaklava (SA)	Yellow and purple leaves	1	0	1[N]	TBIA, PCR, AT	New record
Asteraceae							
Sonchus asper	Donald (VIC)	Yellowing on lower leaf margins	5	0	1	TBIA, PCR	Johnstone and Duffus (1984)
Brassicaceae							
Myagrum perfoliatum	Horsham (VIC)	Yellow and purple leaves, stunting	8	0	4[N]	ELISA, TBIA, AT, PCR	New record
Raphanus raphanistrum	St. Arnaud (VIC)	Yellow blotches, stunting	10	0	8	ELISA, TBIA, AT	Coutts and Jones (2000)
Fabaceae							
Medicago truncatula	Kulpura (SA)	Purple and chlorotic leaf margins	7	2	0	ELISA, TBIA, PCR	Schwinghamer et al. (1999)
Medicago truncatula	Kulpura (SA)	Purple and chlorotic leaf margins	7		1[N]	ELISA, TBIA, AT, PCR	New record
Medicago sativa	Narridy (SA)	Yellow leaves	10	1	0	ELISA, PCR	Jones (2004)
Malvaceae							
Malva parviflora	Horsham (VIC)	Reduced size and leaf yellowing	7	0	2	ELISA	Johnstone and Duffus (1984)
Rubiaceae							
Galium tricornutum	Minyip (VIC)	Reddening of top leaves	6	0	3[N]	ELISA, TBIA, AT, PCR	New record

SA South Australia; *N* new record of host; *AT* aphid transmission

[1] All samples tested serologically. Additional testing applied to positive samples only

under study during our cropping season surveys or are recorded as hosts in the literature (Table 3).

Monitoring of aphid vectors

A total of ten aphid species, all of which are vectors of one or more of the six pulse viruses under study, were found colonised on 20 pulse, pasture legume and weed host species during crop surveys or over summer (between cropping seasons) (Table 4). Seven of these aphid species were found colonising a range of weed hosts and self-sown leguminous plants over summer, between cropping seasons.

Experimental weed host range of AMV, CMV, BYMV, PSbMV, BLRV and BWYV

Of the 36 species mechanically inoculated with AMV, CMV, BYMV and PSbMV, a total of 13 species tested positive to AMV or CMV or both by ELISA or TBIA (Table 5) but none of the species were positive to BYMV or PSbMV. The 13 species included three experimental hosts of CMV in the Brassicaceae which had not been previously reported and were confirmed by PCR and mechanical inoculation. A further eight CMV and five AMV hosts were found, all of which had been previously reported in the literature or found in our cropping season surveys. The 23 species which were inoculated but tested negative to all four viruses were as follows: *Amaranthus albus*, *Conium maculatum*, *Pseudognaphalium luteoalbum*, *Sonchus hydrophillus*, *S. tenerimus*, *Amsinkia intermedia*, *Brassica carinata*, *B. chinensis*, *B. nigra*, *Cardaria draba*, *S. arvensis*, *C. myriocarpus*, *Euphorbia peplus*, *E. terracina*, *Medicago scutellata*, *Fumaria densiflora*, *F. parviflora*, *S. verbenaca*, *Argemone ochroleuca*, *Papaver dubium*, *P. hybridum*, *E. australis* and *R. crispus*.

Of the seven weed species which were inoculated with BWYV by aphid transmission, three species tested positive by ELISA, including two new experimental hosts which were confirmed by PCR (Table 5). A further four species tested negative to BWYV as follows: *H. echioides*, *M. vulgare*, *S. verbenaca* and *R. crispus*. None of the seven species inoculated with BLRV by aphid transmission tested

Table 3 Weed species found in a summer green bridge survey in 2002 in south eastern Australia, identified as hosts of AMV, BYMV, CMV, PSbMV, BLRV or BWYV during the 2000 and 2001 growing season surveys, or in the literature

