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Whitefly-Transmitted Geminiviruses and Associated Disorders in the Americas and the Caribbean Basin

Plant viruses transmitted by whiteflies cause over 40 diseases of vegetable and fiber crops worldwide (1,2,12,14–16,24, 25,27,29). During the past decade, both prevalence and distribution of whitefly-transmitted plant viruses have increased (3–6,14,15,24,29), and the impact has been devastating. Depending on the crop, season, whitefly prevalence, and other factors, yield losses range from 20 to 100%. In many disorders in which whitefly-transmitted plant viruses are implicated, the pathogens have yet to be isolated and characterized (Fig. 1), and the causes remain uncertain.

The biological, morphological, serological, and epidemiological characteristics of whitefly-transmitted viruses and the molecular biology of geminiviruses have been described (1,2,14,19,22,25, 29,32). Our purpose is to present historical and contemporary perspectives on the status of the whitefly-transmitted geminiviruses in the Americas and the Caribbean Basin, where these pathogens are considered the most numerous and widespread group of whitefly-transmitted viruses. In North America, whitefly-transmitted geminiviruses include Abutilon mosaic, bean calico mosaic, bean golden mosaic, chino del tomate, cotton leaf crumple, Euphorbia mosaic, pepper mild tigre, Serrano golden mosaic, Sida mosaic, Sinaloa tomato leaf curl, squash leaf curl, Texas pepper, tomato mottle, and watermelon curly mottle strain of squash leaf curl virus. In the Caribbean Basin and Central America they include Abutilon mosaic, bean golden mosiac, Euphorbia mosaic, Jacquemontia mosaic, Jatropha mosaic, Macroptilium mosaic, Rhynchosia yellow mosaic, Sida mosaic, tobacco leaf curl, and tomato yellow mosaic. In South America they include Abutilon mosaic, bean dwarf mosaic, bean golden mosaic, Euphorbia mosaic, potato yellow mosaic, tomato golden mosaic, and tomato yellow mosaic.

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Historical Perspectives

The first transmission of a viruslike pathogen by *Bemisia tabaci* Gennadius (Fig. 2) was demonstrated in the early 1930s with tobacco leaf curl virus in tobacco and African cassava mosiac virus in cassava (15). The first transmission of a viruslike agent by *B. tabaci* in the tropical Americas was reported in 1946, when "infectious chlorosis of Malvaceae = *Abutilon* variegation mosaic" (Abutilon mosaic virus) was transmitted by the whitefly from plant to plant of *Sida rhombifolia* L. Four years later, H. S. Costa and C. W. Bennett accomplished the first mechanical transmission of a whitefly-transmissible agent, with what is now known as Euphorbia mosaic virus (Fig. 3). Ease of sap transmissibility proved to be an uncommon characteristic of whitefly-transmitted pathogens (1,2,12,14,25).

During the 1950s, surveys in the tropical Americas and the Caribbean Basin revealed widespread rugaceous diseases described at the time as incited by agents transmitted by *B. tabaci* but of uncertain etiology. Foliar malformations, leaf curling, enations, and brilliant yellow mosaic were characteristic symptoms. In Puerto Rico, these symptoms were associated with *B. tabaci*-infested weed species, including *Jatropha gossypifolia* L., *Macroptilium lathyroides* (L.) Urb., *Merremia quinquefolia* (L.) Hall., *Poinsettia heterophylla* (L.) Small, *Rhynchosia minima* DC., and *Sida carpinifolia* L. Many of the associated viruslike agents were eventually studied and characterized (1,2,12,17,25).

During the 1960s, a similar situation was documented during field surveys in Vieques, an offshore island municipality of Puerto Rico, and in St. Croix, St. John, and St. Thomas of the U.S. Virgin Islands. Whitefly populations and golden mosaic symptoms were associated with malvaceous and euphorbiaceous weeds exposed to bright sunlight and growing under semiarid conditions. During this same period, and on into the 1970s, similar observations were made in other locations in the tropics, and the prevalence of whitefly-transmitted viruslike agents also escalated in Brazil, Colombia, Venezuela, and Central America (1–3, 9,12,24–27). In the late 1970s and early 1980s, the coastal areas, inner valleys, highlands, semiarid regions, and cultivated lowlands of the Dominican Republic were surveyed, and symptomatic weeds infested with *B. tabaci* were routinely observed. In addition, high population levels of *B. tabaci* accompanied by a high incidence of golden mosaic symptoms were observed in bean fields for the first time (J. Bird, *personal observation*).

