

Origins of Leafhopper Vectors of Maize Pathogens in Mesoamerica

L. R. Nault

Professor, Department of Entomology, The Ohio State University, Ohio Agricultural Research and Development Center, Wooster, OH 44691

Much of the unpublished information presented here was supplied by my colleagues and students: Susan Heady, Larry Madden, Bill Styer, and Bruce Triplehorn. Their assistance and review of this manuscript are greatly appreciated.

Salaries and research support provided by State and Federal funds, especially grant No. 81-CRCR-1-0646 from the U.S. Dept. of Agriculture, Competitive Research Grants Office, appropriated to The Ohio State University, Ohio Agricultural Research and Development Center.

ABSTRACT

Nault, L. R. 1983. Origins of leafhopper vectors of maize pathogens in Mesoamerica. Pages 75-82 in D. T. Gordon, J. K. Knoke, L. R. Nault, and R. M. Ritter, eds. Proceedings International Maize Virus Disease Colloquium and Workshop, 2-6 August 1982. The Ohio State University, Ohio Agricultural Research and Development Center, Wooster, Ohio. 266 pp.

Two auchenorrhynchos homopterans, the corn leafhopper (*Dalbulus maidis*) and the corn delphacid (*Peregrinus maidis*), are responsible for vectoring five maize pathogens in Mesoamerica. The leafhopper transmits the corn stunt spiroplasma (CSS), the maize bushy stunt mycoplasma (MBSM), and the maize rayado fino virus (MRFV). The delphacid vector transmits the maize mosaic virus (MMV) and maize stripe virus (MStpV). Evidence strongly suggests that the corn leafhopper and its *Dalbulus* relatives have a long history of association with maize (*Zea mays*) and its teosinte (*Zea* spp.) and gamagrass (*Tripsacum*) ancestors in Mexico. The corn leafhopper and seven other *Dalbulus* leafhoppers have been collected from these grassy relatives of maize over the past 1/2 yr in Mexico. Three of these species were discovered for the first time, and the first definitive field hosts were discovered for three other species. Laboratory studies have provided evidence that two species, the corn leafhopper and the Mexican corn leafhopper (*D. elimatus*) are maize specialists and behave like r-selected species. When compared to *D. gelbus*, whose field hosts are several perennial *Tripsa-*

cum spp., *D. maidis* and *D. elimatus* develop more rapidly, have shorter generation times and life spans, and are more fecund and mobile. Although six *Dalbulus* spp. and one *Balduulus* sp. are experimental vectors of CSS, MBSM, and MRFV, the corn leafhopper is judged the most effective. CSS is pathogenic to all *Dalbulus* and *Balduulus* leafhoppers tested except *D. maidis*. MBSM is pathogenic to all but *D. gelbus* and *D. elimatus*. Both pathogens may be influential in determining the distribution and host ranges of *Dalbulus* leafhoppers in Mesoamerica.

The corn delphacid is the sole vector of MMV and MStpV. The only known relatives of *P. maidis* occur in Central Africa. *Sorghum* spp. are suggested as the ancestral plant hosts for both *P. maidis* and the two viruses it transmits. I propose that the vector and viruses adapted to maize as a host in post-Columbian times. This is in conflict with J. L. Brewbaker's hypothesis that *P. maidis* and MMV originated on maize in the southern Caribbean Islands and were responsible for collapse of the classic Maya civilization in pre-Columbian times. A critique of each hypothesis is given.

Fewer than 10 viral and mycoplasmal diseases of maize (*Zea mays* L.) are known to cause serious or potentially serious losses to maize in the Americas. Two insect species are responsible for the transmission of five pathogens that incite five of these diseases. The first of these, the corn leafhopper [*Dalbulus maidis* (DeLong & Wolcott)], transmits the maize rayado fino virus (MRFV), the corn stunt spiroplasma (CSS), and the maize bushy stunt mycoplasma (MBSM). The second vector, the corn delphacid [*Peregrinus maidis* (Ashmead)], transmits the maize mosaic virus (MMV) and the maize stripe virus (MStpV). The corn leafhopper occurs only in the Americas, from the southern U.S. to Argentina in South America (Oman, 1948; Nault and

Knoke, 1981). The three maize pathogens vectored by *D. maidis* occur throughout the range of their vector. The corn delphacid occurs worldwide in tropical and subtropical regions, as do MMV and MStpV. The recent discovery that these five pathogens cause most of the principal maize viral and mycoplasmal diseases in Peru (Castillo and Nault, 1982; Nault *et al.*, 1979, 1981), and perhaps in the rest of Latin America, raised questions concerning the origins of these pathogens and their vectors. Answers to these questions could reveal critical information on the biology and ecology of vectors and pathogens and, hopefully, lead to new approaches for disease control. In the following discussion I shall concentrate on the difficult task of vector origins. Informa-

tion concerning pathogen origins is scant and interpretation of the data is highly speculative.

ORIGIN OF *DALBULUS MAIDIS*

High populations of *D. maidis* occur on maize throughout its range at both low and high altitudes. Corn stunt, the most important of the three diseases associated with the vector, is highly damaging to maize from low-lying areas of the Pacific coast of Central America (R. Gamez, *personal communication*) to the high valleys of the Peruvian Andes (Nault *et al.*, 1981). However, neither Central nor South America is a likely site of origin for *D. maidis*, and recent evidence suggests that the high valleys of Central Mexico are its place of origin and that its evolution is closely tied to the wild ancestors of maize that also occur in this region.

