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Research Papers

Resistance and virulence patterns in the pea seed-borne mosaic virus (PSbMV) / lentil (*Lens culinaris*) pathosystem

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Summary. Pea seed-borne mosaic virus (PSbMV) can reach high levels of seed infection in Australian field peas, resulting in severe crop losses. Endemic, pea-derived PSbMV strains can cause lentil seed infection under experimental conditions, but PSbMV transmission has not been detected in grain harvested from lentil crops in Australia. In contrast, specialised PSbMV strains that are seed-borne in lentils occur in countries with long histories of lentil cultivation. A total of 29 PSbMV isolates were obtained from seeds of 11 exotic lentil accessions held at the Australian Grains Genebank, and the isolates were identified as the P2 pathotype using the standard set of pea differentials. However, testing with an additional set of lentil genotypes revealed two distinct pathotypes, tentatively designated P2a and P2b. Screening of lentil accessions previously reported to possess resistance to PSbMV or to bean yellow mosaic virus (BYMV), as well as Australian (25) and North American (3) cultivars, identified resistance to the P2b pathotype in several entries. In contrast, resistance to the more virulent P2a pathotype was only detected in three germplasm accessions that were previously reported to be BYMV resistant. Incursions of lentil seed-borne PSbMV strains pose major risks to the Australian lentil industry. Collaboration with research programmes in countries where lentil seed-borne PSbMV is present will facilitate resistance screening against a possible wider range of pathotypes, and support research on virulence genes and virus genes controlling seed transmission. As large-scale testing with exotic virus strains is difficult to implement in Australia, development of molecular markers for resistance to the most virulent PSbMV strains is desirable.

Keywords. Lentil seed-borne PSbMV strains, BYMV, virus resistance, pathogenicity test, pathotypes.

INTRODUCTION

Lentil (*Lens culinaris* Medik.) is one of the world's oldest domesticated crops (Zohary, 1972) and ranks third in global cool-season food legume production, after chickpea and field pea (FAOSTAT, 2026). Lentil cultivation benefits farming systems through its ability to fix nitrogen, and more generally by providing grain that is rich in protein, carbohydrates, fibre, vitamins

and minerals (Montejano-Ramírez and Valencia-Cantero, 2024).

Cultivation of lentils in Australia is recent. Less than 40 years ago, lentil was considered an experimental crop (Knights, 1987), and in 1993 the area of lentil production was estimated to be only 980 ha (FAOSTAT, 2026). By 2023, Australia was one of the world's largest producers of lentils, with 1.41 million tons of grain harvested from 0.80 million ha (FAOSTAT, 2026). This increase was made possible as Australian broad-acre grain growers recognised the benefits of introducing a grain legume into their rotations for soil health and fertility and was underpinned by research programmes that developed adapted varieties and improved agronomic practices (Materne and Reddy, 2007). Within their short history, the Australian lentil breeding programmes have focussed on improved harvestability, tolerance to boron toxicity and salinity, and resistance to *Ascochyta* blight and *Botrytis* grey mould (Materne and Reddy, 2007; Thackwray *et al.*, 2024). However, comparatively little attention has been given to breeding for virus resistance.

More than 30 virus species have been reported to infect lentils. Among these, the viruses considered most economically important internationally include alfalfa mosaic virus (AMV, *Alfamovirus*), bean leafroll virus (BLRV, *Luteovirus phaseoli*), bean yellow mosaic virus (BYMV, *Potyvirus phaseoluteum*), beet western yellows virus (BWYV, *Polerovirus*), cucumber mosaic virus (CMV, *Cucumovirus*), pea enation mosaic virus 1 (PEMV-1, *Enamovirus*), pea seed-borne mosaic virus (PSbMV, *Potyvirus pisumsemenportati*) and soybean dwarf virus (SbDV, *Luteovirus glycinis*) (Kumari *et al.*, 2009). Lentils are particularly vulnerable to virus infections, as they are preferred hosts for efficient virus vectors including the pea aphid (*Acyrtosiphon pisum*) (Wale *et al.*, 2000).

Seed-transmitted viruses are important, because sowing infected seed results in infection foci throughout crops early in growing seasons, whereas other viruses must rely on viruliferous aphids migrating from off-season hosts. Lentil sowing rates are also substantially higher than those of larger-seeded pulses, further increasing lentil crop vulnerability to seed-borne viruses. PSbMV, CMV, AMV, BYMV and broad bean stain virus (BBSV, *Comovirus viciae*) are reported to be transmitted through lentil seed (Kumari *et al.*, 2009). Of these only BBSV is not present in Australia (Jones and Congdon, 2024).

Limited virus survey data from Australian commercial lentil crops have been published. Freeman (2014) reported surveys conducted between 2000 and 2005 in Australia's main winter pulse growing regions of South

Australia and Victoria and found that lentil crops were more prone to virus infections than crops of faba bean, field pea or chickpea. CMV was the most prevalent virus detected in lentils, which was attributed to high levels of seed infections. Similarly, limited information is available on lentil viruses in Canada and the United States of America (USA), despite recognition of their potential importance to pulse industries in these countries (Rashed *et al.*, 2018). In contrast, much information has been published over the past three decades on the presence of lentil viruses in countries with long histories of lentil cultivation. Virus incidences determined by tissue blot immunoassays on randomly collected plants from farmer fields have been reported from nine surveys across eight countries. In five of these surveys, PSbMV was the most frequently identified virus (Table 1).

