Inheritance of Resistance to White Lupin Mosaic Virus in Common Pea

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Abstract. Resistance to white lupin mosaic virus (WLMV), a recently characterized member of the potyvirus group, was found in pea (*Pisum sativum* L.) plant introductions from Ethiopia (PI 193835) and India (PI 347485). In cross and backcross populations between plants of resistant PI 193835 with those of susceptible 'Bonneville' and PP-492-5, this resistance was demonstrated to be governed by a single recessive gene. This gene was distinct from other genes previously found in PI 193835 and PP-492-5 (from PI 347492, India) conferring resistance to clover yellow vein virus (CYVV) and three strains of pea seedborne mosaic virus (PSbMV). Indirect evidence suggests that this newly recognized viral resistance gene, *wlv*, is a member of a cluster of closely linked genes located on chromosome 6. This gene cluster includes *sbm-1*, *sbm-3*, and *sbm-4*, which govern resistance to three PSbMV pathotypes, and *cyy-2*, which governs resistance to CYVV.

White lupin mosaic virus (WLMV) originally was isolated from lupin (*Lupinus albus* L.) grown at Kimberly; Idaho. This virus resembles bean yellow mosaic virus (BYMV), but is serologically distinct from members of the BYMV potyvirus subgroup (Hampton et al., 1992). WLMV also lacks the ability to infect red clover (*Trifolium pratense* L.) and most beans (*Phaseolus vulgaris* L.). Experimentally, this newly recognized potyvirus induced a mild to moderate green mosaic in some pea cultivars, while in others it caused rapid and severe systemic necrosis. Considering the potential importance of this virus to the pea crop, a search for sources of resistance was undertaken among domestic and foreign pea cultivars and land races. Resistance was lo-

cated in some lines from Ethiopia and India that previously demonstrated resistance to the three pea seedborne mosaic virus (PSbMV) pathotypes and clover yellow vein virus (CYVV) (Provvidenti and Alconero, 1988a, 1988b). The purpose of this study was to elucidate the inheritance of resistance to WLMV in PI 193835 (Ethiopia) and determine whether this resistance is inherited independently from the other resistance factors previously found in this line and exploited in breeding (Provvidenti and Muehlbauer, 1990; Provvidenti et al., 1991).

Seeds of plant introductions from Ethiopia and India originally were obtained from the Northeast Regional Plant Introduction Station, Geneva, N. Y., whereas domestic and foreign cultivars were secured from commercial sources. WLMV-resistant PI 193835 plants were crossed with those of the susceptible cultivar Bonneville and PP-492-5, a single plant selection of PI 347492 from India. PI 193835 and PI 347492 had shown resistance to the PSbMV pathotypes and CYVV

(Provvidenti and Alconero, 1988c). 'Bonneville' is resistant to several viruses, including the NL-8 strain of bean common mosaic virus (BCMV-NL8), BYMV, CYVV, pea mosaic virus (PMV), PSbMV-L (lentil strain), and watermelon mosaic virus 2 (WMV-2) (Provvidenti and Muehlbauer, 1990). An isolate of WLMV, originally from white lupin, was maintained in 'Bonneville'. The inoculum was prepared by triturating young infected pea leaves with phosphate buffer 0.05 M K_2HPO_4 at pH 8.5. All test plants were inoculated mechanically twice, with an interval of 96 h, to minimize escapes. F₁, F₂, and backcross plants were assayed routinely by enzyme-linked immunosorbent assay to confirm infectivity in susceptible plants. WLMV antiserum had been prepared previously while identifying and characterizing this virus (Hampton et al., 1992). All plants were grown in an insect-free greenhouse maintained at 25 to 28C and periodically treated with 2-methyl-2-(methylthio)propanal *O* -[(methylamino)carbonyl]oxime (aldicarb, Temik).

Most of the pea cultivars tested with WLMV developed a light- and dark-green mosaic that could have been attributed to BYMV infection. This group included 'Alaska 4683', 'Bonneville', 'Campbell Scotch', 'Dwarf Gray Sugar', 'Dwarf Telephone', 'Freezonian', 'Garfield', 'Giant Stride', 'Latah', 'Laxton Progress No. 9', 'Laxton Superb', 'Little Marvel', 'Hundred Fold', 'Knight', 'Mammoth Melting', 'Perfected Freezer', 'Perfected Freezer 60', 'Ranger', 'Scout', 'Sparkle', 'Tall Telephone', 'Tracer', 'Wando', 'World's Record', PI 172339 (Holland), PI 165897 (India), PI 391630 (China), and PI 269818 (former USSR). Other pea lines responded with severe reactions, which included local and systemic necrosis, wilting, and premature death. This group included 'Alaska', 'Alderman', 'Dark Green Perfection', 'Lincoln', and PI 140295 (Iran). PI 193835 (Ethiopia) and PI 347485 (India) plants were uniformly resistant to this virus, while those of PI 193586 (Ethiopia) and PI 347492 (India) were a mixture of resistant and susceptible individuals.

PI 193835 plants, which were chosen for inheritance studies, remained free of local and systemic infection when inoculated with WLMV and were highly resistant or immune (Table 1). 'Bonneville' plants responded with persistent green mosaic and some stunting,

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while those of PP-492-5 exhibited green mosaic followed by yellowing and prominent stunting. All F₁ (PI 193835 × 'Bonneville') and F₂ (PI 193835 × PP-492-5) plants developed symptoms closely resembling those of the susceptible parents. The recessive nature of this resistance was confirmed in the F₂ populations of the same crosses, which segregated in a ratio of 3 susceptible: 1 resistant. All plants of the backcross (PI 193835 × 'Bonneville') × 'Bonneville' were susceptible, whereas those of (PI 193835 × 'Bonneville') × PI 193835 Segregated at a ratio of 1 resistant: 1 susceptible (Table 1). Thus, the high level of resistance to WLMV present in the Ethiopian pea line was conferred by a single recessive gene, *wlv*. The gene for resistance to WLMV differs from those conferring resistance to the PSbMV pathotypes and CYVV (Table 2).