Until I began my investigation in 1979, little was known about leafhoppers in the genus *Dalbulus* with the exception of *D. maidis* and the Mexican corn leafhopper, *D. elimatus* (Ball). The latter species is known principally from Mexico, the southwestern U.S. (Barnes, 1954), and possibly Central America (R. Gamez, *personal communication*). *D. maidis* was originally described by DeLong in the genus *Cicadula* (DeLong and Wolcott, 1923) but was later placed in *Baldulus* by Dorst (1937). DeLong (1950) erected the genus *Dalbulus* and separated it from *Baldulus* by characteristics of the male aedeagus and the shape of the head (vertex). *Dalbulus* was represented by *D. elimatus* (the genotype), *D. maidis*, and four Mexican species DeLong described at that time: *D. guevarai* DeLong, *D. longulus* DeLong, *D. gelbus* DeLong, and *D. acus* DeLong. Left in *Baldulus* were *B. montanus* Oman (the genotype) from southern Arizona and two Mexican species described by DeLong: *B. bilineatus* DeLong and *B. tropicus* DeLong. Of the nine leafhopper species, hosts were known for only *D. maidis* and *D. elimatus*. The others were swept from unknown grasses by DeLong, Oman, and other collectors.

Barnes (1954) conducted an extensive survey of leafhoppers on maize in Mexico in the early 1950's and found that *D. maidis* was most prevalent at low elevations, whereas *D. elimatus* was found principally at high elevations. Low numbers of *D. gelbus* and *D. longulus* were also collected, but there was no evidence that they were breeding on maize. Later Ramirez *et al.* (1975) collected *D. guevarai* from maize plots at the Tlaltizapan, Morelos Experiment Station of the International Center for the Improvement of Maize and Wheat (CIMMYT). The species was successfully reared on maize in the laboratory and used as a vector of one of the corn stunting mollicutes (either CSS or MBSM).

Other reports influential in my decision to focus on Mexico as the site of origin of *D. maidis* came not from Mexico but from the U.S. In searching for hosts other than maize for *D. maidis*, Pitre (1967, 1970; Pitre *et al.*, 1966) discovered that the leafhopper oviposits on and the resultant nymphs complete their development on eastern gamagrass, *Tripsacum dactyloides* L. Soon thereafter, a new leafhopper species was taken from *T. dactyloides* in Maryland and described as *Baldulus trip-*

saci by Kramer and Whitcomb (1968). The new leafhopper was later experimentally used as a vector of Mesa Central corn stunt (= MBSM) by Granados and Whitcomb (1971).

Tripsacum (gamagrass) along with the teosintes (*Zea* spp.) are the closest relatives of maize (Doebley, 1983; Doebley and Iltis, 1980; Galinat, 1977; Iltis and Doebley, 1980; Wilkes, 1972). The gamagrass and teosinte species are more abundant in southern Mexico than elsewhere. Moreover, I noted that the Mexican *Baldulus* and *Dalbulus* described by DeLong in 1950 had a distribution that overlapped that of wild relatives of maize (Nault and DeLong, 1980). I proposed the hypothesis that these leafhoppers utilize teosinte and gamagrass as hosts and that these insects have a long history of association with these grasses, perhaps co-evolving with them. Field studies in Mexico (Nault, 1983, *unpublished*; Nault and DeLong, 1980; Nault *et al.*, 1983) as well as laboratory studies (Nault, *unpublished*) strongly support this hypothesis.

From 1979 through 1982 *Tripsacum*, maize, and the teosintes were examined for presence of leafhoppers in seven Mexican states: Durango, Mexico, Morelos, Guerrero, Jalisco, Oaxaca, and Veracruz. Eight *Dalbulus* spp. were collected, including three new species (Table 1, Fig. 1) (Nault, *unpublished*; Nault and DeLong, 1980; Nault *et al.*, 1983), but no *Baldulus* leafhoppers were taken. *D. maidis* and *D. elimatus* were the two most commonly collected species from maize and teosinte. Also occasionally found on maize were *D. guevarai*, *D. gelbus*, and *D. longulus*. Interestingly, *D. guevarai*, *D. longulus*, and *D. elimatus* were never found together on maize, although each occurred in mixed populations with *D. maidis*. *D. guevarai*, *D. longulus*, *D. elimatus*, and *D. guzmani* DeLong and Nault form a sister species group. Isolating mechanisms may prevent *D. guevarai*, *D. longulus*, and *D. elimatus* from occurring sympatrically (Fig. 2). At only one locality was *D. maidis* consistently taken from *Tripsacum*; the site was adjacent to maize fields where *D. maidis* was abundant. Perhaps *D. maidis* was utilizing *Tripsacum* as a feeding host only, having migrated from the nearby maize that matured and dried more quickly than the perennial *Tripsacums*.

Tripsacum served as a principal source of *D. guevarai*, *D. longulus*, and *D. gelbus* as well as the three new species, *D. guzmani*, *D. tripsacoides* DeLong and Nault, and *D. quinquenotatus* DeLong and Nault. There does not appear to be a host specific relationship between gamagrasses and *Dalbulus* leafhoppers, *i.e.*, a given *Tripsacum* sp. does not harbor a specific *Dalbulus* sp. (Table 1). For example, *D. quinquenotatus* was found on six of the nine *Tripsacum* species surveyed and seven *Dalbulus* spp. were taken from *T. pilosum* Schrib. and Merrill. It is possible that certain *Dalbulus* spp. may prefer and thrive best on a specific *Tripsacum* sp., but field collections to date are insufficient to indicate this. Planned laboratory experiments will test this possibility of host preference for various *Dalbulus* and *Baldulus* spp.

In other laboratory tests we have compared the biol-

TABLE 1. Collections of *Dalbulus* leafhoppers from *Tripsacum* and *Zea* spp from 1979-1981 in Mexico.

Plant species	<i>Dalbulus</i> species							
	<i>maidis</i>	<i>elimatus</i>	<i>longulus</i>	<i>guevarai</i>	<i>gelbus</i>	<i>quiquenotatus</i>	<i>tripsacoides</i>	<i>guzmani</i>
<i>Z. mays mays</i>	+ ^b	+	+	+	+			
teosinte ^a	+ ^b	+						
<i>T. andersonii</i>						+		
<i>T. bravum</i>					+			
<i>T. dactyloides</i>	+	+		+	+	+ ^b	+	
<i>T. lanceolatum</i>						+ ^b		
<i>T. latifolium</i>						+ ^b		
<i>T. laxum</i>	+		+			+ ^b	+	
<i>T. maizar</i>				+			+ ^b	
<i>T. pilosum</i>	+	+		+	+ ^b	+	+	+
<i>T. zopilotense</i>				+		+ ^b		

^a Includes *Z. m. mexicana*, *Z. m. parviglumis*, *Z. diploperennis* and *Z. perennis*.

