

Differential Pathogenicity of Corn Stunting Mollicutes to Leafhopper Vectors in *Dalbulus* and *Baldulus* species

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ABSTRACT

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The effect of corn stunt spiroplasma (CSS) and maize bushy stunt mycoplasma (MBSM) on adult survival of six leafhopper vectors in *Dalbulus* spp. and one *Baldulus* sp. was determined. Newly discovered vector-mollicute associations were: *D. gelbus*—CSS, MBSM; *D. guevarai*—CSS, MBSM; *D. quinquenotatus*—CSS, MBSM; *D. tripsacoides*—CSS, MBSM; and *B. tripsaci*—CSS. Confirmed associations were: *D. maidis*—CSS, MBSM; *D. elimatus*—CSS, MBSM; and *B. tripsaci*—MBSM. Leafhopper survival was measured by the quartiles of the survival distribution (eg, median survival time [t_{50}] and time to 25% survival [t_{25}]), as well as estimated parameters of the Weibull model representing

survival of each species. CSS reduced t_{50} for five species and t_{25} for six. Only *D. maidis* was unaffected by CSS. MBSM reduced t_{50} for only two species and t_{25} for five. *D. elimatus* and *D. gelbus* were unaffected by MBSM. The effect of MBSM was significantly less than CSS for four species. Rate of population decline, as measured by the Weibull scale parameter, was increased for six species exposed to CSS and five species exposed to MBSM. Affected species were the same as those determined by values of the 25% quartile. The differential pathogenicity of CSS and MBSM to their vectors can be rationalized according to the geographic distributions and host ranges of leafhoppers and pathogens.

Additional key words: survival analysis, *Tripsacum* spp., *Zea mays*.

Mollicutes cause two important systemic, stunting diseases of corn (*Zea mays* L.). The corn stunt spiroplasma (CSS), which is the causal agent for the "Rio Grande" strain of corn stunt, is distributed from the southern United States to Argentina (23). Symptoms produced by CSS include plant stunting, chlorotic spots and stripes at the bases of younger leaves, and reddening at the tips of older leaves (17). Maize bushy stunt mycoplasma (MBSM) is the causal agent for the "Mesa Central" and "Louisiana" strains of corn stunt (17,20). MBSM has been reported from the southern United States, Mexico, Peru, and Colombia, and probably has the same geographic distribution as CSS. In Mexico, MBSM is more prevalent than CSS at high elevations (2,000 m) and the reverse is true at mid-to-low elevations (<2,000 m) (6,7). MBSM causes more severe plant stunting and reddening of older leaves than CSS, but does not produce chlorotic stripes at the bases of younger leaves (17). MBSM can also cause a proliferation of axillary and basal shoots.

Both pathogens are efficiently transmitted by leafhoppers (Homoptera: Cicadellidae) in the genera *Dalbulus* and *Baldulus*; deltocephaline leafhoppers from other genera are less efficient vectors (17). The corn leafhopper, *Dalbulus maidis* (DeLong & Wolcott), occurs in high populations on corn throughout the neotropics. The Mexican corn leafhopper, *D. elimatus* (Ball), is found principally in Mexico, although it has been reported from the southwestern United States and possibly Central America (19). In Mexico, *D. maidis* is most prevalent at mid-to-low elevations (<750 m), whereas *D. elimatus* is found principally at higher elevations (>750 m) (1,18). Both *D. maidis* and *D. elimatus* are well adapted to corn, and *D. maidis*, apart from its importance as a vector, is a corn pest. Seven other *Dalbulus* species are known from Mexico, some of these having been discovered recently (19,21,22).

These other *Dalbulus* species are better adapted to gamagrasses (*Tripsacum* spp.), close relatives of maize, than they are to *Zea* spp.; however, all leafhopper species can be laboratory reared on maize (*unpublished*). The related genus, *Baldulus*, consists of four species, one of which, *B. tripsaci* Kramer & Whitcomb (12), utilizes *Tripsacum* as a host in nature.

Granados and Meehan (9) have shown that CSS is highly pathogenic to *D. elimatus*; limited studies suggested that CSS is also pathogenic to *D. maidis*, but to a lesser degree than to *D. elimatus*. Prior to this study it was not known if MBSM is a pathogen of its leafhopper vectors or if CSS is a pathogen of other leafhopper species. The objective of this study was to evaluate the effect of CSS and MBSM on the adult survival of six *Dalbulus* and one *Baldulus* species. To achieve this objective, statistical distributions were fit to the survival data to determine probabilities of death at various times after mollicute acquisition.

