AN ABSTRACT OF THE THESIS OF

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Title: Genetic Relationships Between Pea Seedborne Mosaic Virus Resistance and Horticultural Characteristics, Powdery Mildew, Enation Mosaic Virus and Red Clover Vein Mosaic Virus Resistance in Pisum sativum L.

Abstract approved: /James R. Baggett

Because early stages of an Oregon State University (OSU) pea breeding program suggested there may be unfavorable linkages or associations which could hinder the development of Pea Seedborne Mosaic Virus (PSbMV)-resistant cultivars with acceptable horticultural characteristics, this study was made to determine if it was possible to incorporate PSbMV resistance into pea cultivars having desirable horticultural characteristics and resistance to Pea Enation Mosaic Virus (PEMV), Red Clover Vein Mosaic Virus (RCVMV) and powdery mildew (Erysiphe pisi Syd.).

OSU breeding lines with good horticultural characteristics and resistance to PEMV, RCVMV and powdery mildew were crossed with plant introduction lines having PSbMV resistance but several poor horticultural characteristics. 1376 F_3 families from these crosses were evaluated for resistance to PSbMV and powdery mildew in the greenhouse. Evaluations for resistance to PEMV and RCVMV,

plant habit, number of pods per node, flower color, flavor, seed type and the presence of edible pods were made in the field at the OSU Vegetable Research Farm at Corvallis.

Correlations and Chi Square tests indicated that no general relationships existed between PSbMV resistance and PEMV resistance, RCVMV resistance, plant habit or number of pods per node. There was a tendency for PSbMV resistance and smooth seeds to be associated. PSbMV resistance was generally negatively correlated with resistance to powdery mildew although results were inconsistent. An association between PSbMV resistance and the presence of edible pods existed in 1 of the 2 crosses segregating for the edible pod character, but further studies are necessary to determine if this association is general. Associations existed between PSbMV resistance, white flower color, and good flavor, and white flower color was highly correlated with good flavor. Previous findings that PSbMV resistance is conditioned by a single recessive gene were confirmed. Other secondary associations observed included general relationships between PEMV severity and RCVMV severity, and dwarf plant habit and the presence of edible pods.

It was concluded from the results obtained that there are no major hindrances to the development of pea cultivars having good horticultural characteristics and PSbMV resistance.

Genetic Relationships Between Pea Seedborne Mosaic Virus Resistance and Horticultural Characteristics, Powdery Mildew, Enation Mosaic Virus and Red Clover Vein Mosaic Virus Resistance in *Pisum sativum* L.

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INTRODUCTION

The pea seedborne mosaic virus (PSbMV) is an important problem of the pea (Pisum sativum L.) seed and processing industry in the United States, especially in the Pacific Northwest where most of North America's pea seed is produced. The main threat from PSbMV comes from its transmission through the seed, although transmission by aphids and mechanical means also occurs. The presence of this virus in North America forces breeders and seed companies to maintain constant vigilance and often the use of laboratory detection methods to insure freedom of seedstocks from seedborne infection. Movement of seedlots and exchange of breeding materials among breeders, seed companies, and countries is hindered.

Genetic resistance is the best control measure to remove the threat of seed stock contamination. Resistance to the virus, found in 16 plant introduction (P.I.) lines homogeneous for immunity (24), has been shown to be due to a single recessive gene, sbm (17).

This study was an attempt to determine the relationships between certain distinct genetic characteristics of the pea and resistance or susceptibility to PSbMV. Hybridization of PSbMV resistant and susceptible parents produced populations of lines

which differed in such characters as resistance to pea enation mosaic virus (PEMV), red clover vein mosaic virus (RCVMV), powdery mildew, plant height, flower color, number of pods per node, smooth or wrinkled seed, flavor, and lack of parchment (edible pod). The approach used was to describe these populations for horticultural characteristics, test them for resistance to PSbMV, PEMV, RCVMV and powdery mildew, and to establish correlations by statistical analysis.

LITERATURE REVIEW

Pea Seedborne Mosaic Virus

Description of PSbMV

PSbMV was first detected in Czechoslovakia in 1964 (49) and has been reported in Japan (36), the Netherlands (6), New Zealand (10), and Canada (20). The first observances in the United States occurred in Wisconsin and Washington in 1968 (22, 48, 65).

PSbMV has been referred to as pea leaf rolling virus (42), pea leaf rolling mosaic virus (50), and pea fizzletop virus (23). Isolates of this virus from Japan, the United States, Czechoslovakia and the Netherlands were compared by symptomatology in selected hosts, serology and modal particle length at six locations worldwide. Evidence was found that these isolates are variants of a single virus (31).

The virus has been transmitted to 47 plant species in 12 families (2) but is known to occur only naturally in peas. Its effects are most noticeable in midseason Perfection types (48). The intensity of symptoms may vary among cultivars and plants infected in the field often develop transitory symptoms or may fail to express symptoms under certain growing conditions (32). Levels of seed transmission may vary from 0 to 90% depending on the cultivar (48, 68). Severely infected plants may suffer partial or complete loss of yield.

A member of the Potato Virus Y group, PSbMV is a single-stranded virus containing RNA and having flexuous, rod-shaped particles, approximately 770 nm x 12 nm in size. The virus produces pinwheel inclusions in leaf cells, but rarely in root cells. When initially prepared, juice from the pea leaf or root tissue is highly infective. Juice from infected pea root tissue remains infectious for 96 hours while juice from the leaf tissue must be diluted to 10^{-1} or 10^{-2} to remain infectious for this length of time. This suggests the presence of an inactivating substance or inhibitor in the pea leaf tissue (40). The dilution end point is between 10^{-3} and 10^{-4}. Only traces of infectivity remain after 10 minutes at $55^{o}C$, and infectivity is lost on freezing. The virus has a sedimentation coefficient of 154 S and a buoyant density in CsCl of 1.329 g/cm^3 (30).

PSbMV can be readily purified from pea root tissue, but a strong tendency to aggregate makes purification from pea leaf tissue more difficult (40). Procedures for purification are available (21,38,40,68).

Symptoms in pea seedlings from infected seed are most commonly mild to severe downward leaf roll and/or vein protrusion, and stunting. Other seedling symptoms can include brittleness of upper stems, leaves more cartilaginous than normal, shortened internodes, slightly abnormal curl of one or more leaves, and plants which are more erect and rigid than normal (23).

Mechanically inoculated seedlings show transient vein clearing 5 to 6 days after inoculation. Two weeks after inoculation, a permanent chlorotic mottle develops on young leaves. Mild leaf distortion, shortening of internodes, rosetting, and tight curling of tendrils appear by 3 weeks after inoculation (48).

Symptoms on field-infected, mid-season pea cultivars include a progressive shortening of the internodes which results in terminal rosettes on the main stem and side branches, smaller dark green leaves and stipules, slightly thickened and tightly curled tendrils, and development of a few distorted flowers which may produce pods (48). The small pods show surface irregularities and have blank ovules or uneven ovule development. A prolonged flowering and vegetative condition exists in PSbMV-infected plants, and these plants are more resistant to frost damage than healthy plants (27).

Symptoms can range from slight leaf rolling and/or vein clearing to rapid whole-plant necrosis 5 to 9 days after inoculation. This range of responses to PSbMV appears to result from modification of susceptibility or sensitivity by genetic and/or environmental means. Whole plant necrosis is presumably caused by the action of modifier genes which decrease a plant's tolerance to the virus, while infection without symptoms is presumably caused by modifiers which increase a plant's tolerance. Tolerance or resistance to PSbMV might be mistaken for immunity, in which case the pathogen would not multiply in the host beyond the point of

inoculation. Immunity is qualitative, while the varying degrees of resistance or tolerance are quantitative. The difference between resistant and immune plants is the presence or absence, respectively, of systemic infection (25).

Cultivars display varying degrees of susceptibility to PSbMV, with symptoms being the most pronounced in mid-season Perfection types (27). The later maturing, more determinate cultivars are more severely affected than earlier maturing, indeterminate cultivars such as Small Sieve Alaska (41).

Chiko and Zimmer (7) found that growth stage at the time of inoculation did not significantly affect seed yields or levels of virus transmission through seed of either cultivar studied. Average yields of plots inoculated at each of 3 stages of growth were reduced 8% and 10% in 'Trapper' and 'Century' respectively. However, Kraft and Hampton (41) found that losses in green pea and seed yields were greater in all cultivars when inoculation was 2 weeks compared to 3 weeks after emergence.

Lower temperatures may account for a decrease in both PSbMV symptoms and yield losses. Mink et al. (48) found that few inoculated plants developed symptoms when grown in an 18°C greenhouse than when grown in a 29°C growth chamber. Kraft and Hampton (41) observed fewer plants with visible symptoms and reduced yields in the cooler growing season of 1978 than in 1977. However, they did not determine whether the inoculum was equally infectious in both years.

Stevenson and Rand (69) found that symptom progression was accelerated at higher temperatures, but final severity of symptoms was not significantly affected by temperature. In their study, Alaska and Dark Skin Perfection cultivars were inoculated 14 days after planting, then moved to 16°C, 20°C, 24°C and 28°C locations in the greenhouse. Vein clearing reached maximum severity 3 days after inoculation at 28°C, 4 days at 24°C and 5 days at 20°C and 16°C. Apical malformation, the final symptom, was apparent at all temperatures within 4 weeks after inoculation, but occurred first at higher temperatures.

Seed Transmission

Seed transmission of PSbMV has been reported as high as 90% (48). Studies have been done to determine if time of inoculation, length of seed storage, differences in cultivars, seed size and seed condition affect the rate of seed transmission. Stevenson and Hagedorn (66) studied correlations between transmission of PSbMV and seed size and seed coat condition in Perfection types. They found no significant differences in percent seed transmission between seeds sized 12/64 through 19/64. All seed size groups contained a similar percentage of seed capable of transmitting the virus. They found a significant difference between seeds with intact seed coats which transmitted PSbMV at 4%, and seeds with growth cracks which transmitted the virus at 33%. Seeds with

cracked seed coats had a mean germination percentage of 91%, while that of seeds with intact seed coats was 97%.

