Chapter 16

BEETLE-TRANSMITTED VIRUSES

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The beetle-borne viruses of common beans have become widely distributed in the major bean-production areas of the world. The abundance of insect vectors, the high concentration of these mechanically transmissible viruses in infected plants, and seed transmission of some of these viruses are the main epidemiological factors. Although beetle-borne viruses belong to different virus groups, they all have isometric particles, are 25-30 nm in diameter, and their beetle vectors belong to the families of Chrysomelidae, Coccinellidae, and Meloidae.

Bean Southern Mosaic Virus

Bean southern mosaic virus (BSMV) is undoubtedly the most widely distributed of the beetle-borne viruses which infect beans. This virus was first observed in southern United States (hence its name) and now is present in all the main bean-production nations of the world (Costa, 1972; Cupertino et al., 1982; Ferault et al., 1969; Jayasinghe, 1982; Murillo, 1967; Yerkes and Patiño, 1960; Zaumeyer and Thomas, 1957). BSMV can cause significant yield losses of over 50% by reducing the amount and weight of seed produced by infected bean plants. The virus has a host range restricted to legumes with the possible exception of cucumber (*Cucumis sativus* L.) (Jayasinghe, 1982). Susceptible legumes include soybean (*Glycine max* (L.) Merrill), common bean (*Phaseolus vulgaris* L.), tepary bean (*P. acutifolius* A. Gray var. *acutifolius*), lima bean (*P. lunatus* L.), pea (*Pisum sativum* L.), *Trifolium alexandrinum* L., *Cyamopsis* sp., *Melilotus indica* (L.) All., and cowpea (*Vigna unguiculata* (L.) Walp. ssp. *unguiculata*)

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(Boswell and Gibbs, 1983; Jayasinghe, 1982). The type (bean) strain infects bean, soybean, and lima bean, but not cowpea, while the cowpea strain infects cowpea, soybean, pea, and *Cyamopsis* sp., but not bean (Shepherd and Fulton, 1962). In Latin America, BSMV is known as "mosaico sureño" (Spanish) or "mosaico-do-sul" (Portuguese).

In *Phaseolus vulgaris* BSMV can induce diverse symptoms such as mosaic or mottle, rugosity, epinasty, vein yellowing, stunting, and necrotic local lesions, depending on the variety inoculated (Boswell and Gibbs, 1983; Jayasinghe, 1982; Tremaine and Hamilton, 1983). Most Pinto lines such as Pinto U.I. 114, are good local-lesion assay hosts. The cultivar Bountiful is recommended for maintaining the virus and as a propagation host. *P. acutifolius* is particularly sensitive to BSMV, exhibiting various necrotic reactions upon inoculation with this virus. Several accessions of *P. coccineus* L. (scarlet runner bean), on the contrary, proved to be resistant to BSMV (Jayasinghe, 1982). In nature, however, BSMV is often isolated from bean plants that show mild leaf mottling and moderate leaf curling (Figure 119). Southern bean mosaic virus is often encountered in a mixture with other viruses such as bean rugose mosaic virus (BRMV) or bean yellow stipple virus (BYSV).

Bean southern mosaic virus is the type member of the sobemovirus group which characteristically have isometric particles 28-30 nm in diameter and contain one molecule of positive-sense single-stranded RNA (Boswell and Gibbs, 1983; Tremaine and Hamilton, 1983) (Figure 120). These virus particles are often present inside vacuoles of an infected mesophyll cell (Jayasinghe, 1982). BSMV has a thermal inactivation point between 90 and 95 ^{0}C, a dilution end point of 10^{-5} to 10^{-6}, and longevity in vitro of over three months at room temperature. There are several purification methods for virus isolation (Boswell and Gibbs, 1983; Jayasinghe, 1982; Tremaine and Hamilton, 1983).

The virus is seed-borne and can be carried both in the embryo (Uyemoto and Grogan, 1977) or as a contaminant on the seed coat (McDonald and Hamilton, 1972 and 1973). This virus, however, becomes inactivated upon the dehydration or storage of contaminated seeds (Cheo, 1955). Secondary transmission occurs naturally by several species of chrysomelid beetles such as *Cerotoma facialis*

Erickson, *C. trifurcata* Forster, *Diabrotica adelpha* Harold, *D. balteata* Le Conte, and *Epilachna varivestis* Mulsant (Boswell and Gibbs, 1983; Fulton and Scott, 1974 and 1977; Murillo, 1967; Tremaine and Hamilton, 1983; Walters, 1964b and 1965). These insect vectors acquire the virus after feeding on infected plants for periods of less than a day and can retain it for several days afterward (Walters and Henry, 1970). The virus is also readily transmitted by mechanical means (Tremaine and Hamilton, 1983).