Family/species	No. of locations where found (/225)	AMV, BYMV, CMV, PSBMV, BLRV, BWYV, found in weed species in growing season surveys in this study	AMV, BYMV, CMV, PSBMV, BLRV, BWYV, found in the same weed species in other studies[1]
Amaranthaceae			
Amaranthus retroflexus	1		AMV, CMV, BWYV
Asteraceae			
Lactuca serriola	46	CMV	BWYV[1,3]
Sonchus asper	8	BWYV	BWYV
Sonchus oleraceus	28	AMV, CMV	AMV, CMV, BWYV[1,3]
Brassicaceae			
Myagrum perfoliatum	1	BWYV	New record (Table 2)
Raphanus raphanistrum	1	BWYV	CMV, BWYV
Chenopodaceae			
Chenopodium album	4	No virus detected	AMV, BYMV, CMV, PSbMV
Fabaceae			
Medicago sativa	2	AMV, BLRV	AMV, BYMV, CMV, PSbMV[4], BLRV, BWYV
Trifolium repens	1	No virus detected	AMV, BYMV, CMV, BLRV, BWYV
Trifolium subterraneum	1	BYMV	AMV, BYMV, CMV, BLRV, BWYV
Vicia sativa	1	PSbMV	AMV[2], BYMV, CMV, PSbMV, BLRV, BWYV
Malvaceae			
Malva parviflora	9	BWYV	AMV, CMV, BWYV[1,3]
Polygonaceae			
Rumex crispus	88	No virus detected	BWYV[3]
Solanaceae			
Solanum nigrum	5	AMV	AMV, CMV, PSbMV

[1] All references from Brunt et al. (1996) unless otherwise stated; [2] Latham and Jones (1999); [3] Johnstone and Duffus (1984); [4] ICTVdB Management (2006)

positive by ELISA, including *H. echioides*, *R. rugosum*, *S. alba*, *M. vulgare*, *T. angustifolium*, *S. verbenaca* and *R. crispus*.

Discussion

In this study, we found that 15 common weed species were natural hosts of the six major pulse viruses (AMV, CMV, BYMV, PSbMV, BLRV and BWYV). These included nine hosts of AMV, CMV, BYMV and PSbMV (Table 1) and eight hosts of BLRV and BWYV (Table 2). Ten of the 15 species were found to over-summer in fallow paddocks, roadsides, fence lines, water channels and undisturbed lands, even under severe drought conditions (Table 3).

Fourteen weed species found in the summer surveys were identified as hosts of one or more of the six viruses under study from survey results during the cropping season or from the literature (Table 3), although the summer samples were not virus-tested. The four most commonly found over-summering weed species were *H. echioides* (bristly oxtongue), *R. crispus* (curled dock), *L. serriola* (prickly lettuce) and *S. oleraceus* (commom sowthistle). *L. serriola* was found infected with CMV and *S. oleraceus* was found infected with AMV and CMV during the cropping season. In another Australian study, *L. serriola, S. oleraceus* and *Rumex* species were found naturally infected with BWYV (Johnstone and Duffus 1984). These findings suggest that these weeds probably play a major role in the survival of pulse viruses between cropping seasons in the area of study.

Ten species of aphids, all of which are known vectors of the pulse viruses under study, were found colonising pulse crops and weeds during and between the cropping seasons. Five, six, two, three, one and four species of the known aphid vectors of AMV, CMV, BYMV, PSbMV, BLRV and BWYV respectively, were found on weed species which were known hosts of the virus. Seven aphid species were found over-summering by colonising weed species, many of which were hosts of the viruses under study. These findings suggest that infectious aphids are likely to occur prior to the sowing of crops and have the potential to move

Table 4 Aphid species and hosts on which they were found in the 2000–2002 surveys of south eastern Australia (including vector and virus host records)

