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Inheritance of resistance to the bean-pod weevil (*Apion godmani* Wagner) in common beans from Mexico

Received: 15 August 1995 / Accepted: 8 September 1995

Abstract The bean-pod weevil (BPW), *Apion godmani* Wagner, often causes heavy losses in crops of common bean (*Phaseolus vulgaris* L.). Farmers need resistant bean cultivars to minimize losses, cut production costs, stabilize seed yield, and reduce pesticide use and consequent health hazards. To design effective breeding methods, breeders need new and better sources of resistance and increased knowledge of their modes of inheritance. We therefore: (1) compared sources of resistance to BPW, (2) studied the inheritance of resistance, and (3) determined whether the sources possess similar or different genes for BPW resistance. The following sources of resistance, originating from the Mexican highlands, were evaluated for 3 years at INIFAP-Santa Lucía de Pías, Texcoco, Mexico: ‘Amarillo 153’, ‘Amarillo 169’, ‘Hidalgo 58’, ‘J 117’, ‘Pinto Texcoco’, ‘Pinto 168’, and ‘Puebla 36’. All except ‘Puebla 36’ were crossed with the susceptible cultivar ‘Jamapa’. ‘Amarillo 153’ and ‘Puebla 36’ were crossed with another susceptible cultivar, ‘Bayo Mex’. The parents, F₁ hybrids, and F₂ populations were evaluated for BPW damage in 1992. Backcrosses of the F₁ of Jamapa/Pinto 168 to the respective susceptible and resistant parents were also evaluated in 1992. All seven resistant accessions were crossed in all possible combinations, excluding reciprocals. The resulting 21 F₁ hybrids and 21 F₂ populations were evaluated for BPW damage in 1994. ‘J 117’ had the highest level of resistance to BPW. ‘Pinto Texcoco’ and ‘Puebla 36’ had the highest mean damage score of all seven sources of resistance. The F₁ hybrids between susceptible parents and resistant sources were generally intermediate. Two genes segregating independently

controlled the BPW resistance in each accession. One gene, *Agm*, has no effect when present alone, whereas the other gene, *Agr*, alone conferred intermediate resistance. When both genes were present, resistance to BPW was higher. Based on mean BPW damage scores, all 21 F₁ hybrids and their F₂ populations, derived from crosses among seven resistant accessions, were resistant. However, data from individual plant damage scores in F₂ populations of Amarillo 169/Pinto 168 and Pinto Texcoco/Pinto 168 suggested that at least one gene in each of the three accessions was non-allelic. Data also indicated that ‘Amarillo 169’ had a dominant gene that conferred high levels of BPW resistance, irrespective of the alleles at the other locus; and that ‘Pinto Texcoco’ and ‘Pinto 168’ possessed two different genes for intermediate resistance.

Key words *Apion godmani* · Bean-pod weevil · Breeding for resistance · Common bean · Inheritance · *Phaseolus vulgaris*

Introduction

Although the geographical distribution of the bean-pod weevil (BPW), *Apion godmani* Wagner (Coleoptera: Curculionidae), is restricted to Mexico, Guatemala, El Salvador, Honduras, and northern Nicaragua (McKelvey et al. 1947; Mancía 1973), it causes severe yield losses in common bean (*Phaseolus vulgaris* L.). The economic importance of BPW varies considerably (Shivakoti et al. 1989) depending on the cultivars used, the sowing time, cropping system and agronomic practices employed, prevailing environmental conditions, and BPW populations. But, in some endemic areas of Central America, yield losses from the insect can be as high as 90% (Ramírez et al. 1959; Cardona 1989). Larvae of BPW feed on immature seeds inside developing pods of the common bean. Thus, seed yield, seed quality, seed germination, and market value are all adversely affected.

Communicated by A. L. Kahler

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Cardona (1989) described the biology of BPW. Adults usually appear when common bean crops are about to flower. Before mating, they may feed on young leaves and flowers, causing only slight damage. To oviposit, females chew small holes in the mesocarp of newly formed pods (1–4 cm long) and insert semitranslucent eggs – one per hole – usually above the developing seeds. Eggs hatch in 8–9 days and the first larval instar burrows through the pod wall to the seed, where it spends its second and third instars as it feeds on the developing seeds, causing yield losses. The three instars together take 3 weeks. One larva per infested seed is normal but, when infestations are very high, 3–5 larvae per seed may be found. When ready to pupate, the larva forms a chamber inside the pod. After about 10 days, newly formed adults emerge from the mature, dehiscent pods and disperse to forested areas to return when the next bean crop is about to flower. Thus, the insect completes its life cycle of about 6 weeks on common bean. Usually one generation of BPW develops per cropping season.