PSbMV is internationally considered a major virus in pea (*Pisum sativum*), largely because of its ability to be transmitted at high rates in pea seed (Khetarpal and Maury, 1987). In Australia, high incidences of PSbMV in commercial field pea crops were found to be strongly associated with PSbMV transmission levels in the seed used for sowing (Latham and Jones, 2001a; Freeman *et al.*, 2013; Congdon *et al.*, 2016). Minor levels of seed transmission were found in commercial seed lots of faba bean and chickpea (Latham and Jones, 2001b), but there are no reports of PSbMV seed transmission in Australian commercial lentil seed lots, and PSbMV infection of lentil crops has only been found near pea crops (Agriculture Victoria, 2022). Internationally, the only reported investigation of seed transmission of PSbMV in non-experimental lentil seed lots is from Ethiopia, where 84 of 270 farmer-saved seed lots were PSbMV infected, with the greatest seed-to-plant transmission rate being 16.8% (Abraham and Makkouk, 2002). Hampton (1982) detected seed-borne PSbMV in USDA Genbank accessions originating from a range of West Asian, North African, European and South American countries, indicating that PSbMV seed transmission in lentils could be widespread.

PSbMV strains isolated from lentil seed were found to be similar to pea-derived strains in host range, symptomatology, seed transmission capacity and serological reaction, but were unable to infect BYMV resistant pea varieties (Hampton, 1982; Goodell and Hampton, 1984; Alconero *et al.*, 1986) and therefore considered to be a distinct pathotype. Originally coded PSbMV-L or PSbMV-L1, the lentil pathotype was renamed P2 to align with the existing nomenclature of pea-derived PSbMV strains (Kasimor *et al.*, 1997).

Resistance and virulence genes within the PSbMV / *Pisum sativum* pathosystem have been studied exten-

Table 1. Published surveys in which incidences of lentil viruses were determined by tissue blot immunoassays (TBIA) on randomly collected plants from farmer fields.

Country	Year(s)	Reference	Fields surveyed	Plants tested	Virus incidence (%) ^a					Other viruses ^b	Most frequently identified virus
					Seed-borne viruses						
					PSbMV	CMV	AMV	BYMV	BBSV		
Syria	1991-1993	Kumari <i>et al.</i> (1993)	161	3,320	0.19	nt	nt	nt	0.91	nt	BBSV
Türkiye	1996	Bayaa <i>et al.</i> (1998)	39	7,800	0.03	nt	nt	0.01	0.24	nt	BBSV
Pakistan	1997	Makkouk <i>et al.</i> (2001)	29	2,085	16.26	1.06	0.00	0.00	0.00	0.72	PSbMV
Ethiopia	1998	Tadesse <i>et al.</i> (1999)	32	4,670	9.87	0.04	0.00	0.02	0.02	3.00	PSbMV
Iraq	2000	El-Muadhidi <i>et al.</i> (2001)	10	1,700	0.00	0.00	0.00	1.82	0.00	0.35	BYMV
Iran	2001, 2002	Makkouk <i>et al.</i> (2003)	34	6,080	0.61	0.00	0.16	0.05	0.66	7.81	luteo
Ethiopia	2004	Bekele <i>et al.</i> (2005)	11	810	15.43	0.00	0.00	0.12	0.00	6.05	PSbMV
Azerbaijan	2007, 2008	Mustafayev <i>et al.</i> (2011)	9	1,291	15.41	0.00	0.00	0.00	0.00	14.18	PSbMV
Nepal	2024	Khadka <i>et al.</i> (2024)	94	4,711	12.12	0.53	nt	nt	nt	nt	PSbMV

^a nt: not tested.

^b Other viruses: PEMV-1, luteo- and poleroviruses (as determined by the 5G4 monoclonal antibody), faba bean necrotic yellows virus (FBNYV, *Nanovirus necroflaviviciae*), chickpea chlorotic dwarf virus (CpCDV, *Mastrevirus cicerparvi*).

sively. Single, recessively inherited resistance genes have been identified in field pea that correspond to the four known pathotypes (P1–P4). These genes include: *sbm1*, which confers resistance to all four PSbMV pathotypes; *sbm1^l*, a different allele of the *sbm1* gene, which provides resistance to the P1 and P2 pathotypes; and *sbm2*, which confers resistance to the P2 and P3 pathotypes (Johansen *et al.*, 2001; Gao *et al.*, 2004). Among these, *sbm2* is strongly linked to the *mo* gene for BYMV resistance (Provvidenti and Alconero, 1988), or possibly the same gene with an allele of different specificity (Bruun-Rasmussen *et al.*, 2007).

