Inheritance of Resistance to a Strain of Passionfruit Woodiness Virus in Pea (*Pisum sativum* L.)

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Abstract. An Australian strain of passionfruit woodiness potyvirus (PWV-K) infected peas and caused a light to moderate mosaic consisting of chlorotic spots, veinal chlorosis, and some plant stunting. Resistance to PWV-K was found in pea cultivars and plant introductions (PI) known to be resistant to bean yellow mosaic virus (BYMV). In cross and backcross populations involving the resistant cultivar Bonneville (United States) and PI 140295 (Iran) with the susceptible cultivar Ranger, a single recessive gene was responsible for the high level of resistance to PWV-K. From crosses involving PI 391630 (China), which is resistant to BYMV but susceptible to PWV-K, and the cultivar Bonneville (resistant to both viruses), it was evident that different genetic factors conferred resistance to these two potyviruses. The symbol *pwv* is tentatively assigned to this newly recognized pea resistance gene. Three other Australian strains of PWV did not infect peas.

Passionfruit woodiness potyvirus (PWV) was originally reported by McKnight (1953) to infect *Passiflora edulis* Simms. and other *Passiflora* species in Australia, causing a variety of foliar symptoms, all of which include hardening of the fruit's pericarp (woodiness). PWV has also been found to infect several legume species, including bean (*Phaseolus vulgaris* L.), peanut (*Arachis hypogaea* L.), and soybean [*Glycine max* (L.) Merr.] (Greber, 1971; Taylor and Greber, 1973). Strain differentiation has been based primarily on the symptoms that they incite on naturally infected hosts, since serologically they appeared to be closely related (Taylor and Greber, 1973).

Some potyviruses causing woodiness of passionfruits (*P. edulis*) in the American, African, and Asian tropical and subtropical regions of the world have been considered to be strains of PWV (Bakker, 1974; Chagas et al., 1981; Graca, 1976; Martin, 1962; Wang, 1983). Recent studies, however, have indicated that some of these strains may be distinct viral entities (Niblett et al., 1991; Provvidenti et al., 1992). In the last 2 years, we compared some of the biological properties of passionfruit potyviruses from Puerto Rico, Taiwan, Thailand, and Australia, using bean (*Phaseolus vulgaris* L.) and pea cultivars. All of these viruses were able to infect beans, but some cultivars were resistant, and specific factors were found to differentiate them (Provvidenti, 1992, 1993). None of these viruses infected peas, except the strain from Thailand (PWV-

T) and one of four strains from Australia (PWV-K). Apparently, all of the lines tested were susceptible to PWV-T, while some lines were susceptible and others resistant to PWV-K. Because resistance to PWV-K occurred mainly in peas known to be resistant to bean yellow mosaic virus (BYMV) (Provvidenti, 1992), the purpose of this study was to 1) determine the reaction of a larger number of domestic and foreign pea lines to these two viruses and 2) establish whether the resistance to PWV-K and BYMV was conferred by the same or different genetic factors.

Materials and Methods

Pea seeds of commercial cultivars were obtained from several sources, while those of plant introductions (PIs) were secured from the Northeast Regional Plant Introduction Station, Geneva, N.Y. 'Bonneville' and PI 140295 (Iran), previously found to be resistant to PWV-K, BYMV, and other viruses (Provvidenti, 1990, 1991), were crossed with the susceptible 'Ranger'. PI 391630 (China), which is resistant to BYMV but susceptible to other viruses (Provvidenti, 1987), was crossed with 'Bonneville'. BYMV and PWV-K were maintained in 'Ranger' peas, and inoculum was prepared by triturating young infected pea leaves with phosphate buffer 0.05 M K_2HPO_4 at pH 8.5. From 16 to 20 plants of each pea line were inoculated either with PWV-K or BYMV. To minimize escapes, plants were mechanically inoculated twice, using the first two expanded leaves and then the third leaf. To confirm infectivity, all plants were assayed by inoculating 'Ranger' peas, by enzyme-linked immunosorbent assay (ELISA), or by both techniques. Antiserum to BYMV had been prepared using a strain from New York

(Uyemoto et al., 1972), whereas an antiserum to PWV was provided by R. Greber (Australia).

All plants were grown in a greenhouse in sterilized clay pots (550-ml volume) containing Cornell artificial mix [sphagnum peat, horticultural vermiculite, ground limestone (dolomite) 0N-20superphosphate-0K, calcium nitrate, 18N-6P-12K Osmocote, 7N-40P-6K MagAmp, trace elements 555, and calcium sulfate (gypsum)]. They were also fertilized weekly (water-soluble 14N-28P-14K) and treated with 2-methyl-2-(methylthio) propanol O-[(methylamino) carbonyl] oxime (aldicarb, Temik) every 3 weeks for aphid and whitefly control. Populations grown between November and April received natural light supplemented with fluorescent light for 16 h daily. The greenhouse ranged from 25 to 30C, with a relative humidity of 40% to 60%.