Chemical control of BPW is not easy because the adults, the only targetable stage, are active only during the crop's brief flowering period. Host-plant resistance is thus pivotal, and offers a more sustainable approach, to the integrated management of this pest, especially in areas where common bean is grown by poor farmers with tiny holdings. These farmers often cannot afford chemicals, and even if they could, do not necessarily recognize the insect nor time insecticide applications properly. Moreover, insecticides are hazardous to both the farmers' health and the environment.

For the past 50 years, repeated efforts have been made to screen and identify common-bean germ plasm resistant to BPW. For example, McKelvey et al. (1947) identified sources of resistance in common beans from Mexico. Some of these were later reconfirmed by Guevara (1961) in Mexico and by Mancía (1973) in El Salvador. Other highly resistant germ plasm accessions have been reported in cultigens by Beebe et al. (1993) and Garza and Muruaga (1993), and in wild common bean by Acosta et al. (1992).

Garza (1992) suggests two possible resistance mechanisms against BPW: ovipositional non-preference and hypersensitivity. In hypersensitivity, resistant cultivars display a healing mechanism that encapsulates the egg after it has been deposited by the female. As a result, the newly emerged, first-instar larva cannot penetrate the pod wall to reach the developing seed and thus dies. This mechanism, however, appears to be influenced by environmental conditions during pod and seed formation (Acosta et al. 1992). The biochemical basis of resistance to BPW is unknown.

Some resistant lines were developed in Mexico (Guevara 1961; Guevara et al. 1962), and probably in El Salvador, during the 1960s. In 1977, however, a coordinated regional research project (PROFRIJOL), funded by the Swiss Development Corporation, was initiated in collaboration with national research pro-

grams in Mexico, Central America, and the Caribbean (Beebe et al. 1993). Some sources of BPW resistance from the Mexican highlands (> 2000 m elevation), or lines derived from these, were incorporated into crosses. Although resistance levels were adequate, the lines recovered did not have acceptable commercial seed characteristics. Nor were they adapted to the more tropical Central American environments. Considerable progress was made when new and better adapted sources of resistance (e.g., de Celaya) were incorporated into a pedigree program to develop lines possessing combined resistance to bean common mosaic virus (BCMV) and BPW (Beebe et al. 1993). Some of the lines bred yielded as well as, or even better than, local cultivars in the absence of the insect, and were superior to check under high levels of BPW infestation.

While high levels of BPW resistance have been successfully transferred to some susceptible cultivars, the precise mode of its inheritance is not known. This information is essential for designing alternative methods of gene recombination and selection for resistance to BPW. This study has (1) compared levels of resistance of some sources of BPW resistance, (2) analyzed the inheritance of resistance, and (3) determined whether the sources possess similar or different genes for resistance.

Materials and methods

Plant materials

Seven accessions of common bean, previously identified as resistant to BPW, were used in this study; they were 'Amarillo 153', 'Amarillo 169', 'Hidalgo 58', 'J 117', 'Pinto Texcoco', 'Pinto 168', and 'Puebla 36'. They originated from different locations in the Mexican highlands, and differed in seed type and other agronomic characteristics (see Table 1). All, except 'Pinto Texcoco', were landraces. 'Pinto Texcoco' was selected from a three-way cross, Canario/Zac-9-1-7//Canario 101. All resistant sources, except 'Puebla 36', were crossed with a susceptible cultivar 'Jamapa', using manual emasculation and pollination (Buishand 1956; Bliss 1980). 'Amarillo 153' and 'Puebla 36' were crossed with another susceptible cultivar, 'Bayo Mex'. All crosses were made in a greenhouse (at CIAT-Palmira, Colombia) or in a screenhouse (at CIAT-Popayán, Colombia). Seed from each of the eight F_1 s and their parents was sown in either the greenhouse or screenhouse to check for hybrid origin, make backcrosses onto the respective parents, and to produce selfed (F_2) seeds. The seven resistant sources were also crossed in all possible combinations (diallel crosses), excluding reciprocals. Each of the 21 F_1 hybrids was selfed to produce F_2 seeds.