Aphid species found in this study	Common name	Records as vector of AMV, BYMV, CMV, PSBMV, BLRV, BWYV[1]	Plant hosts on which aphids were found in this study	Record of listed weed as host of AMV, BYMV, CMV, PSBMV, BLRV, BWYV in this study or the literature[1, 9]	Aphid colonisation of weed host during (D) and between (B) cropping seasons D	B
Acyrthosiphon kondoi	Lucerne blue green aphid	AMV, BYMV, CMV	*Medicago sativa*	AMV, BYMV, CMV, PSbMV[8], BLRV, BWYV	Y	Y
Aphis craccivora	Cowpea aphid	AMV, BYMV, CMV, PSBMV, BLRV, BWYV[2]	*Cicer arietinum*	AMV, BYMV, CMV, PSbMV[7], BLRV, BWYV	Y	Y
			Medicago sativa	AMV, BYMV, CMV, PSbMV[8], BLRV, BWYV	Y	Y
			Medicago scutellata	BYMV	Y	Y
			Vicia faba	AMV, BYMV, CMV, PSBMV, BLRV, BWYV	Y	Y
			Vicia sativa	PSBMV[7,] BLRV, BYMV	Y	Y
Aulacorthum solani	Foxglove aphid	AMV, BYMV, CMV PSBMV, BWYV[2]	*Emex australis*	No records	U	Y
Brevicoryne brassicae	Cabbage aphid	BYMV, CMV, PSBMV, BWYV	*Myagrum perfoliatum*	BWYV[9]	U	Y
Hyperomyzus lactucae	Sowthistle green aphid	BYMV, CMV	*Sonchus oleraceus*	AMV, CMV, BWYV[4]	Y	Y
Myzus ornatus	Ornate aphid	AMV, CMV, BWYV	*Emex australis*	No records	Y	U
			Helminthotheca echioides	No records	Y	U
			Rumex crispus	BWYV[4]	Y	U
			Sonchus oleraceus	AMV, CMV, BWYV[4]	Y	U
Myzus persicae	Green peach aphid	AMV, BYMV, CMV, PSBMV, BLRV, BWYV	*Amsinkia intermedia*	No records	U	Y
			Cucumis myriocarpus	No records	U	Y
			Malva parviflora	AMV, CMV[5], BWYV[4]	U	Y
			Solanum nigrum	AMV, CMV, PSBMV	U	Y
Rhopalosiphum padi	Wheat aphid	PSBMV[2]	*Lens culinaris*	AMV, CMV, BYMV, PSBMV, BWYV, BLRV	Y	U
Therioaphis trifolii	Alfalfa spotted aphid	AMV[6]	*Megicago sativa*	AMV, BYMV, CMV, PSBMV[8], BLRV, BWYV	Y	U
Uroleocon sonchi	Sowthistle brown aphid	CMV[3]	*Sonchus oleraceus*	AMV, CMV, BWYV[4]	U	Y

Y yes; *U* Unknown;

[1] All records from Edwardson and Christie (1991), unless otherwise stated; [2] Brunt et al. (1996); [3] Raccah (1983); [4] Johnstone and Duffus (1984); [5] Eid (1983); [6] Garren and Gibbs (1982); [7] Latham and Jones 2001a; [8] ICTVdB Management (2006); [9] New records from this study (Tables 1 and 2)