In a later study over a 1-year period, Stevenson and Hagedorn (68) found that, during the first year, seed transmission was limited primarily to the small seeds and seeds with growth cracked seed coats. In the second year, seed transmission was restricted to abnormally shaped seeds and small seeds. Seed transmission was generally not associated with seeds of normal size and shape.

Kraft and Hampton (41) found no obvious correlation between seed size, shape or condition and seed transmission of PSbMV. Seed infected with PSbMV was found in all sizes from 4.4 to 6.4 mm, in cracked and non-cracked seed, and in shrunken and normal seed of all 6 cultivars tested.

When testing 1835 P.I. lines, Hampton and Braverman (28) found that many seeds with split or stained seed coats produced healthy plants and many normal seeds produced infected seedlings, and that these features were not correlated with seed transmission of PSbMV.

Stevenson and Hagedorn (68) found that high percentages (> 15%) of seed transmission were generally restricted to the early maturing Alaska and Alsweet types, rather than Perfection types. Five of the 38 tested cultivars (Alaska 14A, Eureka, Bridger, Valley Perfection, and Freezer 63240) showed no seed transmission although all exhibited typical PSbMV symptoms. Cultivars differed in the type of seed which showed the highest

rate of seed transmission. Seed transmission of PSbMV in 'Star', and Alaska type, was restricted to small sized seed, while transmission in 'Cascade', a Perfection type, was restricted to seeds with growth-cracked seed coats. This study also showed that the time of inoculation did not influence the seed transmission rate in 'Dark Skin Perfection'.

Knesek and Mink (39) reported that PSbMV could be recovered from dry seed stored for longer than 1 year.

Distribution of PSbMV in the pea seed and inflorescence has been studied (68). PSbMV has been associated with the embryo, endosperm and testa of immature seeds, and in the embryo and cotyledons of mature seeds with growth-cracked seed coats. The virus has been isolated from sepals, petals, carpels, filaments and pollen of the inflorescence. To determine if pollen transmission of PSbMV occurs, crosses were made between two susceptible cultivars, using 'Dark Skin Perfection' as the female, and 'Alaska' as the male. Seedlings were mechanically inoculated with the virus 3 weeks after planting. Seedlings from crosses between infected females and healthy males had 5.83% seed transmission. (The selfed, infected female 'Dark Skin Perfection' gave rise to seedlings with 6.01% seed transmission.) Seed transmission of 0.85% PSbMV was found in seedlings from the cross between healthy females and infected males. There was no evidence of infection of the female parent plant resulting from pollination with pollen from an infected plant. It was not determined if infection of the

ovule or infection of the developing embryo was the primary source of PSbMV from the infected female parent.

Vectors

At least 9 aphid species can transmit PSbMV in a non-persistent manner (30). Principal vectors include *Acyrthosiphon pisum* Harris, the pea aphid; *Myzus persicae* Sulzer, the green peach aphid; *Macrosiphum euphorbiae* Thomas, the potato aphid; and *Rhopalosiphum padi* L., the birdcherry oat aphid (1). The other species include *Dactynotus escalantii* Knowlton, *Macrosiphum rosae* L., *Ovatus crataegarius* Walker, *Aphis craccivora* Koch., and *Aphis fabae* Scopoli (30). The pea, green peach and potato aphids transmit PSbMV in a typical stylet-borne manner; i.e., after single probe acquisitions and with very short retention periods (11).

More detailed discussions on vectors of PSbMV can be found in Gonzales and Hagedorn (11), Aapola and Mink (2), and Kvicala and Musil (42).

Hosts

Initially it was found that PSbMV had a limited host range compared to other legume viruses. *Pisum sativum*, *Lathyrus odoratus* L., *Medicago hispida* Gaertn., 4 species of *Vicia* and a few *Phaseolus vulgaris* L. cultivars were the only legume species reported as hosts (36, 48, 65).

Aapola et al.(1) found that, depending on inoculation procedure, 47 plant species in 12 families became infected with PSbMV. They tested 121 species in 21 families using both rub inoculation with crude juice from infected pea leaf tissue and two species of aphids, Acyrthosiphon pisum and Myzus persicae. Susceptibility to PSbMV was divided into 3 groups: highly susceptible species; marginally susceptible species in which only 1 or 2 plants were infected regardless of inoculation method; and species whose apparent susceptibility was dependent upon inoculation technique. Highly susceptible species included Pisum sativum, 20 species of Vicia, Lens culinaris Medic., Lathyrus odoratus and Chenopodium foetida. Infected plants exhibited prominent symptoms which ranged from stunting and leaf rolling to chlorotic leaf mottle. Marginally susceptible species included Vinca rosea L., Gomphrena globosa L., Beta vulgaris L., Beta vulgaris L. var. cicla, Chenopodium Botrys L. and possible Tetragonia expansa Murr. although it ws not infected by M. persicae. Capsella bursa-pastoris (L.) Medic. was infected using viruliferous green peach aphids. All of the infected plants in this category remained symptomless.

In addition to these susceptible species, Mink et al (48) found that Chenopodium amaranticolor Coste and Reyn., C. capitatum (L.) Asch. and C. quinoa Wild. developed chlorotic or necrotic mottling of inoculated leaves without systemic symptoms.

The winter annual habit of hairy vetch, Vicia villosa Roth, makes it an ideal overwintering host for PSbMV. Under experi-

mental conditions in Wisconsin, Stevenson and Hagedorn (68) found that both peas and hairy vetch serve as reservoirs for aphid vectors, PSbMV overwintered effectively in seedlings of hairy vetch, and that PSbMV is not seedborne in vetch. However, Musil (51) found that seed transmission occurred in 1 cultivar of vetch. In addition to PSbMV, Stevenson and Hagedorn found PEMV, RCVMV and pea streak virus in the vetch seedlings.

Strains of PSbMV

In addition to the standard U.S. strain of PSbMV, several other strains have been reported. PSbMV-L, the lentil strain, is distinguished by its nonpathogenicity to most pea cultivars, by pathogenicity to lentil, Lens culinaris germ plasm sources independently of PSbMV-immunity-conferring gene sbv, by an inoculum reservoir restricted to infected lentil seed, by comparative enzyme-linked immunosorbent assay (ELISA), and by intrinsic particle instability. Hosts of PSbMV-L other than lentil include 'Tempter' pea, Vicia faba var. minor and Chenopodium amaranticolor. PSbMV-L is readily transmitted by the pea aphid (26).

PSbMV was first detected in New Zealand in 1978 by Fry and Young (10). The strain most frequently isolated in New Zealand differs from many of the other strains in being unable to infect pea cultivars homozygous for mo, a recessive gene which confers resistance to the pea strain of bean yellow mosaic virus (BYMV) (54).

The Washington strain of PSbMV is aberrant in terms of aphid transmission, and in its ability to infect Chenopodium amaranticolor in that fewer local lesions are produced and they take longer to develop than with the standard U.S. strain (R.O. Hampton, personal communication).

The "Yugoslavian strain" of PSbMV, first reported in 1978 (47) has been tested and shown to be the same as the standard U.S. strain (R.O. Hampton, personal communication).

Inheritance of Resistance to PSbMV

Hagedorn and Gritton (17) determined the inheritance of resistance to PSbMV in P.I. Lines 193586 and 193835 by crossing them with 8 susceptible commercial cultivars. All F_1 plants were susceptible to PSbMV, while the F_2 plants segregated 3 susceptible : 1 resistant. Backcrosses of the F_1 to the resistant parent segregated 1 susceptible : 1 resistant. These results indicate that resistance results from the homozygous condition of a single recessive gene pair, designated sbm. These results were confirmed by Hampton and Marx (29).

Sources of resistance to PSbMV include numerous P.I. lines obtained mainly from northern India and Peru (28). P.I. 193586, a tall, indeterminate, late-maturing pea found resistant to PSbMV, was obtained from Ethiopia (4). P.I. 193586 was tested many times by several researchers and was originally found to be a homogeneous line resistant to PSbMV (67,3). Current studies have

shown that P.I. 193586 consists of a mixture of 80% resistant and 20% susceptible plants (31). Hagedorn and Gritton (17) reported that occasional susceptible plants have been observed in both P.I. 193586 and P.I. 193835.

Two PSbMV-resistant breeding lines, one a canning pea and the other a freezing type, were released in 1971 by Gritton and Hagedorn of the University of Wisconsin. In 1977, PSbMV resistant breeding lines B442-15 and B445-66, were released by Baggett and Hampton (4) of Oregon State University. These lines, also resistant to PEMV, are medium height, double-podded freezing type peas. Recently, 10 additional breeding lines resistant to both PSbMV and PEMV were released by Baggett (personal communication). These lines have varying degrees of resistance to powdery mildew, and some have the edible pod character. Most are mid-season Perfection type freezer peas with good commercial qualities.

Pea Enation Mosaic Virus

Pea Enation Mosaic Virus (PEMV), formerly known as Pea Virus I (53), is an important virus disease in the United States, especially in certain Northwest pea growing areas. The disease has also been reported in Czechoslovakia, West Germany, the Netherlands, Switzerland and England (16).

Symptoms of infected seedlings include pronounced vein clearing in the youngest leaflets and stipules, retardation of terminal

growth buds and foliage surrounding the buds becoming distorted, turned downward or twisted to one side. Low temperatures (12°-14°C) tend to lessen the severity of disease symptoms, especially terminal bud distortion (70). Older plants show a reduction in size, wrinkled leaves, numerous chlorotic to translucent spots and pod malformation. Blisterlike ridges called "enations" may develop on the undersides of leaves, stipules and pods. A California PEMV isolate produces giant stem enations (58).

PEMV is mainly transmitted in a circulative manner by the aphids Acyrthosiphon pisum and Macrosiphum solanifolii Aschmead (53). Other aphid vectors include Cerosipha gossypii (Glover), A. solani Kalt. and Myzus ornatus Laing (16).

Some isolates of PEMV are not as easily and consistently transmitted mechanically as are others (16). The virus is not known to be seedborne (62).