Field trials

All parents, eight sets of F_1 hybrids and F_2 populations of single crosses, and two backcrosses to the susceptible and resistant parents for the F_1 of Jamapa/Pinto 168 were evaluated for BPW damage under rainfed field conditions at the Santa Lucía de Prías Research Station of the Mexican Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP), Texcoco (2250 m altitude, 16 °C, 70% RH), in 1992. This site usually has a heavy and uniform infestation of BPW with little or no interference from other pests. A randomized complete block design with two or three replications was used. The parents and F_1 hybrids were grown in single-row, 5-m-long plots. The number of rows for each F_2 population and backcrosses

depended on the availability of seed. The parents, F₁ hybrids, and F₂ (and backcrosses in one case) populations for each source of resistance were also grouped together for evaluations. In addition, 'Jamapa', a susceptible check, was planted every 8 to 12 rows to monitor distribution of insect damage throughout the nurseries. The distance between rows was 80 cm and between plants within the row approximately 15 cm. Plots were kept free of weeds and diseases during the entire growing season. Occasional low populations of the Mexican bean beetle (*Epilachna varivestis* Mulsant) were hand-picked to avoid using insecticides.

The field trial involving seven resistant parents and 'Jamapa' and their seven sets of F₁ hybrids, F₂ populations, and backcrosses to both parents was also grown in 1993 at the same site, using the same experimental design with three replications. Because BPW infestation levels were less than 25% in the susceptible parent, Jamapa, segregation data were not analyzed for this study.

To test for allelism, seven sources of BPW resistance, and their 21 F₁ hybrids and 21 F₂ populations were grown at the same location in 1994. Parents and F₁ hybrids were sown in single-row, 3-m-long plots. The number of rows in the F₂ varied from three to five, depending on the availability of seed. A randomized complete block design with three replications was used for the study.

Evaluation for BPW

For each parent and F₁ hybrid in 1992 and 1994, and 19 F₂ populations in 1994, a random sample of 30 and 50 pods per plot (one pod per plant), respectively, were taken at maturity. For all F₂ populations and backcrosses in 1992 and for 2 of 21 F₂ populations in 1994, all mature pods from each individual plant were evaluated separately. Each pod was first examined by carefully opening along the ventral suture and removing each seed, which was then checked for BPW damage. The numbers of damaged seeds and total seeds were counted, and the percentage of damaged seeds calculated. Subsequently, they were classified into susceptible (> 50% damage compared with susceptible 'Jamapa' or 'Bayo Mex'), intermediate (> 30% and ≤ 50% damage of 'Jamapa' or 'Bayo Mex'), and resistant (≤ 30% damage of 'Jamapa' or 'Bayo Mex'). Chi-square tests were performed to test the goodness-of-fit of the expected segregation ratios.

Results

BPW infestation levels were highest in 1994 and lowest in 1993 (Table 1). Damage levels in susceptible 'Jamapa' ranged from 22.9% in 1993 to 88.7% in 1994. For resistant parents, damage ranged from a mean of 2.7% for 'J 117' to a mean of 15.8% for 'Pinto Texcoco'. Consistently, 'J 117' was the most resistant landrace in all years, followed by 'Amarillo 153', 'Amarillo 169', and 'Pinto 168'.

All F₁ hybrids between the resistant sources and susceptible parents had intermediate damage scores (Table 2). F₂ populations between the susceptible parent and 'Amarillo 153', 'Amarillo 169', 'Hidalgo 58', 'J 117', 'Pinto 168', 'Pinto Texcoco', and 'Puebla 36' segregated into ratios of 9 resistant: 3 intermediate: 4 susceptible (Table 2).

The F₁ of Jamapa/Pinto 168 backcrossed to 'Jamapa' gave a good fit to 1 resistant:1 intermediate:2 susceptible (Table 2). Similarly, despite a few intermediate and susceptible plants, the backcross of the F₁ to the resistant parent gave a good fit to 1 resistant:0 intermediate:0 susceptible.