During the 1950s, *B. tabaci* was recognized as a sporadic pest on cotton in subtropical Mexico and in the deserts of Arizona, California, and Texas (8), and cotton leaf crumple disease (Fig. 4) was documented for the first time. Similar observations were made concurrently in Cuba and throughout the Caribbean. By the mid-1980s, the insect had become a serious pest and virus vector on cotton,

Fig. 1. Tobacco from the Dominican Republic infected with an uncharacterized geminivirus first observed widespread in tobacco plantings during the winter and spring of 1990–1991.

cucurbits (Fig. 5), lettuce, pepper (Fig. 6), and tomato (Fig. 7) throughout these regions. Predictably, on the basis of earlier trends in tropical regions, whitefly-transmitted viruses became commonplace in many vegetable crops and now cause epidemics resulting in annual losses of millions of dollars. During 1980–1990, nearly every country in the tropical and fringe temperate latitudes of the Americas and Caribbean Basin that produces fiber and vegetable crops has experienced high-level infestations of *B. tabaci* and the serious disease losses now routinely associated with whitefly-transmitted geminiviruses (3–7, 14,16,27). Several new phytotoxic disorders associated with feeding by *B. tabaci* nymphs and adults have been reported in crop species in the United States and Caribbean Basin. For example, the squash silverleaf and uneven ripening of tomato disorders first documented in Florida in 1987 have also been noted in Puerto Rico (J. Bird, *personal observation*), the Dominican Republic, the eastern Caribbean, and the southwestern United States (J. K. Brown, *unpublished*).

Another indication that significant changes are occurring in agroecosystems in the region is the recent documentation of *B. tabaci* infestations in cassava, pumpkin, tomato, lettuce, pepper, and cucurbitaceous and solanaceous weed species in the Caribbean Basin and the Mexican-U.S. border region (J. K. Brown and J. Bird, *unpublished*). In the past, most of these species did not serve as hosts of *B. tabaci* in the Caribbean region or North America, although infestations were often documented in Africa, the Middle East, and the Far East. Thus, whitefly-transmitted geminiviruses and *B. tabaci*, once only resident or indigenous members of western ecosystems, have become pandemic and nearly cosmopolitan throughout the tropical Americas and the Caribbean Basin (3,8,28,31). Although the precise reasons for these dramatic shifts are not clear, the conditions defined by contemporary agricultural ecosystems favor an increased incidence of geminiviruses and prevalence of whitefly vector populations. Indeed, a case can be made against the expansion of monoculture production of most food and fiber crop plants accompanied by the increase in pesticide use on both a regional and a worldwide basis.

Fig. 2. Adult *Bemisia tabaci*, referred to as the cotton, sweetpotato, or tobacco whitefly.

Fig. 3. *Datura stramonium* from Puerto Rico (1977) infected with Euphorbia mosaic virus, an example of a whitefly-transmitted geminivirus from the region that infects an euphorbiaceous host.

The Viruses

Whitefly-transmitted viruses can infect singly or in mixtures. Complexes of these viruses are common, which compounds

Fig. 4. Cotton from Arizona (1981) infected with cotton leaf crumple virus, the only whitefly-transmitted virus isolated from cotton.

Fig. 5. Zucchini from Arizona (1982) infected with the watermelon curly mottle strain of squash leaf curl virus.

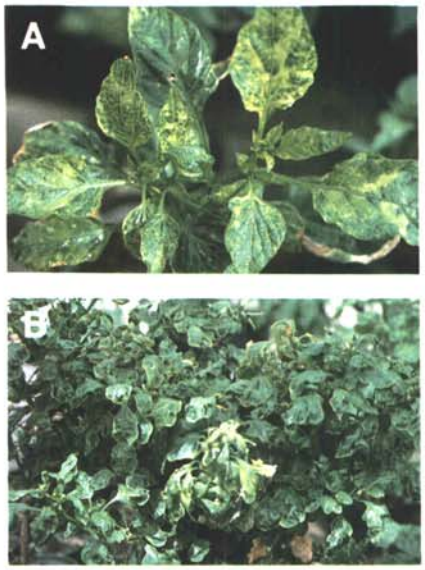

Fig. 6. (A) Pepper from Mexico (1989) infected with Serrano golden mosiac virus and (B) pepper from Mexico (1987) with tigre disease incited by a mixture of chino del tomate virus, the tentatively designated pepper mild tigre virus, and an unidentified third virus.