In addition to Pisum sativum, major hosts of PEMV include the field pea, P. sativum L. var. arvense (Poir.); alfalfa, Medicago sativa L.; and subclover, Trifolium subterraneum L. Other species which can be infected include lentil, Lens culinaris; bean, Phaseolus vulgaris; 5 species of Trifolium; 5 species of Vicia; 5 species of Lathyrus; 3 species of Lupinus; 2 species of Medicago; 2 species of Melilotus; soybean, Glycine max L.; chick-pea, Cicer arietinum L.; milk vetch, Astragalus rubyi Gr.-Morr. (46); Anthyllis vulneraria L.; Lotus tetragonolobolus L; button medic,

Medicago orbicularis All.; Melilotus indica; and Nicotiana clevelandii Gray (18).

Resistance to PEMV is conditioned by a single dominant gene, En, located on chromosome 3 (14). This gene gives the plant the ability to grow and reproduce normally even though it may be systemically infected with PEMV. All U.S. pea breeding lines resistant to PEMV descended from G 168, a selection from P.I. 140295 (61).

Red Clover Vein Mosaic Virus

RCVMV, also known as Wisconsin Pea Stunt Virus (19) and Pea Stunt Virus (16), causes vein clearing 12 to 14 days after inoculation, rosetting of terminal foliage, profuse axillary bud growth, chlorosis of middle and lower leaves, and a streaking or necrosis along the stems. Severe stunting from reduced internode length causes infected plants to reach only 25-50% of their normal height. Any pods which form are usually poorly filled (16,52).

The virus is transmitted mechanically and by several species of aphids in the non-persistent manner. Vectors include Acyrthosiphon pisum, Therioaphis ononidis (Kalt.), Myzus persicae, Cavariella aegopodii Scopoli, C. theobaldi Gillette and Bragg (72), and Myzocallis ononidis Kalt. (12).

RCVMV is not known to be seedborne in Pisum sativum, but has been found to be seedborne in red clover, Trifolium pratense L. (72), and broad bean, Vicia faba L. (59). Hosts include P.

sativum, P. sativum var. arvense, Trifolium pratense, T. dubium Sibth., T. hybridum L., T. repens L., T. repens latum McC., T. incarnatum L., Vicia faba, V. sativa L., Melilotus alba Desv. (72), M. officinalis Lam., Medicago lupulina L. (12), and Lathyrus odoratus (37).

The inheritance of resistance to RCVMV has not been determined, but is assumed to be multigenic. P.I. 193845, 203066, 212029 and 261677 are sources of resistance (9).

Powdery Mildew

Worldwide in distribution, powdery mildew in peas is caused by the fungus Erysiphe pisi Syd. (syn. E. polygoni DC.) The disease adversely affects total plant weight, plant height, weight of shelled peas, number of peas per pod, number of nodes per plant, pod and shelled pea appearance, and raises tenderometer readings which lowers the quality of the crop. Usually, late-sown crops are the most liable to infection, as the fungus thrives during prolonged warm, dry daytime conditions and when the nights are cool enough for dew formation (63).

Small grayish-white, felt-like patches of mycelium appear first on lower leaves, then enlarge and cover entire leaves with a powdery coating of spores or conidia, which are disseminated to other plants by air currents. Petioles, stems and pods may also be infected. The pea vines become dwarfed, leaves are yellowed, malformed and become dry and brittle. Severe infection can cause

death. Infected pods become spotted or streaked and the fungus may penetrate to the seeds which often become grayish brown (8). Crawford (8), Van Hook (71), and Stevens (64) found that the disease may be transmitted by infected seed.

Harland (33) and Pierce (55) found that resistance is conferred by a single recessive gene. Other researchers (57,35,60) have confirmed their results. The gene, er, is located on chromosome 3 (44). Sources of resistance of powdery mildew are OSU 42, Geneva 59-29, P.I. 142775, 142777, 180792, 201497, 203064, 'Strategem' (63), P.I. 222069 and 244155 (9).

Horticultural Characteristics

Edible Pod

Edible pod or "sugar peas" lack the fibrous, indigestible inner parchment of the pod at all stages of growth. The endocarp is reduced or absent, and the mesocarp becomes thickened, fleshy and juicy, giving a body to the pod which is different from the thin shell-like structure of the pods of other peas. The pods are usually wider and flatter than those of other peas, and are constricted between the seeds (34).

Mendel, Tschermak and Lock (74) all found edible pod to be conditioned by a single recessive gene. Hampton and Marx (29) state that the gene for edible pod, p, located on chromosome 6, is linked with wlo (waxlessness of leaves) and sbm, resistance to PSbMV.

White (75) determined that 2 pairs of genes, P-p and V-v, control the edible pod character. Lamprecht demonstrated that V is located on chromosome 4 (56). A continuous parchment layer or patches of parchment are conditioned by the gene P in the absence of V, while only strips of parchment at the sutures of the pod wall are determined by V in the absence of P. Complete absence of parchment is found in plants with the genotype ppvv. Crossing the non-parchmented genotypes PPvv and ppVV yields all parchmented F_1 plants, and 9 parchmented : 7 non-parchmented in the F_2 generation.

Number of Flowers per Inflorescence

Lamprecht (43) found that 2 genes, Fn and Fna, located on chromosomes 2 and 4 respectively (56), are involved in producing the number of flowers per inflorescence. Low flower number is dominant, with Fn Fna producing a single flower, Fn fna or fn Fna causing 2 flowers to develop and fn fna responsible for 3 or more flowers.

Lamprecht (43) found that environmental conditions favoring vigorous growth may cause an Fn Fna plant to produce some 2 flowered peduncles, while poor growing conditions have the reverse effect, but do not reduce the higher numbers to 2.

Flower Color

Tschermak (76) was the first to propose that a basic color gene, A, is necessary for flower color. A alone gives only faint color, and a large number of genes affecting color in various parts of the plant depend on A for their expression. Am, also referred to as Aw by Wellensiek (73), with A gives the purple flower color (15). Wellensiek (73) found that A is the basic gene for leaf axil color, which is not affected by Aw. Both A and Am are located on chromosome 1 (56). B, located on chromosome 3, also gives purple flower color (76). Cr and Ce, both on chromosome 5, condition crimson and cerise colored flowers respectively. Cv is a modifying gene which strengthens flower color (73).

Plant Habit

Height in peas, although affected by environment, is determined primarily by 2 genes. T, located on chromosome 4, conditions plants with a large number of internodes and thick stems. Le, also on chromosome 4, is responsible for long internodes, while le is characteristic of plants having short internodes and zigzag stem growth (37). Tall plants (T_Le_), which are dominant over dwarf, have 20-60 long internodes, and range from 150 to 360 cm in height. Half-dwarfs (T_lele and ttLe__) have 20-40 short internodes or 8-20 long internodes respectively, and range in height from 60-150 cm. Dwarf plants (ttlele) are typically 20-60 cm in height and have 8-20 short internodes. Classification of

all segregates with long internodes, regardless of the number, as tall, and all those with short internodes as dwarf, gives 3:1 tall:dwarf, which is the ratio Mendel found in his study of height in peas (75).

Two additional genes for internode length are coe (20-32 mm) and cot (33-64 mm). Four additional genes, mie, mier, mine and miu are responsible for decreasing the number of internodes (56).

Seed Type

Round, smooth seeds are dominant to wrinkled, angular seeds. This single gene, R, is located on chromosome 7. Round seeds have simple starch grains, while those of wrinkled seeds are usually compound, although simple starch grains can occur in the presence of rb, which is found on chromosome 3 (56).

Dimpled seeds are characterized by shallow, wide depressions on the seed surface, distinctly separate by smooth areas, as opposed to the small, deep pits which occur on round seeds as a result of soil, location and/or moisture factors (34). Dimpled seed is due to di, which is hypostatic to r, therefore being observable only on R or round seeds. It is also hypostatic to A and so requires a (absence of anthocyanin pigment) for expression (56).

Indent seeds have normally 2 large, deep impressions, 1 over the radicle and the other opposite. This is a pericarp character and therefore is determined by the genotype of the maternal plant.

Indent is dominant to round, smooth seed and is characterized by L, found on chromosome 3. The genes a and z (basic gene for part-colored seed coat) inhibit the effect of L (56).

MATERIALS AND METHODS

Parent Materials

The crosses used as sources of pea lines tested in this study were as follows:

Code	Identification Symbol	Parentage	Year
11	B 508	S 582 x 442-15	1977
11-R	B 508R	442-15 x S 582	1977
13	B 544	B 504-5 x S 434	1979
13-R	B 544R	S 434 x B 504-5	1979
15	B 546	B 504-5 x S 605	1979
15-R	B 546R	B 605 x B 504-5	1979
17	B 549	B 504-18 x M 187	1979
17-R	B 549R	M 187 x B 504-18	1979
19	B 550	B 504-18 x M 190	1979
20	B 580	B 505-16 x S 605	1979
20-R	B 580R	S 605 x B 505-16	1979
22	B 599	S 434 x B 506-24	1979
22-R	B 599R	B 506-24 x S 434	1979
1	C-1	S 604 x P.I. 193586	1980
1-R	C-1R	P.I. 193586 x S 604	1980
3	C-3	S 582 x P.I. 193586	1980
3-R	C-3R	P.I. 193586 x S 582	1980

(continued next page)

Code	Identification Symbol	Parentage	Year
5	C-5	S 523 x P.I. 193586	1980
5-R	C-5R	P.I. 193586 x S 523	1980
7	C-7	S 441 x P.I. 193586	1980
7-R	C-7R	P.I. 193586 x S 441	1980
9	C-9	M 183 x P.I. 193586	1980
9-R	C-9R	P.I. 193586 x M 183	1980

All parents except P.I. 193586 are white-flowered lines of dwarf habit developed at the Oregon State University Vegetable Research Farm, Corvallis, Oregon. P.I. 193586, the tall PSbMV-resistant line segregating for white and purple flowers, was obtained from the Plant Introduction collection of Pisum at Geneva, N.Y.

Table 1. Disease resistance[z] and horticultural characteristics[y] of parent pea lines.