Table 5 Experimental weed hosts of the six pulse viruses under study

Family/species	AMV	BYMV	CMV	PSbMV	BLRV	BWYV	Testing methods[1]	References
Asteraceae								
Lactula serriola	0	0	+	0	−	−	MI, ELISA	Zitter (2001)
Sonchus oleraceus	+	0	0	0	−	−	MI, ELISA	Ndunguru and Kapooria (2000)
Brassicaceae								
Capsella bursa-pastoris	+	0	+	0	−	−	MI, ELISA	Zitter (2001)
Rapistrum rugosum	−	−	−	−	0	$+^N$	TBIA, AT	Brunt et al. (1996)
Sinapsis alba	0	0	$+^N$	0	−	−	MI, ELISA, TBIA, PCR	
Sinapsis alba	−	−	−	−	0	+	AT, ELISA, TBIA, PCR	
Sisymbrium irio	0	0	$+^N$	0	−	−	MI, ELISA, TBIA, PCR	
Sisymbrium orientale	0	0	$+^N$	0	−	−	MI, ELISA, TBIA, PCR	
Caryophyllaceae								
Stellaria media	+	0	+	0	−	−	MI, ELISA	Brunt et al. (1996), Zitter (2001)
Fabaceae								
Lupinus angustifolius	0	0	+	0	−	−	MI, ELISA	Jones (1988)
Trifolium angustifolium	−	−	−	−	0	$+^N$	AT, TBIA, PCR	
Trifolium subterraneum	+	0	0	0	−	−	MI, ELISA	Jones (1992)
Portulacaceae								
Portulaca oleracea	0	0	+	0	−	−	MI, ELISA	Zitter (2001)
Solanaceae								
Datura stramonium	+	0	+	0	−	−	MI, ELISA	Zitter (2001)
Solanum nigrum	−	0	+	0	−	−	MI, TBIA, PCR	Zitter (2001)
Urticaceae								
Urtica urens	0	0	+	0	−	−	MI, ELISA	Zitter (2001)

+= positive; $+^N$ = this shows positive and new record; 0 = negative;—not tested, MI = mechanical inoculation, AT = aphid transmission. [1] All hosts inoculated by MI or AT and virus recovery by serology. Additional testing applied to positive samples only. Note: No host came up positive to BYMV, PSBMV or BLRV

into newly sown crops and infect them. The likelihood of this being significant in south-eastern Australia undoubtedly depends on the amount of summer and early autumn rainfall and subsequent build up of weed and aphid numbers, as found in Western Australia (Thackray et al. 2004; Maling et al. 2008; Maling et al. 2010). Of the ten aphid species found, *Aphis craccivora* was found most frequently during and between cropping seasons. Coutts and Jones (2002) studied the spread of a number of viruses within mixed species perennial pastures in Western Australia and they also found *A. craccivora* to be the most abundant aphid species. It is a vector of five of the six pulse viruses under study (AMV, BYMV, CMV, PSbMV and BLRV). Of interest was the fact that in our study, *A. pisum,* the pea aphid, was not found in either crop or weed surveys.

The importance of legume pastures as reservoirs of pulse viruses depends on the farming system. In the Wimmera area of Victoria, many farmers no longer run sheep or maintain legume pastures but focus on cropping only, rotating cereals, canola and pulses. However legume pastures are still common in other parts of the cropping zone in western Victoria. Alternate legume pastures were not surveyed in this study, although a number of species of *Medicago, Trifolium* and *Vicia* were found as weeds in crops and on roadsides, and all six viruses were found in one or more of these species. Pulse crop species were also found as self-sowns, particularly after poor seasons (drought) when crops were left unharvested. Studies in Western Australia of alternate annual pasture and forage legumes found that many of these species were hosts of AMV, CMV, BYMV and PSbMV and that the viruses were seedborne in many of these species (McKirdy and Jones 1995; McKirdy et al. 2000; Latham and Jones 2001b; Latham et al. 2001).

Lucerne is commonly grown as a pasture legume in south eastern Australia, but in this study lucerne paddocks were not systematically surveyed (due to drought); Lucerne, however, was sampled from a small number of paddocks to as a weed on roadsides etc. The significance of lucerne as host for pulse viruses is probably underestimated in this study; however, it is probably the largest perennial source of AMV in this region as has been found in WA and NSW (Jones 2001; Jones and Harman 2002; Van Leur and Kumari 2011; Garren and Gibbs 1982). During regular Victorian surveys, we have found *Acyrthosiphon kondoi* and *A. craccivora* in lucerne

stands all year. We have also found AMV-infected lucerne paddocks and adjacent faba bean crops severely infected with AMV, suggesting the movement of infective aphids from the lucerne into newly sown crops. The persistently transmitted viruses under study, BLRV and BWYV, differ from seed-borne, non-persistently transmitted viruses in that they need a green bridge (alternate host) between cropping seasons to survive. Lucerne is a host of both BLRV and BWYV (Jones and Harman 2002). It is a likely host for the over-summering of BLRV, which has a narrow host range, restricted mainly to the Fabaceae. BLRV was not found in any weed hosts over summer and only in leguminous weeds during the cropping season.