The mean percent of damage for 21 F₁ hybrids obtained from diallel crosses among seven sources of resistance to BPW varied from 5.4% for Amarillo 169/Hidalgo 58 to 24.4% for Amarillo 169/Pinto Texcoco (Table 3). Similarly, the values for 21 F₂ populations ranged from 6.8% for Amarillo 153/J 117 to 22.3% for Pinto Texcoco/Pinto 168. When individual plant data from two of the 21 F₂ populations were examined, some recombinants in both populations were found to

Table 1 Origin, seed color, 100-seed weight, and percentage of damage caused by *A. godmani* in resistant and susceptible common-bean accessions evaluated in 1992, 1993, and 1994 at INIFAP-Santa Lucía de Pías, Texcoco, Mexico

Identification	Origin	Race ^b	Growth habit ^c	Phaseolin type	Seed color	100-seed weight (g)	Percentage of damage			
							1992	1993	1994	Mean
Resistant accessions										
Amarillo 153	Tepeaca, Puebla	Jalisco	III	S	Yellow	32	8.8	1.7	11.1	7.3
Amarillo 169	San Martín Texmelucan, Puebla	Jalisco	III	S	Yellow	29	8.7	1.8	13.1	7.9
Hidalgo 58	Pachuca, Hidalgo	Jalisco	III	S	Yellow	30	12.9	2.3	19.1	11.4
J 117	Atlacomulco, México State	Jalisco	III	S	Yellow	30	2.9	0.3	4.9	2.7
Pinto Texcoco ^a	Texcoco, México State	—	III	S	Pink striped	28	12.7	3.6	31.1	15.8
Pinto 168	Huichapán, Hidalgo	Durango	III	S	Pink spotted	30	10.1	0.9	12.9	8.0
Puebla 36	Zacapoxtla, Puebla	Jalisco	III	S	Gray spotted	33	3.3	2.6	37.8	14.6
Mean						30	8.5	1.9	18.6	9.7
Susceptible accessions										
Bayo Mex	México State	Nueva Granada	I	T	Beige	42	50.1	38.5	—	44.3
Jamapa	Veracruz State	Mesoamerica	II	S	Black	20	47.1	22.9	88.7	52.9

^a Unlike the other accessions, which are landraces, this is derived from a 3-way cross: Canario/Zac-9-I-7//Canario 101

^b According to Singh et al. (1991)

^c According to Singh (1982)

Table 2 Mean percentage of damage for mid-parent, F₁, F₂, and backcrosses; and segregation for resistant, intermediate, and susceptible genotypes for *A. godmani* in eight F₂ and two backcross

Population	Mean percentage of damage			Phenotypic segregation			Expected ratio	χ^2
	Mid-parent	F ₁	F ₂	Resistant (R)	Intermediate (I)	Susceptible (S)		
Bayo Mex/Amarillo 153	30.0	32.2	17.9	53	27	10	9R:3I:4S	13.13 ^a
Bayo Mex/Puebla 36	27.3	29.5	26.6	32	18	23	9R:3I:4S	4.60
Jamapa/Amarillo 153	27.6	15.8	19.3	33	13	19	9R:3I:4S	0.87
Jamapa/Amarillo 169	27.6	30.6	15.2	49	10	16	9R:3I:4S	2.08
Jamapa/Hidalgo 58	29.6	37.9	20.2	31	17	30	9R:3I:4S	3.97
Jamapa/J 117	24.6	11.9	14.4	32	12	11	9R:3I:4S	0.86
Jamapa/Pinto Texcoco	30.7	27.1	15.6	60	26	28	9R:3I:4S	1.27
Jamapa/Pinto 168	28.3	18.5	17.7	40	17	26	9R:3I:4S	2.42
Jamapa//Jamapa/Pinto 168	26.5	28.5	–	16	13	42	1R:1I:2S	2.63
Pinto 168//Jamapa/Pinto 168	11.8	9.1	–	25	5	3	1R:0I:0S	1.94

^a Probability < 0.05. All other probabilities > 0.05

Table 3 Percentage of damage by *A. godmani* for mid-parent, F₁, and F₂ for 21 diallel crosses among seven resistant accessions of common bean evaluated at INIFAP-Santa Lucía de Pías, Texcoco, Mexico, in 1994