Line	Disease[z]				Horticultural Characteristic[y]		
	PSbMV	Powdery Mildew	PEMV	RCVMV	Use Type	Seed Type	Pods per Node
M 183	S	R	R	R	Can	Wr	3
M 187	S	R	R	R	Fr	Wr	2
M 190	S	R	R	R	Fr	Wr	2
S 434	S	R	R	R	Fr	Wr	2
S 441	S	R	R	R	Fr	Wr	2
S 523	S	S	R	R	Fr	Wr	2

Table 1 (continued)

Line	Disease[z]				Characteristic[y]		
	PSbMV	Powdery Mildew	PEMV	RCVMV	Use Type	Seed Type	Pods per Node
S 582	S	R	R	R	Ed	Dimp	2
S 604	S	R	R	R	Fr	Wr	2-3
S 605	S	R	R	R	Fr	Wr	2
442-15	R	S	R	R	Fr	Wr	2
B 504-5	R	S	R	R	Fr	Wr	2
B 504-18	R	R	R	R	Fr	Wr	2
B 505-16	R	S	R	R	Fr	Wr	2
B 506-24	R	S	R	R	Fr	Wr	2
P.I. 193586	R	S	S	S	None	Sm	1

[z] PSbMV = Pea Seedborne Mosaic Virus
PEMV = Pea Enation Mosaic Virus
RCVMV = Red Clover Vein Mosaic Virus. The parental lines other than P.I. 193586 exhibited varying degrees of resistance to RCVMV, from no visible infection to mild infection when observed in the field.

[y] R = resistant S = susceptible
Fr = freezer Can = canner Ed = edible pod
Wr = wrinkled Sm = smooth Dimp = dimpled

General Methods of Plant Culture

Plants were grown in the greenhouse during the Fall, Winter and early Spring, and in the field at the Oregon State University Vegetable Research Farm during the late Spring and summer months.

Greenhouse plants were grown in 15-cm diameter cans on benches. The soil mix consisted of 22% sandy loam, 22% fine peat,

22% mason sand and 34% crushed pumice. A complete commercial fertilizer was incorporated after steam sterilization of the soil. To insure uniform germination, the top of the soil was smoothly packed and the seeds were covered with measured quantities of mason sand. Day temperatures were maintained at 65°-70°F and night temperatures fluctuated from 50°-60°F.

Field plantings were made in May and June in Chehalis silty clay loam. The field received preplant fertilizer banded at the rate of 600 kg/hectare of 8.0 N - 10.3 P - 6.6 K. Sprinkler irrigation was applied as necessary for optimum growth. No insecticides were used to control aphids. Seeds were planted with a belt-type hand planter, spaced 5-8 cm apart in rows 0.9 m apart.

Hybridization between pea lines was accomplished by means of standard hand emasculation and pollination methods. All crosses were made in the greenhouse.

Chronological History of the Development and Testing of Genetic Populations

Winter 1979-1980. The initial crosses and reciprocal crosses were made between P.I. 193586 and OSU 183, 441, 523, 582 and 604.

Spring 1980. F_1 seed was grown in the greenhouse to insure a supply of F_2 seed in case of crop failure in the field.

Summer 1980. F_1 seed was grown in the field. F_2 seed was harvested separately from all plants of each of the C 1 - C 9-R crosses. Seed was also harvested separately from single F_2 plants

of the B 508-B 599 crosses, which originated at OSU in 1977 and 1979 in the PSbMV-resistant breeding program. In the C 1 - C 9-R crosses, the number of single plant selections harvested varied from 28 to 122 per cross, with a mean of 75.2, for a total of 752. In the B 508-599 lines, the number of single plant selections harvested per cross varied from 40 to 51, with a mean of 48, for a total of 624. Plant losses occurred from powdery mildew, Fusarium root rot, and birds.

Fall 1980 to Spring 1981. 26 seeds of P.I. 193586 were planted in the greenhouse to test for their susceptibility to PSbMV, PEMV, RCVMV and powdery mildew. A separate identity was maintained for each plant grown. Enzyme-linked Immunosorbent Assay (ELISA) was the serological test used to confirm the identify and presence of the viruses.

Tests for resistance to PSbMV and powdery mildew were begun on the single plant selections harvested from the field and on all parents. Seed type of each selection was noted. Each family consisted of 6-11 plants per can. All but 1 plant per can were rub-inoculated at the 3-leaf stage. Initial symptoms occurred 1 week after inoculation, and disease classifications were made after 3 weeks.

Powdery mildew resistance was also noted at this time. No inoculations were necessary, as the fungus was already present in the greenhouse.

Summer 1981. F_2 seeds harvested from the single plant selections of crosses C1-C9R during the summer of 1980 were planted at the

OSU Vegetable Research Farm. Plantings were made June 23 - June 26. A total of 752 F_3 families from C1-C9R were grown in addition to the 624 4-meter plots of the lines from crosses B 508-599. Observations were made of the individual plots regarding resistance to PEMV, RCVMV, powdery mildew, pods per node, flower color, tall or dwarf stature, flavor and presence of edible pod.

Fall and Winter 1981. PSbMV and powdery mildew resistance tests were continued in the greenhouse on the F_3 families not tested the previous winter. Retests were made when classifications were questionable.

General Inoculation Methods

The inoculum used for testing was prepared from young infected pea leaves thoroughly macerated by means of a mortar and pestle. During the grinding of the leaves, sufficient 0.02 M Na_2HPO_4 buffer, pH 7.0, was added to dilute the plant extract to 10^{-1}.

Plants were inoculated at the 3-leaf stage. Before inoculation, each leaf was dusted with 400-mesh silicon carbide powder. The diluted sap extract was gently rubbed over the leaf surface with gloved fingers. Control plants were inoculated in the same manner, using only the buffer solution. Plants were washed with water following inoculation.

Sources of Virus Cultures

The PSbMV inoculum, isolate #25, was originally supplied in the form of infected seeds from A. Slinkard, University of Saskatoon, Saskatoon, Saskatchewan, Canada. The inoculum was then maintained in the greenhouse at OSU by repeated transfers from infected to healthy plants of pea lines OSU 441, 183 and 604.

Inoculum of PEMV-3, a mechanically transmitted isolate, was obtained for greenhouse PEMV tests from D.J. Hagedorn, University of Wisconsin.

The RCVMV inoculum, ATCC-PV-110, was obtained from the American Type Culture Collection in Rockville, Maryland.

PEMV and RCVMV cultures were maintained in the greenhouse by repeated transfers from infected to healthy susceptible 'Little Marvel' plants. PEMV and RCVMV are transmitted from natural reservoirs by species of aphids when peas are grown at the OSU Vegetable Research Farm. No mechanical inoculations are necessary for field infection.

Disease Classification

Pea Seedborne Mosaic Virus

A system for rating disease severity was established to evaluate the degree of PSbMV infection in the greenhouse. A resistant pea plant, cultivar, or line, is defined as one in which no systemic symptoms are produced when rub-inoculation is

employed. Localized necrosis may occur on the inoculated leaves only.

Disease Score	Degree of Infection
1	No infection, plants resistant.
2	Mild infection; slight downward rolling of leaf margins and vein swelling, slightly shortened internodes.
3	Moderate infection; marked downward leaf margin rolling and vein clearing, shortened internodes, plants somewhat stunted.
4	Moderate-severe infection; marked downward leaf margin rolling and vein clearing, leaf shape deformed, leaf size reduced, plants moderately stunted.
5	Severe infection; extreme downward rolling of leaf margins, vein clearing, leaf shape deformed, leaf size greatly reduced, plants severely stunted.

Pea Enation Mosaic Virus

The system for rating disease severity for PEMV was similar to that for PSbMV. Classifications were made in the field.

Disease Score	Degree of Infection
1	No infection, resistant.
2	Trace, latent, no damage.
3	Mild infection, presence of enations on pods.
4	Moderate infection, presence of enations on leaves and pods, some mottling and chlorotic (sometimes necrotic) flecking of newly unfolded leaves, some twisting and distortion of apical growth.

5	Severe infection, presence of enations on leaves and pods, pronounced mottling and flecking of leaves, much twisting and distortion of apical growth.

Red Clover Vein Mosaic Virus

The classification system for RCVMV as noted in the field is as follows:

Disease Score	Degree of Infection
1	No apparent infection.
2	Trace, latent, no damage.
3	Mild infection, slight vein chlorosis.
4	Moderate infection, vein chlorosis, curling of young leaves, plants stunted.
5	Severe infection, pronounced vein chlorosis and curling of young leaves, plants severely stunted.

Powdery Mildew

Disease scores were made in the greenhouse for powdery mildew according to the following classifications:

Disease Score	Degree of Infection
1	Considered resistant, mycelium and spores present on leaves only, no other symptoms.
2	Family segregating resistant and susceptible.
3	Family susceptible, mycelium and spores present on leaves and stems, affected areas often die, pods often develop

small brown to black necrotic spots, plant dwarfed if infected early.

Classification of Lines for Horticultural Characteristics

Flower Color. Two flower colors were observed and were assigned numbers as follows: white = 1, segregating white and purple = 2, purple = 3.

Growth Habit. Dwarf stature plants were designated by 1, combination of dwarf and tall or wild type by 2, and tall by 3.

Seed Type. Wrinkled seeds were designated as 1, dimpled seeds as 2, and smooth as 3.

Flavor. Peas with above average flavor were designated by 1, average flavor by 2, strong or undesirable flavor by 3, and astringent, unacceptable flavor by 4.

Pods Per Node. Single pods per node and single-double segregating were designated as 1, double pods and double-triple segregating were designated as 2, and triple pods and single-double-triple segregating designated as 3.

Edible Pod. Families having edible pods were designated as 1, segregating edible-non-edible as 2, and non-edible pod as 3.

Data Analysis

Relationships were evaluated by contingency table Chi Square tests and correlation coefficients. Values obtained were tested for significance at 4 decimal places but were rounded off to 2 significant figures for table presentation.

Some of the populations were biased by selection for horticultural characteristics such as plant habit and seed type, therefore Mendelian ratios were not attempted. Chi Square tests for goodness of fit showed that the expected 1:2:1 (susceptible:segregating:resistant) ratio was observed in almost all crosses tested for PSbMV resistance regardless of the altered ratios for some of the horticultural characteristics.

