

Whitefly-Borne Viruses and Virus Epidemiology in Western USA

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ABSTRACT

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The whitefly-transmitted viruses cause significant crop losses throughout the world. The agents are transmitted by at least three whitefly species in the nonpersistent, semipersistent, and persistent manners. In recent years we have found several whitefly-transmitted viruses in the western USA. A compilation of available data on these viruses would suggest at least three groups of viruses differing in type of virus particle, symptomatology, and vector relationships. These include geminiviruses, and viruses similar to the closteroviruses and nepoviruses. The sweet potato whitefly, *Bemisia tabaci* (Gennadius), has become increasingly important in the United States since its outbreak occurrence in the southwest deserts in 1981. The insect has caused losses of more than 100 million dollars in vegetable production in the region for its role as a vector of lettuce infectious yellows virus and squash leaf curl virus. During the fall of 1990 apparent changes in host preferences of *Bemisia* were noticed in California and isolations of the whiteflies were shown to be a mixture of two biotypes. The population prevalent in California since 1981 has been termed the "A" biotype and the new population has been termed "B" biotype. The biotypes differ in a number of ways including their ability to induce silverleaf of squash, host preference, larval development, esterase banding patterns, and transmission of viruses. The introduction of the new biotype into the southwest desert, coupled with its inefficiency to transmit important viruses, has significantly altered epidemiological characteristics of the whitefly transmitted viruses of the region. The demonstration of vector specificity between biotypes implies that similar vector specificity may occur in other areas of the world and that virus distribution may be dependent on the geographical distribution of the whitefly biotypes. An esterase isozyme analysis on polyacrylamide gels was made on the populations of the biotypes maintained on different hosts. Populations which were maintained on sweet potato or bean shifted to the "A" biotype, whereas, those maintained on broccoli and melon shifted to the "B" biotype. It seems that host suitability plays a major role in the adaptability of whitefly biotypes to different regions. Manipulating hosts may be useful in changing the predominant whitefly biotype in a region.

Key words: whitefly-borne viruses, virus epidemiology, whitefly biotype.

INTRODUCTION

The whiteflies are small piercing and sucking insects belonging to the family Aleyrodidae in the order Homoptera. They are responsible for the natural spread of a large number of economically important diseases in the tropical and subtropical areas. Serious losses are induced on cassava, cotton, cowpea, bean, tobacco, soybean, tomato, squash, melon, watermelon, lettuce, sugarbeet, carrot, pepper, sweet potato, and cucumber (1,2,3,4,5,6,9,10,11,12,13,15,16,19,20,29,31,32). There are about 1156 known whitefly species worldwide (30). The sweet potato whitefly, *Bemisia tabaci* (Gennadius), is

one of the most important whitefly vectors. In recent years there has been an awareness of disease losses caused by two other whitefly species, *Trialeurodes vaporariorum* (Westwood) and *T. abutilonea* (Hald.), in temperate areas of the United States, Europe, Australasia, and Asia (14,23,26,28,33,34).

WHITEFLY-TRANSMITTED VIRUSES IN WESTERN USA

The sweet potato whitefly, *B. tabaci*, was found in California in the 1920's. It became a major problem in

the USA since its outbreak in Palo Verde and Imperial valleys and western Arizona in 1981. It damages plants in several ways including direct damage from feeding individuals, production of honeydew upon which sooty mold fungus can grow, and transmission of viruses. In recent years we have found several whitefly-transmitted viruses in the western USA.

Lettuce infectious yellows virus.

A yellowing disease of lettuce, sugarbeet, carrot and other crop and weed hosts was found in the desert areas of southwestern United States in 1981 (15). The inciting virus, lettuce infectious yellows virus (LIYV), was transmitted by *B. tabaci* in a semipersistent manner. This virus was not mechanically transmissible. The virus was retained by viruliferous whiteflies for 3 days in serial transfers on susceptible hosts. LIYV has a wide host range including 45 species in 15 plant families and causes economically significant losses in lettuce, sugarbeet, cantaloupe, watermelon, and squash. Purified virus preparations had an $A_{260/280nm}$ ratio of 1.28 and contained long flexuous particles 13–14 nm wide and 1,800–2,000 nm long (16). A single protein with a MW of 32,000 daltons was detected by SDS-PAGE. Nucleic acid extracted from purified LIYV virion revealed a single species of single-stranded RNA of ca. 7,000 nucleotide bases (24). We have no direct evidence that these whitefly-transmitted flexuous rods are closteroviruses. The particles, however, are of similar size and flexibility. Cytopathological examination of infected tissues indicates that infections are associated with intracellular inclusions including vesicles which are similar to those associated with infection by known closteroviruses (21).