BWYV has a much wider host range than BLRV including more than 150 species in 23 families (Brunt et al. 1996) and was found in a number of weed species throughout the year. It infects not only pulse crops but also canola, which is grown in the same cropping systems as pulses in temperate Australia. It has been reported in canola in Tasmania (Johnstone and Duffus 1984), Victoria (Marcroft 2000) and NSW (Coutts and Jones 2000) and in canola and wild radish (*R. raphanistrum*) in Western Australia (Coutts and Jones 2000). The seven weed species identified in this study as natural hosts of BWYV include one member of the Fabaceae (medic) and two members of the Brassicaceae (Table 2). *M. parviflora* (marshmallow) was identified as a perennial source of BWYV in this study. It has also been reported as a host of BWYV in Tasmania (Johnstone and Duffus 1984). The two annual cruciferous BWYV hosts found in this study, *M. perfoliatum* (muskweed) and *R. raphanistrum* (wild radish) occur frequently in the cropping zone and are difficult to eradicate from canola production areas. In a recent survey in Victoria, in which farmers ranked weeds causing the most serious problems on their farms, *M. perfoliatum* and *R. raphanistrum* were ranked first and sixth (Niknam et al. 2002). *M. perfoliatum* was frequently found colonised by large numbers of cabbage aphids (*Brevicoryne brassicae*). *R. raphanistrum* was surveyed by Coutts and Jones (2000) as a potential source of viruses for spread to canola. Samples were collected from a range of sites in a number of districts over 2 years and BWYV was detected in the majority of samples. Although BWYV has a wide host range and seven natural weed hosts were found in this study, only two additional experimental host species tested were found susceptible (Tables 2 and 5).

The results of the present study show that the respective host ranges of the pulse viruses AMV, CMV, BYMV, PSbMV, BLRV and BWYV include common weed and pasture species, some of which survive all year and which were found to support populations of aphid vectors. This suggests that weeds are a major source of viruses and vectors and that they are likely to act as a primary source of infection for crops in the area. Therefore, removal of weeds from paddocks to adjacent roadsides, ditches etc., a demonstrated component of effective virus management in other crops (E.g. Hobbs et al. 2000; Rist and Lorbeer 1991), should be a component of any strategy aimed at managing viruses in pulse crops in the area of study.

Weed management in preparation for crop production and during crop growth is normal practice for farmers in the Australian winter cropping zone (Jones et al. 2000). Weed management of areas adjacent to crops is sometimes undertaken to reduce weed seed or to reduce fire risk. There is no technical difficulty or significant additional cost involved in farmers extending their weed control to include locations adjacent to crop paddocks. Summer weed management has demonstrated benefits to subsequent winter crop production, including increased soil moisture and potential for increased grain yields (Fromm and Grieger 2002). Summer weed eradication has the added advantage of effectively reducing virus reservoirs and aphid populations thus reducing early crop infection.

Contamination of crop seed with weed seed occurs widely and a recent study of farmers' seed in the Victorian Wimmera and Southern Mallee regions (Niknam et al. 2002) quantified these contaminations in cereal and lentil seed. Only 18% of lentil samples tested were weed-free, and the most frequent contaminants included a number of the hosts of pulse viruses found in our study (*M. perfoliatum*, *M. parviflora*, *V. sativa*, *R. raphanistrum* and *Medicago* spp). Therefore, cleaning crop seed is an important part of managing weeds and preventing the introduction of new weed species. Strategies to minimise virus infections in pulse crops should include the sowing of weed-free pulse seed which is virus-tested (if available) or selected from crops with no apparent virus symptoms to the reduction of weed hosts, which are potential virus and aphid reservoirs, during and between cropping seasons.

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