Cross	Mid-parent	F ₁	F ₂
Amarillo 153/Amarillo 169	17.3	8.2	13.8
Amarillo 153/Hidalgo 58	18.1	11.5	15.1
Amarillo 153/J 117	10.9	10.0	6.8
Amarillo 153/Pinto Texcoco	22.8	24.1	17.1
Amarillo 153/Pinto 168	16.3	17.4	13.4
Amarillo 153/Puebla 36	17.0	15.7	14.3
Amarillo 169/Hidalgo 58	15.3	5.4	7.0
Amarillo 169/J 117	8.1	9.0	7.4
Amarillo 169/Pinto Texcoco	20.1	24.4	17.4
Amarillo 169/Pinto 168	13.6	13.1	18.4
Amarillo 169/Puebla 36	14.2	18.9	13.0
Hidalgo 58/J 117	8.9	13.1	7.3
Hidalgo 58/Pinto Texcoco	20.9	19.1	15.1
Hidalgo 58/Pinto 168	14.4	10.0	7.8
Hidalgo 58/Puebla 36	15.0	18.1	15.9
J 117/Pinto Texcoco	13.9	17.0	11.7
J 117/Pinto 168	7.1	10.3	7.7
J 117/Puebla 36	7.8	7.6	9.0
Pinto Texcoco/Pinto 168	19.2	20.3	22.3
Pinto Texcoco/Puebla 36	19.8	16.3	20.6
Pinto 168/Puebla 36	13.3	10.7	20.6

be susceptible. Moreover, the F₂ population Amarillo 169/Pinto 168 segregated into 12 resistant: 3 intermediate: 1 susceptible (Table 4). The F₂ of Pinto Texcoco/Pinto 168 gave a good fit to 9 resistant:6 intermediate:1 susceptible.

Table 4 Segregation for resistant, intermediate, and susceptible genotypes for damage by *A. godmani* in two F₂s of resistant × resistant crosses of common bean evaluated at INIFAP-Santa Lucías de Pías, Mexico, in 1994

Cross	Resistant (R)	Intermediate (I)	Susceptible (S)	Expected ratio	χ^2
Amarillo 169/Pinto 168	69	19	7	12R:3I:1S	0.34 ^a
Pinto Texcoco/Pinto 168	48	26	8	9R:6I:1S	2.42 ^a

^a Probability > 0.05

populations of common bean obtained by crossing resistant sources with susceptible testers (cv Bayo Mex and/or Jamapa) and evaluated in 1992 at INIFAP-Santa Lucía de Pías, Texcoco, Mexico

Discussion

Variation in the percentage of damage from one year to the next (Table 1) was caused largely by differences in BPW infestation levels. Similar differences in BPW damage levels throughout BPW-affected regions, cropping systems, and years have been recorded by Shivakoti et al. (1989) and Garza and Castillo (1991) in Mexico, and by Beebe et al. (1993) in Central America. Because rearing the insect in captivity and obtaining uniform levels of artificial infestation are not feasible, access to a reliable site such as Santa Lucía de Pías in Mexico is essential for successful germ plasm evaluation and genetic and selection studies. Moreover, the damage scores shown in Table 1 suggest that more dependable evaluations would be obtained from data obtained across environments, and that no absolute values for BPW damage can be assigned to resistant versus susceptible genotypes. Susceptible and resistant checks must therefore be grown repeatedly at frequent intervals in each nursery and in each environment, and resistant genotypes should be identified on the basis of their lack of damage, compared with susceptible checks. Because insect pressure may not be uniform throughout the nursery, necessary adjustments (e.g., use of moving mean values) must also be made to accurately differentiate between resistant and susceptible genotypes.

Two genes probably control the inheritance of resistance to BPW in each of 'Amarillo 153', 'Amarillo 169',

'Hidalgo 58', 'J 117', 'Pinto 168', 'Pinto Texcoco', and 'Puebla 36' since: (1) the F_1 of crosses between the susceptible cultivar 'Jamapa' and/or 'Bayo Mex' and seven sources of resistance was intermediate to resistant, and (2) the F_2 populations gave a good fit to 9 resistant: 3 intermediate: 4 susceptible segregation pattern (Table 2). However, when one dominant gene was present alone, intermediate levels of resistance to BPW were expressed. When the other dominant gene was alone, it had no effect (a null allele) and a susceptible genotype resulted. But when dominant alleles for both genes were present, their interaction resulted in a higher BPW resistance. The gene symbols *Agr* (*A. godmani* resistance) and *Agm* (for *A. godmani* resistance modifier) are proposed for the two independently segregating genes for BPW resistance.

Compared with the expected ratios, the number of susceptible plants was lower and the number of plants with intermediate resistance was higher in the cross Bayo Mex/Amarillo 153. These differences may have resulted from misclassification through low BPW pressure. Moreover, segregation distortions also have been reported by Koenig and Gepts (1989), Paredes and Gepts (1995) and Welsh et al. (1995) in interracial and intergene pool crosses of common bean. 'Amarillo 153' belongs to the Middle American race Jalisco, whereas 'Bayo Mex' belongs to the Andean race Nueva Granada (Singh et al. 1991).