Squash leaf curl virus.

A whitefly-borne disease, described as squash leaf curl in 1981 by Flock and Mayhew (18), caused high mortality and drastical yield reduction in squash (*Cucurbita* sp.). It caused severe stunting and leaf curl symptoms on all cultivars of *C. maxima*, *C. moschata*, and *C. pepo* that were tested, and induced a green mosaic and leaf distortion in *Phaseolus vulgaris*. The disease agent, squash leaf curl virus (SLCV), is a geminivirus transmitted by *B. tabaci* in a circulative manner. Serological studies demonstrated that SLCV is related to cassava latent virus and melon leaf curl virus, but not to other geminiviruses (6).

Melon leaf curl virus.

A whitefly-transmitted geminivirus causing leaf curl symptoms on melons has been isolated from the Imperial Valley, California in 1985 (17). The infectious

agent, melon leaf curl virus (MLCV), which affects melon, watermelon, cucumber, cantaloupe, pumpkin, squash, and bean, is transmitted by *B. tabaci* and by mechanical inoculation. MLCV virions appeared identical to SLCV on the basis of particle morphology and ELISA tests. However, SLCV does not infect melon, watermelon, and cucumber; also, SLCV antiserum did not react with MLCV in agar double diffusion tests.

Tomato necrotic dwarf virus.

A newly discovered whitefly-transmitted virus, tomato necrotic dwarf virus (TNDV), which infects tomato, pepper, eggplant, and other Solanaceous crops and weeds. It is transmitted by *B. tabaci*, besides its being mechanically transmissible. Purified virus has been shown containing three distinct isometric components ca. 30 nm in diameter (22). The middle and bottom components contain single-stranded RNA with a molecular weight of 1.8×10^6 and 2.7×10^6 daltons, respectively. Sedimentation coefficients of the three types of particles were 57s, 117s, and 138s. Mechanical inoculation tests indicated that both middle and bottom components are required for infection. Viruses with apparently close affinities to TNDV are the nepoviruses and the comoviruses. These two groups have bipartite genomes, isometric particles ca. 30 nm in diameter, and three sedimentary components. The nepoviruses are transmitted by nematodes and the comoviruses are transmitted by beetles.

Beet pseudoyellows virus.

The greenhouse whitefly, *T. vaporariorum* is one of the most important pests of greenhouse crops throughout the world. However, the most important damage by this insect is that it transmits a virus, termed beet pseudo-yellows virus (BPYV), which was described by Duffus in 1965 from the United States (14). BPYV has a wide host range of crops, weeds, and ornamentals. The virus induces stunting, unthriftness, and interveinal yellowing or reddening. BPYV has become increasingly important and appears to be spreading rapidly in recent years. Purified preparations contained long, flexuous rod-shaped particles approximately 12 nm wide and 1,500 to 1,800 nm long (26). Other two *Trialeurodes*-transmitted entities, cucumber yellows virus (CYV)(34) and muskmelon yellows virus (MYV)(27), appeared to have host ranges somewhat different from BPYV and were thus considered as distinct viruses. However, recent evidence (27,35) indicated that the insect transmission and host range characteristics of CYV and MYV are identical to BPYV.

EPIDEMIOLOGY OF LETTUCE INFECTIOUS YELLOW S VIRUS

The major parameters in the epidemiology of insectborne viruses are the sources of infection, the vector population dynamics and distribution, the percentage of inoculative insects, and the virus-vector relationships.