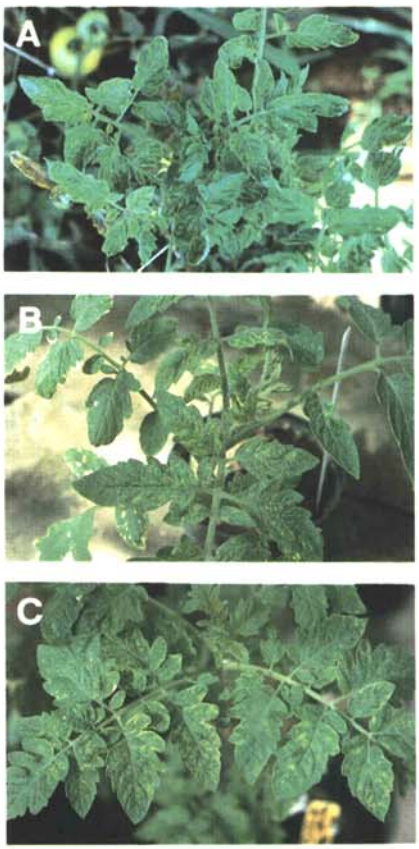

Fig. 7. (A) Tomato from Costa Rica (1988) infected with yellow leaf curl virus, the first economically important geminivirus of tomato in that country. (Courtesy R. Lastra) (B) Tomato from Mexico (1983) infected with chino del tomate virus, the first geminivirus isolated from tomato in North America. (C) Tomato infected with tomato mottle geminivirus, responsible for an epidemic in Florida during 1989–1990.

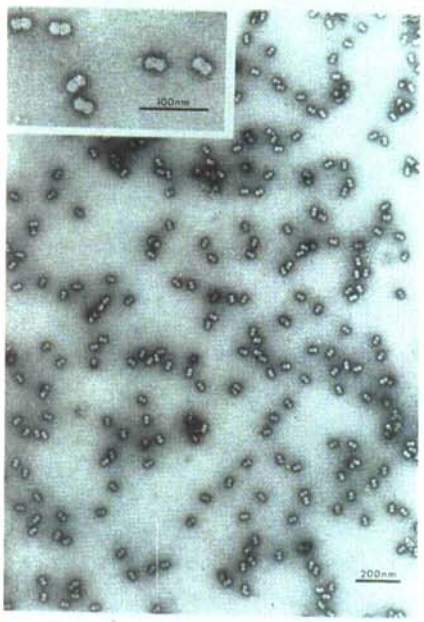

Fig. 8. Electron microscopic view of characteristic geminivirus particles, 20 × 30 nm in diameter. (Courtesy R. Lastra)