RESULTS AND DISCUSSION

Chi Square Tests for Goodness of Fit for Individual Characters

Twenty-one of the 23 crosses segregated for PSbMV resistance as expected (Table 2). When the 3 susceptible + segregating : 1 resistant classification was used (Table 3), only 1 cross deviated slightly from the expected ratio. When tested against a 1 susceptible : 2 segregating : 1 resistant ratio, 2 crosses gave Chi Square values higher than expected (Table 2). These results indicate that accurate scorings were made for PSbMV resistance, and that resistance is conferred by a single recessive gene as was determined by Hagedorn and Gritton (17) and confirmed by Hampton and Marx (29).

Schroeder and Barton (61) determined that resistance to PEMV is conditioned by a single dominant gene. Therefore, F_3 families from resistant x susceptible parents should segregate 1 resistant : 2 segregating : 1 susceptible. Using this classification, Chi Square values were significant at .01 probability for 9 of the 10 crosses segregating for PEMV resistance (Table 4). Seven of the 10 crosses had Chi Square values significant at .01 probability when a 3 resistant + segregating : 1 susceptible classification was used (Table 5). For most of the crosses, there was a lack of susceptible families. This indicates that misclassification for PEMV resistance may have occurred due to the presence of RCVMV symptoms in the same plants. A more likely explanation is that

many of the families escaped infection. Because of the late planting date, the potential for virus infection in the field was declining. Although the susceptible check varieties showed 100% infection, some of the families from resistant x susceptible parents may have tended to escape infection even though they were genetically susceptible, possibly because of modifying factors.

Resistance to powdery mildew is conferred by a single recessive gene, as was determined by Harland (32) and Pierce (55). F_3 families from resistant x susceptible parents should segregate 1 resistant : 2 segregating : 1 susceptible. Significant Chi Square values were obtained for 14 of the 21 crosses segregating for powdery mildew resistance when the 1 resistant : 2 segregating : 1 susceptible classification was used (Table 6). The 3 susceptible + segregating : 1 resistant classification decreased the number of significant Chi Square values to 4 (Table 7). For both classifications, however, a consistent pattern of too many susceptible or resistant families was not evident. This inconsistency was most likely due to the highly qualitative scoring system used for powdery mildew resistance, and the effect of modifying genes from either of the parents. However, since the PSbMV resistance ratios were as expected, the altered ratios for powdery mildew resistance should have no bearing on the determination of the relationship of PSbMV resistance to powdery mildew resistance when contingency table Chi Square tests are used.

Table 2. Chi Square values for inheritance of pea seedborne mosaic virus (PSbMV) resistance in pea progenies.

Cross	Total Families	Observed			Expected			Chi Square
		Res[z]	Seg	Sus	Res	Seg	Sus	
1	83	13	34	36	20.75	41.50	20.75	15.46**
1-R	89	21	49	19	22.25	44.50	22.25	1.99
3	87	18	51	18	21.75	43.50	21.75	2.59
3-R	68	16	43	9	17.00	34.00	17.00	6.20
5	63	16	31	16	15.75	31.50	15.75	0.01
5-R	27	3	13	11	6.75	13.50	6.75	4.78
7	122	30	61	31	30.50	61.00	30.50	0.02
7-R	59	18	25	16	14.75	29.50	14.75	1.51
9	128	28	54	46	32.00	64.00	32.00	8.19
9-R	27	10	12	5	6.75	13.50	6.75	2.15
11	49	11	23	6	12.25	24.50	12.25	2.15
11-R	46	11	24	11	11.50	23.00	11.50	0.08
13	51	9	34	8	12.75	25.00	12.75	6.91
13-R	50	17	27	6	12.50	25.50	12.50	5.16
15	50	11	18	21	12.50	25.00	12.50	7.92
15-R	50	13	22	15	12.50	25.00	12.50	0.88
17	50	7	23	20	12.50	25.00	12.50	7.08
17-R	50	12	31	7	12.50	25.00	12.50	3.99
19	49	15	29	5	12.25	24.50	12.25	5.74
20	49	14	27	8	12.25	24.50	12.25	1.98
20-R	47	15	27	5	11.75	23.50	11.75	5.30
22	43	7	27	9	10.75	21.50	10.75	1.69
22-R	49	15	32	2	12.25	24.50	12.25	11.28**

[z] Res = resistant, Seg = segregating, Sus = susceptible families.
[y] Significant at 1% (**).

Table 3. Chi Square values for inheritance of pea seedborne mosaic virus (PSbMV) resistance in pea progenies, combining segregating and susceptible families.

Cross	Total Families	Observed		Expected		Chi Square
		Res[z]	Seg+Sus[y]	Res[z]	Seg+Sus[y]	
1	83	13	70	20.75	62.25	3.37
1-R	89	21	68	22.25	66.75	0.04
3	87	18	69	21.75	64.25	0.65
3-R	68	16	52	17.00	51.00	1.01
5	63	16	47	15.75	47.25	1.01
5-R	27	3	24	6.75	50.25	2.08
7	122	30	92	30.50	91.50	0
7-R	59	18	41	14.75	44.25	1.39
9	128	28	100	32.00	96.00	1.51
9-R	27	10	17	6.75	20.25	8.59**
11	49	11	29	10.00	30.00	0.03
11-R	46	11	35	11.50	34.50	0
13	51	9	42	12.75	38.25	1.10
13-R	50	17	33	12.50	37.50	1.71
15	50	11	39	12.50	37.50	0.35
15-R	50	13	37	12.50	37.50	0
17	50	7	43	12.50	37.50	2.67
17-R	50	12	38	12.50	37.50	0
19	49	15	34	12.25	36.75	0.55
20	49	14	35	12.25	36.75	0.17
20-R	47	15	32	11.75	35.25	0.86
22	43	7	36	10.75	32.25	1.31
22-R	49	15	34	12.25	36.75	0.55

[z] Res = resistant families.
[y] Seg + Sus = segregating and susceptible families combined.
[x] Significant at 1% (**).

Table 4. Chi Square values for inheritance of pea enation mosaic virus (PEMV) resistance in pea progenies.

Cross	Total Families	Observed Res[z]	Seg	Sus	Expected Res	Seg	Sus	Chi Square
1	83	13	4	49	20.75	41.50	20.75	76.47**[y]
1-R	89	21	33	19	22.25	44.50	22.25	12.81**
3	87	18	56	6	21.75	43.50	21.75	15.48**
3-R	68	16	42	5	17.00	34.00	17.00	11.29**
5	63	16	26	4	15.75	31.50	15.75	20.97**
5-R	27	3	5	4	6.75	13.50	6.75	25.22**
7	122	30	50	14	30.50	61.00	30.50	35.06**
7-R	59	18	29	4	14.75	29.50	14.75	16.42**
9	128	28	64	12	32.00	64.00	32.00	25.00**
9-R	27	10	11	4	6.75	13.50	6.75	5.66

[z] Res = resistant, Seg = segregating, Sus = susceptible.
[y] Significant at 1% (**).

Table 5. Chi Square values for inheritance of pea enation mosaic virus (PEMV) in pea progenies, combining resistant and segregating families.

Cross	Total Families	Observed Res+Seg[z]	Sus[y]	Expected Res+Seg[z]	Sus[y]	Chi Square
1	83	34	49	62.25	20.75	10.44**
1-R	89	70	19	66.75	22.25	0.45
3	87	81	6	65.25	21.75	14.25**
3-R	68	63	5	51.00	17.00	10.37**
5	63	59	4	47.25	15.75	10.72**
5-R	27	23	4	20.25	6.75	0.94
7	122	108	14	91.50	30.50	11.19**
7-R	59	55	4	44.25	14.75	9.49**
9	128	116	12	96.00	32.00	12.82**
9-R	27	23	4	20.25	6.75	0.94

[z] Res + Seg = resistant and segregating families combined.
[y] Sus = susceptible families.
[x] Significant at 1% (**).

Table 6. Chi Square values for inheritance of powdery mildew resistance in pea progenies.

Cross	Total Families	Observed Res[z]	Seg	Sus	Expected Res	Seg	Sus	Chi Square
1	83	22	26	35	20.75	41.50	20.75	15.66**
1-R	89	29	34	26	22.25	44.50	22.25	5.16
3	87	31	29	27	21.75	43.50	21.75	10.03*
3-R	68	22	30	16	17.00	34.00	17.00	1.99
5	63	0	0	63	0	0	63.00	-
5-R	27	0	0	27	0	0	27.00	-
7	122	33	56	33	30.50	61.00	30.50	0.81
7-R	59	20	29	1	14.75	29.50	14.75	3.41
9	128	34	35	59	32.00	64.00	32.00	36.05**
9-R	27	7	13	7	6.75	13.50	6.75	0.04
11	49	15	12	13	10.00	20.00	10.00	6.60
11-R	46	11	7	28	11.50	23.00	11.50	34.82**
13	51	23	13	15	12.75	25.50	12.75	14.76**
13-R	50	13	9	28	12.50	25.00	12.50	29.48**
15	50	25	8	17	12.50	25.00	12.50	15.68**
15-R	50	42	7	1	12.50	25.00	12.50	93.16**
17	50	23	16	11	12.50	25.00	12.50	12.24**
17-R	50	9	18	23	12.50	25.00	12.50	11.76**
19	49	17	13	19	12.25	24.50	12.25	10.96**
20	49	8	22	19	12.25	24.50	12.25	5.45
20-R	47	11	8	28	11.75	23.50	11.75	32.74**
22	43	13	12	18	10.75	21.50	10.75	9.56*
22-R	49	8	16	25	12.25	24.50	12.25	15.69**

[z] Res = resistant, Seg = segregating, Sus = susceptible families.
[y] Significant at 1% (**), and 5% (*).

Table 7. Chi Square values for inheritance of powdery mildew resistance in pea progenies, combining segregating and susceptible families.