MATERIALS AND METHODS

Leafhoppers. With one exception, leafhoppers used in this study were from Mexico. Colonies of *D. maidis* and *D. elimatus* were established from specimens collected from maize near Tepexpan, Mexico, October 1980. Colonies of *D. guevarai* DeLong and *D. quinquenotatus* DeLong & Nault were started from adults taken from *Tripsacum dactyloides* (L.) L. and *T. zopilotense* Hern. & Randolph near Teloloapan, Guerrero, October 1981. The colony of *D. tripsacoides* was started from adults taken from *T. maizar* Hern. & Randolph near La Huerta, Jalisco, October 1981. The colony of *D. gelbus* DeLong was established from adults taken from *T. pilosum* Scribn. & Merrill near Zapopan, Jalisco, October 1980, and *B. tripsaci* from adults on *T. dactyloides*, Raleigh, NC, USA, October 1981. Except for *D. maidis* and *D. elimatus*, these species are best adapted to *Tripsacum*, although *D. gelbus* and *D. guevarai* have been collected on several occasions from maize in Mexico (19,22). Colonies of the seven species were maintained in separate 30.5 × 30.5 × 18-cm cages at ~26 C. Cages contained approximately six maize (cultivar Aristogold Bantam Evergreen)

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plants, some of which were replaced weekly with plants at the six-leaf stage. *B. tripsaci* and *D. tripsacoides* required *Tripsacum* as an egg-laying host and feeding host for early instars; maize served as the sole feeding host for later instars and adults.

Approximately 40 mid-instar nymphs of each species were placed in cages with either CSS-infected, MBSM-infected, or healthy corn plants for a 1-wk acquisition access period (AAP). We used the same isolate of CSS as in previous studies (17). MBSM was obtained from infected *Zea mays* ssp. *parviglumis* Iltis & Doebley in Teloloapan, Guerro, Mexico, on 2 October 1980. After the AAP, 25 emerging adults of each species and treatment (exposure to mollicute) were transferred to plastic tube cages (30.5 × 15 cm) containing two healthy corn plants in approximately the six-leaf stage. Cages were kept in growth chambers set at 26 C. On a weekly basis, surviving leafhoppers were counted and placed in tube cages with new healthy six-leaf corn plants. Preliminary tests indicated there was no difference in survival of males and females (*unpublished*); therefore, sex of individual leafhoppers was not determined. The experiment was repeated three times and terminated when all leafhoppers were dead.

Mollicute transmission. Enzyme-linked immunosorbent assay (ELISA) was used as a check to be certain that a high proportion of leafhoppers acquired and were infected with CSS. Separate groups of *D. maidis*, *D. elimatus*, *D. gelbus*, *D. guevarai*, and *D. quinquenotatus* were given a 1-wk AAP (as in previous experiments), transferred to healthy corn plants for a 2-wk incubation period, then individually sacrificed for ELISA according to procedures developed by D. T. Gordon and L. R. Nault (*unpublished*) to be published in a separate article. Antiserum is not available for MBSM, therefore, it was not possible to check for its presence in leafhoppers; we assume that acquisition and infection rates for both mollicutes are equivalent.

In parallel tests to determine if all seven species are vectors of CSS and MBSM, mid-instar nymphs of each species were placed in cages with CSS- or MBSM-infected corn plants for a 1-wk AAP. Leafhoppers were placed in new cages with disease-free corn for a 2-wk incubation period, and then surviving insects were placed in tube cages (one insect per plant) for an inoculation access period (IAP) of 5–7 days. The number of plants showing symptoms after ~8 wk was recorded for each species, and the resulting proportions transmitting each mollicute were determined.

