# Comparative Responses of Selected *Phaseolus vulgaris* Germ Plasm Inoculated Artificially and Naturally with Bean Golden Mosaic Virus

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**ABSTRACT**

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A total of 44 bean (*Phaseolus vulgaris* L.) genotypes was evaluated for disease reactions to bean golden mosaic virus (BGMV) by mechanical and whitefly inoculation under glasshouse and field conditions, respectively. Most of the genotypes reacted similarly under both screening conditions, with a few discrepancies ascribed to the poor adaptation of some temperate bean genotypes to the tropical conditions of the field evaluation site (Monjas, Guatemala). The mechanical inoculation technique made possible the observation of different plant responses, namely delayed symptom expression, tolerance, and disease escape in diverse cultivars. However, most of the bean cultivars tested were severely affected when test plants were mechanically inoculated with BGMV at the beginning of the primary leaf stage. The glasshouse evaluation of six parental genotypes used to develop two highly BGMV-resistant lines, DOR 303 and A 429, showed all six parents to be BGMV-susceptible, suggesting the occurrence of transgressive segregation. The experimental bean lines NW 59 and 63, selected for their immunity to a leafhopper-transmitted bean geminivirus (beet curly top virus), proved susceptible to BGMV under both field and glasshouse conditions, demonstrating a marked difference in the genetics of resistance to these two geminiviruses in *P. vulgaris*. It is concluded here that, while field evaluations are needed to screen segregating populations, the mechanical inoculation of bean genotypes with BGMV yields valuable information on their response to the virus and potential use as parents for breeding purposes.

Bean golden mosaic is the most devastating viral disease of beans (*Phaseolus vulgaris* L.) in Latin America, particularly in Brazil, Mexico, Dominican Republic, and Guatemala (7). This disease is caused by a geminivirus, bean golden mosaic virus (BGMV), transmitted by the whitefly *Bemisia tabaci* Genn. (7). This virus characteristically induces intense foliar yellowing, severe pod distortion, and plant stunting in susceptible bean cultivars (6). Yield losses are often 100% due to the malforming effect of the virus on the pods (7) and, also, to the high incidence of flower abortion in BGMV-infected plants. To date, not a single bean cultivar among thousands of germ plasm accessions tested has proved to be immune to the virus. Some black-seeded cultivars, however, are not as severely affected under moderate BGMV incidence (7). These cultivars, particularly Porrillo Sintetico and Turrialba 1, have been extensively used as parents to develop over 95% of all the bean lines bred for golden mosaic resistance in Latin America.

The golden mosaic evaluation of local and improved bean germ plasm has traditionally taken place under field conditions due to the difficulty of achieving successful mechanical transmission of BGMV and of maintaining *B. tabaci* colonies. Although knowledge of the field behavior of bean germ plasm under natural BGMV incidence is critical, several factors often hinder the interpretation of field data. One of the main limitations is the direct relationship that exists between BGMV incidence and the dynamics of whitefly populations. A low or late incidence of viruliferous whiteflies often results in a low disease incidence and a moderate disease reaction. Also, other pathogens, pests, and abiotic factors affect plants in nature, and it is difficult to discriminate between plant and insect resistance mechanisms in germ plasm evaluated in the field. All of these variables have important implications in the design and outcome of BGMV breeding projects. This paper analyzes the results of the comparative evaluation of selected bean genotypes for their reaction to BGMV transmitted by *B. tabaci* under field conditions and mechanically under glasshouse conditions.