In contrast, PSbMV resistance genes in lentils have received far less attention. Haddad *et al.* (1978) screened 568 lentil accessions from the USDA Genebank, using mechanical inoculations with a non-pathotyped PSbMV strain that originated from pea. Resistance was assessed based on absence of symptoms, with symptomless plants re-inoculated and their progenies tested. Of four accessions identified as immune, one (PI 368648) was crossed with two susceptible varieties, ‘Tekoa’ and ‘Precoz’, demonstrating that resistance was controlled by a single recessive gene. Crosses of PI 368648 with another of the resistant selections, PI 212610, indicated that both selections shared the same resistance gene, for which the code *sbv* was proposed. Hampton (1982) compared an isolate derived from the Greek lentil accession PI 297772 (PSbMV-L) with a pea-derived PSbMV isolate, by inoculating lentil accessions known to be either immune or susceptible to PSbMV, and found a differential reaction to both strains in some accessions. No follow-up has been

reported to identify more resistant germplasm or to develop PSbMV resistant lentil varieties. Furthermore, no studies have examined potential linkages between potyvirus resistance genes in lentil, comparable to those described in pea (Provvidenti and Hampton, 1991; Bruun-Rasmussen *et al.*, 2007).

Testing seed of lentil accessions from the Australian Grains Genebank (AGG) that originated from the USDA Genebank has identified PSbMV in several lines, but no cross infection to neighbouring accessions during seed increases was detected (van Leur *et al.*, 2013a). To date, no lentil seed-borne PSbMV infections have been found in Australian commercial seed increases or production fields. However, an incursion of lentil seed-borne PSbMV strains into lentil crops could have major impacts on the Australian lentil industry, particularly as production expands from winter rainfall environments into sub-tropical regions that are likely to be virus-prone. Breeding for resistance is a cost-effective and environmentally sustainable strategy for virus management. To support this approach, Australian lentil breeding programmes require knowledge of PSbMV resistance in locally adapted varieties, and should have access to sources of PSbMV resistance.

The aim of the present study was to evaluate resistance of lentil varieties and germplasm accessions to lentil seed-derived PSbMV isolates, in order to identify potential sources of resistance that can be exploited by lentil breeding programmes to pre-emptively develop germplasm combining local adaptation with effective PSbMV resistance.

MATERIALS AND METHODS

Virus diagnostics

Tissue blot immunoassays (TBIA) were used for all diagnoses, as these assays provide a reliable, rapid, and cost-effective methodology for testing large numbers of individual plants for virus infections (Freeman *et al.*, 2013; van Leur *et al.*, 2025). After blotting growing tips of plants on nitrocellulose membranes (Schleiger & Schuell Protran, 0.45 µm pore size), the membranes were processed using polyclonal antibodies specific to PSbMV (DSMZ, AS-0129) or BYMV (DSMZ, AS-0717), following the procedures described by Kumari *et al.* (2022).

Germplasm tested and virus isolates used

Five lentil germplasm accessions with reported resistance or tolerance to PSbMV (Haddad *et al.*, 1978; Hampton, 1982; Kumari and Makkouk, 1995), and seven accessions with reported BYMV resistance (McKirdy *et al.*, 2000; Al Khalaf *et al.*, 2009; Kanawaty *et al.*, 2017), were obtained from the Australian Grains Genebank (AGG, Horsham, Victoria; Table 2). Single plant selections were made from several Genebank accessions to minimise possible heterogeneity. The AGG also supplied seed of additional lines that were identified during the study as potential donors of resistance. Twenty-five Australian lentil varieties were obtained from the National Lentil Breeding Program (Horsham, Victoria) or commercial seed merchants.

Four pea seed-derived PSbMV strains were used for initial screening of lentil germplasm. These were: Ps11-11/16 (P1 pathotype, isolated from a ‘Kaspa’ seed lot harvested at the Plant Breeding Institute in Narrabri, New South Wales (NSW)); Ps11-13/19 (P2 pathotype, isolated from a ‘Dundale’ seed lot harvested at the Wagga Wagga Agricultural Institute, NSW); Ps11-16/16 (P3 pathotype, isolated from an ‘Excell’ seed lot harvested in a farmer’s field in southern NSW); and Ps11-10/2 (P4 pathotype, isolated from an ‘Excell’ seed lot harvested at the Wagga Wagga Agricultural Institute, NSW). Isolation and pathotyping procedures for these strains were described in a previous study (van Leur *et al.*, 2025).

All PSbMV isolates obtained from lentil were first pathotyped on a *Pisum sativum* differential set (van Leur *et al.*, 2025), consisting of genetically homogeneous single plant progenies from PI 193835 (*sbm1* resistance gene, resistant to all PSbMV pathotypes), PI 269774 (*sbm1^l* gene, resistant to P1 and P2 pathotypes) and ‘Dark Skin Perfection’ or ‘Greenfeast’ (*sbm2* gene, resistant to P2 and P3 pathotypes). Single plant progenies of

lentil genotypes were used for further pathotype differentiation of lentil strains. A PSbMV- and BYMV-susceptible lentil variety (‘PBA Jumbo2’ or ‘PBA Kelpie XT’) was included as a susceptible control in each test. Tests were repeated if controls were not or poorly infected.