Survival analyses. Let T be the time of death of an individual leafhopper, ie, length of a leafhopper life span. $S(t)$ is the probability that a leafhopper lives at least to time t , or equivalently, the probability that T is greater than t . This probability can be written as:

$$S(t) = Pr \{ T > t \} \quad (1)$$

in which $Pr \{ \cdot \}$ is the probability of an event occurring (13). In experiments that are not terminated until all individuals die (uncensored data), $S(t)$ is estimated from the survival curve, ie, $S(t)$ equals the proportion alive at any time t . This is equivalent to an l_x schedule of life-table analysis (25). Our objective was to find a model for $S(t)$, or equivalently, a model for the distribution of deaths for each species and treatment. Properties of the model must include: $S(0) = 1$; and $S(\infty) = 0$, in which ∞ represents positive infinity.

The two-parameter Weibull model was chosen because of its flexibility and relative mathematical simplicity (13). The Weibull survival function can be written as:

$$S(t) = \exp(-(t/b)^c) \text{ for } t > 0 \quad (2)$$

in which: $\exp(\cdot)$ is e (2.718) raised to a specified power, b is a scale parameter which is inversely related to death rate (ie, larger b means slower decline of the population) and has units of time; and c is a unitless shape parameter that allows the model to take on many forms. When $c = 1$, the Weibull model reduces to the exponential (13). The cumulative distribution of deaths (ie, mortality) is given by $F(t) = 1 - S(t)$. The Weibull is perhaps the most common model for representing survival distributions in both engineering and

medical research (13). $F(t)$ of the expanded three-parameter Weibull model has also been used in a more empirical manner, with different interpretations of the variables and parameters, to represent plant disease epidemics and crop loss due to plant diseases (14,24).

The hazard rate or hazard function, $h(t)$, is a useful reexpression of survival and is given by: $h(t) = -S'(t)/S(t)$, in which $S'(t)$ is the first derivative of $S(t)$ with respect to t and equals the probability density function of T (13). In human epidemiology, $h(t)$ is called the "force of mortality." The hazard rate, when multiplied by Δt , a small increment of t , is approximately equal to the probability of dying in the interval $[t, t + \Delta t]$ provided the individual survived until time t . The Weibull hazard rate is given by:

$$h(t) = (c/b)((t/b)^{c-1}) \quad (3)$$

When $c = 1$, $h(t)$ equals $1/b$; for $c > 1$, $h(t)$ is an increasing function of t .

The parameters b and c were estimated for each species, replication, and treatment using a maximum likelihood procedure (5,28). Additionally, b and c were estimated for each species and treatment with the data pooled across replications. Confidence intervals for the estimated parameters of the pooled data were calculated using the method of Billman et al (2). In general, the 95% confidence intervals for the estimated parameters included the mean of the estimated parameters obtained from the separate analyses of the three replications. For all other analyses and comparisons, therefore, the estimated parameters from the individual replications were used.

Tests were performed to determine if the leafhopper survival distributions were best fit by the Weibull, or by either of two other fairly common survival models, the exponential and the more complicated log-normal. The test for Weibull vs. exponential model was based on the maximum likelihood estimates of c (11); large values of c indicated that the exponential was not appropriate. The test for log-normal vs. Weibull model was based on a likelihood ratio test which is fully explained in Dumonceaux and Antle (8).

The survival experiment consisted of a randomized factorial with three main effects, replication, species, and treatment. The treatments were leafhopper exposure to CSS-infected, MBSM-infected, or healthy corn. In addition to the b and c parameters from the Weibull model, quartiles of the survival distributions were calculated and compared. The quartiles are the times to 75 (t_{75}), 50 (t_{50}), and 25% (t_{25}) survival. The 50% quartile is equivalent to the median survival time. Analysis of variance (ANOVA) was used to determine the effect of species, treatment, and the species × treatment interaction. Duncan's Bayesian least significant difference (BLSD) test was used for mean separations at $k = 100$ ($P \approx 0.05$) (29).

RESULTS

Average survivals of the seven leafhopper species are plotted in Fig. 1. In general, all leafhoppers in the controls were dead by 18 wk or less. The effect of CSS on survival can be readily seen for all species except *D. maidis*. MBSM had an obvious effect on *D. guevarai*, *D. quinquenotatus*, *D. tripsacoides*, *B. tripsaci*, and to a lesser extent on *D. maidis*.