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## MATERIALS AND METHODS

**Virus source and inoculation procedures.** The field evaluation was conducted in the locality of Monjas, Guatemala (elevation 961 m; mean temperature 28 C, and mean annual rainfall 957 mm). The main breeding host for the whitefly vector in the area is tomato. The BGMV isolate used in the glasshouse for the mechanical transmission tests was also obtained at this locality. Tissue from 14-day-old bean plants showing initial golden mosaic symptoms was ground (1:4, w/v) in cold 0.1 M potassium phosphate buffer, pH 7.6 (1). The inoculum was applied onto Carborundum-dusted (600 mesh) primary leaves of 8-day-old Topcrop bean seedlings using sterile cotton swabs. The inoculated test plants were maintained for a day under reduced light conditions (870 $\mu E \cdot m^{-1} \cdot s^{-1}$ av.) and then transferred to a glasshouse with a maximum light intensity of 1,100 $\mu E \cdot m^{-1} \cdot s^{-1}$, an average temperature of 27 C, and relative humidity of 75%. The test plants remained under these conditions until physiological maturity. This artificial inoculation procedure in the glasshouse was repeated several times, especially in those cases where golden mosaic symptoms were not clearly expressed or whenever an interesting observation was made. The field data were also supported by previous evaluations made by other members of the CIAT Bean Program.

**Effect of plant age.** In order to investigate the effect of seedling age at the time of inoculation on plant susceptibility to BGMV, the cultivar Porrillo Sintetico was sown in the glasshouse at 24-hr intervals for a week and then mechanically

inoculated with BGMV 1 wk after the last sowing date. In a different test, three 8-day-old and five 12-day-old seedlings of each of three bean cultivars, Great Northern 31, Porrillo Sintetico, and Red Mexican 35, were inoculated mechanically with BGMV. One month later, the inoculated plants were individually assayed for BGMV using the immunosorbent electron microscopy (ISEM) technique (4,11).

**Virus purification.** Bean golden mosaic virus was purified from systemically-infected Topcrop bean leaves harvested 8 days after the plants were mechanically inoculated. Frozen (−80 C) leaf tissue (30 g) was homogenized with a blender in 60 ml of 0.1 M phosphate buffer, pH 7.5, containing 1% 2-mercaptoethanol and 0.1% Driselase (9). This mixture was stirred at 10 C for 1 hr, filtered through cheesecloth, and then centrifuged at 10,400 *g* for 15 min. The resulting supernatant was mixed with 4% polyethylene glycol (PEG 8,000), 1% sodium chloride, and 0.5% Triton X 100, and then stirred at 10 C for 2 hr. The mixture was centrifuged at 10,400 *g* for 15 min, and the resulting pellet was resuspended overnight in 10 ml of 0.01 M phosphate buffer, pH 7.5, at 4 C. This suspension was centrifuged at 12,100 *g* for 10 min, and the resulting supernatant was centrifuged at 170,000 *g* for 90 min. The pellet obtained after the second centrifugation was allowed to resuspend for 2 days in 1 ml of 0.01 M phosphate buffer, pH 7.5, at 4 C, before a final centrifugation at 12,100 *g* for 10 min. The clarified supernatant was then layered on a log-linear sucrose gradient (2) prepared in 0.01 M phosphate buffer, pH 7.5, and centrifuged at 150,000 *g* for 270 min in a Beckman SW-41 rotor. An ultraviolet-absorbing band located approximately 22 mm from the bottom of the 12-ml tube (14 × 89 mm) was recovered with the aid of an ISCO density gradient fractionator. The collected fraction was diluted with 0.01 M phosphate buffer, pH 7.5, to a final volume of 10 ml, and then subjected to high speed centrifugation at 170,000 *g* for 90 min. The resulting pellet was left 4 days resuspending in 0.5 ml of 0.01 M phosphate buffer, pH 7.5, at 4 C. This suspension was further purified in a preformed 20–30% $CsSO_4$ gradient prepared in 0.01 M phosphate buffer, pH 7.5, by centrifuging at 120,000 *g* for 270 min in a Beckman SW 65 rotor. A visible zone located 20 mm from the bottom of the 5.5-ml tube was collected in a dropwise manner through a needle hole punched in the bottom of the tube. The fraction collected was diluted with 0.01 M phosphate buffer and concentrated by ultracentrifugation at 170,000 *g* for 90 min. The pellet obtained was finally resuspended in 0.3 ml of 0.01 M phosphate buffer, pH 7.5.