Bean southern mosaic virus is best controlled by planting resistant cultivars. Resistance to BSMV in *P. vulgaris* is expressed mainly as hypersensitivity rather than as immunity (Jayasinghe, 1982; Yerkes and Patiño, 1960; Zaumeyer and Thomas, 1957).

Because few existing bean cultivars are resistant, the virus is managed directly by planting virus-free seed and indirectly by chemically controlling the insect vector. Because maize is one of the preferred hosts of some chrysomelid vectors of BSMV, the common association of maize with beans sometimes aggravates the incidence of bean southern mosaic virus.

Bean Mild Mosaic Virus

Bean mild mosaic virus (BMMV) has been isolated from infected bean plants in El Salvador (Waterworth et al., 1977) and Colombia (Jayasinghe, 1982; Waterworth, 1981). This virus probably has a wider geographical range since the mild symptoms it induces are not easily recognized. In Spanish, the name of the virus is "virus del mosaico suave del frijol."

Although BMMV alone does not seem to affect bean plants significantly, in mixed infection the virus acts synergistically, enhancing symptom expression (Jayasinghe, 1982; Waterworth et al., 1977). The bean cultivars 27 R, Top Crop, and Widusa are diagnostic hosts (Boswell and Gibbs, 1983; Waterworth, 1981).

BMMV infects several legumes: soybean (*Glycine max*), *Lablab purpureus* (L.) Sweet, *Canavalia gladiata* (Jacq.) DC., *C. ensiformis* (L.) DC., siratro (*Macroptilium atropurpureum* (DC.) Urb.), *M. lathyroides* (L.) Urb., tepary bean (*Phaseolus acutifolius* var. *acutifolius*), scarlet runner bean (*P. coccineus* L.), common bean (*P.*

vulgaris), *Rhynchosia minima* (L.) DC., and *Sesbania exaltata* (Raf.) V.L. Cory (Boswell and Gibbs, 1983; Waterworth, 1981). *Gomphrena globosa* L. and *Chenopodium quinoa* (Willd.) are susceptible to the Central American isolate of BMMV but not to the Colombian isolate (Boswell and Gibbs, 1983; Jayasinghe, 1982; Waterworth, 1981).

The symptoms induced by BMMV in *P. vulgaris* are expressed as vein yellowing and mild mosaic (Figure 121). Systemically infected plants tend to recover and latent infections are common (Boswell and Gibbs, 1983; Jayasinghe, 1982).

The bean mild mosaic virus consists of isometric particles of about 28 nm in diameter and containing single-stranded RNA. This virus is not serologically related to other viruses of similar morphology and physicochemical properties and, therefore, is still ungrouped. It has a thermal inactivation point of 84 ^{0}C, dilution end point of 10^{-8}, and longevity in vitro of 42 and 65 days for the Central American and Colombian isolates, respectively (Boswell and Gibbs, 1983; Jayasinghe, 1982; Waterworth, 1981). Crystalline virus aggregates have been observed in root phloem of infected *P. acutifolius* cells (Jayasinghe, 1982).

The bean cultivars Nep-2, Pinto, and Top Crop have been used as propagative hosts in different purification procedures (Jayasinghe, 1982; Waterworth et al., 1977). The purified virus is a good immunogen (Boswell and Gibbs, 1983; Waterworth, 1981).

The bean mild mosaic virus is readily transmitted by mechanical means, especially by contaminated tools. The virus is also transmitted by the chrysomelids *Cerotoma ruficornis* Olivier, *Diabrotica undecimpunctata howardii* Barber, *D. balteata*, *Epilachna varivestis* Mulsant, and *Gynandrobrotica variabilis* (Boswell and Gibbs, 1983; Hobbs, 1981; Waterworth, 1981; Waterworth et al., 1977). It can also be seed-borne in *P. vulgaris* (Jayasinghe, 1982).