ANOVA revealed a significant effect ($P = 0.05$) of species, treatment, and the species × treatment interaction on the quartiles of the survival distributions. The t_{50} values for CSS-exposed leafhoppers were significantly different from those of the controls for all species except *D. maidis* and *D. quinquenotatus* (Fig. 2). CSS-exposed leafhoppers had values of t_{50} ranging from 2.3 to 7.5 wk. MBSM had a lesser impact on median survival; only MBSM-exposed *D. guevarai* and *D. tripsacoides* had t_{50} values significantly different from those of the controls. Time to 50% survival for the MBSM-exposed leafhoppers ranged from 3.8 to 7.6 wk. The t_{50} values for the controls were remarkably similar for the seven species; values ranged from 5.0 to 8.3 wk, and few means were significantly different from each other.

Exposure to CSS-infected corn significantly reduced the t_{25} for all species except *D. maidis* (Fig. 3); exposure to MBSM-infected corn significantly reduced t_{25} for all species except *D. elimatus* and *D. gelbus*. The t_{25} after CSS exposure was significantly shorter than the t_{25} after MBSM-exposure for *D. elimatus*, *D. gelbus*, *D. guevarai*, and *B. tripsaci*. The effect of MBSM also was more delayed than CSS. For example, MBSM reduced the median survival time for only two species compared to the controls, but reduced t_{25} for five species. On the other hand, CSS reduced t_{50} for five species and t_{25} for six.

There were significant effects of species, treatment, and the species \times treatment interaction ($P = 0.05$) for both the b and c parameters of the Weibull model. Mean maximum likelihood estimates for b and c are listed in Table 1. For CSS-exposed

leafhoppers, the values of b were significantly lower (ie, faster rate of population decline) than those of the control for all species except *D. maidis*; for MBSM-exposed leafhoppers, the b s were significantly lower for all species except *D. elimatus* and *D. gelbus*. Values of b for CSS-exposed leafhoppers were significantly lower than those of MBSM-exposed leafhoppers for *D. elimatus*, *D. gelbus*, *D. guevarai*, and *B. tripsaci*. For CSS-exposed leafhoppers, the values of c were significantly greater than those of the controls for all species except *D. maidis* and *D. guevarai*; for MBSM-exposed leafhoppers, the c values were significantly greater for only *D. quinquenotatus* and *D. tripsacoides*. The c values for the controls of the seven species were not significantly different from each other.