A total of 29 lentil seed-borne PSbMV strains were pathotyped. Fifteen strains were isolated in 2012 from seed of AGG accessions (van Leur *et al.*, 2013a). These accessions were duplicates from the USDA Genebank, and had been previously reported as PSbMV infected (Hampton 1982; Goodell and Hampton, 1984). The remaining 14 strains were isolated during 2018, 2024 or 2025, and originated from AGG accessions, evaluated as part of ongoing studies to identify resistance to a range of lentil viruses. All strains were increased on PSbMV-susceptible *Vicia faba* lines, including the varieties ‘PBA Amberley’ or ‘Fiesta’ and germplasm selections Ac1206 (originating from China) or Ac1229 (from Ecuador). PSbMV infection in inoculated faba bean plants was confirmed by TBIA before leaf tissue was used as inoculum. Virus strains were preserved by drying infected faba bean tissue over silica gel and storing at 5–8°C in paper envelopes placed inside airtight plastic boxes on silica gel.

Testing for BYMV resistance in accessions reported as resistant was carried out using mechanical inoculations with BYMV isolates originating from northern NSW; isolated from faba beans growing in commercial crops (isolates By20-05 and By22-15) or from red clover (*Trifolium pratense*) growing in pastures (isolates By23-01 and By23-02). The BYMV isolates from red clover were found to be more virulent than those from faba bean, and formed a separate phylogenetic group in molecular analyses (Maina *et al.*, 2025). However, all four isolates failed to infect the pea variety ‘Greenfeast’, which contains the single recessive *mo* gene conferring resistance to BYMV (van Leur *et al.*, 2013b).

Screening tests

For each genotype / pathotype combination one 0.33 L plastic pot was sown with six seeds. The pots contained a commercial potting mixture, adjusted with lime to pH 6.8–7.0, and were after sowing placed into an aphid-proof, temperature controlled (18–24°C) greenhouse. Late emerging and poorly growing seedlings were removed 10 to 14 d after sowing, and the remaining plants were then each mechanically inoculated by rubbing a virus suspension into the first and second leaf. Virus inoculum was prepared by homogenising 3 to 5 g of fresh PSbMV infected young faba bean leaves with 3 g of silicon carbide in 15 to 25 mL of cold 0.01 M sodium phosphate buffer (pH 7.0). Plants were TBIA-tested for

Table 2. Lentil accessions and varieties with reputed resistance to PSbMV or BYMV, tested in the present study.

Name	AGG ^a	ILL ^b	PI ^c	Origin ^d	Type ^d	Virus Resistance (Reference)
ILL0217	70094	217	212610	Afghanistan	Landrace	PSbMV resistant (Haddad <i>et al.</i> , 1978) PSbMV-L resistant, PSbMV susceptible (Hampton, 1982)
ILL0277	71162	277	297745	Greece	Landrace	PSbMV resistant (Haddad <i>et al.</i> , 1978)
ILL1931	71601	1931	368648	North Macedonia	Improved cv	PSbMV resistant (Haddad <i>et al.</i> , 1978) PSbMV-L resistant, PSbMV resistant (Hampton, 1982)
ILL1935 ^e	71604	1935	368651	North Macedonia	Improved cv	PSbMV-L resistant, PSbMV susceptible (Hampton, 1982)
Red Chief	72936		477921	USA	Improved cv	PSbMV tolerant (Kumari and Makkouk, 1995)
ILL0083	74515	83		Afghanistan	Landrace	BYMV resistant (Al Khalaf <i>et al.</i> , 2009)
ILL0336	75305	336	298122	France	Unknown	BYMV resistant (Al Khalaf <i>et al.</i> , 2009)
ILL0518	71489	518	320951	India	Landrace	BYMV highly resistant (Kanawaty <i>et al.</i> , 2017)
ILL1949	71624	1949	379372	Serbia	Landrace	BYMV highly resistant (Kanawaty <i>et al.</i> , 2017)
ILL4736	75304	4736		Canada	Breeding line	BYMV resistant (Al Khalaf <i>et al.</i> , 2009)
ILL5005		5005		Spain	Landrace	BYMV moderately resistant (Kanawaty <i>et al.</i> , 2017)
ILL7163	74059	7163		Pakistan	Breeding line	BYMV highly resistant (McKirdy <i>et al.</i> , 2000) BYMV resistant (Al Khalaf <i>et al.</i> , 2009)

^a Accession number with the Australian Grains Genebank, Horsham, Victoria, Australia (AGG).

^b International Legume Lentil (ILL) accession number with the International Center for Agricultural Research in the Dry Areas (ICARDA).

^c Plant Introduction (PI) accession number with the United States Department of Agriculture's Agricultural Research Service (USDA-ARS).

^d Origin and Type, according to GENESYS (Accessed January 15, 2026, from <https://www.genesys-pgr.org/>).

^e PI 368651 is heterogeneous for PSbMV-L resistance (Hampton, 1982).

virus presence 3 weeks after the inoculations. Infection percentages were calculated based on the numbers of inoculated seedlings.