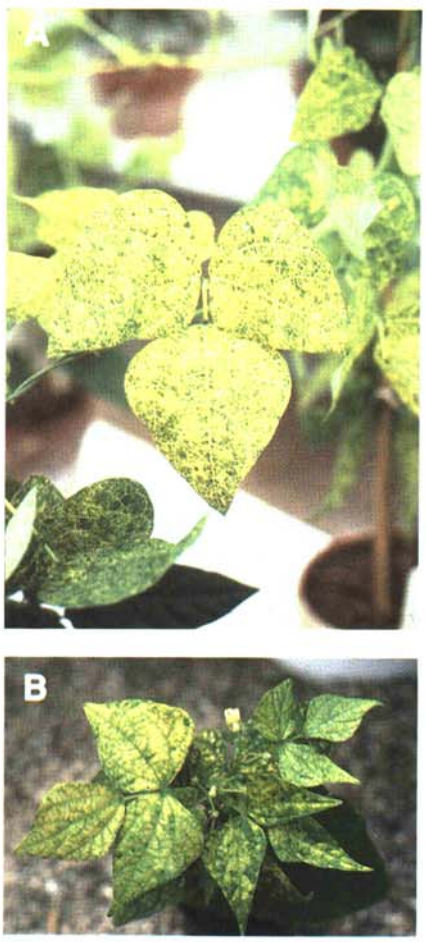

Fig. 9. (A) Lima bean from Puerto Rico (1975) infected with bean golden mosaic virus, the type isolate of the bean geminiviruses from the Caribbean Basin. (B) Pinto bean from Mexico (1985) infected with bean calico mosaic virus, the northernmost isolate of the bean geminiviruses in North America.

the difficulties of diagnosing diseases and identifying and characterizing viruses. Much of the information on whitefly-transmitted viruses has come from time-consuming studies using virus-vector-host complexes to define pathogen-insect relationships and host ranges. Such information is crucial to developing strategies for disease control. Biochemical characterization and investigations of fundamental aspects of whitefly-transmitted viruses require the establishment and maintenance of homogeneous virus cultures. The need for routine serial transfer of viruses from plant to plant using the whitefly vector has complicated and delayed the investigation of many whitefly-transmitted viruses. A shortage in the tropical Americas and Caribbean Basin of experimental facilities suitable for biological and biochemical studies has also limited progress. Until the recent awareness of the nearly global nature of these disease problems, the impact of the whitefly-transmitted plant viruses on food and fiber production was recognized solely from local or regional perspectives.

The whitefly-transmitted plant viruses fall into one of three groups of plant viruses, based on particle morphology and nucleic acid composition: carlavirus-like, closterovirus-like, and geminiviruses (11,14). The largest, most recently recognized group is the geminiviruses, established as a taxon in 1978. Geminiviruses have a geminate, or paired, particle morphology (Fig. 8) and a circular, single-stranded DNA genome of 2.6 kb (monopartite) and about 5.2 kb (bipartite) and are transmitted by whiteflies and leafhoppers, respectively (19,22,32).

In the mid-1970s, researchers in Brazil made the first breakthrough in identifying and characterizing whitefly-transmitted viral agents. The first geminivirus particles were purified from tomato plants infected by tomato golden mosaic virus (TGMV) and observed by electron microscopy. Shortly thereafter, the viral nucleic acid was isolated and shown to be DNA, and the infectivity of the viral DNA was demonstrated by the reproduction of golden mosaic symptoms in tomato after mechanical inoculation (26).

Nearly concurrent with this discovery was the purification of morphologically similar virus particles from beans infected with golden mosaic virus in Colombia (17). Virions were visualized by transmission electron microscopy, and the viral nucleic acid was isolated and found to be DNA (9). Subsequently, geminivirus particles were purified from lima beans infected with golden mosaic virus in Puerto Rico (Fig. 9). Infectious DNA isolated from virions was shown to be circular and single-stranded, an unprecedented characteristic among plant viruses (19).

The next important breakthrough in the early biochemical characterization of whitefly-transmitted geminiviruses was the discovery in 1975 that the genome of bean golden mosaic virus from Puerto Rico (BGMV-PR) was bipartite and that each of the two DNA components was housed in a separate particle (20). During the same year, the bipartite nature of the Brazilian geminivirus, TGMV, was demonstrated and the requirement for two distinct DNA components to confer infectivity was shown using infectious DNA clones of both TGMV (21) and BGMV-PR (22,32). A bipartite DNA genome had also recently been shown for African cassava mosaic virus (ACMV) (32), the prototype whitefly-transmitted virus from Africa for which a whitefly vector had first been demonstrated by Storey in the 1930s.

In response to the emergence of these data, the International Committee on the Taxonomy of Viruses (ICTV) established the geminivirus group as a new and distinct virus taxon in 1978. At first, the geminivirus group included both leafhopper-transmitted and whitefly-transmitted viruses. Since then, representatives have been provisionally added to both subgroups on the basis of insect transmission characteristics. In 1990, a proposal was made to the ICTV for recognition of three subgroups of geminiviruses: 1) leafhopper-transmitted, monopartite, monocot hosts, 2) leafhopper-transmitted, monopartite, dicot hosts, and 3) whitefly-transmitted, bipartite, dicot hosts. Recently, the whitefly-transmitted geminivirus tomato yellow leaf curl was shown to be infectious as a cloned monopartite genome, although a second component similar to those described for other bipartite geminiviruses was also found in infected tissues (30). Additional data may set a precedent for the establishment of yet another distinct geminivirus subgroup.