A single dominant gene for resistance to BPW may exist in each of these common-bean accessions from the Mexican highlands. In addition, the role and expression of another dominant gene are probably dependent on the prevailing environment (temperature, humidity, light quality, BPW population pressure). These two factors may explain (1) the lack of resistance found in Guatemalan sources of resistance when grown in Mexican highlands, and (2) the loss of resistance in Mexican highland sources that have been transferred into germ plasm adapted to Central American tropical lowland environments and brought back to the Mexican highlands (our unpublished data). The interaction between resistance genes, environments, and BPW infestation levels merits further research.

The mean percentages of damage by the BPW to the 21 F_1 hybrids and 21 F_2 populations from crosses among seven sources of resistance give the impression that the F_1 hybrids and F_2 populations were all resistant. If this were true, and no evidence for susceptible recombinants were found in any F_2 population, then we could conclude that the resistance genes present in the seven landraces were one and the same. Moreover, differences in their levels of resistance would result from an allelic series at either locus and/or modifying genes. The data taken on individual plants in the two F_2 populations, however, showed some susceptible segregants (Table 4). Moreover, the approximate segregations into 12 resistant:3 intermediate:1 susceptible for Amarillo 169/Pinto 168 or 9 resistant:6 intermediate:1 susceptible for Pinto Texcoco/Pinto 168 indicated that

two dominant genes control resistance to BPW in these common-bean accessions and that the genes were not necessarily allelic in all three parents. For example, 'Pinto 168' and 'Pinto Texcoco' had different, independently segregating genes that conditioned intermediate resistance when present alone, but their combined action imparted higher levels of resistance. Similarly, one of the dominant genes in 'Amarillo 169' expressed resistance, irrespective of the alleles at the other locus whose dominant allele, when alone, conditioned intermediate resistance. Why was the effect of this resistance gene not fully expressed when crossed with susceptible 'Jamapa' and evaluated in 1992? How did the role of the modifier gene *Agm* change in these resistant \times resistant crosses in 1994? The reasons may lie in the occurrence of the *Agm* gene, whose action and interaction may change with environment, genetic background, and/or BPW population pressure.

Although the resistant and susceptible parents have been evaluated for BPW damage for 3 or more years, no attempts had been made to pure-line them before initiating this study. Thus, the possibility of some parents being genotypic mixtures, albeit in low frequency, means that the existence of some susceptible genotypes cannot be ruled out. To detect and eliminate environmental effects and to clarify further the allelic or non-allelic nature of BPW resistance genes, we need further research on purifying parental lines; additional crosses, backcrosses, and F_3 -progeny tests; developing and evaluating recombinant inbred lines; and identifying molecular markers linked to the resistance genes. Such research will also minimize our dependence on natural infestation by BPW for germ plasm evaluation and genetic and selection studies, and thus expedite breeding processes. At present, only one crop per year can be grown in the Mexican highlands under conditions of BPW infestation.

Once different non-allelic genes for BPW resistance have been determined for common bean accessions, efforts should be made to combine them so to broaden the genetic base and increase resistance levels. Immunity to BPW, however, has not yet been found in any accession; thus justifying continued germ plasm screening for better and newer sources of resistance.

The fact that resistance was controlled by two genes may help explain the relative ease of transferring resistance into susceptible Central American common-bean cultivars by conventional pedigree and F_2 -derived family methods of evaluation and selection (Beebe et al. 1993). Moreover, it should be feasible to combine BPW resistance with other desirable agronomic traits such as resistance to BCMV, bruchids (*Zabrotes subfaciatus* Boheman), anthracnose (caused by *Colletotrichum lindemuthianum* (Sacc. and Magnus)), bean golden mosaic virus, and common bacterial blight (caused by *Xanthomonas campestris* pv *phaseoli* (Smith and Dye)). Evaluating common-bean pods and seeds for BPW damage is tedious, laborious, and time-consuming. The population size needed for screening increases exponen-

tially every filial generation, which further delays evaluation and selection. Now that we know that BPW resistance is either dominant or intermediate, we suggest that multiple parent F_1 hybrids be screened for BPW damage, and that gamete selection (Singh 1994) be used to facilitate simultaneous improvement of the above-mentioned agronomic traits and BPW resistance.