BYMV inoculation procedures were the same as those described above.

Seed transmission trial

Seed transmission in mechanically inoculated lentil varieties was assessed in 2018 (five varieties) and 2019 (two of the five varieties tested in 2018), using virus strains isolated from lentil seed (three in 2018 and two in 2019) or pea seed (four in 2018 and three in 2019). Eight seeds per variety were sown into 4 L capacity pots, using the potting mixture and greenhouse conditions described above. One pot for every strain / variety combination was used in 2018. Because of poor seed yields in 2018, the number of varieties was reduced in 2019, when two pots per strain / variety combination were sown.

All emerged seedlings were inoculated at the 2-3 leaf development stage. Virus presence was assessed 2-3 weeks later, and four infected plants per pot were retained and grown to maturity. Seed harvested from these plants was grown in trays in the greenhouse, and emerged seedlings were individually TBIA-tested for presence of PSbMV. Seed-to-plant transmission percentages were calculated based on the number of emerged seedlings.

RESULTS AND DISCUSSION

Strain differentiation among lentil seed-derived PSbMV isolates

All lentil seed-derived PSbMV strains were unable to infect the *sbm1*, *sbm1¹* and *sbm2* pea differential lines, and were therefore classified as pathotype P2. However, initial testing of lentil seed-derived strains on ILL0277, a germplasm accession previously reported as resistant to a pea-derived PSbMV strain (Haddad *et al.*, 1978), revealed variations, even when a single-seed progeny of this accession was used. ILL0277 was resistant to all pea seed-derived PSbMV strains, but lentil seed-derived strains segregated into two distinct groups. These were tentatively classified as separate pathotypes: P2a, comprising strains able to infect ILL0277, and P2b, comprising strains unable to infect ILL0277.

Strain isolations from lentil seed in 2012 identified the more virulent P2a pathotype in two accessions originating from Chile, AGG71307 (PI 299222) and AGG71315 (PI 299233). Isolates from the Iranian accession AGG72306 (PI 432218) were mixed, with three strains pathotyped as P2a and one as P2b, whereas all four strains isolated from the Greek accession AGG71189 (PI 297772) were pathotyped as P2b (Table 3). Hampton (1982) previously isolated a PSbMV strain from PI 297772 seed (PSbMV-L), and showed a unique virulence pattern for this strain across a range of lentil germplasm.

Between 2018 to 2025, more than 500 lentil accessions were received from the AGG to be evaluated for resistance to a range of viruses of importance to the Australian lentil industry. Of these, 58 accessions were selected for seed testing based on PSbMV susceptibility and geographic origin, of which seven showed seed infections. Seven P2a pathotype strains were isolated from accessions collected in Ethiopia and Greece, and seven P2b strains were isolated from two accessions originating from Nepal (Table 3).

The germplasm accessions used for isolations have undergone multiple regeneration cycles since collection, and may have been exposed to infections originating from diverse sources. Consequently, the pathogenicity of the isolates does not necessarily reflect the PSbMV population present in the respective countries of origin.

PSbMV strain-specific resistance in lentil germplasm and breeding lines

None of the five accessions previously reported as PSbMV resistant showed resistance to the P2a strain; however, ILL1931, ILL1935 and 'Red Chief' reacted similarly to ILL0277, with resistance to the P2b strain (Table 4).

Testing of seven lentil lines with reputed BYMV resistance yielded three lines (ILL0083, ILL0518 and ILL1949) with resistance to both lentil seed-derived

PSbMV pathotypes (P2a and P2b) and two lines (ILL0336 and ILL4736) that were resistant to P2b, but susceptible to P2a, exhibiting a resistance pattern similar to ILL0277.

Lentil genotype resistant to P2a and P2b, as well as those resistant only to P2b, also showed complete immunity to the four pea seed-derived pathotypes, P1, P2, P3 and P4 (Table 4).

Twenty-five Australian lentil varieties were tested with pea seed-derived PSbMV strains. The varieties 'Aldinga', 'Boomer', 'Commando', 'Nipper', 'Northfield', 'Nugget', 'PBA Blitz', 'PBA Flash', 'PBA Giant', 'PBA Greenfield', 'PBA Jumbo', 'PBA Jumbo2', 'PBA Kelpie XT', 'GIA Leader', 'GIA Metro', and 'GIA Sire' reacted as susceptible. In contrast, 'PBA Ace', 'PBA Bolt', 'PBA Hallmark XT', 'PBA Herald' and 'ALB Terrier' all showed complete resistance. 'PBA Highland XT', 'PBA Hurricane XT', 'GIA Lightning' and 'GIA Thunder' gave heterogeneous reactions, with up to 25% susceptible plants. Heterogeneous resistance reactions were expected, because all tested varieties were developed prior to commencement of the National Lentil Breeding Program deliberate selection for resistance to endemic (pea seed-derived) PSbMV strains in 2022. The varieties resistant to the pea seed-derived virus strains were also tested with the lentil seed-derived P2a and P2b strains. All were resistant to the P2b strain, but all were susceptible to P2a.