Cross	Total Families	Observed		Expected		Chi Square
		Res[z]	Seg+Sus[y]	Res	Seg+Sus[y]	
1	83	13	61	20.75	62.25	0.04
1-R	89	21	60	22.25	66.75	2.35
3	87	18	56	21.75	65.25	4.69
3-R	68	16	46	17.00	51.00	1.59
7	122	30	89	30.50	91.50	0.17
7-R	59	18	39	14.75	44.25	2.04
9	128	28	94	32.00	96.00	0.09
9-R	27	10	20	6.75	20.25	0.01
11	49	11	25	10.00	30.00	2.70
11-R	46	11	35	11.50	34.50	0
13	51	9	28	12.75	38.25	9.94**[x]
13-R	50	17	37	12.50	37.50	0
15	50	11	25	12.50	37.50	15.36**
15-R	50	13	8	12.50	37.50	89.71**
17	50	7	27	12.50	37.50	10.67**
17-R	50	12	41	12.50	37.50	0.96
19	49	15	32	12.25	36.75	1.96
20	49	14	41	12.25	36.75	1.53
20-R	47	15	36	11.75	35.25	0.01
22	43	7	30	10.75	32.25	0.37
22-R	49	15	41	12.25	36.75	1.53

[z] Res = resistant families.
[y] Seg + Sus = segregating and susceptible families combined.
[x] Significant at 1% (**).

Although White (75) determined that 2 genes, p and v, are responsible for the edible pod character, most commercial pea lines have either p or v, but rarely both (personal communication, G.A. Marx). It may be assumed that in this study, the presence of edible pods is due to a single recessive gene, and F_3

families from edible x non-edible pod parents will segregate 1 edible pod : 2 segregating : 1 non-edible pod.

One of the 2 crosses segregating for the edible pod character gave a Chi Square value significant at .01 probability when both 1:2:1 and 3 non-edible + segregating : 1 edible pod classifications were used (Tables 8 and 9). For this cross, twice the expected number of edible pod families were observed, while the expected value for segregating families was twice the observed value. Although the population was biased by selection for plant habit (50% dwarf and 50% tall families) only 25% of the families were expected to have edible pods. It appears that the abnormally large number of edible pod segregates was the result of linkage between edible pod and dwarf plant habit. Selecting a biased sample for plant height (excessive number of dwarf plants) could result in an excessive number of edible pod plants.

Table 8. Chi Square values for inheritance of edible pod character in pea progenies.

Cross	Total Families	Observed			Expected			Chi Square
		Non	Seg	Ed	Non	Seg	Ed	
3	87	20	24	43	21.75	43.50	21.75	29.64**[y]
3-R	68	22	29	17	17.00	34.00	17.00	2.21

[z] Non= non-edible pod, Seg = segregating, Ed = edible pod families.
[y] Significant at 1% (**).

Table 9. Chi Square values for inheritance of edible pod character in pea progenies, combining segregating and non-edible pod families.

Cross	Total Families	Observed		Expected		Chi Square
		Non + Seg[z]	Ed[y]	Non + Seg[z]	Ed[y]	
3	87	44	43	65.25	21.75	26.39**[x]
3-R	68	51	17	51.00	17.00	0.02

[z] Non-edible pod and segregating families combined.
[y] Edible pod families.
[x] Significant at 1% (**).

PSbMV Resistance vs. PEMV Resistance

There was generally no relationship between PSbMV resistance and PEMV resistance. Correlation coefficients varied from moderate to very small and positive to negative. The value for Cross 1-R was significant at .01 probability and negative. Values were equally divided between positive and negative. Chi Square values were all non-significant with the exception of that for P.I. 193586 x OSU 582 (Cross 3-R), which had a Chi Square value significant at .05 probability, and a moderate, positive correlation coefficient (Table 10).

The small correlation values including the significant one may have resulted from misclassification for PEMV, represented by varying degrees of correlation values. A reduced incidence of PEMV infection in the field, because of late planting, might have reduced expression in some susceptible families. Modifying factors could have affected symptom expression and classification.

Table 10. The relationship between pea seedborne mosaic virus (PSbMV) resistance and pea enation mosaic virus (PEMV) resistance in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	6.53	-.12
1-R	P.I. 193586 x OSU 604	89	8.33	-.23**[x]
3	OSU 582 x P.I. 193586	87	3.22	-.03
3-R	P.I. 193586 x OSU 582	68	10.96*	.19
5	OSU 523 x P.I. 193586	63	2.98	.11
5-R	P.I. 193586 x OSU 523	27	2.83	-.14
7	OSU 441 x P.I. 193586	122	7.13	.18
7-R	P.I. 193586 x OSU 441	59	4.95	-.14
9	M 183 x P.I. 193586	128	7.98	.08
9-R	P.I. 193586 x M 183	27	2.42	-.04
11	OSU 582 x 442-15	40	5.11	.11
11-R	442-15 x OSU 582	46	6.25	.10

[z] Number of families = n.
[y] Significant at 5% (*), and 1% (**).
[x] = PSbMV resistance associated with PEMV susceptibility.

PSbMV Resistance vs. RCVMV Resistance

There was no apparent relationship between PSbMV resistance and RCVMV resistance. Twelve of the 21 crosses observed to segregate for resistance to RCVMV as measured by disease severity gave negative correlation values for PSbMV resistance vs. RCVMV resistance, and 2 of these values were significant at .05 probability. One of the remaining 9 crosses (Cross 22) gave a positive correlation value significant at .05 probability. The other 8 crosses gave low positive correlation values. Four Chi Square values were significant at .05 probability (Crosses 5-R, 13-R, 17 and 22), with remaining values moderate to small (Table 11).

For this particular characteristic, most of the crosses did not offer clearcut differences in resistance to RCVMV with the exception of OSU 582 x P.I. 193586 (Cross 3) and its reciprocal. OSU 582 consistently showed strong resistance to RCVMV while P.I. 193586 was highly susceptible. Crosses between these 2 parents should have given progeny segregating for resistance. The remaining parents showed moderate RCVMV symptoms, which should have yielded progeny with less pronounced segregation.

A low incidence of RCVMV infection in the field may have led to misclassification, since values varied from positive to negative and moderate to small throughout the crosses. Inaccurate scoring for RCVMV may have been the result of PEMV symptoms occurring simultaneously in the same plants, masking or magnifying RCVMV symptoms.

Table 11. The relationship between pea seedborne mosaic virus (PSbMV) resistance and red clover vein mosaic virus (RCVMV) resistance in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	3.90	.01
1-R	P.I. 193586 x OSU 604	89	1.86	-.09
3	OSU 582 x P.I. 193586	87	1.76	-.04
3-R	P.I. 193586 x OSU 582	68	3.26	.12
5	OSU 523 x P.I. 193586	63	3.48	.10
5-R	P.I. 193586 x OSU 523	27	11.22*	-.23
7	OSU 441 x P.I. 193586	122	2.67	-.01
7-R	P.I. 193586 x OSU 441	59	6.78	-.03
9	M 183 x P.I. 193586	128	2.24	-.01
9-R	P.I. 193586 x M 183	27	4.91	.20
11	OSU 582 x 442-15	40	4.89	-.07
11-R	442-15 x OSU 582	46	9.18	-.36*[x]
13	B 504-5 x OSU 434	51	1.59	.01
13-R	OSU 434 x B 504-5	50	10.98*	-.03
15	B 504-5 x OSU 605	50	4.56	-.18
15-R	OSU 605 x B 504-5	50	3.27	.07
17	B 504-18 x M 187	50	13.00*	-.33*[x]
20	OSU 605 x B 505-16	49	3.13	-.23
20-R	OSU 434 x B 506-24	47	2.44	.20
22	OSU 434 x B 506-24	43	7.92*	.35*[w]
22-R	B 506-24 x OSU 434	49	0.97	.04

[z] Number of families = n.
[y] Significant at 5% (*).
[x] PSbMV resistance associated with RCVMV susceptibility.
[w] PSbMV resistance associated with RCVMV resistance.

PSbMV Resistance vs. Powdery Mildew Resistance

Generally, resistance to powdery mildew was negatively correlated with PSbMV resistance. Of the 21 crosses segregating for powdery mildew resistance, 3 crosses (Crosses 11-R, 13-R and 22-R) had correlation values significant at .05 probability, and 2 (Crosses 15 and 20) at .01 probability. Remaining correlation coefficients were usually negative and small, although 4 crosses gave values which were positive and small. Crosses 19 and 20 had Chi Square values significant at .05 probability, and Cross 13-R gave a value significant at .01 probability. Remaining Chi Square values were small (Table 12).

These results were inconsistent as to cross and male or female parent. This most likely was the result of using a highly qualitative classification system for powdery mildew resistance. Modifying genes associated with 1 of the parents depending on the cross affected the severity of the mildew reaction, thus affecting disease classification.

Table 12. The relationship between pea seedborne mosaic virus (PSbMV) resistance and powdery mildew resistance in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	7.34	-.12
1-R	P.I. 193586 x OSU 604	89	6.99	-.15
3	OSU 582 x P.I. 193586	87	1.90	-.02
3-R	P.I. 193586 x OSU 582	68	2.35	-.12
7	OSU 441 x P.I. 193586	122	4.27	-.03
7-R	P.I. 193586 x OSU 441	59	4.05	-.01
9	M 183 x P.I. 193586	128	3.90	.03
9-R	P.I. 193586 x M 183	27	7.15	-.14
11	OSU 582 x 442-15	40	3.09	-.01
11-R	442-15 x OSU 582	46	5.06	-.30*[x]
13	B 504-5 x OSU 434	51	2.36	-.17
13-R	OSU 434 x B 504-5	50	18.37**	-.35*[x]
15	B 504-5 x OSU 605	50	10.17	-.38**[x]
15-R	OSU 605 x B 504-5	50	3.78	-.02
17	B 504-18 x M 187	50	4.52	.19
17-R	M 187 x B 504-18	50	2.09	.06
19	B 504-18 x M 190	49	11.18*	-.14
20	OSU 605 x B 505-16	49	12.43*	-.38**[x]
20-R	B 505-16 x OSU 434	47	5.34	-.06
22	OSU 434 x B 506-24	43	1.18	.08
22-R	B 506-24 x OSU 434	49	6.50	-.34*[x]

[z] Number of families = n.
[y] Significant at 5% (*), and 1% (**).
[x] Powdery mildew resistance associated with PSbMV susceptibility.