Occurrence of LIYV hosts in the field

Lettuce infectious yellows virus is found in the desert southwest of the United States at all times of the year. The peak periods of LIYV incidence are November through January when virtually all the major crops (including carrot, cucumber, lettuce, melon, sugarbeet, and watermelon) are 100% infected with the virus. In addition *Malva parviflora* L. (cheese-weed), *Rumex crispus* L. (dock), *Chenopodium murale* L. (sowbane), *Sonchus oleraceus* L. (sowthistle), *Lactuca scariola* L. (wild lettuce), *Physalis wrightii* Gray (ground cherry) and *Helianthus annuus* L. (sunflower) are heavily infected. The incidence of LIYV in the various weed hosts drops from the peak period in the fall to lower levels in the May-June period. Some annual species such as cheese-weed and sowthistle virtually disappear during the hot summer season. Fall melon has a high incidence of LIYV and virtually becomes 100% infected in November.

Whitefly monitoring

Whiteflies were collected with a vacuum collector (8) throughout the year in the desert areas. Mark increases in population occurred during the May-June period. Whitefly populations were low on weeds such as wild lettuce, sowthistle, and sunflower in early summer, but when ground cherry first appeared the whitefly population dramatically increased on this host. Population of this insect increases very rapidly on cotton during the early summer period.

It is obvious that each growing season the growth cycles of crops, weeds and whiteflies may vary in the desert southwest. Data collected over several years on whitefly populations in the region, however, were remarkably similar and probably represent the general whitefly population cycle. Initial build up is probably on weeds such as wild lettuce, sowthistle, sunflower and ground cherry. Ground cherry, cotton, and fall melon are the hosts that serve as the major increase hosts during July, August, and September.

CONTROL STRATEGIES OF LETTUCE INFECTIOUS YELLOW S VIRUS

LIYV is found in the region at all times of the year and highest incidence occurs during October and November when the susceptible crops and weeds are essentially 100% infected. During the months of January through May whitefly populations drop to a very low level and evidence indicates the LIYV incidence in the weeds also drops as the weed matures and dies.

On the above evidence, control of LIYV in the desert region should be based on the elimination of overwintering weed hosts during the period January through July, after winter lettuce has been harvested and before fall melons are planted. During this period, whitefly populations are at a low level and weed hosts of the virus are relatively few. Once fall melons emerge in late July the very rapid increase in whiteflies and virus incidence in melons makes control at this stage virtually impossible.

Whitefly population changes

During the fall of 1990 isolations of *B. tabaci* from California desert regions were found to contain a mixture of two biotypes. The population prevalent in California since 1981 has been termed as "A" biotype and the new population has been termed "B" biotype. The biotypes differ in a number of ways including their ability to induce silverleaf of squash, host preference, larval development and virus transmission (7). These two biotypes could not be distinguished morphologically but could be distinguished by esterase isozyme banding patterns (Fig. 1)(25). LIYV was transmitted 100 times less efficiently by the "B" biotype. SLCV was retained by whiteflies of A biotype for 26 days as compared with only 14 days for the "B" biotype. Populations of the "B" biotype exploded in the southwest deserts during 1991, reaching populations 10 times those previously recorded for the region. LIYV levels in desert sugarbeets and lettuce were less than 1.0% in 1991 in comparison to over 70% in 1990 and in previous seasons.

Preliminary crossing experiments between the biotypes using virgin males and females produced no detectable hybrids. Limited analysis of field collected whiteflies from the desert region in 1991 indicated an almost complete shift in the population from the previously occurring "A" biotype to the newly