**Serology.** An antiserum to BGMV was prepared by injecting a New Zealand white rabbit with a purified virus preparation standardized to a concentration of 1 mg/ml, using an extinction coefficient of 7.7 (8). A series of four injections of 0.15 ml each of the virus, emulsified with an equal volume of Freund's complete (first injection) or incomplete (subsequent injections) adjuvant, was given to the rabbit at weekly intervals using the toe-pad immunization technique (12). The rabbit was first bled 1 wk after the last injection.

The immunosorbent electron microscopy (ISEM) tests involved a modification of the technique described by Roberts et al (11). Formvar- and carbon-coated 200-mesh copper grids were incubated for 1 hr with a drop of 1:50 dilution of bean golden mosaic virus antiserum in 0.01 M phosphate buffer, pH 7.5, at room temperature. Young trifoliate leaves of bean golden mosaic-affected Topcrop bean plants were ground in 200 µl of 0.01 M phosphate buffer and centrifuged at 8,000 *g* for 15 min. After incubation for 1 hr with the diluted antiserum, the grids were washed with 0.01 M phosphate buffer, pH 7.5, and floated on a drop of infected plant extract for 4 hr at 4 C. The grids were then washed with bidistilled water and stained with a drop of a 2% aqueous solution of uranyl acetate for 2 min. The grids were observed at 50,000 magnification using JEOL 100 SX electron microscope.

**Test cultivars and experimental lines.** A total of 44 bean genotypes was selected for this study according to different criteria. Four black-seeded cultivars (ICA-Pijao, Porrillo 70, Porrillo Sintetico, and Turrialba 1) were chosen as the most common sources of BGMV resistance used to date, together with the first four cultivars (ICTA-Jutiapan, ICTA-Quetzal, ICTA-Tamazulapa, and Negro Huasteco) derived from these parents. Two new experimental lines, A 429 and DOR 303, recently found to possess the highest level of BGMV resistance observed so far, and their parents Garrapato × (Porrillo Sintetico × G 02115), and (Porrillo Sintetico × Cacahuate 72) × (Moeda × Cacahuate 72) × Red Kloud, respectively, were also included in the test (G 02115 and Moeda were only tested by mechanical inoculation). A set of 19 cultivars (Amanda, Black Turtle Soup, Dubbele Witte, Great Northern 31, Great Northern 123, Improved Tendergreen, Imuna, Jubila, Michelite, Monroe, Pinto 114, Puregold Wax, Red Mexican 34, Red Mexican 35, Redlands Greenleaf B, Redlands Greenleaf C, Stringless Green Refugee, Topcrop, and Widusa) used to characterize bean common mosaic virus (BCMV) strains (6) was tested because of its different genetic composition. Alubia, Blanco INIA, Michigan Dark Red Kidney, Mochis 440, Pompadour Checa, Rabia de Gato, and Royal Red were tested as representative grain types found in some golden mosaic-affected regions of Latin America. Finally, three experimental lines (NW 59, NW 63, and NW 395), released as curly top immune or resistant bean cultivars by the USDA and the Agricultural Experiment Stations of Idaho, Oregon, and Washington, were also tested here despite the different insect vector (leafhoppers) of the beet curly top geminivirus (BCTV). Three main symptoms were recorded for all test plants, mosaic, stunting, and flower abortion, on the understanding that the expression of these symptoms can be affected by adverse environmental conditions or plant adaptation problems.