Improving resistance to *Ascochyta* blight (caused by *Ascochyta lentis*) has been a high priority for the

Table 3. Pathotyped PSbMV strains isolated from lentil seed accessions kept at the Australian Grains Genebank.

Lentil accession			Origin	Isolation Year	PSbMV strain codes	
AGG ^a	ILL ^b	PI ^c			Pathotype P2a	Pathotype P2b
71307		299222	Chile	2012	PsL12-11/1; PsL12-11/2; PsL12-11/3; PsL12-11/4	
71315	404	299233	Chile	2012	PsL12-6/1; PsL12-6/3; PsL12-6/5	
71189	304	297772	Greece	2012		PsL12-5/1; PsL12-5/3; PsL12-5/5; PsL12-5/7
72306		432218	Iran	2012	PsL12-8/2; PsL12-8/3; PsL12-8/4	PsL12-8/1
70465	4895		Ethiopia	2018	PsL18-13/1	
70527	5912		Ethiopia	2018	PsL18-14/1 ^d	
73624			Greece	2024	PsL24-1/1; PsL24-1/2; PsL24-1/3	
74312	7857		Nepal	2024		PsL24-2/1; PsL24-2/2; PsL24-2/3; PsL24-2/4; PsL24-2/5; PsL24-2/6
74314	7859		Nepal	2024		PsL24-3/1
73612			Greece	2025	PsL25-1/1	
73614			Greece	2025	PsL25-2/1	

^a Accession number with the Australian Grains Genebank, Horsham, Victoria (AGG).

^b International Legume Lentil (ILL) accession number with the International Center for Agricultural Research in the Dry Areas (ICARDA).

^c Plant Introduction (PI) accession number with the United States Department of Agriculture's Agricultural Research Service (USDA-ARS).

^d PsL18-14/1 showed inconsistent reactions in eight pathogenicity tests, with six tests showing P2a reactions, and two tests showing P2b reactions.

Table 4. PSbMV and BYMV resistance^a of selected^b lentil accessions and varieties.

Accession name	Origin	Reported resistance	PSbMV pathotype						BYMV strain	
			P2a	P2b	P1	P2	P3	P4	Moderate ^c virulence	High ^c virulence
ILL0217 ^d	Afghanistan	PSbMV	S	S	S	nt	nt	S	S	S
ILL0277 ^d	Greece	PSbMV	S	R	R	R	R	R	MR	MR
ILL1931	North Macedonia	PSbMV	S	R	R	R	R	R	S	S
ILL1935	North Macedonia	PSbMV	S	R	R	nt	nt	R	R	MR
Red Chief	USA	PSbMV	S	R	R	nt	nt	R	S	S
ILL0083 ^d	Afghanistan	BYMV	R	R	R	R	R	R	MR	S
ILL0336 ^d	France	BYMV	S	R	R	R	R	R	S	S
ILL0518 ^d	India	BYMV	R	R	R	nt	nt	R	R	MR
ILL1949 ^d	Serbia	BYMV	R	R	R	nt	nt	R	R	MR
ILL4736 ^d	Canada	BYMV	S	R	R	R	R	R	MR	S
ILL5005 ^d	Spain	BYMV	S	S	S	nt	nt	S	MR	S
ILL7163 ^e	Pakistan	BYMV	S	S	S	nt	nt	S	S	S

^a R: complete resistance, MR: low infection ($\leq 20\%$ plants tested positive), S: susceptible, nt: not tested.

^b Origin and background provided in Table 2.

^c BYMV moderate virulence; By20-05 and By22-15 isolated from faba bean, BYMV high virulence; By23-01 and By23-02 isolated from red clover (Maina *et al.*, 2025).

^d Genetically homogeneous single plant progenies used for pathogenicity tests.

^e Two sources of ILL7163 were tested; (1) Australian Grains Genebank, (2) imported from the International Center of Agricultural Research. Both showed a similar reaction.

Australian lentil breeding programme, and the Canadian variety ‘Indianhead’ was used as a main donor for this resistance (Thackwray *et al.*, 2024). ‘Indianhead’ (PI 320952, AGG 70793) is a black-seeded lentil intended for use as a green manure crop (Slinkard, 1988) and was selected at the University of Saskatchewan, Canada, from a germplasm accession originating from former Czechoslovakia (<https://www.genesys-pgr.org/>). In the present study, ‘Indianhead’ reacted similarly to ILL0277; resistant to the pea seed-derived pathotypes P1 to P4 and the lentil seed-derived pathotype P2b, but susceptible to pathotype P2a, and could be an unintentional donor of the strain-specific PSbMV resistance found in the limited number of Australian cultivars. ‘Indianhead’ has also been used as a donor of *Ascochyta* blight resistance in the lentil breeding programmes in Canada and the USA (Thackwray *et al.*, 2024). The Canadian breeding line ILL4736 (University of Saskatchewan breeding code G-118), reportedly resistant to BYMV, showed a PSbMV reaction similar to ILL0277 (Table 4), although pedigree information for ILL4736 is not publicly available. The reportedly PSbMV tolerant variety ‘Red Chief’ also reacted like ILL0277 (Table 4). ‘Red Chief’ was selected at Washington State University from a cross between PI 181886 and PI 329171 (Wilson and Muehlbauer, 1983). In the present study, PI 181886 (AGG 71068, originating from Syria) was PSbMV-susceptible and PI 329171 (AGG

71505, originating from Iran), was heterogeneous for PSbMV resistance.