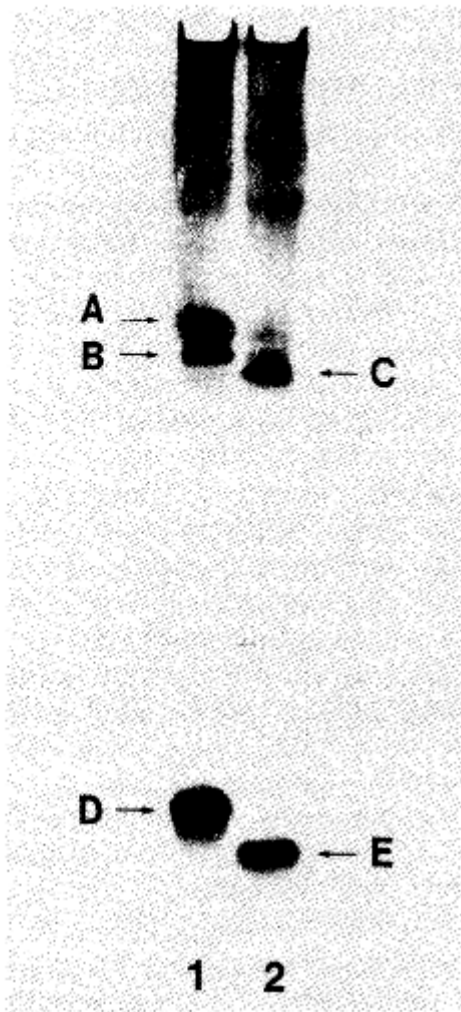


Fig. 1. Esterase patterns of individual *Bemisia tabaci* from colonies of "A" biotype (1) and "B" biotype (2). The whiteflies of "A" biotype show 3 major bands (A,B) and (D). While the whiteflies of "B" biotype only show 2 major bands (C and E).

introduced "B" biotype. It was of interest to determine in the laboratory how this shift in population took place. Equal numbers of males and females of both biotypes (25 "A" males + 25 "A" females + 25 "B" males + 25 "B" females) were enclosed in muslin-covered cages. An esterase isozyme analysis on polyacrylamide gels was made on the caged mixed population at approximately monthly intervals. Populations maintained on sweetpotato and bean shifted quickly to the "A" biotype, whereas, those maintained on broccoli and melon shifted to the "B" biotype (Fig. 2). After four months, segregates or recombinations of the "A" and "B" biotypes as determined by isozyme patterns (Fig. 3) were present on all hosts.

An isozyme analysis of *Bemisia* from California, Florida, Texas, Israel, Mexico, Nigeria and the Canary Islands indicates that these populations have a range of isozymes representative of the variations or segregations of the "A" and "B" populations (Fig. 4). However, the Israel population had an additional band not present in populations from the other regions. It seems that host suitability plays a major role in the adaptability of

whitefly biotype to different regions. Manipulating hosts may be useful in changing the predominant whitefly biotype in a region.