Many geminiviruses are not mechanically transmissible and thus must be manipulated exclusively through the use of the whitefly vector. Investigations of whitefly-transmitted geminiviruses have also been hampered by the phloem-limited or phloem-restricted nature of the viruses. In addition, virus titers are strongly influenced by environmental conditions (light and temperature), purification attempts yield only small quantities of virions, and the virus particles have proved extremely labile in some cases. It is not surprising, therefore, that the unusual geminate particle morphology of the group was revealed by electron microscopy only slightly less than two decades ago. Exciting progress has been made in the study of several whitefly-transmitted viruses in recent years, and knowledge of the biological, biochemical, and molecular nature of the pathogens has increased with the emergence of new technologies and improved communications systems. Even

so, future challenges and opportunities exist to increase our knowledge of this unique plant virus group.

The Whitefly Vector

Among the 1,100 recognized species of whiteflies in the world, only three are recognized as vectors of plant viruses (28). *B. tabaci*, also known as the cotton, sweetpotato, or tobacco whitefly, was first described as a pest of tobacco in Greece in 1889 and was designated *Aleurodes tabaci* Genn. (8,11,18,28,31). *B. tabaci* is now recognized as the most common and important whitefly vector of plant viruses worldwide and is the only known whitefly vector of geminiviruses (14,18,22).

Whiteflies constitute the family Aleyrodidae in the order Homoptera. Under favorable conditions, 11–15 generations may be completed in 1 year and females may deposit 100–300 eggs in a 3- to 6-week lifetime. Four of the five whitefly instars are nearly or entirely immobile (sessile) on the host plant; thus, the adult is the only important vector (8,11,18). In the early literature, several genera and species were designated for what are now collectively recognized as *B. tabaci* (31). *B. tabaci* is believed to have originated either in the Orient or in Pakistan and to have been dispersed to Africa, Europe, and the Americas by human transport of plant materials. The taxonomy and classification of whiteflies are complex because the adults of many species have similar gross morphology; the fourth instar (termed pupal case) is therefore used for identification purposes (11,18, 28,31).

Whiteflies feed on the phloem contents by means of a stylet (11,18), thus deriving amino acids and carbohydrates directly from the food transport system of the host plant. The stylet passes intercellularly through leaf tissues to reach the phloem contents. This feeding specialization is an effective means of acquiring and subsequently transmitting geminiviruses, which characteristically infect phloem-associated tissues (23).

Transmission of geminiviruses by *B. tabaci* is considered to be similar to the persistent, circulative type described for other homopterans (14). For efficient transmission of most geminiviruses, an acquisition-access feed of 2–24 hours followed by an inoculation-access feed of 2–3 days is optimum. Usually, transmission occurs only after a latent period of 4–10 hours. After acquisition, whiteflies can transmit virus for 5–20 days, with a gradual loss in transmission efficiency over time. Little is known about the mechanism(s) involved in this highly specific transmission process.

B. tabaci is polyphagous, and at least 506 plant species in 74 families (dicots and monocots) have been reported as hosts (8,11,18). For example, 96 host species have been recorded for Fabaceae, 56 for Compositae, 35 for Malvaceae, 33 for Solanaceae, 32 for Euphorbiaceae, 20 for Convolvulaceae, and 17 for Cucurbitaceae (11). There are, however, several reports of apparent adaptation to or preference for a particular repertoire of plant species, as defined by the differential ability of some populations to colonize only given host species. Host specialization has been observed particularly with populations that were previously and/or continually reared on a particular plant species under laboratory or field conditions.