## RESULTS AND DISCUSSION

Table 1 shows a close agreement between the field and glasshouse results

**Table 1.** Evaluation of improved bean genotypes and their parents for golden mosaic resistance under field and glasshouse inoculation conditions

| | Symptoms[a] and inoculation method | |
|---|---|---|
| Bean genotype | Field (whitefly vector) | Glasshouse (mechanical) |
| A 429 | ML, SL, AL | ML, SL, AL |
| Cacahuate 72 | MH, SL, AI*[b] | MH, SL, AI |
| DOR 303 | V (0, MH, SH, AH) | V (0, MH, SI, AH) |
| Garrapato | ML, SI, AI | ML, SI, AH |
| G 2115 | ··· | MH, SI, AH |
| ICA-Pijao | MI, SL, AI | MI, SL, AI |
| ICTA-Jutiapan | MI, SL, AI | MI, SL, AI |
| ICTA-Quetzal | MI, SL, AI | MI, SL, AI |
| ICTA-Tamazulapa | MI, SL, AI | MI, SL, AI |
| Moeda | ··· | MH, SI, AH |
| Negro Huasteco | MI, SL, AI | MI, SL, AI |
| Porrillo 70 | MI, SL, AI | MI, SL, AI |
| Porrillo Sintetico | MI, SL, AI | MI, SL, AI |
| Red Kloud | MI, SL, AH | MH, SL, AH |
| Turrialba 1 | MI, SL, AI | MI, SL, AI |

[a] First letter: 0 = symptomless, M = mosaic, S = stunting, A = flower abortion, V = variable reaction (combinations of 0 and M, S, and A). Second letter is degree of symptom expression: L = mild, I = moderate, H = severe, ··· = not tested.

of the evaluation of selected bean cultivars and experimental lines. The glasshouse inoculation test of experimental lines A 429 and DOR 303 confirms the high level of resistance observed during this investigation for A 429 (moderate symptom expression and acceptable yield) and DOR 303 (symptomless plants are observed under moderate disease pressure) under field conditions. Some DOR 303 plants, however, exhibited severe stunting and plant malformation under both field and glasshouse conditions. Another interesting observation in relation to these two experimental lines is that none of their parents (Cacahuate 72, Garrapato, G 2115, Moeda, Red Kloud, or Porrillo Sintetico) exhibits a level of resistance as high as their offspring, suggesting the occurrence of transgressive segregation.

The three ICTA cultivars, Negro Huasteco, and their parents (Porrillo Sintetico, Porrillo 70, ICA-Pijao, and Turrialba 1), reacted similarly to BGMV under both field and glasshouse conditions (Table 1). These black-seeded genotypes share common parents (Porrillo and Turrialba 1) and possess similar agronomic characteristics, including adaptation to a wide range of geographical environments. All eight genotypes tend to delay symptom expression and are not severely affected when infected after the first month of plant development.

Results in Table 2 indicate that the increasing age of Porrillo Sintetico plants causes them to become resistant to mechanical inoculation with BGMV. The steep infection gradient over time, observed in the glasshouse, is not apparent under natural conditions, probably due to the continuous exposure of field-grown plants to viruliferous whiteflies. In our glasshouse experiments, Porrillo Sintetico is consistently one of the last cultivars to show golden mosaic symptoms, and, if inoculated 10 days after sowing, many plants do not develop symptoms. All 15 of the Porrillo Sintetico, Great Northern 31, and Red Mexican 35 plants mechanically inoculated with BGMV 12 days after sowing remained symptomless, and the virus could not be detected by ISEM in any of the 45-day-old plants tested. On the contrary, all nine plants of these three cultivars mechanically inoculated 8 days after sowing showed characteristic golden mosaic symptoms, and BGMV was detected by ISEM (Fig. 1) in all nine of the plants at age 45 days, with an average particle increase factor of approximately 190 (11). The ability of Porrillo Sintetico and related genotypes, such as ICA-Pijao and the ICTA cultivars, to produce pods when infected with BGMV is variable under both field and glasshouse conditions, and seems to be negatively affected by adverse environmental conditions (mainly high temperature) that aggravate the incidence of flower abortion induced by the virus.