None of the survival distributions were adequately described by

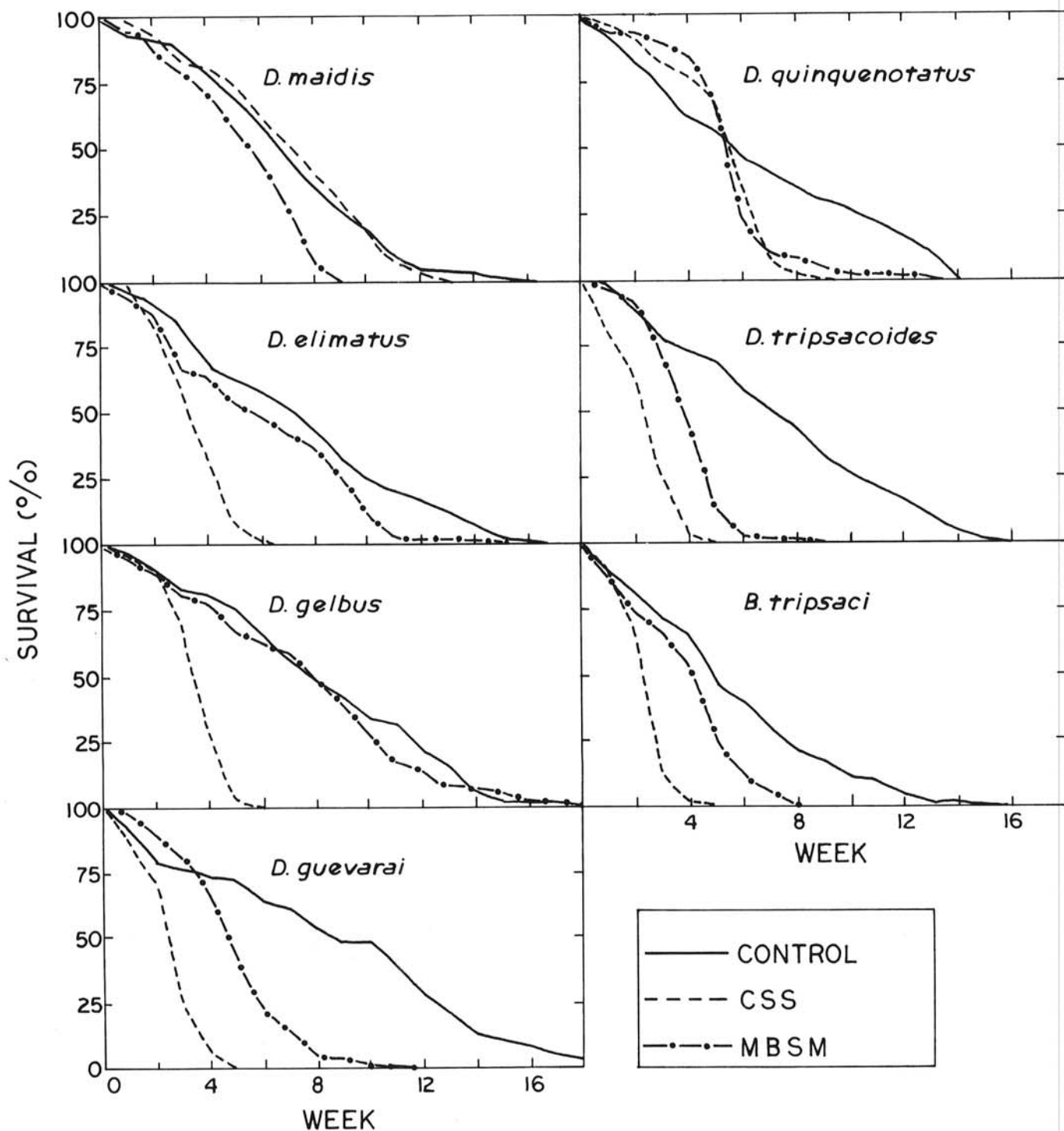


Fig. 1. Adult survival of leafhoppers in six *Dalbulus* and one *Baldulus* species on corn after exposure to corn stunt spiropasma (CSS), maize bushy stunt mycoplasma (MBSM), or healthy corn (control) for 1 wk. Curves represent the average of three replications.

the simple exponential model ($P = 0.01$) according to the test of Klimko et al (11). Results of the likelihood ratio test (8) indicated that only ~20% of the survival distributions were better described by the log-normal model than by the Weibull model. This percentage was not high enough to warrant further modeling with the log-normal distribution, since the log-normal has some undesirable properties. Firstly, there is no closed-form expression for $S(t)$, ie, $S(t)$ can only be represented as the integral: $1 - \int_0^t f(u) du$, in which $f(u)$ is the log-normal probability density function evaluated at $t = u$, and du is a small increment of u (13). The integral can only be solved numerically. Secondly, the hazard rate of the log-normal model has the undesirable property of reaching a maximum and then declining at large values of t (13). Declining hazard rates after reaching a maximum are not commonly observed.

The effects of c on the theoretical Weibull $S(t)$ and $h(t)$ functions are presented in Fig. 4. Except for $c = 1$, the parameter values are typical for leafhopper survival in this study. Values of 2, 3, and 4 approximately correspond to the average c values for all leafhopper species exposed to healthy corn, MBSM, and CSS, respectively. The case when $c = 1$ is shown in order to present the typical curve for the exponential distribution. The hazard rate is a power function of c , ie, hazard rate increases exponentially as c increases linearly. For $c = 4$, the hazard rate extends beyond the scale of this plot and equals 9.7 at $t = 18$ wk. To interpret the hazard rate,

consider the case when $t = 9$ wk. The probability of a leafhopper dying immediately after 9 wk given that it survived 9 wk equals $1.22\Delta t$ (ie, $h(9) = 1.22$) when $c = 4$; this probability equals $0.37\Delta t$ when $c = 2$. Thus, the conditional probability of death given survival for 9 wk when $c = 4$ is 3.3 ($1.22/0.37$) times greater than when $c = 2$.

The effect of three typical values of b , at a constant value for c , on theoretical $S(t)$ and $h(t)$ functions are shown in Fig. 5. Values of 5 and 7 wk approximately correspond to the average values of b for all species exposed to CSS and MBSM, respectively. Values of b equal to 9 wk or higher are typical for most species exposed to healthy corn. $S(t)$ drops off quickly at smaller values of b . The hazard rate is inversely proportional to b .