^b Nymphs as well as adults collected.

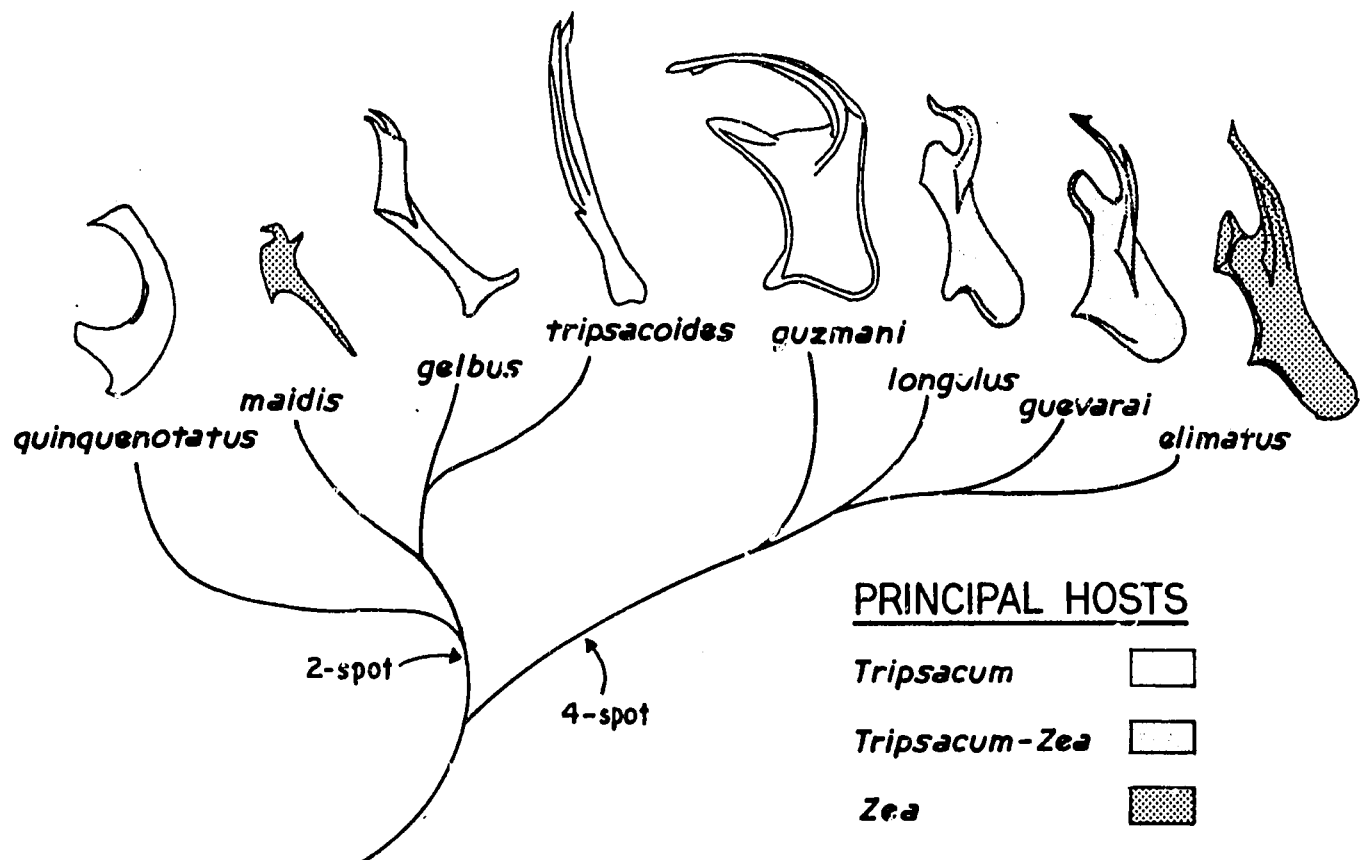


Fig. 1. Preliminary phylogeny of eight Mexican *Dalbulus* leafhopper species showing lateral views of aedeagus (male genitalia). The two major groups are divided by number of head spots (two or four).