Results and Discussion

Of 60 pea lines, 31 were susceptible and 29 were resistant to PWV-K. Plants of susceptible lines developed a light to moderate mosaic that consisted of chlorotic spots, veinal chlorosis, some plant stunting, and pod distortion. This group included 'Alaska', 'Alderman', 'Dwarf Gray Sugar', 'Dwarf Telephone', 'Early Sweet 11', 'Elf', 'Freezonian', 'Galaxie', 'Garfield', 'Giant Stride', 'Green Bay', 'Green Harrow', 'Late Alaska', 'Laurel', 'Lincoln', 'Mammoth Melting Sugar', 'Midget', 'Midfreezer', 'Miragreen', 'Nugget', 'Oregon Sugar Pod', 'Pixie', 'Progress No 9', 'Ranger', 'Rocket', 'Scout', 'Sprite', 'Tall Telephone', 'Thomas Laxton', 'World's Record', and PI 391630 (China). Resistant cultivars included 'Ace', 'Bonneville', 'Cascade', 'Dark Skin Perfection', 'Early Frosty', 'Eureka', 'Galaxie', 'Jade', 'Knight', 'Laxton Superb', 'Laxtonian', 'Little Marvel', 'Mar', 'Melody', 'Medalist', 'Midway', 'Perfected Freezer 60', 'Pride', 'Shoshon', 'Sparkle', 'Sugar Snap', 'Surprise', 'Target', 'Wando', PI 140295 (Iran), PI 174319 (Turkey), PI 174924 (India), PI 180669 (Germany), and PI 236493 (Sweden). These cultivars and PIs were classified as highly resistant, since no virus was recovered from the first three inoculated leaves and two apical leaves of plants that had reached the pod stage. All cultivars and PIs resistant or susceptible to PWV-K were also found to be resistant or susceptible to BYMV, except PI 391630 (BYMV resistant).

F₁ plants of ('Ranger' x 'Bonneville'), (PI 140295 x 'Ranger'), and (PI 391630 x 'Bonneville') were infected by PWV-K and exhibited symptoms identical to those affecting the susceptible parents (Table 1). The F₂ populations of the same crosses segregated in a ratio of 3 susceptible : 1 resistant, confirming the recessive nature of this resistance. Plants of backcross populations involving the resistant parents (PI 140295 x 'Ranger') x PI 140295, ('Ranger' x 'Bonneville') x 'Bonneville', and (PI 391630 x 'Bonneville') x 'Bonneville' segregated about in the ratio 1 resistant : 1 susceptible. Plants of the other

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Table 1. Inheritance of resistance in pea to an Australian strain of passionfruit woodiness potyvirus (PWV-K).

Parents and cross progeny	No. plants		Expected ratio (R : S)	χ^2	Goodness of fit (P)
	Resistant	Susceptible			
Bonneville ^z	74	0			
PI 391630 ^y	0	53			
PI 140295 ^z	60	0			
Ranger ^y	0	59			
Ranger x Bonneville					
F ₁	0	26			
F ₂	23	83	1:3	0.62	0.45
BC (F ₁ x Bonneville)	36	45	1:1	1.00	0.32
BC (F ₁ x Ranger)	0	55			
PI 140295 x Ranger					
F ₁	0	23			
F ₂	16	66	1:3	1.32	0.26
BC (F ₁ x PI 140295)	21	27	1:1	0.75	0.40
BC (F ₁ x Ranger)	0	63			
PI 391630 x Bonneville					
F ₁	0	15			
F ₂	24	83	1:3	0.374	0.55
BC (F ₁ x Bonneville)	29	34	1:1	0.397	0.54
BC (F ₁ x PI 391630)	0	71			

^zResistant.^ySusceptible.

backcross populations involving the susceptible parents (PI 140295 x 'Ranger') x 'Ranger', ('Ranger' x 'Bonneville') x 'Ranger', and (PI 391630 x 'Bonneville') x PI 391630 succumbed to infection. Hence, we conclude that the high level of resistance to PWV found in the two pea lines from the United States and Iran was conferred by a single recessive gene.

While pea lines resistant to BYMV were also resistant to PWV-K, PI 391630 was an exception and succumbed to PWV-K. Consequently, the *mo* gene known to confer resistance to BYMV and watermelon mosaic virus 2 (Schroeder and Provvidenti, 1971) was not involved in the resistance to PWV-K. 'Bonneville' and PI 140295 are also resistant to the NL-8 strain of BCMV, clover yellow vein virus, pea mosaic virus, and the lentil strain of pea seedborne mosaic virus (Provvidenti, 1987, 1990, 1991; Provvidenti and Alconero, 1988). The pertinent genes for resistance to these potyviruses *bcm*, *cyv-1*, *pmv*, and *sbm-2* are located on chromosome 2 (Provvidenti, 1987, 1990, 1991; Provvidenti and Alconero, 1988). If any one of these genes confers resistance to PWV-K, all the tests that could be performed may not provide conclusive evidence because the genes are closely linked. In host range, serology, and coat protein structure, PWV-K seems to differ from most of the other potyviruses listed above (Shukla et al., 1988; Taylor and Kimble, 1964;

Teakle and Wildermuth, 1967). Thus, we are tentatively assigning the symbol *pwv* (passionfruit woodiness virus) to this genetic factor to differentiate it from other viral resistance genes.

A literature search failed to reveal any reference regarding the natural occurrence in pea crops of any known strain of PWV or other potyviruses causing passionfruit woodiness. PWV-K and PWV-T cause symptoms that closely resemble those incited by other legume viruses; therefore, their presence in peas can be easily overlooked.

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