Results of ELISA indicated that CSS acquisition and infection rates for the five tested species were very high. For *D. maidis*, *D. elimatus*, *D. gelbus*, *D. guevarai*, and *D. quinquenotatus*, 100, 80, 100, 93, and 96%, respectively, were positive for CSS. These results suggest that mortality of mollicute-exposed leafhoppers was due to the mollicutes and not differences in nutrition or other factors between healthy and infected plants.

CSS and MBSM transmission rates for the seven leafhopper species are listed in Table 2. All species transmitted both mollicutes, although rates were variable. CSS, and to a lesser extent MBSM, killed many leafhoppers before the end of the test period. Of the six species affected by CSS, transmission rates ranged from 9 to 38%.

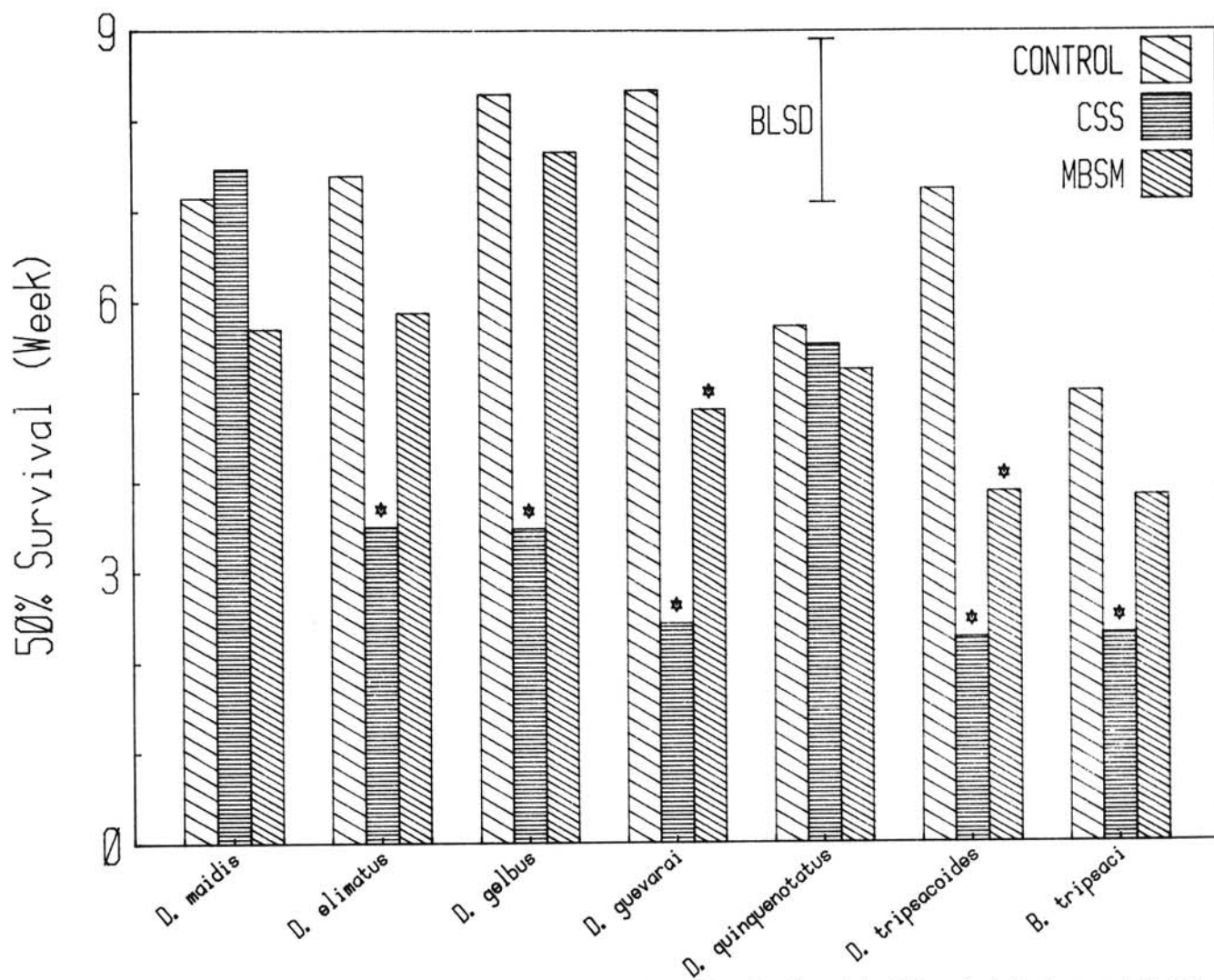


Fig. 2. Effect of corn stunt spiroplasma (CSS) and maize bushy stunt mycoplasma (MBSM) on time (in weeks) to 50% survival of leafhoppers in six *Dalbulus* and one *Balbulus* species. Bars represent means of three replications. For each species, bars topped with an asterisk are significantly different from the control according to Duncan's Bayesian least significant difference (BLSD, $k = 100$, $P \cong 0.05$) test. BLSD was drawn on the plot and equaled 1.80 wk; this value can be used for making any pairwise comparison of means.

Of the five species affected by MBSM, rates ranged from 35 to 71%. There was no significant difference in transmission rates of the two species not affected by MBSM, *D. elimatus* and *D. gelbus*.

DISCUSSION

D. maidis and *D. elimatus* have been used frequently as experimental vectors of CSS and MBSM (see review by Nault and Bradfute [20]). *B. tripsaci* was used as a vector of MBSM (= "Louisiana corn stunt") by Granados and Whitcomb (10). Ramirez et al (27) used *D. guevarai* as a corn stunt (= "achaparramiento") vector, but it is not clear whether CSS or MBSM was involved. We have shown that all seven leafhopper species used in this study are vectors of both mollicutes.