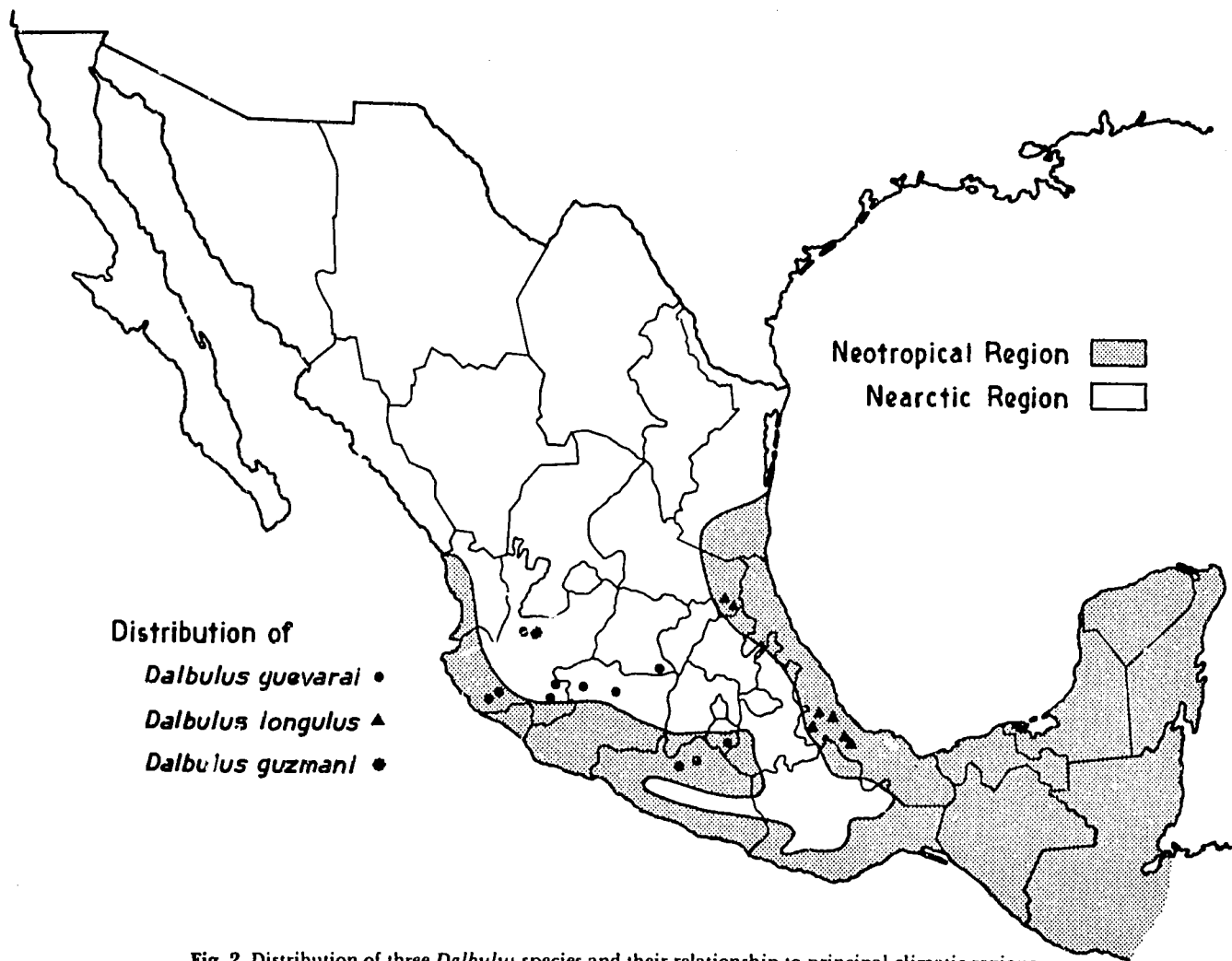


Fig. 2. Distribution of three *Dalbulus* species and their relationship to principal climatic regions.

ogy and behavior of three *Dalbulus* spp.: *D. maidis*, considered the best adapted maize specialist and the only species reported as a maize pest (Bushing and Burton, 1974); *D. elimatus*, also a maize specialist; and *D. gelbus*, a species occasionally found on maize but best adapted to *Tripsacum*. I anticipated that *D. maidis* and *D. elimatus*, which exploit annuals, would respond like "r-selected" species, whereas *D. gelbus* which lives on a perennial would likely behave as a "K-selected" species (Pianka, 1970; Southwood, 1977). These terms are taken from the well-known logistic equation in which the rate of change in a population (dN/dt) is related to the population (N) and the intrinsic rate of reproduction (r_{max}), as modified by an additional factor ($1-N/K$) which is dependent on the extent to which the population approaches the carrying capacity of the habitat (K), i.e.:

$$dN/dt = N \cdot r_{max} (1-N/K)$$

Rates of reproduction are greatest when N is small compared to K and other conditions favor high reproductive rates. These rates are smallest when N approaches K and where K-selected species prevail. Although insects in general are considered r-selected and verte-

brates K-selected, within a group of related insects such as *Dalbulus* there may be a continuum of r- to K-selected species. In the stable habitat of a long-lived perennial, such as *Tripsacum*, a leafhopper would be expected to establish more constant population levels.

Pianka (1970) and Southwood (1977) suggested features common to r- and K-selected species. For example, when compared to a K-selected species, an r-strategist has a more rapid rate of development and a shorter life span and generation time, is more fecund and mobile, and frequents unstable habitats.

Our tests with *D. maidis*, *D. elimatus*, and *D. gelbus*, all performed on sweetcorn, are consistent with these features. At all temperatures from 17 to 32 C, *D. maidis* developed more quickly than *D. elimatus* which in turn developed more quickly than *D. gelbus*. At 32 C, only *D. maidis* survived from egg to adult. The number of eggs and resultant progeny produced by *D. maidis* was greater than for *D. elimatus* and both were significantly more productive than *D. gelbus*. The intrinsic rate of increase (r_{max}) was significantly greater for *D. maidis* than *D. gelbus*, with *D. elimatus* being intermediate. On the other hand, *D. gelbus* lived significantly longer than *D. maidis* with *D. elimatus* being intermediate.

Mobility was measured by counting leafhoppers taking flight in response to a mechanical disturbance; *D. elimatus* was significantly more mobile than *D. gelbus* with *D. maidis* being intermediate. Additional studies similar to the above are planned for *D. guevarai*, *D. guzmani*, *D. longulus*, *D. quinquenotatus*, *D. tripsacoides*, and *B. tripsaci*, whose principal host is *Tripsacum*. These tests will be performed on *Tripsacum* as well as sweet corn. In preliminary trials, *D. gelbus* utilized *T. dactyloides* as a host better than did *D. maidis*.

Seven *Dalbulus* species are vectors of CSS, MBSM, and MRFV (*D. guzmani* has not been tested). They are not equally efficient as vectors. One reason is that most species are highly sensitive to these plant pathogens (CSS and MBSM), i.e., they also serve as leafhopper pathogens (Madden and Nault, 1983; Nault, unpublished). With the exception of *D. maidis*, CSS is pathogenic to all other *Dalbulus* spp. as well as *B. tripsaci*. Although pathogenic effects are less severe, MBSM reduces the longevity of *B. tripsaci* and *Dalbulus* spp. with the exception of *D. gelbus* and *D. elimatus*. Earlier Granados and Meehan (1975) showed CSS to be highly pathogenic to *D. elimatus* but only slightly so to *D. maidis*.