As shown in Table 3, there were some discrepancies between field and glasshouse evaluations. Cultivars Blanco INIA (Great Northern 164557), Michigan Dark Red Kidney, Royal Red, and the NW lines developed for temperate environments, showed poor adaptation in Guatemala. Under such conditions, it is difficult to discriminate between BGMV symptoms, such as stunting and flower abortion, and poor plant adaptation. Most of these cultivars grew better under glasshouse conditions where light intensity, temperature, and day length were partially controlled. The glasshouse evaluation of these cultivars led to the detection of genotypes, such as Blanco INIA, which possess potentially valuable disease resistance traits. The susceptible reaction of the NW lines to BGMV (Table 3) clearly indicates that the genetics of resistance to BGMV and BCTV in *P. vulgaris* is not the same. The large, white-seeded cultivar Alubia proved to be one of the most BGMV-susceptible genotypes both in the glasshouse and field tests. The comparative field and glasshouse evaluations of Mochis 440 (BGMV-tolerant cultivar from Mexico), Rabia de Gato (BGMV-susceptible cultivar from Guatemala), and Pompadour Checa (BGMV-susceptible cultivar from Dominican Republic) were also very similar (Table 3).

Most of the 19 BCMV differential cultivars showed poor adaptation in Guatemala, emphasizing the value of the artificial inoculation procedure to screen exotic bean germ plasm for golden mosaic resistance. In the glasshouse, the genotypes tested showed a variety of disease reactions (Table 4). For instance, the cultivar Redlands Greenleaf C was easily infected by mechanical means and it showed early golden mosaic symptoms, but it did not suffer severe growth or yield reduction. Therefore, Redlands Greenleaf C is considered in this study as a BGMV-tolerant genotype. Pinto 114 exhibited only moderate golden mosaic symptoms in the field, and many mechanically-inoculated plants did not develop symptoms in the glasshouse. Many Great Northern 31 and Blanco INIA plants also remained symptomless after mechanical inoculation, although the significance of this observation could not be investigated under field conditions due to the poor adaptation of these genotypes in

**Table 2.** Effect of plant age on susceptibility of the bean cultivar Porrillo Sintetico to infection by mechanical inoculation with bean golden mosaic virus under glasshouse conditions

| Plant age[a] (days) | Percentage of plants showing golden mosaic symptoms[b] | |
|---|---|---|
| | Trial 1 | Trial 2 |
| 7 | 100 | 100 |
| 8 | 80 | 100 |
| 9 | 50 | 90 |
| 10 | 20 | 60 |
| 11 | 0 | 50 |
| 12 | 0 | 0 |
| 13 | 0 | 0 |

[a] Age (from sowing time) when the test plants were inoculated.
[b] Ten plants mechanically inoculated per sowing date.

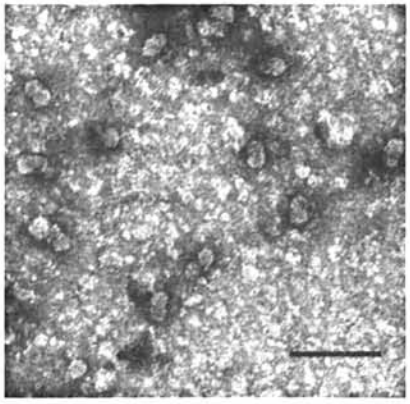

**Fig. 1.** Bean golden mosaic virus particles detected by immunosorbent electron microscopy in infected bean tissue extracts. Scale bar = 100 nm.

**Table 3.** Reaction of selected bean cultivars to bean golden mosaic virus inoculated under field conditions by the whitefly vector, and in the glasshouse by mechanical means

| Bean cultivar | Symptoms[a] and inoculation method | |
|---|---|---|
| | Field (whitefly vector) | Glasshouse (mechanical) |
| Alubia | MH, SH, AH | MH, SH, AH |
| Blanco INIA | ML, SI, AI | V (0, MI, SI, AI) |
| Michigan Dark Red Kidney | MH, SI, AI | MH, SL, AI |
| Mochis 440 | MI, SI, AI | MI, SI, AI |
| NW 59 | MI, SI, AH | V (0, MH, SI, AH) |
| NW 63 | MI, SI, AH | V (0, MH, SI, AH) |
| NW 395 | MI, SI, AH | V (0, MI, SL, AI) |
| Pompadour Checa | MH, SH, AI | MH, SI, AL |
| Rabia de Gato | MH, SI, AI | MH, SI, AI |
| Royal Red | MH, SI, AI | MH, SL, AI |

[a] First letter: 0 = symptomless, M = mosaic, S = stunting, A = flower abortion, V = variable reaction (combinations of 0 and M, S, and A). Second letter is degree of symptom expression: L = mild, I = moderate, H = severe.