Acknowledgements We are most grateful to the Swiss Development Corporation and PROFRIJOL for financial support to carry out field evaluations in Mexico, to Henry Terán for data analysis, to Aracelly Fernández and Beatriz Arenas for secretarial assistance, and to Elizabeth de Páez for editorial help. Our special thanks are due to Dr. Daniel Debouck and his associates for phaseolin-protein analysis of resistant and susceptible parents used in hybridization.

References

- Acosta J, Rosales R, Garza R (1992) Resistance to the pod weevil in wild *Phaseolus vulgaris*. *Annu Rep Bean Improv Coop (CO)* 35:103–104
- Beebe S, Cardona C, Díaz O, Rodríguez F, Mancía E, Ajuquey S (1993) Development of common bean (*Phaseolus vulgaris* L.) lines resistant to the pod weevil, *Apion godmani* Wagner, in Central America. *Euphytica* 69:83–88
- Bliss FA (1980) Common bean. In: Fehr WR, Hadley HH (eds) *Hybridization of crop plants*. American Society of Agronomy, Madison, Wisconsin, pp 273–284
- Buishand TJ (1956) The crossing of bean (*Phaseolus* spp.). *Euphytica* 5:41–50
- Cardona C (1989) Insects and other invertebrate bean pests in Latin America. In: Schwartz HF, Pastor-Corrales MA (eds) *Bean production problems in the tropics*, 2nd edn. CIAT, Cali, Colombia, pp 505–570
- Garza R (1992) Identificación de los componentes de la resistencia al ataque del picudo del ejote, *Apion godmani*, que poseen los materiales de frijol seleccionados. In: Informe de investigación 1991 del proyecto *Apion* en México. SARH-INIFAP-CEVAMEX, Chapingo, Mexico, pp 13–22
- Garza R, Castillo S (1991) Selección de genotipos de frijol resistentes al ataque del picudo del ejote *Apion* spp. In: Informe 1990 del proyecto *Apion* en México. SARH-INIFAP-CEVAMEX, Chapingo, Mexico, pp 2–12
- Garza R, Muruaga JS (1993) Resistencia al ataque del picudo del ejote *Apion* spp. en frijol *Phaseolus* spp. *Agron Mesoam* 4:77–80
- Guevara J (1961) El combate del picudo del ejote mediante la combinación de variedades resistentes e insecticidas. *Agríc Téc Méx* 1(2):17–19
- Guevara J, Patiño G, Casas E (1962) Selección de variedades de frijol resistentes al picudo del ejote. *Agríc Téc Méx* 1(10):10–12
- Koenig R, Gepts P (1989) Segregation and linkage of genes for seed proteins, isozymes, and morphological traits in common bean (*Phaseolus vulgaris*) *J Hered* 80:455–459
- Mancía JE (1973) Evaluación de variedades de frijol tolerantes al picudo de la vaina *Apion godmani* (Wagn). *SIADES (El Salvador)* 2:15–20
- McKelvey JJ, Guevara J, Cortés A (1947) *Apion* pod weevil: a pest of beans in Mexico. *J Econ Entomol* 40:476–479
- Paredes OM, Gepts P (1995) Segregation and recombination in inter-gene pool crosses of *Phaseolus vulgaris* L. *J Hered* 86:98–106
- Ramírez M, Casas E, Rubio A (1959) Susceptibilidad de algunas variedades de frijol al picudo del ejote en la Mesa Central. *Agríc Téc Méx* 1(7):6, 37–38
- Shivakoti GP, Domínguez B, Vera J (1989) Pérdidas en frijol causadas por el picudo del ejote *Apion godmani* Wagn. *Agrociencia* 76:231–241
- Singh SP (1982) A key for identification of different growth habits of *Phaseolus vulgaris* L. *Annu Rep Bean Improv Coop (CO)* 25:92–94
- Singh SP (1994) Gamete selection for simultaneous improvement of multiple traits in common bean. *Crop Sci* 34:352–355
- Singh SP, Gepts P, Debouck DG (1991) Races of common bean (*Phaseolus vulgaris*, Fabaceae). *Econ Bot* 45:379–396
- Welsh W, Bushuk W, Roca W, Singh SP (1995) Characterization of agronomic traits and markers of recombinant inbred lines from intra- and inter-racial populations of *Phaseolus vulgaris* L. *Theor Appl Genet* 91:169–177