The Weibull model was acceptable for representing the survival of adult leafhoppers in *Dalbulus* and *Baldulus* species. Our results provide additional evidence for the wide applicability of the Weibull model for describing survival in engineering, health sciences (13), and zoology (26). The effect of the mollicutes on leafhopper survival can be directly quantified by values of the scale parameter, *b*, and shape parameter, *c*. The closed-form expressions of the Weibull model allow the representation of the probability of leafhopper survival at a particular time (*S(t)*), as well as the probability of death during the interval [*t*, *t* + Δt] given that the leafhopper survived until *t* (*h(t)*). These probabilities are essential for our planned development of a simulation model of these leafhopper species.

D. maidis was the most efficient CSS vector and the only species tested whose adult life span was unaffected by the spiroplasma. This does not agree with Granados and Meehan (9) who reported that CSS was marginally pathogenic to *D. maidis* in limited studies;

TABLE 1. Effect of exposure to corn stunt spiroplasma (CSS) and maize bushy stunt mycoplasma (MBSM) on the maximum likelihood estimates of the scale (*b*) and shape (*c*) parameters of the Weibull distribution representing survival of adult leafhoppers in six *Dalbulus* and one *Baldulus* species^a

Species	<i>b</i>			<i>c</i>		
	Control	CSS	MBSM	Control	CSS	MBSM
<i>D. maidis</i>	9.60	8.44	6.95* ^b	2.33	2.86	3.40
<i>D. elimatus</i>	9.22	4.35*	7.96	2.15	3.78*	2.13
<i>D. gelbus</i>	10.14	4.42*	10.10	2.42	4.90*	2.15
<i>D. guevarai</i>	12.66	4.04*	6.23*	2.02	3.20	2.77
<i>D. quinquenotatus</i>	9.11	6.48*	6.85*	2.06	3.53*	3.66*
<i>D. tripsacoides</i>	8.97	3.94*	5.00*	2.09	3.52*	3.66*
<i>B. tripsaci</i>	8.44	3.33*	6.04*	1.95	5.48*	2.69
BLSD ^c	1.83			1.41		

^aValues are the average of three replications; *b* is in units of time (wk) and *c* is unitless.

^bFor each species and variable, value followed by an asterisk is significantly different from the control according to Duncan's Bayesian least significant difference ($k = 100$, $P \approx 0.05$) test.

^cDuncan's Bayesian least significant difference (BLSLSD) for making pairwise comparisons of *b* or *c* ($k = 100$, $P \approx 0.05$).