No recent information on PSbMV resistance in North American lentil cultivars is available, but the results from ‘Indianhead’, ‘Red Chief’ and ILL4736 indicate that resistance to the pea strains and the P2b lentil strain is present within the Canadian and USA breeding programmes.

BYMV resistance in lentil germplasm

Several accessions showed moderate resistant reactions, expressed as less than 20% of plants infected by BYMV, even after repeated tests on homogenous genotypes derived from single seed progenies. No host accession displayed complete resistance to all four of the BYMV isolates. However, two accessions previously reported as highly resistant to Syrian BYMV isolates, ILL0518 and ILL1949 (Kanaway *et al.*, 2017), were only infected by highly virulent isolates derived from red clover. The previously reported high virulence on faba bean of these isolates (Maina *et al.*, 2025) was confirmed on lentils in the present study. The susceptibility of accessions previously reported to be highly BYMV resistant such as ILL7163 (McKirby *et al.*, 2000), indicates significant regional differences in pathogen virulence.

Table 5. Seed to plant transmission rates (%) of five PSbMV susceptible lentil varieties after mechanical inoculations with pea seed- and lentil seed-derived PSbMV strains in greenhouse trials.

PSbMV strain	Isolated from	Pathotype	Seed to plant transmission rates (%)						
			PBA Flash		PBA Jumbo2		PBA Blitz	Boomer	Nipper
			2018	2019	2018	2019	2018	2018	2018
PsL12-11/1	Lentil	P2a	17.5	nt ^a	0.0	nt	2.9	2.5	5.2
PsL12-6/5	Lentil	P2a	15.8	28.1	16.7	20.2	14.3	10.5	19.8
PsL12-5/3	Lentil	P2b	0.0	nt	0.0	nt	7.0	0.0	2.1
PsL12-8/1	Lentil	P2b	nt	21.3	nt	22.0	nt	nt	nt
Ps11-11/16	Pea	P1	7.9	4.3	0.0	2.2	6.5	0.0	2.2
Ps11-13/19	Pea	P2	0.0	nt	0.0	nt	nt	0.0	0.0
Ps11-16/16	Pea	P3	0.0	0.0	0.0	0.0	nh ^b	0.0	2.0
Ps11-10/2	Pea	P4	13.5	1.0	0.0	0.0	10.4	0.0	6.7

^a nt: not tested.

^b nh: not harvested.

While the single recessive gene (*mo*) within the *Pisum sativum* gene pool provides complete immunity to all BYMV isolates regardless of origin or virulence, no comparable gene was identified in lentil (*Lens vulgaris*) in this study.

PSbMV seed transmission in lentils under greenhouse conditions

Mechanical inoculations of PSbMV onto lentil varieties, grown in pots under greenhouse conditions, resulted in severe growth reductions, irrespective of virus isolate origin (from lentil or pea seed) or pathotype. Seed yields from the greenhouse-grown plants were very low compared with field-grown plants, and seed transmission tests were therefore conducted on only 40 to 100 harvested seeds per strain/variety combination. Seed transmission results were highly variable, but the only strain that failed to be seed transmitted in any of the tested lentil varieties was the pea seed-derived strain Ps11-13/19 (P2 pathotype). The lentil seed-derived strain PsL12-6/5 (P2a pathotype) showed the greatest level of seed transmission in both years (Table 5). Because of the limited number of seeds tested, these are only indicative results. However, they confirm earlier results showing that pea-derived PSbMV strains can be seed transmitted in lentils under experimental conditions (Hampton and Muehlbauer, 1977; Coutts *et al.*, 2008).

CONCLUSIONS

The results of this study demonstrate that the PSbMV/*Lens culinaris* pathosystem is distinct from the

well-characterised PSbMV/*Pisum sativum* pathosystem. When PSbMV strains isolated from lentil seed held at the Australian Grains Genebank were tested on a standard pea differential set, all were classified as pathotype P2. However, testing these strains on lentil germplasm accessions with reported PSbMV resistance revealed two distinct pathotypes, tentatively designated P2a and P2b. Lentil genotypes resistant to the P2a pathotype were also resistant to the P2b, whereas the reverse was not observed. Lentil genotypes resistant to either P2a or P2b were also resistant to all pea seed-derived PSbMV pathotypes (pathotypes P1, P2, P3 and P4).

Several recently developed Australian lentil varieties were resistant to the P2b pathotype and to pea-derived pathotypes. Australian lentil breeding programmes share research sites with pea breeding programmes, and high PSbMV infection levels are common in Australian pea crops, particularly at research stations (van Leur *et al.*, 2025). Symptoms of PSbMV in field peas can be difficult to identify under field conditions (Khetarpal and Maury, 1987). However, in lentils, PSbMV can have severe effects, irrespective of whether the infecting strain originated from pea or lentil seed. It is therefore possible that Australian lentil breeders have inadvertently selected for resistance to the PSbMV pea strains present in their trial fields.