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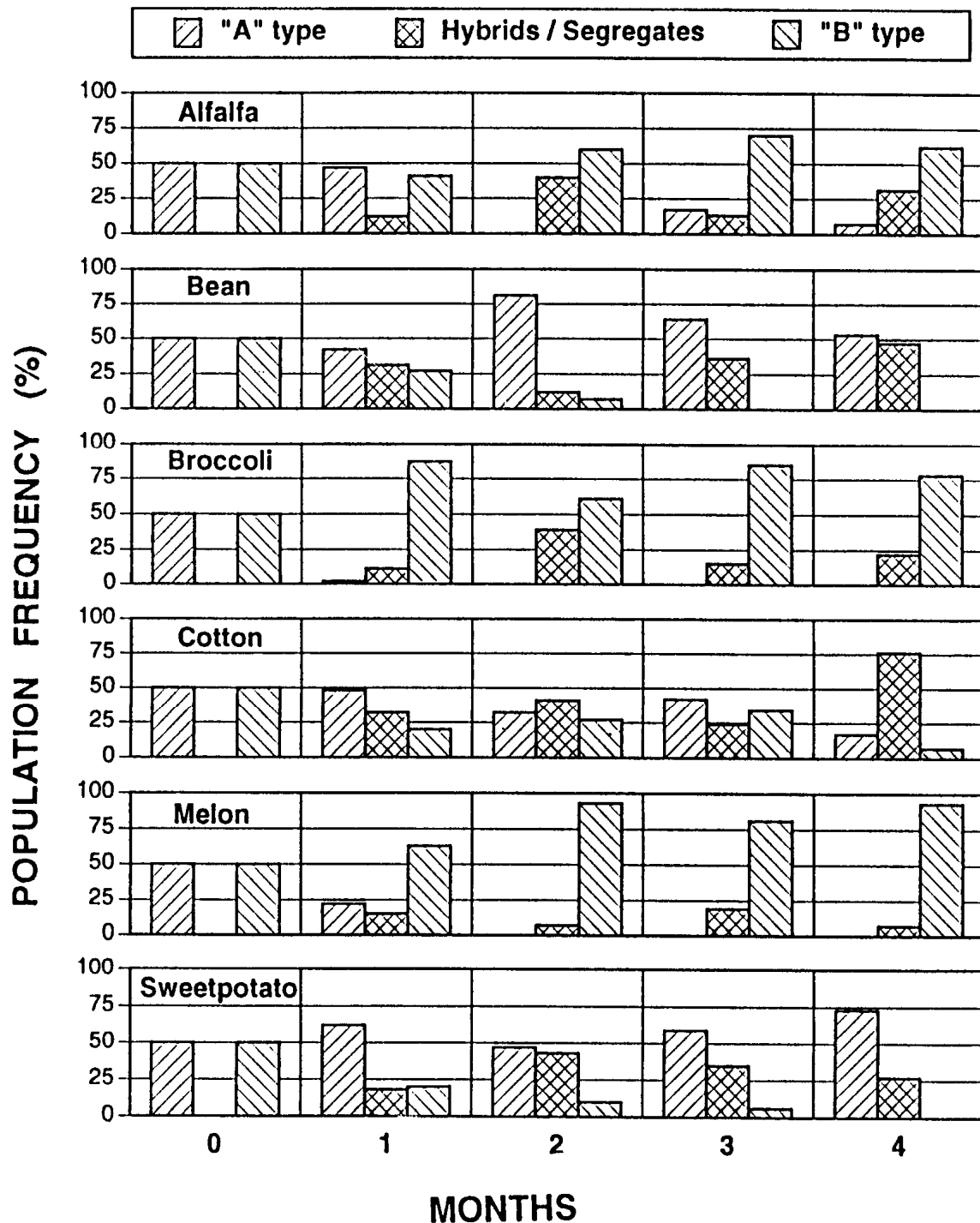


Fig. 2. The frequency of different biotypes in the caged mixed populations maintained on alfalfa, bean, broccoli, cotton, melon and sweet potato at approximately monthly interval. Populations maintained on sweet potato and bean shifted quickly to the "A" biotype, whereas, those maintained on broccoli and melon shifted to the "B" biotype. After four months, segregates or recombinations of the "A" and "B" biotypes as determined by isozyme patterns were present on all hosts.