Resistance to BMMV has been found only in *Phaseolus leptostachyus* Bentham, *P. filiformis* Bentham (immunity), and *P. lunatus* (hypersensitive resistance) (Boswell and Gibbs, 1983; Jayasinghe, 1982). Consequently, the current recommendations for bean mild mosaic virus control aim to reduce chrysomelid vector populations in the field.

Bean Rugose Mosaic Virus

Bean rugose mosaic virus (BRMV) was first detected in Costa Rica in 1964 (Gámez, 1972a) and, later, in Guatemala (Gámez, 1971), El Salvador (Granillo et al., 1975), Colombia, and Brazil (Kim, 1977). The economic importance of this virus is not yet known. The virus causes systemic infection in common bean (*Phaseolus vulgaris*), tepary bean (*P. acutifolius* var. *acutifolius*), *Macroptilium lathyroides*, lima bean (*P. lunatus*), broad bean (*Vicia faba* L.), *Trifolium incarnatum* L., soybean (*Glycine max*), chickpea (*Cicer arietinum* L.), and pea (*Pisum sativum*) (Gámez, 1972a). The cowpea (*Vigna unguiculata* ssp. *unguiculata*) also has been reported as susceptible to BRMV (Cartín-González, 1973).

Common names frequently used for bean rugose mosaic virus in Latin America include "mosaico rugoso," "ampollado," "arrugamiento," "encarrugamiento," and "mosaico em desenho."

The bean rugose mosaic virus reactions in beans include systemic infection, local lesions, or immunity (Gámez, 1972a; Zaumeyer and Thomas, 1957). Severity of the systemic infection depends upon the virus strain and plant cultivar infected. In general, plants infected by BRMV exhibit a severe mosaic, rugosity, malformation, and leaf puckering (Figure 122). Pods of infected plants exhibit varying degrees of malformation and mottling, although in some cultivars mottling is not present (Cartín-González, 1973; Gámez, 1972a; Granillo et al., 1975).

Bean cultivars used as diagnostic species for BRMV are Stringless Green Refugee, Kentucky Wonder, Sure Crop Wax, Michelite, Sanilac, Potomac, Tender Green, Top Crop, Great Northern U.I. 60, Plentiful, ICA Pijao, and 27 R. Cowpea cultivars such as Monarch and Early Ramshorn, and soybean cultivars such as Lee, Hill, Hood, Improved Pelican, Hampton, Beinville, and Biloxi, have also been used. *Chenopodium amaranticolor* Coste *et* Reynier is a local lesion host. Many bean cultivars produce local lesions after inoculation with BRMV. The bean cultivars Colección 109 R, 27 R, and ICA Gualí have been used to propagate BRMV (Cartín-González, 1973; Gámez, 1972a).

The bean rugose mosaic virus is a comovirus with isometric particles 28-29 nm in diameter. It has three component particles, two of which contain single-stranded RNA. The thermal inactivation point of BRMV is between 65 and 79 °C. It has a dilution end point between 10^{-4} and 10^{-5}. It remains infectious in crude extracts for 48-96 hours at 22 °C (Gámez, 1972a; Zaumeyer and Thomas, 1948). Virus particles can be found in the cytoplasm of infected cells, forming vacuolate and cytoplasmic crystalline diagnostic inclusions (de Camargo et al., 1976; Gálvez et al., 1977; Kitajima et al., 1974).

The bean rugose mosaic virus can be mechanically transmitted. However, it is disseminated in the field by insect vectors of the subfamily Galerucinae, family Chrysomelidae (Fulton et al., 1975a). Bean rugose mosaic virus is transmitted by *Cerotoma ruficornis*, *Diabrotica balteata* (Figure 123), and *D. adelpha* (Cartín-González, 1973; Fulton and Scott, 1977; Gámez, 1972a). The virus can be acquired by its vectors during feeding periods of less than 24 hours. As with many virus-vector associations, a high percentage of insects transmits the virus for as long as two days. The transmission rate then drops markedly, although occasionally some insects transmit the virus for longer periods (Fulton et al., 1975a; Selman, 1973; Walters, 1969). *Cerotoma ruficornis* can transmit the virus for as long as seven to nine days, but *D. balteata* and *D. adelpha* transmit it for only one to three days (Cartín-González, 1973; Gámez, 1972a).