In early studies, this type of host adaptation was attributed to distinctive populations referred to as races or ecological biotypes (2,25). In Puerto Rico, one population of *B. tabaci* could feed and reproduce only on *Jatropha multifida* L., *J. gossypifolia*, and *Croton lobatus* L. and subsequently transmitted Jatropha mosaic virus to and from these hosts exclusively. In contrast, populations of the "*Sida* race" of *B. tabaci* from the same region preferred malvaceous hosts such as *S. carpinifolia* L. and several members of other plant families. Plant species considered to be poor hosts or nonhosts for *B. tabaci* in the Caribbean Basin included cassava, cotton, crucifers, pepper, and tomato (2,25).

In Brazil, *B. tabaci* populations were well documented on malvaceous hosts, such as *Abutilon striatum* Dicks. ex Lindl. and cotton, and on solanaceous species. Consistent with the Puerto Rican populations, however, Brazilian *B. tabaci* did not colonize cassava (1,11). These observations contrasted with those for populations in Israel, reported as pests of cucurbits, crucifers, and tomatoes, in the 1950s and 1960s, and with those in Africa, where *B. tabaci* had been recognized as an important pest and virus vector in cassava since at least the 1930s (15).

J. Bird introduced the "race" concept in which *B. tabaci* populations can be distinguished according to ability to colonize a distinct repertoire of plant species (1,2). He also suggested that *B. tabaci* populations evolving in the Old World could be distinguished from those evolving in the New World by the continual association with particular plant species in the respective environments. A possible corollary is that whitefly-transmitted geminiviruses might have evolved in distinct lines after isolation from and/or strict association with particular host plant species as defined by host adaptation of *B. tabaci* populations found in Old World and New World environments. Thus, coevolution of geminiviruses with their host plants may be dictated primarily by vector-host interactions rather than virus-host interactions. These hypotheses have not been substantiated by experimental evidence.

Movement of plants by humans may be partially responsible for the changes in population dynamics of *B. tabaci* witnessed in the pantropics, as, for example, the introduction of soybean, okra, and eggplant into the New World and the transportation of cassava from South America to Africa. Differential host adaptability may be alterable from generation to generation and thus be expressed as transient, but stable, host preferences among some *B. tabaci* populations. Also, the tendency of *B. tabaci* to associate exclusively with certain hosts as a result of continual exposure may ultimately become a genetically fixed characteristic. Both scenarios may be possible, since present-day *B. tabaci* populations include those with both narrow and wide host range potentials (2,11,13). Recent studies have shown the existence of at least four distinct races or biotypes of *B. tabaci* in North America and the Caribbean Basin based on the ability to utilize differential host species for feeding and reproduction, on the demonstration of differential isozyme patterns, and on the ability or inability to induce silverleaf symptoms by bioassay to a *Cucurbita* indicator host (13; J. K. Brown et al, *unpublished*). Whether there is an absolute correlation between these parameters remains to be determined.

Definition and application of the "race" or "biotype" concept to *B. tabaci* will require application of standardized experimental techniques and an investigation of biological and genetic characteristics of whitefly populations worldwide. Improved understanding could lead to better methods for monitoring short- and long-distance dispersal and potentially to effective control measures for both whiteflies and the geminiviruses they transmit.

Virus Detection and Disease Diagnosis

The whitefly-transmitted geminiviruses studied thus far are serologically related to one another (14,22,32). Polyclonal antisera raised against most whitefly-transmitted geminiviruses are probably suitable for virus detection by serologically specific electron microscopy, enzyme-linked immunosorbent assay (ELISA), and western blot analysis but not for precise virus identification. Recent investigations using a panel of monoclonal antibodies yielded differential reactions among geminiviruses of diverse geographic origins (B. D. Harrison and J. K. Brown, *unpublished*). Further studies may lead to the development of virus- or strain-specific antibodies, which will facilitate disease diagnosis and virus identification and which may help to define relationships among whitefly-transmitted geminiviruses.

Visualization of nuclear inclusion bodies by light microscopy (10) and

ultrastructural localization of virions in plant cells by transmission electron microscopy (23) are also useful means for detecting whitefly-transmitted geminiviruses. Some variation has been detected among geminiviruses with respect to the precise locations and types of cytopatholgical structures induced in different geminivirus-host combinations. However, ultrastructural differences are not virus-specific and cannot be used to differentiate whitefly-transmitted geminiviruses at this time.