PSbMV Resistance vs. Plant Habit

There was no general relationship between PSbMV resistance and plant habit, although 3 of the 10 crosses segregating for plant habit (Crosses 3, 7-R, and 9) had correlation values significant at .05 probability (Table 13). Cross 3, which gave a significant positive correlation value, did not have a significant Chi Square value. The 2 crosses (7-R and 9) with significant negative correlation values also had significant Chi Square values. The reciprocal of Cross 9 gave a moderately sized correlation value which was in agreement with Cross 9, although the value was not statistically significant. However, these values were not large and it is unlikely that a strong association exists between PSbMV resistance and tall plants, the combination found in the resistant parent. Chi Square values for the other crosses were moderate to low, as were correlation values, which varied from positive to negative. There is a disagreement in the direction of significant values, but the significance is not large enough to be convincing that any association exists.

Table 13. The relationship between pea seedborne mosaic virus (PSbMV) resistance and plant habit in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	8.80	.07
1-R	P.I. 193586 x OSU 604	89	1.55	.01
3	OSU 582 x P.I. 193586	87	6.87	.24*
3-R	P.I. 193586 x OSU 582	68	5.54	-.08
5	OSU 523 x P.I. 193586	63	4.77	.09
5-R	P.I. 193586 x OSU 523	27	2.28	.29
7	OSU 441 x P.I. 193586	122	5.55	.12
7-R	P.I. 193586 x OSU 441	59	13.03*	-.27*[x]
9	M 183 x P.I. 193586	128	13.91**	-.21*[x]
9-R	P.I. 193586 x M 183	27	5.41	-.36

[z] Number of families = n.
[y] Significant at 5% (*), and 1% (**).
[x] PSbMV resistance associated with tall plants.

PSbMV Resistance vs. Number of Pods Per Node

There was no consistent association between PSbMV resistance and single or multiple pod bearing habit. Chi Square values were insignificant and ranged from moderate to small (Table 14). Two crosses, Cross 13 (B 504-5 x OSU 434) and its reciprocal, Cross 13-R, gave correlation values significant at .05 probability, indicating that in these crosses an association was present between PSbMV resistance and multiple pods per node. However, in these 2 crosses PSbMV segregation did not fit the expected ratio, possibly indicating the presence of selfs or seed mixtures, which may have led to an incorrect correlation between PSbMV resistance and number of pods per node. Remaining crosses gave small correlation values which varied from positive to negative, indicating that no general relationship existed between PSbMV resistance and number of pods per node.

Table 14. The relationship between pea seedborne mosaic virus (PSbMV) resistance and number of pods per node in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	1.32	.11
1-R	P.I. 193586 x OSU 604	89	4.06	.06
3	OSU 582 x P.I. 193586	87	1.99	.15
3-R	P.I. 193586 x OSU 582	68	1.42	.06
5	OSU 523 x P.I. 193586	63	0.84	-.05
5-R	P.I. 193586 x OSU 523	27	3.14	-.30
7	OSU 441 x P.I. 193586	122	0.21	-.04
7-R	P.I. 193586 x OSU 441	59	1.63	.09
9	M 183 x P.I. 193586	128	4.02	.02
9-R	P.I. 193586 x M 183	27	-	-
11	OSU 582 x 442-15	40	0.17	-.03
11-R	442-15 x OSU 582	46	1.61	-.09
13	B 504-5 x OSU 434	51	3.75	-.27*
13-R	OSU 434 x B 504-5	50	5.11	-.32*
15	B 504-5 x OSU 605	50	3.62	.22

[z] Number of families = n.
[y] Significant at 5% (*).

PSbMV Resistance vs. Seed Type

There was no strong relationship between PSbMV resistance and seed type, but there was a tendency for smooth seeds and resistance to be associated, which is the combination found in the resistant parent.

In the 12 crosses which were segregating for wrinkled, smooth and dimpled seeds, correlation values between resistance to PSbMV and seed type were variable from cross to cross, with values ranging from moderate to small (Table 15). Crosses 3 and 7 gave negative correlation values significant at .05 probability, and 1 of these crosses (Cross 3) gave a Chi Square value significant at .05 probability. The negative correlation values meant that PSbMV resistance was associated with smooth seeds.

Table 15. The relationship between pea seedborne mosaic virus (PSbMV) resistance and seed type in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	1.09	-.04
1-R	P.I. 193586 x OSU 604	89	2.80	.05
3	OSU 582 x P.I. 193586	87	7.85*	-.24*[x]
3-R	P.I. 193586 x OSU 582	68	1.15	.12
5	OSU 523 x P.I. 193586	63	1.71	.16
5-R	P.I. 193586 x OSU 523	27	2.01	.12
7	OSU 441 x P.I. 193586	122	6.59	-.21*[x]
7-R	P.I. 193586 x OSU 441	59	8.64	-.23
9	M 183 x P.I. 193586	128	2.71	-.11
9-R	P.I. 193586 x M 183	27	1.90	.06
11	OSU 582 x 442-15	40	6.82	-.12
11-R	442-15 x OSU 582	46	6.93	.04

[z] Number of families = n.
[y] Significant at 5% (*).
[x] PSbMV resistance associated with smooth seeds.

PSbMV Resistance vs. Flower Color

There was no general association between PSbMV resistance and flower color for the 3 crosses segregating for purple and white flowers. Cross 7 (OSU 441 x P.I. 193586) gave both a Chi Square and a positive correlation value significant at .01 probability, indicating an association between PSbMV resistance and white flowers. The other 2 crosses had small Chi Square and correlation values (Table 16).

Table 16. The relationship between pea seedborne mosaic virus (PSbMV) resistance and flower color in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	8.36	-.12
7	OSU 441 x P.I. 193586	122	24.11**	0.37**[x]
9	M 183 x P.I. 193586	128	1.97	0.21

[z] Number of families = n.
[y] Significant at 1% (**).
[x] PSbMV resistance associated with white flower color.

PSbMV Resistance vs. Flavor

Crosses 1, 7, and 9 included families which were segregating for purple and white flower color. Since purple flowers are generally associated with unacceptable flavor, it was necessary to analyze white and purple-flowered families separately. Different results were obtained using this method than when analyzing all the families together (Table 17).

No general relationship was found between PSbMV resistance and flavor among purple-flowered families and their relatives (Table 18). Among the white-flowered families, Cross 1 (OSU 604 x P.I. 193586) gave a Chi Square value significant at .01 probability and a positive correlation coefficient significant at .05 probability (Table 19). These results suggest that this specific cross with OSU 604 as the female parent tends to segregate PSbMV-resistant peas having good flavor.

Table 17. The relationship between pea seedborne mosaic virus (PSbMV) resistance and flavor in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	15.16*	.23*[x]
1-R	P.I. 193586 x OSU 604	89	2.65	.10
3	OSU 582 x P.I. 193586	87	2.34	.14
3-R	P.I. 193586 x OSU 582	68	3.40	-.08
5	OSU 523 x P.I. 193586	63	2.12	.15
5-R	P.I. 193586 x OSU 523	27	1.09	.20
7	OSU 441 x P.I. 193586	122	24.14**	.29**[x]
7-R	P.I. 193586 x OSU 441	59	1.35	.04
9	M 183 x P.I. 193586	128	4.17	.10
9-R	P.I. 193586 x M 183	27	4.57	-.32
11	OSU 582 x 442-15	40	4.27	.16
11-R	442-15 x OSU 582	46	0.41	-.13
13	B 504-5 x OSU 434	51	1.61	.05
13-R	OSU 434 x B 504-5	50	3.03	.16
15	B 504-5 x OSU 605	50	6.61	-.07
15-R	OSU 605 x B 504-5	50	1.20	.05
17	B 504-18 x M 187	50	2.53	.06
19	B 504-18 x M 190	49	2.31	-.19

[z] Number of families = n.
[y] Significant at 5% (*), and 1% (**).
[x] PSbMV resistance associated with good flavor.

Table 18. The relationship between pea seedborne mosaic virus (PSbMV) resistance and flavor in families having all purple flowers or segregating for purple and white flowers, within crosses 1, 7 and 9.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	5	2.22	.61
7	OSU 441 x P.I. 193586	13	2.36	.43
9	M 183 x P.I. 193586	6	3.33	-

[z] Number of families = n.

Table 19. The relationship between pea seedborne mosaic virus (PSbMV) resistance and flavor in families having only white flowers within crosses 1, 7 and 9.

1	OSU 604 x P.I. 193586	78	14.19**	.26*[x]
7	OSU 441 x P.I. 193586	109	3.36	-.11
9	M183 x P.I. 193586	122	3.00	.11

[z] Number of families = n.
[y] Significant at 1% (**), and 5% (*).
[z] PSbMV resistance associated with good flavor.

PSbMV Resistance vs. Edible Pod

One of the 2 crosses segregating for the presence of edible pods (Cross 3) gave a Chi Square value significant at .05 probability and a positive correlation value significant at .01 probability between PSbMV resistance and the presence of edible pods (Table 20). These values were calculated using data obtained when classifying PSbMV resistance using a 1 susceptible : 2 segregating : 1 resistant ratio. Since the population was too small to correctly classify genotypically, the greater than expected number of PSbMV-segregating families and the less than expected number of PSbMV-susceptible families were combined in the same phenotypic class to give totals which were close to expected values (Table 21). Using the 3:1 (susceptible + segregating : resistant) ratio rather than the 1:2:1 ratio for PSbMV resistance, a non-significant Chi Square value is obtained for the relationship between PSbMV resistance and the presence of edible pods (Table 20).

The significant Chi Square value obtained for Cross 3 for PSbMV resistance vs. edible pod presence was the result of a larger than expected number of edible pods occurring within the PSbMV-resistant category (Table 21). Since data were taken in the field when pods were mature enough for the parchment to be evident, misclassification of edible pods was unlikely. Therefore, in this 1 cross, with the edible pod parent as the female, an association between PSbMV resistance and the presence of edible pods exists. Linkage between the gene for PSbMV resistance and

the gene for the presence of edible pod (lack of parchment) is known (29). Both are closely located on 1 end of chromosome 6. There is the possibility that a crossover occurred in OSU 582 x P.I. 193586 differently from that of the reciprocal, resulting in the significant Chi Square and correlation values.

Table 20. The relationship between pea seedborne mosaic virus (PSbMV) resistance and the presence of edible pods in pea progenies.