Several cultivars which react with local lesions can be used as resistance sources. Inheritance is monogenic and governed by three alleles, the first of which is dominant over the other two and confers immunity to the virus. The second is dominant over the third and confers hypersensitivity. The third determines susceptibility to systemic infection (Machado, 1973; Machado and Pinchinat, 1975). Chemical control of vectors, as for all other beetle-transmitted viruses, is possible.

Bean Pod Mottle Virus

Bean pod mottle virus (BPMV) is known to occur in North America. The bean cultivars Pinto, Black Valentine, and Bountiful have been suggested as diagnostic hosts (Boswell and Gibbs, 1983). Other susceptible plant species are *Chenopodium quinoa*, pea (*Pisum sativum*), *Sesbania exaltata*, *Canavalia ensiformis*, lentil (*Lens culinaris* Med.), and lima bean (*Phaseolus lunatus*) (Boswell and Gibbs, 1983; Moore and Scott, 1971).

The bean pod mottle virus significantly affects yield because it characteristically induces malformation of pods and seed abortion (Zaumeyer and Thomas, 1948 and 1957). Leaf blistering and puckering are not diagnostic of BPMV infections. Systemic mottling, stunting, and leaf and pod distortion are symptoms commonly associated with BPMV-infected natural hosts such as common bean (*Phaseolus vulgaris*), soybean (*Glycine max*), and *Desmodium paniculatum*.

The bean pod mottle virus belongs to the comovirus group whose members possess isometric particles 28 nm in diameter and two genome segments of single-stranded RNA, encapsidated in different particles. BPMV has a thermal inactivation point around 70 °C, a longevity in vitro of 62-93 days, and a dilution end point of 10^{-4}. *Glycine max*, Black Valentine, Cherokee Wax, and Bountiful have been used as propagative hosts to isolate the virus (Bancroft, 1962; Boswell and Gibbs, 1983; Moore and Scott, 1971; Zaumeyer and Thomas, 1948). Diagnostic virus-induced inclusions in infected cells have been found only in myelinic bodies and osmiophilic globules, and then only as a few virus particles (Kim and Fulton, 1971 and 1972; Kim et al., 1974).

The virus is transmitted by mechanical means and by beetle vectors such as *Cerotoma trifurcata*, *Diabrotica balteata*, *D. undecimpunctata howardii*, *Colaspis flavida*, *C. lata*, *Epicauta vittata*, and *Epilachna varivestis* (Boswell and Gibbs, 1983; Fulton and Scott, 1974; Fulton et al., 1975a; Horn et al., 1970; Moore and Scott, 1971; Patel and Pitre, 1971; Ross, 1963; Walters, 1964a). BPMV is not seed-borne (Boswell and Gibbs, 1983).

Several sources of resistance are available in *P. vulgaris* which confer immunity or resistance to BPMV (Thomas and Zaumeyer, 1950). Chemical control of the beetle vectors is also recommended in cases where this measure is economically feasible.

Bean Curly Dwarf Mosaic Virus

Bean curly dwarf mosaic (BCDMV) was first isolated from beans in El Salvador in 1971 and detected in Guatemala in 1985. No estimates of yield losses are available but BCDMV reportedly occurred in 1%-15% of plants in bean fields in El Salvador. The host range of BCDMV includes common bean (*Phaseolus vulgaris*), tepary bean (*P. acutifolius* var. *acutifolius*), lima bean (*P. lunatus*), pigeonpea (*Cajanus cajan* (L.) Millsp.), chickpea (*Cicer arietinum*), *Crotalaria juncea* L., soybean (*Glycine max*), *Lathyrus sativus* L., lentil (*Lens culinaris* Med.), *Macroptilium lathyroides*, pea (*Pisum sativum*), *Sesbania exaltata*, broad bean (*Vicia faba*), and mung bean (*Vigna radiata* (L.) Wilczek var. *radiata*) (Meiners et al., 1977).

Susceptible hosts show a range of symptoms, depending upon the cultivar (Figure 124) and stage of plant development. Plants infected at an early stage of development are extremely stunted and produce no yield. Older plants are less severely affected and produce limited yields. Symptoms may be observed only in the terminal growth of some cultivars with an indeterminate growth habit. Symptoms include mosaic, rugose, curling and twisting of leaves, and plant dwarfing. The virus may cause chlorotic and/or necrotic local lesions, vein necrosis, top necrosis, and death, depending upon the cultivar (Meiners et al., 1977).