Several of these findings may explain, in part, why other *Dalbulus* species are less successful in exploiting maize than *D. maidis*. The abundance of *D. maidis* and absence of other *Dalbulus* spp. on maize in the low tropics may be due to its tolerance to high temperatures that have been demonstrated as lethal to *D. elimatus* and *D. gelbus*. Also, the tolerance of *D. maidis* to CSS in regions where the pathogen is common would place it in a favorable position to out-compete other *Dalbulus* spp. *D. elimatus* has rarely been collected at low elevations where CSS is common but is frequently found at high elevations in Mexico where CSS rarely occurs. Unlike CSS, the distribution of MBSM in Mexico is more common at high elevations. MBSM is pathogenic to *D. maidis* but not to *D. elimatus*. The differential susceptibility of *D. maidis* and *D. elimatus* to CSS and MBSM could be an important factor in their distribution. Other *Dalbulus* spp. can avoid CSS and MBSM by remaining on *Tripsacum* which is immune to both mollicutes (Nault, 1980). Lastly, the relatively higher intrinsic rates of increase for *D. maidis* and *D. elimatus* on maize compared to that of *D. gelbus* and perhaps the other *Dalbulus* spp. can explain their success as important maize herbivores.

Much more field and laboratory work is needed before questions concerning the origins and distribution of *Dalbulus* spp. can be answered. Clearly, Mexico is a center of diversity for the genus. However, no surveys for leafhoppers on *Tripsacum* have been made in Central or South America. Northern South America (Peru, Colombia, and Ecuador) is a second center of diversity for *Tripsacum* (de Wet *et al.*, 1981) and may harbor as yet undiscovered *Dalbulus* spp. Among *Dalbulus* spp., only *D. maidis* is known to feed on maize in Peru (Nault *et al.*, 1979, 1981). However, DeLong collected and co-described a leafhopper, *Picchusteles inca* Linnouvari

and DeLong (1976), from grasses found near the ancient Incan City of Machu Picchu. The species is remarkably similar to *Dalbulus*, a point noted by Linnouvari and DeLong. Although *Tripsacum* has not been reported from Machu Picchu, *P. inca* may be an indicator of the presence of gamagrass or of a close andropogonoid relative. Clearly, the type locality of *P. inca* should be revisited, as well as known locations of *Tripsacum* in Peru and elsewhere in South America.

As noted earlier, it is far more difficult to speculate on the origins of the three pathogens vectored by *Dalbulus*. Davis (1983) discusses the relationship of CSS to other Spiroplasmas and *Spiroplasma citri* in particular. If Whitcomb (1981) is correct that CSS is a "maize specialist" that originated from *S. citri*, then it might be quite difficult to determine when and where CSS originated. *S. citri* is found worldwide, has a broad host range, and is transmitted by a number of deltocephaline leafhoppers. If we assume that CSS is a variant of *S. citri*, then this specialization took place somewhere in the neotropics. I suspect that a deltocephaline leafhopper carried *S. citri* from an unknown dicotyledenous host to maize or teosinte. Once in *Zea*, *S. citri* adopted an indigenous *Zea* dwelling leafhopper as its vector. This leafhopper was very likely *D. maidis*. Perhaps at first CSS was highly pathogenic to *D. maidis* as it currently is to other *Dalbulus* spp. With time, resistant mutants appeared as now exist today. My guess is that as pre-Columbian man domesticated maize and carried it with him throughout the Americas, *D. maidis* followed, carrying CSS with it. *D. maidis* and CSS may have been the first pest and disease to plague the early domesticated maize (Nault, 1983). These speculations are far from satisfactory; nevertheless, they form a basis whereby future studies can be structured.

Even less can be said about the origins of MBSM and MRFV. MBSM has not been cultured and nothing is known about its relatedness to other mycoplasma-like organisms. MBSM has a host and vector range that is narrower than that of CSS (Nault, 1980). As for MRFV, only one other plant virus, oat blue dwarf, is considered to be a distant relative (Gamez, 1983). The two viruses have distinct host ranges and leafhopper vectors. Of the three maize pathogens vectored by *Dalbulus*, MRFV is the only one known to infect *Tripsacum* where it produces mild or symptomless infections (Nault *et al.*, 1980). MRFV is less damaging than CSS and MBSM to native land races of maize in Latin America (Gámez, 1980) and is not known to be pathogenic to *D. maidis* (Gámez, 1983). This, along with the susceptibility of *Tripsacum* to MRFV, suggests a long association of the virus with maize and its relatives.

ORIGIN OF PEREGRINUS MAIDIS

Recently Brewbaker (1979) presented the bold but controversial hypothesis that the MMV was responsible for the collapse of the classic Maya civilization 1000 yr ago. Based on reasons given in his lengthy treatise, Brewbaker favors the notion that a devastating disease outbreak in maize, and not foreign invasion, sustained drought, holocaust, human disease epidemic, or socio-

economic decadence was responsible for the collapse. He rather casually dismisses other insect pests and diseases as being responsible and provides his rationale for selecting MMV as the cause.

A synopsis of his argument is as follows. MMV is a devastating disease transmitted by *P. maidis*, a delphacid planthopper restricted to the humid lowland tropics. According to Brewbaker, maize and teosinte are the only definitive hosts for MMV and are the only hosts on which *P. maidis* thrives. The disease is serious only where maize is grown more or less continuously throughout the year in the wet or irrigated tropics. Resistance in maize occurs only in one known form, the Mv gene, that confers a high level of resistance but not immunity. The Mv gene occurs in all seven maize races that evolved in the Caribbean but in none of the Mexican or Central American races. He proposes that MMV originated in northern South America or the southern Caribbean Islands and was spread northward to other Caribbean Islands by the Arawak Indians around the time of Christ. The sympatric origin or selection in maize of the Mv resistant mutant in this region is assumed to have allowed its incorporation into the Caribbean maize races. Brewbaker conjectures that viruliferous *P. maidis* were blown from the Caribbean, perhaps by hurricane winds, to the Peten in northern Guatemala about the time of the eighth century. The disease became epidemic in susceptible maize races, such as Nal-Tel and Tepecintle, grown by the Peten Maya.

I will not comment on the many non-agronomic factors that may have contributed to the Mayan collapse, nor for that matter will I review Brewbaker's dismissal of other potentially contributing insect pests and diseases. Rather I will critique only arguments that he uses to support his hypothesis. Along the way I will suggest my own hypothesis for the origins of *P. maidis*, MMV, and MStpV as well and explain why none could have been responsible for the extinction of the Maya civilization.