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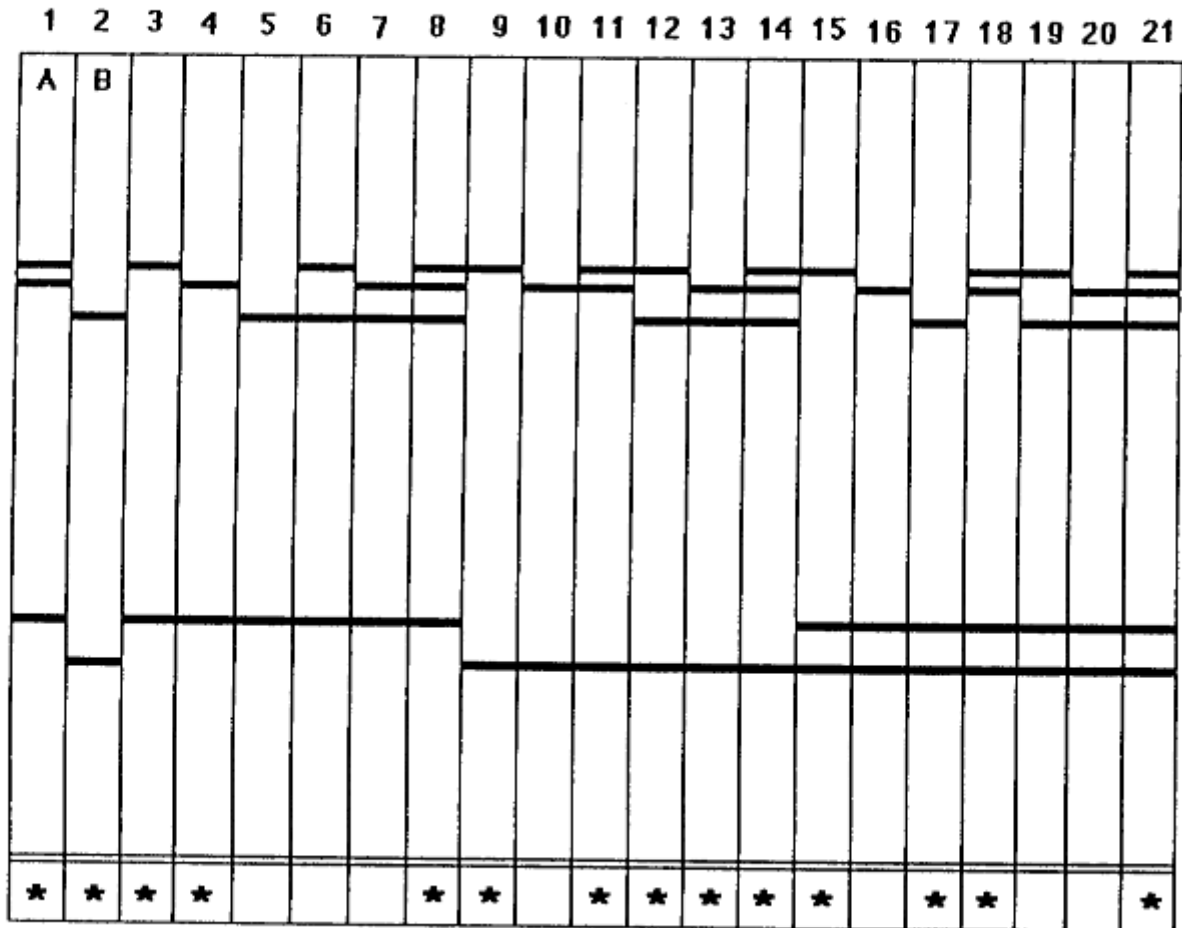


Fig. 3. Esterase patterns of *Bemisia tabaci* from California biotypes "A" and "B" (lanes 1 and 2) and the possible hybrids or segregates (lanes 3 to 21). The "*" indicates the patterns which have been found in the caged mixed populations.