The bean curly dwarf mosaic virus is a comovirus serologically related to quail pea mosaic virus but not to bean rugose mosaic virus (Waterworth et al., 1974). BCDMV particles are 25-28 nm in diameter and infectious in dilutions as weak as 1×10^{-5} in 0.025 M phosphate buffer. Dilutions are still infectious after incubation at room temperature for three weeks or after heating at 50 ^{0}C for 10 minutes (Meiners et al., 1977). A purification method is available (Walters, 1958).

The bean curly dwarf mosaic virus may be transmitted by the spotted cucumber beetle (*Diabrotica undecimpunctata howardii*), Mexican bean beetle (*Epilachna varivestis*), banded cucumber beetle (*D. balteata*), and flea beetle (*Cerotoma ruficornis*) (Meiners et al., 1977; Waterworth et al., 1977). Recently, two other genera, *Gynandrobrotica* and *Paranapiacaba* have also been shown to transmit BCDMV (Hobbs, 1981). The spotted cucumber beetle and Mexican bean beetle retained BCDMV infectiousness for two and three days, respectively, after a 24-hour accession feeding. BCDMV is also transmitted mechanically and by seed (Meiners et al., 1977).

Studies in El Salvador suggest that insect vectors transmit the viruses to beans from infected wild plant species growing on the edge of fields: the incidence of virus-infected plants is less in the center of bean fields than in the outer edges (Meiners et al., 1977). BMMV commonly occurs in mixture with BCDMV (Figure 125). Its economic importance depends on the combined infection with other viruses (Waterworth et al., 1977) or on the susceptibility of certain bean genotypes which react to BCDMV with systemic necrosis. No control measures are reported for bean curly dwarf mosaic virus but chemical control of vectors should be effective.

Bean Yellow Stipple Virus

Bean yellow stipple virus (BYSV) was first isolated in Illinois in 1948 (Zaumeyer and Thomas, 1950) and later in Costa Rica and Cuba in 1972 and 1978, respectively (Gámez, 1972b and 1976). BYSV is synonymous with cowpea chlorotic mottle virus (CCMV) which occurs in southern United States, Mexico, and probably in Central America (Fulton et al., 1975b). There are no studies of its economic importance in beans.

Only leguminous species have been reported susceptible to systemic infection by BYSV. Susceptible plants include common bean (*Phaseolus vulgaris*), tepary bean (*P. acutifolius* var. *acutifolius*), lima bean (*P. lunatus*), *Vigna umbellata* (Thunb.) Ohwi *et* Ohashi, *V. aconitifolia* (Jacq.) Maréchal, *Macroptilium lathyroides* (L.) Urb., cowpea (*Vigna unguiculata* (L.) Walp. ssp. *unguiculata*), *V. unguiculata* ssp. *unguiculata* var. *sesquipedalis* (L.) Verdc., *V. hirta*, soybean (*Glycine max*), *G. javanica*, and pigeonpea *Cajanus cajan* (L.) Millsp. (Gámez, 1976; Kuhn, 1964; Walters, 1958). In other studies, *Cyamopsis tetragonoloba* (L.) Taub., urd bean (*Vigna mungo* (L.) Hepper), and pea (*Pisum sativum*) also were susceptible (Zaumeyer and Thomas, 1950).

The common name frequently used for bean yellow stipple virus in Latin America is "moteado amarillo."

Only systemic infection has been observed in bean cultivars inoculated with BYSV. Infected plants show initial symptoms of very light yellow stippling and, later, small yellow spots on trifoliolate leaves. These may coalesce to form spots or yellow areas with well-defined borders and an irregular shape. The spots decrease in intensity and number on the new leaves formed at flowering. Slight variations in severity occur, depending upon the cultivar, time of infection, and climatic conditions. Some cultivars also exhibit slight growth reduction. In general, the infected plants do not show malformation, rugosity, or mosaics commonly associated with other bean viruses (Gámez, 1972b and 1976; Zaumeyer and Thomas, 1950).