I cannot dispute Brewbaker's contention that MMV can cause "devastating" disease epidemics. Such epidemics have been reported in recent times from several tropical regions of the world. I am surprised, however, that Brewbaker ignores MStpV, the other principal virus also vectored by *P. maidis* (Gingery *et al.*, 1981). On the American continent MStpV is known to occur in Florida, Venezuela, and Peru where both MMV and MStpV occur in the same maize fields. Surely both viruses occur together in the Caribbean and the lowlands of Mexico and Central America. No doubt maize mosaic and maize stripe have been confused and reported by Brewbaker and perhaps others as well as one caused solely by MMV (Nault *et al.*, 1981). The possible presence of MStpV in this region does not argue against Brewbaker's hypothesis, but the possible involvement of MStpV should be considered. It would be particularly instructive to test the responses of the seven Caribbean maize races that contain the Mv gene, as well as the Nal-Tel and Tepecintle races, to MStpV.

A more serious weakness in Brewbaker's argument is

his insistence that *P. maidis* and MMV are maize and teosinte specialists. In the mid-1960's *P. maidis* was reported as a pest of sorghum [*Sorghum bicolor* (L.) Moench] and *Pennisetum typhoides* (Burm.) Stapf and C. E. Hubb. in India where it was also reported as breeding on *Setaria italica* (L.) Beauv., *Echinochloa colonum* (L.) Link, and *Paspalum scrobiculatum* L. (Chelliah and Basher, 1966; Thontadarya and Channa-Basavanna, 1968). Moreover, these authors report that sorghum was the preferred host in laboratory tests. In recent years, *P. maidis* has become a more serious pest with the introduction of new sorghum varieties that mature at different times of the year (Agriwal *et al.*, 1981). Delphacid feeding causes death of top leaves and prevents emergence of the sorghum ear head. Secondary damage is caused by sooty molds that grow on honeydew secreted by planthoppers. Furthermore, Brewbaker should not take lightly the reports of others that *P. maidis* can utilize hosts other than maize (Namba and Higa, 1971). I have observed *P. maidis* using *Rottboellia exaltata* L. as a host in Florida and have confirmed this in laboratory and greenhouse tests (Nault, unpublished).

I also strongly suspect that the reports of MMV in other hosts are correct (Herold, 1972). The second virus, MStpV, unequivocally has a host range that extends beyond the genus *Zea*. We have confirmed that sorghum and *R. exaltata* are hosts (Gingery, *et al.*, 1981). Greber (1981) has recently isolated MStpV from one cultivated and two wild *Sorghum* spp. in Australia and has experimentally infected barley (*Hordeum vulgare* L.), rye (*Secale cereale* L.), and triticale (x *Triticosecale* Wittmack).

The above evidence would suggest that *P. maidis*, MMV, and MStpV may have a stronger link to *Sorghum* and its relatives than to *Zea*. In my 3 yr collecting from teosinte and gamagrass at mid- and high elevations in Mexico, I have never encountered *P. maidis*, MMV, or MStpV.

Africa, rather than the Americas, is the likely place of origin for the corn delphacid, MMV, and MStpV. Only one other *Peregrinus* species is known, *P. iccasta* (Fennah), and it occurs in tropical Central and West Africa. There is also the African genus, *Curtometopum*, as yet only known from females of the type species, *C. turneri* Muir, that could conceivably be allied to *Peregrinus*, but its position will remain uncertain until a male is discovered.

In a letter to me dated 19 July 1979, R. G. Fennah, British Museum of Natural History, an authority on the world's delphacid planthoppers, stated "The facts so far available suggest that tropical Africa is the genetic headquarters of *Peregrinus*, and that (*P.*) *maidis* has spread into India and S.E. Asia in prehistoric times and has taken the same route into the New World as the tapir or delphacids of the genus *Ugyops* (s.l.). *Saccharosydne* is a grass or sugar cane frequenting delphacid genus represented in various warmer parts of the New World by six species, and by a single species extending through Japan, Manchuria and China. Unlike *Peregrinus*, it has no species common to Asia and America.

Its close relative, *Neomalaxa*, includes a single species that extends from Puerto Rico to Brazil. There is a case for considering *Saccharosydne* as of American origin. If *Peregrinus maidis* were American, I should rather expect a comparable situation to exist. But it doesn't."

I take exception to only one part of Fennah's statement, *i.e.*, that *P. maidis* came to the New World by the same route as the tapir. He is, of course, referring to the land bridge (Beringia) that once connected the USSR with Alaska ca. 18,000 yr ago. This land mass would have been exposed during ice age conditions, yet *P. maidis* appears to tolerate only tropical climates. There would also be the problem of adaptation to hosts other than *Sorghum*, since this genus also has a tropical or subtropical distribution.

I favor another hypothesis for the introduction of *P. maidis* to the New World as well as the Oceanic Islands. I postulate that introductions occurred in post-Columbian times as corn and sorghum seed were being transported transoceanically by early travelers. While *P. maidis* cannot feed and survive on the seed itself, I have noted that the hopper can survive for 1 or more weeks on the germinated hypocotyl of maize. The *P. maidis* habit of frequenting secluded areas of its hosts would be compatible with its being a stowaway in bags of sorghum or maize seed, a few seeds of which could germinate when exposed to moisture and serve as sustenance for the hitchhiking hoppers. The situation is also ideal for transport of MMV and MStpV in that both are long-lived in their vector and MStpV transovarially passed through the egg. The adaptation to maize by the corn planthopper and the two viruses may have occurred after their introduction to the New World or may have occurred earlier on the African continent when maize was introduced in the 1500's.