The strong linkage between BYMV resistance and resistance to PSbMV pathotype P2 in field pea (Provvidenti and Alconero, 1988) prompted the present investigation of a possible similar relationship within the PSbMV / *Lens vulgaris* pathosystem. Testing lentil lines reported as BYMV resistant did not identify a gene conferring complete immunity to all the tested BYMV isolates, comparable to the *mo* gene in field pea. However,

the most BYMV resistant lentil accessions (ILL0518 and ILL1949) were immune to all PSbMV pathotypes. Further investigations of resistance in lentils to different potyviruses would therefore be valuable.

More than 40 years ago, Goodell and Hampton (1984) warned of the risk that lentil seed-borne PSbMV strains could escape from genebanks into commercial lentil fields. Nearly three decades later, van Leur *et al.* (2013a) raised the same concern for the emerging Australian lentil industry. Since then, lentil production in the 'new' lentil producing countries – Canada, the USA, and Australia – has expanded substantially, reaching a combined area of more than 2.5 million ha in 2023, representing about half of the global lentil area (FAOSTAT, 2026). Despite this growth, and the widespread presence of PSbMV in pea crops, PSbMV seed transmission has not yet been reported in commercial lentil crops in these countries. The absence of specialised lentil seed-borne strains is the most likely explanation for this discrepancy.

In the present study, all lentil seed-derived PSbMV strains were classified as the P2 pathotype, but the P2 pathotype is not unique to lentils. Alconero and Hoch (1989) pathotyped 189 PSbMV strains isolated from seeds of a wide range of pea germplasm introductions held at the USDA Genebank, and identified 14 isolates reacting as the P2 pathotype using two pea lines capable of differentiating the four PSbMV pathotypes. In addition, a pea seed-derived P2 pathotype strain has previously been identified in Australia (van Leur *et al.*, 2025). Pathotyping of PSbMV isolates using standardised, homogenous pea and lentil genotypes is essential for pea and lentil breeding programmes to identify effective and durable resistance genes. However, single gene virulences in pathogen populations are unlikely to explain complex traits including seed transmission, which are probably controlled by multiple virus genes (Wang and Maule, 1994; Simmons and Munkvold, 2014). To fully understand the uniqueness of lentil seed-borne PSbMV strains, collaboration with research programmes in countries where these strains are endemic is needed, and should include pathotyping as well as studies of seed transmission and host resistance of local germplasm. Ademe *et al.* (2025) examined eight PSbMV strains isolated from lentils grown in farmer fields or research stations in different regions of Ethiopia. Although the strains were isolated from plants, it is likely that they were lentil seed-borne. Phylogenetic analysis showed that six isolates clustered with the published lentil seed-borne PSbMV-L1 strain (GenBank accession code: AJ252242), and were distinct from pea seed-borne strains. However, no pathotyping was undertaken by Ademe *et al.* (2025).

Strict quarantine regulations have undoubtedly played important roles in preventing introduction of lentil seed-borne strains into Australian lentil fields (Maina and Jones, 2023). However, rapidly expanding lentil cultivation, together with increasing international travel and trade, make incursions of lentil seed-borne strains very likely. Pre-emptive breeding is required, using parental material with resistance to the most virulent lentil seed-borne virus strains, but requires better understanding of the inheritance of PSbMV resistance in lentils. The only published study on PSbMV inheritance used a non-pathotyped PSbMV strain originating from field pea and identified a single recessive gene (*sbv*) in both PI 368648 and PI 212610 (Haddad *et al.*, 1978). In the present study, PI 368648 (ILL1931) was resistant to the P2b pathotype, but susceptible to the P2a pathotype, and PI 212610 (ILL0217) was found to be susceptible to PSbMV. Hampton (1982) found that PI 212610 was resistant to the lentil seed-borne strain PSbMV-L, but was susceptible to the pea seed-borne strain. This is contrary to the present study, where lentil lines resistant to a lentil seed-borne strain (either P2a or P2b) were also resistant to all pea seed-borne strains. This discrepancy likely reflects heterogeneity within the germplasm accessions, common in genebank material, and the single-plant progeny tested was not representative of the original accession.

Although the present study has demonstrated substantial differences in PSbMV virulence and resistance patterns between the field pea and lentil pathosystems, lentil germplasm accessions were identified with complete immunity to infections, similar to those observed in field pea. Detailed studies on PSbMV in field pea have revealed different alleles of resistance genes each reacting with specific pathotypes. Similar studies for PSbMV in lentils could facilitate the development of pathotype-specific resistance markers, like those developed for field pea (Swisher Grimm and Porter, 2020). Australian breeding programmes would be greatly assisted by molecular markers capable of identifying resistance to specific PSbMV pathotypes, as large-scale resistance screening using exotic virus strains is both risky and difficult to implement.

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