Bean cultivars susceptible to BYSV include Stringless Green Refugee, Pinto U.I. 111, Bountiful, Michelite, Sanilac, Top Crop, Tender Crop, Tender White, Tender Green, Great Northern U.I. 60, Kentucky Wonder, and Tender Long. The cowpea cultivar Black Eye also is susceptible. Several species of legumes produce local necrotic lesions and include *Lablab purpureus* (L.) Sweet, soybean (*Glycine max*), *Crotalaria juncea*, and *C. paulina*. *Lablab purpureus* has been used in studies on virus infectiousness. *Chenopodium amaranticolor* and *C. album* L. react with whitish local lesions. The bean cultivars Colección 109 R and Pinto U.I. 78 have been used to multiply the virus (Gámez, 1976; Zaumeyer and Thomas, 1950).

Bean yellow stipple virus is a member of the bromovirus group (Harrison et al., 1971; Lane, 1974) with isometric particles 26-30 nm in diameter (Gámez, 1972b and 1976). The virus has a thermal inactivation point of 76 ^{0}C, a dilution end point between 1^{-5} x 10^{-4}, and a longevity in vitro of five days at 18 ^{0}C and one day at 20 ^{0}C (Gámez, 1976; Zaumeyer and Thomas, 1950). Purification procedures have been described (Gámez, 1971). BYSV induces amorphous and filamentous inclusions as well as membranous vesicles which contain virus particles (Kim, 1977).

Bean yellow stipple virus is not seed transmitted (Gámez, 1976; Zaumeyer and Thomas, 1957), but is easily transmitted mechanically. Dissemination occurs principally through beetle vectors such as *Cerotoma ruficornis* and *Diabrotica balteata*. Virus acquisition by the vector can occur in less than 24 hours. *C. ruficornis* can retain the virus from three to six days, but *D. balteata* retains it for only one to three days. As with other groups of viruses which are transmitted by Coleoptera insects, the transmission percentage decreases rapidly during the third day after virus acquisition (Gámez, 1976).

All bean cultivars tested experimentally are susceptible (Gámez, 1976; Zaumeyer and Thomas, 1950). Control of insect vectors is an effective method of reducing virus incidence when it becomes economically important.

References

Bancroft, J. B. 1962. Purification and properties of bean pod mottle virus and associated centrifugal and electrophoretic components. Virology 16(4):419-427.

Boswell, K. F. and Gibbs, A. J. 1983. Viruses of legumes 1983: descriptions and keys from VIDE. Australian National University, Canberra, A.C.T., Australia. 139 p.

Cartín-González, L. Fdo. 1973. Caracterización de dos nuevas razas del virus del mosaico rugoso del frijol (*Phaseolus vulgaris* L.). Thesis. Universidad de Costa Rica, San José, Costa Rica. 42 p.

Cheo, P. C. 1955. Effect of seed maturation on inhibition of southern bean mosaic virus in bean. Phytopathology 45(1):17-21.

Costa, A. S. 1972. Investigações sobre moléstias do feijoeiro no Brasil. In: Anais do I simpósio brasileiro de feijão, Campinas, 22 à 29 de agôsto de 1971, 2 vols. Universidade Federal de Viçosa, Viçosa, MG, Brazil. Vol. 2. p. 305-384.

Cupertino, F. P.; Lin, M. T.; Kitajima, E. W.; and Costa, C. L. 1982. Occurrence of southern bean mosaic virus in central Brazil. Plant Dis. 66(8):742-743.

de Camargo, I. J. B.; Kitajima, E. W.; and Costa, A. S. 1976. Microscopia electrônica do vírus do mosaico-em-desenho do feijoeiro in situ. Fitopatol. Bras. 1(3):207-214.

Ferault, A. C.; Spire, D.; Bannerot, H.; Bertrandy, J. J.; and LeTan, Y. 1969. Identification dans la région parisienne d'une marbrure du haricot comparable au bean southern mosaic virus (Zaumeyer *et* Harter). Ann. Phytopathol. 1:619-626.

Fulton, J. P. and Scott, H. A. 1974. Virus-vectoring efficiencies of two species of leaf-feeding beetles. Proc. Am. Phytopathol. Soc. 1:159. (Abstr.)

——— and ———. 1977. Bean rugose mosaic and related viruses and their transmission by beetles. Fitopatol. Bras. 2(1):9-16.

———; Scott, H. A.; and Gámez, R. 1975a. Beetle transmission of legume viruses. In: Bird, J. and Maramorosch, K. (eds.). Tropical diseases of legumes. Academic Press, New York, NY, USA. p. 123-131.