Perhaps the strongest argument for a relatively recent dispersal of *P. maidis* worldwide is the acknowledgment from Fennah (*personal communication*) that there is little variation (morphological) in the species over its range of occurrence. If dispersal occurred in prehistoric or even pre-Columbian times, particularly to oceanic islands that are notorious for rapid speciation of flora and fauna, then I would have expected morphological variation in *P. maidis* to occur, but it has not. More subtle genetic variation in *P. maidis* is possible and can be measured by a study of its isoenzyme patterns. Perhaps there is more variation than is apparent from a morphologic inspection.

I agree with Fennah that *Peregrinus* has an African origin and that its evolution is more closely linked to *Sorghum* than *Zea*. If *P. maidis* spread from Africa to the Caribbean by natural means in pre-Columbian times, then Brewbaker's theory could still be valid. However, I favor the hypothesis that the delphacid was introduced in post-Columbian times to the Caribbean where native races responded to MMV by selection and spread of the Mv gene. This leaves open the question of the Maya collapse. I remain intrigued by Brewbaker's hypothesis, and being an entomologist and plant pathologist, I favor the notion that a pest or disease played a significant role in man's history. Brewbaker

may be right in part, but he has selected the wrong insect-transmitted pathogen. I favor CSS as the responsible pathogen (Nault, 1983).

Some might argue that the debate between Brewbaker and myself is solely academic and of little consequence to agriculture and the solution of current disease problems. I would disagree! Brewbaker has properly focused attention on the difficulties of producing corn in the low Central American tropics and has discovered a significant source of disease resistance to MMV (Brewbaker, 1981). He has also unintentionally called attention to the unresolved problem of identifying the principal maize stunting pathogens in Central America. Is MMV the most important as Brewbaker suggests, or are the other pathogens discussed in this paper important as well? The answers to such questions could provide reasons for the success or failure of current and future disease control methods (such as use of the Mv gene) in Central America.

LITERATURE CITED

- Agriwal, R. K., R. S. Verma, G. S. Bharaj. 1981. Screening of sorghum lines for resistance against shoot bug, *Peregrinus maidis* (Ashmead) (Homoptera: Delphacidae). JNKVV (Jawaharal Nehru Krishi Vishwa Vidyalaya) Res. J. 12:116.
- Barnes, D. 1954. Biología, ecología y distribución de las chicharritas, *Dalbulus elimatus* (Ball) y *Dalbulus maidis* (DeL. & W.). Oficina de Estudios Especiales, Folleto Técnico No. 11, Mexico, D.F. 112 pp.
- Brewbaker, J. L. 1979. Diseases of maize in the wet lowland tropics and the collapse of the classic Maya civilization. Econ. Bot. 33:101-118.
- Brewbaker, J. L. 1981. Resistance to maize mosaic virus. Pages 145-151 in D. T. Gordon, J. K. Knoke, and G. E. Scott, eds. Virus and Viruslike Diseases of Maize in the United States. South. Coop. Ser. Bull. 247. 218 pp.
- Bushing, R. W. and V. E. Burton. 1974. Leafhopper damage to silage corn in California. J. Econ. Entomol. 67:656-658.
- Castillo, J. and L. R. Nault. 1982. Enfermedades causadas por virus y mollicutes en maíz en el Perú. Fitopatología 17:40-47.
- Chelliah, S. and M. Basheer. 1966. Biological studies of *Peregrinus maidis* (Ashmead) (Araeopidae: Homoptera) on sorghum. Indian J. Entomol. 27:466-471.
- Davis, R. E. and I-M. Lee. 1983. Identities of new spiroplasmas reported in the United States. Pages 51-55 in D. T. Gordon, J. K. Knoke, L. R. Nault, and R. M. Ritter, eds. Proc. Int. Maize Virus Dis. Colloq. and Workshop, 2-6 Aug. 1982. Ohio State Univ., Ohio Agric. Res. Dev. Cent., Wooster. 266 pp.
- DeLong, D. M. 1950. The genus *Dalbulus* and *Dalbulus* in North America including Mexico. (Homoptera: Cicadellidae). Bull. Brooklyn Entomol. Soc. 45:105-116.
- DeLong, D. M. and G. N. Wolcott. 1923. New species. In Wolcott's Insectae Portoricensis, Porto Rico Dept. Agr. J. 7:257-270.
- DeWet, J. M. J., D. H. Timmer, K. W. Hilu, and G. B. Fletcher. 1981. Systematics of South American *Tripsacum* (Gramineae). Am. J. Bot. 68:265-276.
- Doebley, J. F. 1983. The taxonomy and evolution of *Tripsacum* and *Teosinte*, the closest relatives of maize. Pages 15-28 in D. T. Gordon, J. K. Knoke, L. R. Nault, and R. M. Ritter, eds. Proc. Int. Maize Virus Dis. Colloq. and Workshop, 2-6 Aug. 1982. Ohio State Univ., Ohio Agric. Res. Dev. Cent., Wooster. 266 pp.
- Doebley, J. F. and H. H. Iltis. 1980. Taxonomy of *Zea* (Gramineae). I. A subgeneric classification with key to taxa. Am. J. Bot. 67:982-993.
- Dorst, H. E. 1937. A revision of the leafhoppers of the *Macrostelus* group (*Cicadula* of authors) in America North of Mexico. U. S. Dep. Agric. Misc. Publ. 271. 24 pp.
- Galinat, W. C. 1977. The origin of corn. Pages 1-47 in G. F. Sprague, ed. Corn and Corn Improvement. Agronomy Ser. Vol. 18. Am. Soc. Agron., Madison, Wisc. 774 pp.