DNA probes made from partial- or full-length clones of the two genomic components (DNA-1 and DNA-2) of several whitefly-transmitted geminiviruses have been used in DNA hybridization assays for virus detection and, in some cases, for virus identification. DNA hybridization assays incorporating individual probes or probe cocktails (mixtures) of DNA-1 components are useful for virus detection (7). In contrast, the nucleotide sequences of the DNA-2 components of whitefly-transmitted geminiviruses are nearly unique for each virus and can serve as virus- or strain-specific probes (7,22).

Comparative hybridization studies using a panel of whitefly-transmitted geminivirus DNA-1 component probes indicated that there are greater differences among the DNA-1 component nucleotide sequences of geminiviruses in regions defined by geographic barriers within or between continents than among those of geminiviruses on the same continent or in the same geographic region. Further, DNA-2 component probes tested in this same manner have proved to be highly virus-specific (22; J. K. Brown et al, *unpublished*). There are limitations in the utility of DNA hybridization assays for virus diagnosis, imposed primarily by the need to maintain a broad array of virus clones. However, reproducible and differential hybridization patterns resulting from cross-hybridization with a defined panel of probes are potentially indicative of the degrees of similarities or differences among the isolates tested. Thus, hybridization profiles currently yield clues that aid in detecting virus mixtures and/or in revealing separation of mixtures into pure virus cultures (J. K. Brown et al, *unpublished*).

Diagnosis of whitefly-transmitted geminiviruses requires a laboratory assay whose results must be corroborated by tedious biological characterization. A time-consuming, multifaceted diagnostic approach is mandated, particularly with previously unrecognized whitefly-transmitted geminiviruses. Improved diagnostic technologies based on fundamental knowledge of the composition and organization of viral genomes and on virus-encoded polypeptides are needed.

Disease Control

No strategy for control of whitefly-transmitted geminiviruses has proved effective in practice. Whiteflies are difficult to control with insecticides and are often resistant to pesticides (18). The lack of other reliable means for reducing vector populations compounds the problem.

Barriers such as row covers and repellent mulches that affect phototactic responses of whiteflies have shown some promise in delaying or reducing disease incidence but are not practical or effective when levels of whiteflies and virus inoculum are high. Controlling weeds adjacent to cultivated fields, planting trap crops, and implementing cropfree periods may reduce vector populations in certain cropping systems (14,18).

Classical genetic and plant breeding techniques are currently being used to develop resistant cultivars. Several laboratories are applying such biotechnologic methods as coat protein-mediated protection, defective replicase interference, and various antisense strategies to the development of virus-resistant vegetable cultivars. The incorporation of both classical and engineered types of resistance into a single cultivar would likely reduce the potential for breakdown of either type of protection. Long-term strategies and additional creative approaches are needed to reduce the losses currently sustained from whitefly-transmitted geminivirus infections.

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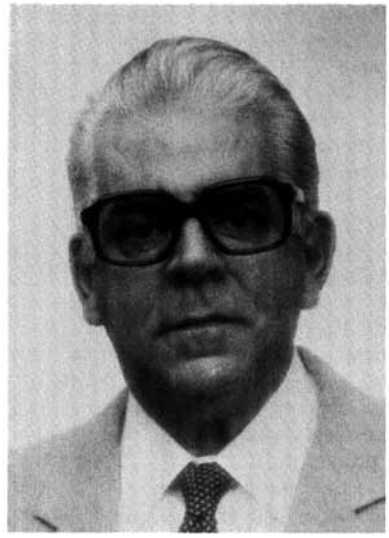

Julio Bird

Dr. Bird is professor emeritus in the Department of Plant Pathology and Botany of the University of Puerto Rico, Rio Piedras, and has been associated with the university's Agricultural Experiment Station there since 1948. He obtained his B.Sc. degree in biology from the University of Puerto Rico in 1948 and his M.Sc. and Ph.D. degrees in plant pathology from the University of Minnesota in 1951 and 1956, respectively. He is best known for his work on whitefly-transmitted viruses, including discovery of three unrelated rugaceous viruses in Puerto Rico, two of which cause serious disease in tobacco. Other areas of investigation have included soil and water transmission of chlorotic streak virus of sugarcane, aphid vectors of virus diseases of plantain and banana, and effects of temperature on expression of virus diseases.

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