———; ———; and ———. 1975b. Cowpea chlorotic mottle and bean yellow stipple viruses. Phytopathology 65(6):741-742.

Gálvez, G. E.; Cárdenas-Alonso, M.; Kitajima, E. W.; Díaz-Ch., A. J.; and Nieto-C., M. P. 1977. Purification, serology, electron microscopy and properties of the ampollado strain of bean rugose mosaic virus. Turrialba 27(4):343-350.

Gámez, R. 1971. Observaciones y estudios preliminares sobre virus del frijol en Guatemala. In: Rulfo-V., F. (ed.). XVII reunión anual del Programa Cooperativo Centroamericano para el Mejoramiento de Cultivos Alimenticios (PCCMCA). Panama. p. 41-42.

———. 1972a. Los virus del frijol en Centroamérica, II: algunas propiedades y transmisión por crisomélidos del virus del mosaico rugoso del frijol. Turrialba 22(3):249-257.

————. 1972b. Some properties and beetle transmission of bean yellow stipple virus. Phytopathology 62(7):759. (Abstr.)

———. 1976. Los virus del frijol en Centroamérica, IV: algunas propiedades y transmisión por insectos crisomélidos del virus del moteado amarillo del frijol. Turrialba 26(2):160-166.

Granillo, C. R.; Díaz-Ch., A. J.; Anaya-G., M. A.; and Jiménez, G. E. 1975. Una nueva enfermedad virosa del frijol transmitida por crisomélidos: "el ampollado." SIADES 4(1):3-4.

Harrison, B. D.; Finch, J. T.; Gibbs, A. J.; Hollings, M.; Shepherd, R. J.; Valenta, V.; and Wetter, C. 1971. Sixteen groups of plant viruses. Virology 45(2):356-363.

Hobbs, H. A. 1981. Transmission of bean curly dwarf mosaic virus and bean mild mosaic virus by beetles in Costa Rica. Plant Dis. 65(6):491-492.

Horn, N. L.; Newsom, A. D.; Carver, R. G.; and Jansen, R. L. 1970. Effects of virus diseases on soybeans in Louisiana. Louisiana Agric. 13:12.

Jayasinghe, W. U. 1982. Chlorotic mottle of bean (*Phaseolus vulgaris* L.). CIAT series 09EB(2)82. Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia. 157 p. (Originally Ph.D. dissertation. Landbouwhogeschool, Wageningen, Netherlands.)

Kim, K. S. 1977. An ultrastructural study of inclusions and disease development in plant cells infected by cowpea chlorotic mottle virus. J. Gen. Virol. 35(part 3):535-543.

——— and Fulton, J. P. 1971. Tubules with viruslike particles in leaf cells infected with bean pod mottle virus. Virology 43(2):329-337.

——— and ———. 1972. Fine structure of plant cells infected with bean pod mottle virus. Virology 49(1):112-121.

———; ———; and Scott, H. A. 1974. Osmiophilic globules and myelinic bodies in cells infected with two comoviruses. J. Gen. Virol. 25(part 3):445-452.

Kitajima, E. W.; Tascon, A.; Gámez, R.; and Gálvez, G. E. 1974. Ultrastructural studies on bean leaf tissues infected with two strains of bean rugose mosaic virus. Turrialba 24(4):393-397.

Kuhn, C. W. 1964. Purification, serology, and properties of a new cowpea virus. Phytopathology 54(7):853-857.

Lane, L. C. 1974. The bromoviruses. Adv. Virus Res. 19:151-220.

Lin, M. T.; Gámez, R.; and Kitajima, E. W. 1981. Bean "mosaico-em-desenho" virus is a member of the bean rugose mosaic virus serogroup. Fitopatol. Bras. 6(2):293-298.

Machado, P. F. Rodrigues. 1973. Herança das reações do feijoeiro (*Phaseolus vulgaris* L.) ao vírus do mosaico rugoso de feijão. M.Sc. thesis. Centro Tropical de Enseñanza e Investigación, Instituto Interamericano de Ciencias Agrícolas de la OEA, Turrialba, Costa Rica. 30 p.

——— and Pinchinat, A. M. 1975. Herencia de la reacción del frijol común a la infección por el virus del mosaico rugoso. Turrialba 25:418-419.

McDonald, J. G. and Hamilton, R. I. 1972. Distribution of southern bean mosaic in the seed of *Phaseolus vulgaris*. Phytopathology 62(3):387-389.