- Gómez, R.** 1983. Maize rayado fino disease: The virus-host-vector interaction in neotropical environments. Pages 62-68 in D. T. Gordon, J. K. Knoke, L. R. Nault, and R. M. Ritter, eds. Proc. Int. Maize Virus Dis. Colloq. and Workshop, 2-6 Aug. 1982. Ohio State Univ., Ohio Agric. Res. Dev. Cent., Wooster. 266 pp.
- Gómez, R.** 1980. Rayado fino virus disease of maize in the American tropics. *Trop. Pest Manage.* 26:26-33.
- Gingery, R. E., L. R. Nault, and O. E. Bradfute.** 1981. Maize stripe virus: Characteristics of a member of a new virus class. *Virology* 112:99-108.
- Granados, R. R. and D. J. Meehan.** 1975. Pathogenicity of the corn stunt agent to an insect vector, *Dalbulus elimatus*. *J. Invertebr. Pathol.* 26:313-320.
- Granados, R. R. and R. F. Whitcomb.** 1971. Transmission of corn stunt mycoplasma by the leafhopper *Balbulus tripsaci*. *Phytopathology* 61:240-241.
- Greber, R. S.** 1981. Maize stripe disease in Australia. *Aust. J. Agric. Res.* 32:27-36.
- Herold, F.** 1972. Maize mosaic virus. No. 94 in *Descriptions of Plant Viruses*. Commonw. Mycol. Inst., Assoc. Appl. Biol. Kew, Surrey, England. 4 pp.
- Iltis, H. H. and J. F. Doebley.** 1980. Taxonomy of *Zea* (Gramineae). II. Subspecific categories in the *Zea mays* complex and a generic synopsis. *Am. J. Bot.* 67:994-1004.
- Kramer, J. P. and R. F. Whitcomb.** 1968. A new species of *Balbulus* from gamagrass in eastern United States with its possible implications in the corn stunt virus problem. *Proc. Entomol. Soc. Wash.* 70:88-92.
- Linnavouri, R. and D. M. DeLong.** 1976. New neotropical leafhoppers from Peru and Bolivia (Homoptera: Cicadellidae). *Rev. Peru. Entomol.* 19:29-38.
- Madden, L. V. and L. R. Nault.** 1983. Differential pathogenicity of corn stunting mollicutes to leafhopper vectors in *Dalbulus* and *Balbulus* species. *Phytopathology* 73:1608-1614.
- Namba, R. and S. Y. Higa.** 1971. Host plant studies of the corn planthopper, *Peregrinus maidis* (Ashmead), in Hawaii. *Proc. Hawaii. Entomol. Soc.* 21:105-108.
- Nault, L. R.** 1980. Maize bushy stunt and corn stunt: A comparison of disease symptoms, pathogen host ranges, and vectors. *Phytopathology* 70:659-662.
- Nault, L. R.** 1983. Origins in Mesoamerica of maize viruses and mycoplasmas and their leafhopper vectors. Pages 259-266 in R. T. Plumb and J. M. Thresh, eds. *Plant Virus Epidemiology*. Blackwell Scientific Publications, Oxford, England. 377 pp.
- Nault, L. R. and D. W. DeLong.** 1980. Evidence for co-evolution of leafhoppers in the genus *Dalbulus* (Cicadellidae, Homoptera) with maize and its ancestors. *Ann. Entomol. Soc. Am.* 73:349-353.
- Nault, L. R. and J. K. Knoke.** 1981. Maize vectors. Pages 77-84 in D. T. Gordon, J. K. Knoke and G. E. Scott, eds. *Virus and Viruslike Diseases of Maize in the United States*. South. Coop. Ser. Bull. 247. 218 pp.
- Nault, L. R., R. E. Gingery, and D. T. Gordon.** 1980. Leafhopper transmission and host range of maize rayado fino virus. *Phytopathology* 70:709-712.
- Nault, L. R., D. T. Gordon, and J. Castillo Loayza.** 1981. Maize virus and mycoplasma diseases in Peru. *Trop. Pest Manage.* 27:363-369.
- Nault, L. R., D. T. Gordon, V. D. Damsteegt, and H. H. Iltis.** 1982. Response of annual and perennial teosintes (*Zea*) to six maize viruses. *Plant Dis.* 66:61-62.
- Nault, L. R., D. M. DeLong, B. W. Triplehorn, W. E. Styer, and J. F. Doebley.** 1983. More on the association of *Dalbulus* (Homoptera: Cicadellidae) with Mexican *Tripsacum* (Poaceae) including the description of two new species of leafhoppers. *Ann. Entomol. Soc. Am.* 76:305-309.
- Nault, L. R., D. T. Gordon, R. E. Gingery, O. E. Bradfute, and J. Castillo Loayza.** 1979. Identification of maize viruses and mollicutes and their potential insect vectors in Peru. *Phytopathology* 69:824-828.
- Oman, P. W.** 1948. Distribution of *Balbulus maidis* (DeLong & Wolcott). *Proc. Entomol. Soc. Wash.* 50(2):34.
- Pianka, E. R.** 1970. On r- and K-selection. *Am. Nat.* 106: 581-588.
- Pitre, H. N.** 1967. Greenhouse studies of the host range of *Dalbulus maidis*, a vector of the corn stunt virus. *J. Econ. Entomol.* 60:417-421.
- Pitre, H. N.** 1970. Notes on the life history of *Dalbulus maidis* on gama grass and plant susceptibility to the corn stunt disease agent. *J. Econ. Entomol.* 63:1661-1662.
- Pitre, H. N., R. L. Combs, and W. A. Douglas.** 1966. Gamagrass, *Tripsacum dactyloides*: A new host of *Dalbulus maidis*, vector of corn stunt virus. *Plant Dis. Rep.* 50:570-571.
- Ramirez, J. L., C. G. DeLeon, C. M. Garcia, and G. R. Granados.** 1975. *Dalbulus guevarai* (DeL.) nuevo vector del achaparramiento del maiz en Mexico. Incidencia de la enfermedad y su relacion con el vector *Dalbulus maidis* (DeL. & W.) en Muna, Yucatan. *Agrociencia* 22:39-49.
- Southwood, T. R. E.** 1977. Habitat, the template for ecological strategies. *J. Anim. Ecol.* 46:337-365.
- Thontadarya, T. S. and G. P. Channa-Basavanna.** 1968. Mode of egg-laying in *Peregrinus maidis* (Ashmead) (Araeopidae: Homoptera). *Mysore J. Agric. Sci.* 2:338-339.
- Whitcomb, R. F.** 1981. The biology of spiroplasmas. *Annu. Rev. Entomol.* 26:397-425.
- Wilkes, H. G.** 1972. Maize and its wild relatives. *Science* 177:1071-1077.