**Table 4.** Reaction of 10 standard groups of bean genotypes used to differentiate strains of bean common mosaic virus to bean golden mosaic virus inoculated under field conditions by the whitefly vector, and in the glasshouse by mechanical means

| Resistance group[a] | Differential cultivar | Symptoms[b] and inoculation method | |
|---|---|---|---|
| | | Field (whitefly vector) | Glasshouse (mechanical) |
| | **Cultivars with recessive alleles of the necrosis gene[c]** | | |
| 1 | Dubbele Witte | MI, SI, AH | MI, SL, AH |
| | Stringless Green Refugee | MH, SI, AH | MH, SI, AH |
| 2 | Redlands Greenleaf C | MH, SI, AI | MH, SL, AL |
| | Puregold Wax | MH, SI, AH | MH, SI, AH |
| | Imuna | MH, SH, AH | MH, SI, AH |
| 3 | Redlands Greenleaf B | MH, SI, AH | MH, SL, AI |
| | Great Northern 123 | MI, SH, AH | MH, SH, AH |
| 4 | Michelite 62 | MI, SH, AH | MH, SI, AH |
| | Red Mexican 34 | MI, SI, AH | MI, SI, AI |
| 5 | Pinto 114 | MI, SI, AL | V (0, MI, SI, AI) |
| 6 | Monroe | MI, SI, AH | MI, SI, AH |
| | Great Northern 31 | ML, SI, AI | V (0, MI, AI) |
| | Red Mexican 35 | MI, SI, AI | V (0, MI, AI, L) |
| | **Cultivars with dominant alleles of the necrosis gene[d]** | | |
| 7 | Widusa | MI, SI, AH | MH, SI, AI |
| | Black Turtle Soup | MI, SI, AH | MH, SI, AH |
| 8 | Jubila | MI, SI, AH | MH, SI, AH |
| 9 | Topcrop | MH, SH, AH | MH, SH, AH |
| | Improved Tendergreen | MH, SI, AH | MH, SI, AH |
| 10 | Amanda | MH, SI, AH | MH, SI, AH |

[a] According to Drijfhout (5) for bean common mosaic virus.
[b] First letter: 0 = symptomless, M = mosaic, S = stunting, A = flower abortion, V = variable reaction (combinations of 0 and M, S, and A), L = local necrotic lesions on inoculated leaves. Second letter is degree of symptom expression: L = mild, I = moderate, H = severe.
[c] Common mosaic-susceptible cultivars.
[d] Common mosaic-resistant cultivars.

Guatemala (Tables 3 and 4). However, both cultivars possess valuable resistance genes to bean common mosaic (6), bean yellow mosaic (F. Morales, *unpublished data*), and bean southern mosaic (10) viruses. Should this ability to remain symptomless prove to be heritable and operative in the presence of the insect vector, it would be worth exploiting in breeding programs. Red Mexican 35 was also difficult to infect with BGMV by mechanical inoculation, and most of the test plants exhibited necrotic local lesions on the inoculated primary leaves (Fig. 2). However, the expression of hypersensitivity in Red Mexican 35 is erratic, and its occurrence does not preclude the possibility of systemic infection of some plants by BGMV. All of the remaining 15 differential bean cultivars evaluated exhibited a high degree of BGMV susceptibility.

This investigation demonstrates that there is a variety of plant responses that may be related to resistance to BGMV in bean genotypes with seed colors other than black, which should be exploited to broaden the narrow genetic base of the existing germ plasm.