Code	Cross	n[z]	Chi Square	Correlation[y] Coefficient	Chi Square	Correlation Coefficient
			PSbMV 1:2:1		PSbMV 3:1[v]	
3	OSU 582 x P.I. 193586	87	10.91*	0.31**[x]	2.99	0.18
3-R	P.I. 193586 x OSU 582	68	1.85	-.11	1.30	-.13

[z] Number of families = n.
[y] Significant at 5% (*) and 1% (**).
[x] PSbMV resistance associated with the presence of edible pods.
[w] PSbMV 1 susceptible : 2 segregating : 1 resistant for F_3 families.
[v] PSbMV 3 susceptible plus segregating : 1 resistant for F_3 families.

Table 21. Segregation of F_3 pea progenies for presence of edible pods within pea seedborne mosaic virus (PSbMV) classes using 1:2:1[z] and 1:3[y] ratios.

		Ed[x]	Pods seg	Non-ed		Ed	Pods seg	Non-ed
Cross 3 (OSU 582 x P.I. 193586)	PSbMV[w] Res	12	4	2	PSbMV Res	12	4	2
	PSbMV Seg	26	16	9	PSbMV Seg+Sus	31	20	18
	PSbMV Sus	5	4	9				
		Ed	Pods seg	Non-ed		Ed	Pods seg	Non-ed
Cross 3-R (P.I. 193586 x OSU 582)	PSbMV Res	3	6	7	PSbMV Res	3	6	7
	PSbMV Seg	11	20	12	PSbMV Seg+Sus	14	23	15
	PSbMV Sus	3	3	3				

[z] PSbMV 1 resistant : 2 segregating : 1 susceptible for F_3 families.

[y] PSbMV 1 resistant : 3 segregating plus susceptible for F_3 families.

[x] Ed = edible pod, Pods seg = segregating for edible pod character, Non-ed = non-edible pods.

[w] PSbMV Res = resistant, Seg = segregating, Sus = susceptible, Seg + Sus = segregating and susceptible families combined.

PEMV Severity vs. RCVMV Severity

Several secondary relationships not involving PSbMV were studied. The data indicate a general relationship between PEMV severity and RCVMV severity within the 10 crosses segregating for PEMV resistance. Crosses 1, 5, and 7 and their reciprocals gave Chi Square values significant at .01 probability. Two of these crosses, Cross 1 (OSU 604 x P.I. 193586) and Cross 5 (OSU 523 x P.I. 193586), and their reciprocals had positive correlation values which were significant at .01 probability (Table 22).

Although these data suggest a relationship between RCVMV severity and PEMV severity, accurate scoring for RCVMV is not possible when PEMV symptoms are strong, as the PEMV symptoms often mask or magnify the RCVMV symptoms.

Table 22. The relationship between pea enation mosaic virus (PEMV) severity and red clover vein mosaic virus (RCVMV) severity in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	92.70**	.56**[x]
1-R	P.I. 193586 x OSU 604	89	60.56**	.44**[x]
3	OSU 582 x P.I. 193586	87	6.14	.15
3-R	P.I. 193586 x OSU 582	68	6.29	-.02
5	OSU 523 x P.I. 193586	63	24.04**	.42**[x]
5-R	P.I. 193586 x OSU 523	27	23.33**	.76**[x]
7	OSU 441 x P.I. 193586	122	36.14**	.17
7-R	P.I. 193586 x OSU 441	59	62.96**[x]	.23
9	M 183 x P.I. 193586	128	6.22	-.01
9-R	P.I. 193586 x M 183	27	5.54	.34

[z] Number of families = n.
[y] Significant at 1% (**).
[x] PEMV severity associated with RCVMV severity.

Edible Pod vs. Plant Habit

Dwarf plant habit was associated with the presence of edible pods in both crosses segregating for the edible pod characteristic. Chi Square values were large and significant at .01 probability as were the positive correlation values (Table 23). When Chi Square values were calculated for Cross 3 (OSU 582 x P.I. 193586) and its reciprocal using a 3:1 ratio for plant habit (tall + segregating : dwarf), large significant Chi Square values were also obtained. These values were 61.32 and 39.57 respectively, using 2 degrees of freedom.

Two genes, p and v, determine the edible pod character. It is not known which of these genes conditions the presence of edible pods in OSU 582, but it is unlikely that both are present. The gene p occurs on chromosome 6, 4 map distances from lm, the gene which shortens internode length by 50%. The gene which is responsible for shortened internodes and a zigzag stem, le, occurs 12 map distances from v on chromosome 4. Linkage probably occurred between p and lm, or between v and le, resulting in the significant Chi Square and correlation values.

Table 23. The relationship between plant habit and the presence of edible pods in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
3	OSU 582 x P.I. 193586	87	89.15**	.82**[x]
3-R	P.I. 193586 x OSU 582	68	85.76**	.88**[x]

[z] Number of families = n.
[y] Significant at 1% (**).
[x] Dwarf plant habit associated with the presence of edible pods.

Flower Color vs. Flavor

Good flavor was highly correlated with white flower color in all 3 crosses segregating for white and purple flowers. Chi Square and correlation values were high and significant at .01 probability (Table 24). Purple flower color, characteristic of some of the P.I. 193586 parents, was always associated with astringency and unacceptable flavor in all stages of seed development.

Table 24. The relationship between flower color and flavor in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	55.76**	.37**[x]
7	OSU 441 x P.I. 193586	122	109.00**	.84**[x]
9	M 183 x P.I. 193586	128	128.00**	.69**[x]

[z] Number of families = n.
[y] Significant at 1% (**).
[x] White flower color associated with good flavor, and purple flower color associated with unacceptable flavor.

Flower Color vs. Seed Type

Two of the 3 crosses segregating for purple and white flower color (Crosses 1 and 7) gave significant Chi Square values for flower color versus seed type. All correlation values were negative, suggesting that there was a tendency for purple flower color and smooth seeds to be associated.

Table 25. The relationship between flower color and seed type in pea progenies.

Code	Cross	n[z]	Chi Square[y]	Correlation[y] Coefficient
1	OSU 604 x P.I. 193586	83	9.56*	-.10
7	OSU 441 x P.I. 193586	122	21.02**[x]	-.18
9	M 183 x P.I. 193586	128	2.71	-.13

[z] Number of families = n.
[y] Significant at 5% (*), and 1% (**).
[x] Purple flower color associated with smooth seeds and white flower color associated with wrinkled seeds.

GENERAL DISCUSSION

The objective of this study was to determine if there are unfavorable linkages or associations which could delay or prevent the incorporation of PSbMV resistance into pea cultivars having desirable horticultural characteristics as well as resistance to PEMV, RCVMV, and powdery mildew. It appeared early in the Oregon State University breeding project that progress in achieving horticultural type in the first cycle of breeding for PSbMV resistance was less than expected.

Although we did not attempt to maintain random Mendelian populations for all characteristics studied, and segregations deviated from the expected ratios for characters other than PSbMV resistance, the relationships found were considered valid. Using the statistical methods of correlation analyses and contingency table Chi Squares, the maintenance of Mendelian populations for all characters should not be necessary. The populations were developed in a manner which should not have biased the randomness of PSbMV segregation or the association of PSbMV with other characteristics. For almost every cross, PSbMV resistance segregated as expected, confirming the findings of Hagedorn and Gritton (17) and Hampton and Marx (29), that resistance is conditioned by a single recessive gene.

Relationships between PSbMV resistance and the presence of edible pods, smooth seeds and good flavor probably exist, but it would be necessary to make more detailed studies in order to

verify these associations. After 3 cycles of crossing, it appears that the breeding program will eventually produce lines of peas with fully acceptable horticultural characteristics and PSbMV resistance. It is possible that 4 or more cycles of crossing, using modest-sized populations in a combination backcross-pedigree system, will be required to achieve this objective.

The present study did not produce positive results by finding strong negative associations which would prevent breeding PSbMV-resistant peas, but has provided useful information for breeders. Further study or breeding experience would be needed to determine if there are additional, more quantitative characteristics which might reduce the possibilities of breeding acceptable PSbMV-resistant cultivars.

SUMMARY AND CONCLUSIONS

PSbMV-susceptible lines with desirable horticultural characteristics were crossed with PSbMV-resistant lines. The resulting 1376 F_3 families were evaluated for horticultural characteristics and tested for resistance to PSbMV, PEMV, RCVMV and powdery mildew. Associations between PSbMV and PEMV resistance, RCVMV resistance, powdery mildew resistance, flower color, flavor, plant habit, seed type, number of pods per node and the presence of edible pods were determined using correlation coefficients and contingency table Chi Square tests. Secondary associations were also determined. The following relationships were indicated:

1. No general relationships existed between PSbMV resistance and PEMV resistance, RCVMV resistance, plant habit or number of pods per node.
2. There was a tendency for PSbMV resistance and smooth seeds to be associated.
3. PSbMV resistance was generally negatively correlated with resistance to powdery mildew. Modifying genes, associated with either of the parents depending on the cross, and the highly qualitative classification for powdery mildew resistance gave inconsistent results.
4. An association between PSbMV resistance and the presence of edible pods existed in OSU 582 x P.I. 193586, the cross using the edible pod parent as the female. A linkage exists on

chromosome 6 between the gene for PSbMV resistance and the gene for the presence of edible pods. It is possible that a crossover occurred in OSU 582 x P.I. 193586 differently from that of the reciprocal cross.

5. An association between PSbMV resistance and white flower color occurred in 1 cross, OSU 604 x P.I. 193586. This cross also showed an association between PSbMV resistance and good flavor. For all 3 crosses segregating for flower color, white flowers were highly correlated with good flavor, and purple flowers were associated with undesirable flavor.
6. PEMV severity was associated with RCVMV severity although accurate scoring for RCVMV is difficult when strong PEMV symptoms are also present.
7. Linkage between the gene for edible pod and the gene which shortens internode length appeared to result in an association between dwarf plant habit and the presence of edible pods in both crosses segregating for the edible pod character.
8. The data in this study support the findings of Hagedorn and Gritton (17) and Hampton and Marx (29) in confirming that PSbMV resistance is conditioned by a single recessive gene.

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