Although resistance to WLMV is conferred by a distinct entity, there is circumstantial evidence that it may be linked closely to the other known resistance genes located on chromosome 6 (Provvidenti and Hampton, 1991). In our tests, the multi-viral resistant lines Marx's G-1000 (Provvidenti et al., 1991) and USDAX-78006 (Provvidenti and Muehlbauer, 1990) were resistant to WLMV (Table 2). During their development, these two lines were tested only with PSbMV-ST; but, for six to eight generations, including backcrossing and selfing, they also maintained their resistance to PSbMV-L, PSbMV-P4, CYVV, and WLMV. The multi-resistance of Marx's G-

1000 and USDA X-78006 was derived from PI 347485 and PI 193835, respectively (Provvidenti and Muehlbauer, 1990; Provvidenti et al., 1991). Hence, a cluster of genes, which includes *sbm-1*, *sbm-3*, *sbm-4*, *cyv-2*, and *wlv*, seems to be present in these two lines. Gritton and Hagedorn (1975) used *wlo* as a marker to establish that *sbm-1* is located on chromosome 6. Line A 1075-239, which was provided by N.F. Weeden (Cornell Univ.) and possesses this marker, was crossed with WLMV-resistant PI 193835. From Table 1, it is evident that, in the F₂ population, the segregation for *wlv* was close to the expected ratio (10 resistant :35 susceptible) (*P* = 0.67) for resistance to WLMV. However, among the 45 tested plants, only two were homozygous for *wlo* and *wlv*. This ratio closely agrees with two independently inherited single recessive factors (*P* = 0.68). The value of *wlo* as a marker for *sbm-1* has been questioned in recent work (Weeden et al., 1991).

WLMV has been found in naturally infected lupin in Idaho, but, since it is a newly characterized pathogen, further studies are needed to determine its presence and distribution in pea and other legumes. Our findings have shown that WLMV can be destructive, particularly to pea cultivars in which it causes foliage and stem necrosis and premature death. Our results have shown that valuable resistance is available in land races from Ethiopia and India and, more specifically, in some advanced multi-viral resistant lines, such as

Marx's G-1000 and USDA X-78006. Both of these lines offer two clusters of genes, one located on chromosome 2 and the other on chromosome 6. The first cluster contains *mo* for BYMV and WMV-2, *pmv* for PMV, *bcm* for BCMV-NL8, *sbm-2* for PSbMV-L, and *cyv-1* for CYVV. Recent evidence has shown that another gene is present in this same cluster and confers resistance to a strain of passion fruit woodiness virus from Australia (Provvidenti et al., 1992). The cluster on chromosome 6 includes *sbm-1* for PSbMV-ST, *sbm-3* for PSbMV-L, *sbm-4* for PSbMV-P4, *cyv-2* for CYVV, and possibly *wlv* for WLMV. However, the genes conferring resistance to CYVV and PSbMV-L, located on chromosomes 2 and 6, maybe duplicate entities (Provvidenti, 1987; Provvidenti and Alconero, 1988a). The presence of eleven resistance genes clustered on two chromosomes makes breeding new cultivars with multi-viral resistance easier, since they are recessive genes conferring a high level of resistance to each of the viruses.

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Table 1. Inheritance of resistance to white lupin mosaic virus in progenies from crosses of *Pisum sativum* PI 193538 (Ethiopia) with susceptible cultivar Bonneville, line PP-492-5 (from PI 347492, India), and line A1075-239.

Progenies	Plant (no.)		Expected ratio (R: S)	Goodness-of-fit (P)
	Resistant (R)	Susceptible (s)		
Bonneville	0	45		
PI 193835	38	0		
PP-492-5	0	37		
A1075-239	0	16		
PI 193835 × Bonneville				
F ₁	0	15		
F ₂	19	67	1:3	0.54
BC (F ₁ × PI 193835)	24	29	1:1	0.45
BC (F ₁ × Bonneville)	0	47		
PI 193835 × PP-492-5				
F ₁	0	20		
F ₂	16	59	1:3	0.47
A1075-239 × PI 193835				
F ₁	0	15		
F ₂	10	35	1:3	0.67

*This line is homozygous for the *wlo* gene.

Table 2. Reaction [resistant (R) or susceptible (S)] of various pea lines to three pathotypes of pea seedborne mosaic virus (PSbMV-ST, PSbMV-L, and PSbMV-P4), clover yellow vein virus (CYVV), and white lupin mosaic virus (WLMV).

Accession	CYVV	PSbMV-ST	PSbMV-L	PSbMV-P4	WLMV
PI 193835	R	R	R	R	R
PP-586-2	R	R	R	R	s
PI 347485	R	R	R	R	R
PP-492-5	R	R	R	R	s
Marx's G-1000	R	R	R	R	R
USDA X-78006	R	R	R	R	R

PP-586-2 was selected from PI 193586 (Ethiopia) and PP-492-5 was selected from PI 347492 (India). Marx's G-1000 line's resistance to WLMV is derived from PI 347485; USDA X-78006's resistance to WLMV is derived from PI 193835.