This study also shows that it is possible to screen bean genotypes by artificial inoculation with mechanically transmissible isolates of BGMV. The main limitation to the implementation of the mechanical BGMV inoculation technique is the apparent existence of non-mechanically transmissible BGMV strains in Brazil (3) and Argentina (F. Morales, *unpublished data*). Fortunately, all of the Central American and Caribbean isolates of BGMV tested can be mechanically transmitted and, also, the Latin American isolates of BGMV seem to differ more in their virulence than in their pathogenicity. In fact, the reported field susceptibility or tolerance of several Argentinian and Brazilian bean genotypes has been confirmed (F. Morales and A. Niessen, *unpublished data*) in mechanical inoculation tests with a Colombian isolate of BGMV.


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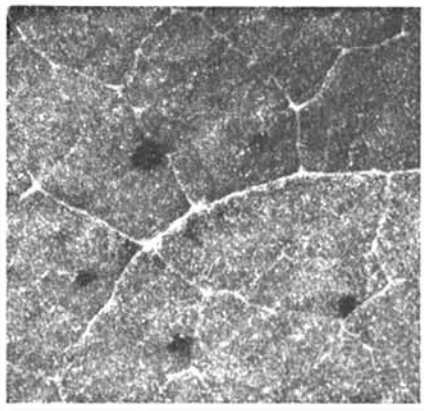

**Fig. 2.** Necrotic local lesions induced in the primary leaves of the bean cultivar Red Mexican 35 by mechanical inoculation with bean golden mosaic virus.

## LITERATURE CITED


1. Bird, J., Rodriguez, R., Monllor, A., and Sanchez, J. 1977. Transmisión del mosaico dorado de la habichuela (*Phaseolus vulgaris*) en Puerto Rico por medios mecánicos. Fitopatologia 12:28-30.
2. Brakke, M. K., and van Pelt, N. 1970. Linear-log sucrose gradient for estimating sedimentation coefficients of plant viruses and nucleic acids. Anal. Biochem. 38:56-64.
3. Costa, A. S. 1965. Three whitefly-transmitted virus diseases of beans in Sao Paulo, Brazil. FAO Plant Prot. Bull. 13:121-130.
4. Derrick, K. S. 1973. Quantitative assay for plant viruses using serologically specific electron microscopy. Virology 56:652-653.
5. Drijfhout, E. 1978. Genetic interaction between *Phaseolus vulgaris* and bean common mosaic virus with implications for strain identification and breeding for resistance. Agric. Res. Rep., Ctr. Agric. Publ. Doc. Wageningen. 98 pp.
6. Drijfhout, E., Silbernagel, M. J., and Burke, D. W. 1978. Differentiation of strains of bean common mosaic virus. Neth. J. Plant Pathol. 84:13-26.
7. Galvez, G. E., and Cardenas, M. R. 1980. Whitefly transmitted viruses. Pages 263-289 in: Bean Production Problems. H. F. Schwartz and G. E. Galvez, eds. Centro Internacional de Agricultura Tropical, Cali, Colombia. 424 pp.
8. Goodman, R. M., and Bird, J. 1978. Bean golden mosaic virus. Descriptions of Plant Viruses. 192. CMI/Assoc. Appl. Biol., Kew, Surrey, England.
9. Jaramillo, S., and Lastra, R. 1986. Purification and properties of the geminivirus Euphorbia mosaic virus. J. Phytopathol. 115:193-203.
10. Jayasinghe, U. 1982. Chlorotic mottle of bean (*Phaseolus vulgaris* L.). Ph.D. thesis. Agricultural University, Wageningen, Netherlands. 156 pp.
11. Roberts, I. M., Robinson, D. J., and Harrison, B. D. 1984. Serological relationships and genome homologies among geminiviruses. J. Gen. Virol. 65:1723-1730.
12. Ziemiecki, A., and Wood, K. R. 1975. Serological demonstration of virus-specific proteins associated with cucumber mosaic virus infection of cucumber cotyledons. Physiol. Plant Pathol. 7:171-177.