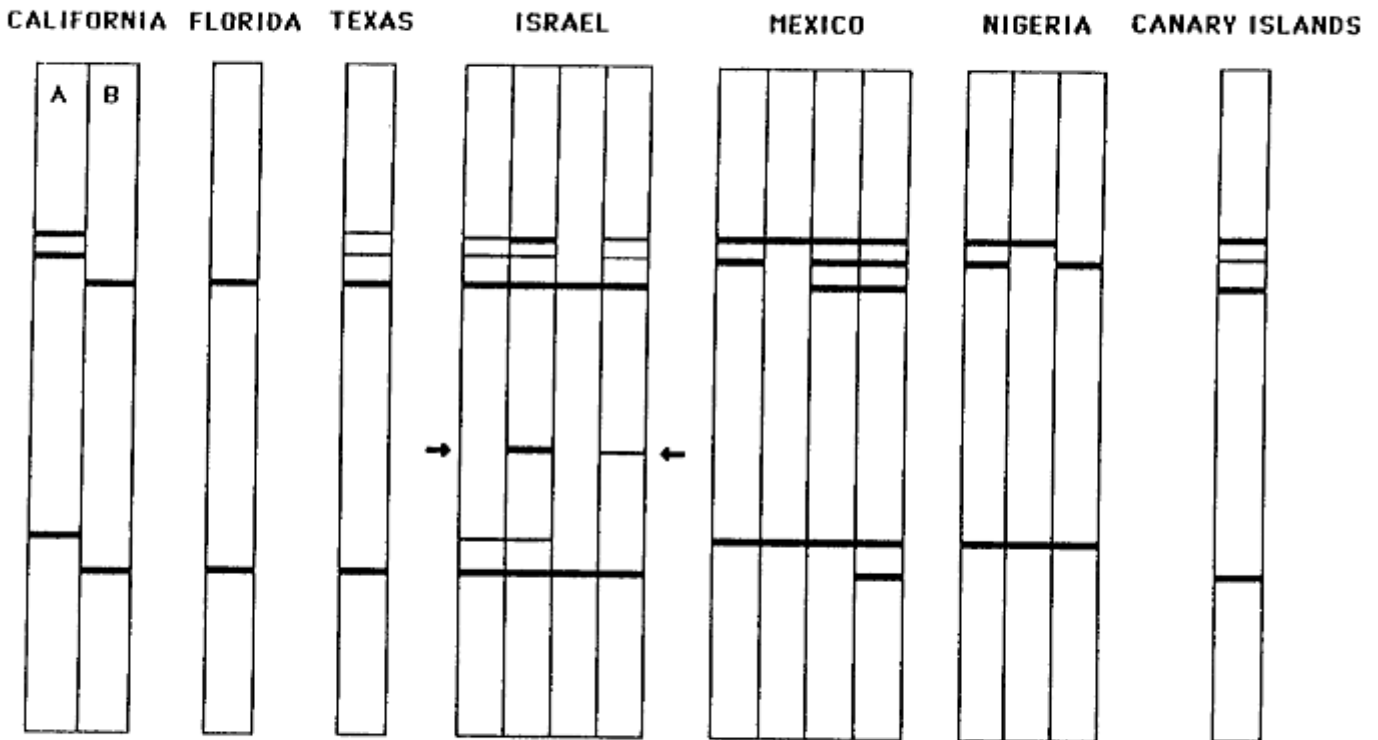


Fig. 4. Esterase patterns of *Bemisia tabaci* from California (biotypes "A" and "B"), Florida, Texas, Israel, Mexico, Nigeria and Canary Islands. These populations have the range of isozymes representative of the variations or segregates of the "A" and "B" populations. However, the Israel population had an additional band (→).

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摘 要

劉興業. 1993. 美國西部粉蝨傳播之病毒及其流行特性. 植病會刊 2:187-194. (USDA-ARS, 1636 East Alisal St., California 93905, USA).

粉蝨傳播之病毒在世界各地造成作物嚴重損失，至少有三種不同粉蝨可傳播病毒，其方式有非持續性、半持續性及持續性者。在美國西部最近幾年有多種粉蝨傳播之病毒大量發生，由既有之報告顯示至少有三種不同病毒存在，其病毒顆粒、病徵及媒介關係均有所不同，此三類病毒包括 geminivirus，及類似 closterovirus 和 nepovirus 之病毒。自 1981 年後，甘藷粉蝨 *Bemisia tabaci* 在美國西部大量發生，其為害日趨嚴重，此粉蝨媒介萵苣黃化病毒 (lettuce infectious yellows virus) 及矮南瓜捲葉病毒 (squash leaf curl virus)，並已在蔬菜生產上造成一億美元的損失。1990 年秋加州之 *Bemisia* 在寄主偏好上發生變化，其族群混有二種不同的生物型出現，由 1980 年以來即發生的舊族群屬於 A 生物型，而新出現的族群稱為 B 生物型。此二生物型有不同之性狀，如在矮南瓜上造成銀葉之能力、寄主偏好、幼蟲發育、脂醣素電泳圖譜，以及病毒之傳播方式等均有不同。在西南部沙漠地區由於新生物型粉蝨的出現，其傳染重要病毒的效率發生變化，造成該地區粉蝨傳播之病毒其流行特徵大幅改變，此種現象亦可能於其他

地區發生，即粉蝨傳播之病毒和媒介昆蟲生物型的地理分布有關。不同生物型的粉蝨族群飼養在不同的寄主後，經脂酵素同功異構酶的電泳分析顯示，維持在甘藷或四季豆的族群會變成 A 生物型，而若飼養在青花菜或甜瓜上之族群會轉化為 B 生物型。此顯示寄主適應性對某一地區粉蝨的生物型的演化有重大關係，因此改變寄主植物之種類應可改變一特定地區粉蝨的生物型。

關鍵詞：粉蝨傳播之病毒、病毒流行特性、粉蝨生物型。