——— and ———. 1973. Analytical density-gradient centrifugation of southern bean mosaic virus from seedcoats of *Phaseolus vulgaris*. Virology 56(1):181-188.

Meiners, J. P.; Waterworth, H. E.; Lawson, R. H.; and Smith, F. F. 1977. Curly dwarf mosaic disease of beans from El Salvador. Phytopathology 67(2):163-168.

Moore, B. J. and Scott, H. A. 1971. Properties of a strain of bean pod mottle virus. Phytopathology 61(7):831-833.

Murillo, J. I. 1967. Estudio sobre dos aislamientos virosos del frijol en Costa Rica. In: Memoria: XIII reunión anual del PCCMCA. Programa Cooperativo Centroamericano para el Mejoramiento de Cultivos Alimenticios (PCCMCA), San José, Costa Rica. p. 52-55.

Patel, V. C. and Pitre, H. N. 1971. Transmission of bean pod mottle virus to soybean by the striped blister beetle, *Epicauta vittata*. Plant Dis. Rep. 55(7):628-629.

Ross, J. P. 1963. Transmission of bean pod mottle virus in soybeans by beetles. Plant Dis. Rep. 47(12):1049-1050.

Selman, B. J. 1973. Beetles: phytophagous Coleoptera. In: Gibbs, A. J. (ed.). Viruses and invertebrates. North-Holland, Amsterdam, Netherlands, and American Elsevier, New York, NY, USA. p. 157-177.

Shepherd, R. J. and Fulton, R. W. 1962. Identity of a seed-borne virus of cowpea. Phytopathology 52(6):489-493.

Thomas, H. R. and Zaumeyer, W. J. 1950. Inheritance of symptom expression of pod mottle virus. Phytopathology 40(11):1007-1010.

Tremaine, J. H. and Hamilton, R. I. 1983. Southern bean mosaic virus. CMI/AAB (Commonw. Mycol. Inst. [and] Assoc. Appl. Biol.) Descr. Plant Viruses. Set 17, sheet 274 (no. 57 revised), 6 p.

Uyemoto, J. K. and Grogan, R. G. 1977. Southern bean mosaic virus evidence for seed transmission in bean embryos. Phytopathology 67(10):1190-1196.

Walters, H. J. 1958. A virus disease complex in soybeans in Arkansas. Phytopathology 48(6):346. (Abstr.)

———. 1964a. Transmission of bean pod mottle virus by bean leaf beetles. Phytopathology 54(2):240.

———. 1964b. Transmission of southern bean mosaic virus by the bean leaf beetle. Plant Dis. Rep. 48(12):935.

———. 1965. Transmission of the cowpea strain of southern bean mosaic by bean leaf beetle. Phytopathology 55(10):1081. (Abstr.)

————. 1969. Beetle transmission of plant viruses. Adv. Virus Res. 15:339-363.

——— and Henry, D. G. 1970. Bean leaf beetle as a vector of the cowpea strain of southern bean mosaic virus. Phytopathology 60(1):177-178.

Waterworth, H. E. 1981. Bean mild mosaic virus. CMI/AAB (Commonw. Mycol. Ints. [and] Assoc. Appl. Biol) Descr. Plant Viruses. Set 15, sheet 231, 3 p.

———; Meiners, J. P.; and Smith, F. F. 1974. Bean curly dwarf mosaic disease caused by a virus serologically related to squash mosaic virus. Proc. Am. Phytopath. Soc. 1:49. (Abstr.)

———; ———; Lawson, R. H.; and Smith, F. F. 1977. Purification and properties of a virus from El Salvador that causes mild mosaic in bean cultivars. Phytopathology 67(2):169-173.

Yerkes, W. D., Jr. and Patiño, G. 1960. The severe bean mosaic virus, a new bean virus from Mexico. Phytopathology 50(5):334-338.

Zaumeyer, W. J. and Thomas, H. R. 1948. Pod mottle, a virus disease of beans. J. Agric. Res. 77:81-96.

——— and ———. 1950. Yellow stipple, a virus disease of beans. Phytopathology 40(9):847-859.

——— and ———. 1957. A monographic study of bean diseases and methods for their control. Rev. ed. Technical bulletin no. 868. United States Department of Agriculture, Washington, DC, USA. 255 p.