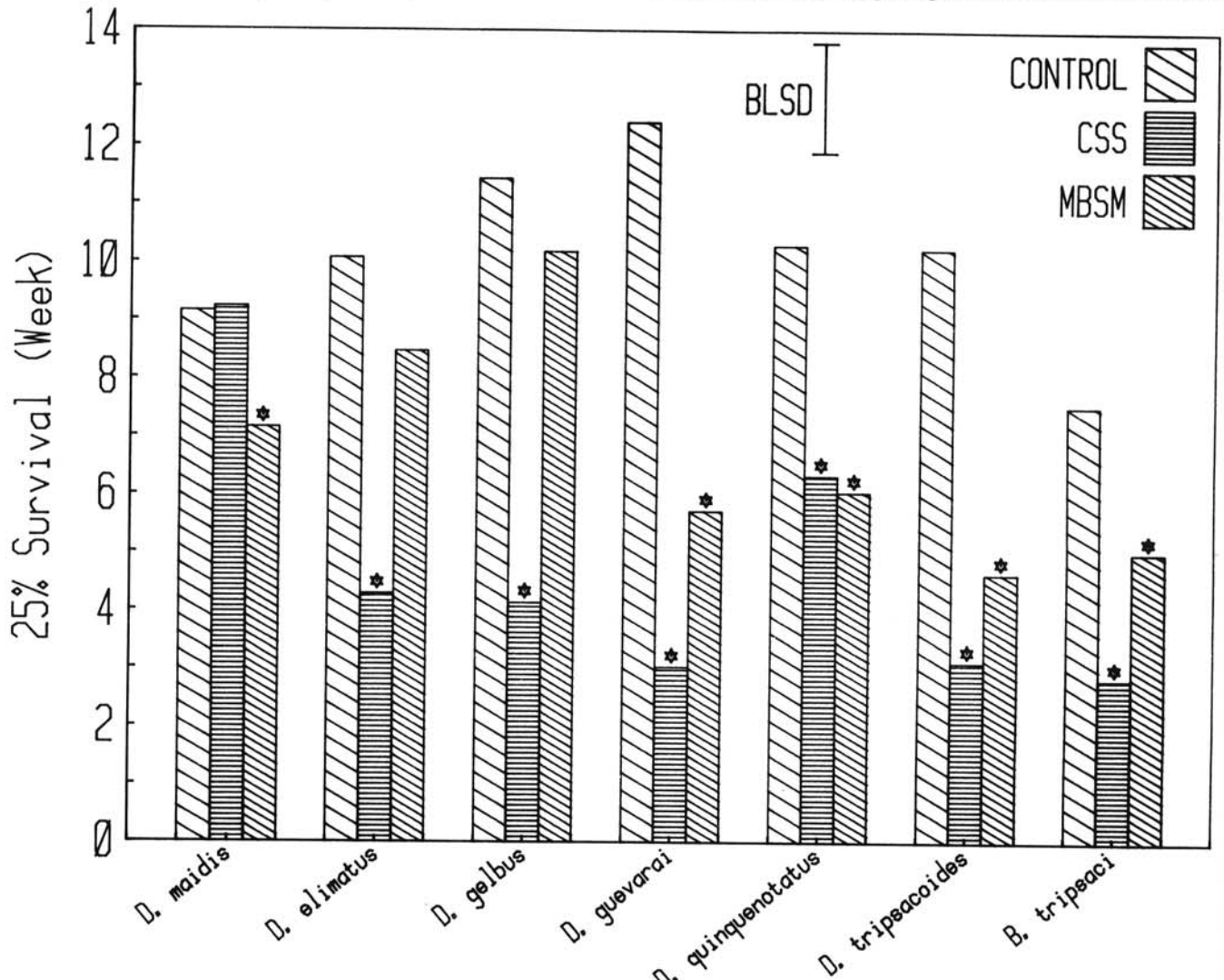


Fig. 3. Effect of corn stunt spiroplasma (CSS) and maize bushy stunt mycoplasma (MBSM) on time (in weeks) to 25% survival of leafhoppers in six *Dalbulus* and one *Baldulus* species. Bars represent means of three replications. For each species, bars topped with an asterisk are significantly different from the control according to Duncan's Bayesian least significant difference (BLSLSD, $k = 100$, $P \approx 0.05$) test. BLSLSD was drawn on the plot and equaled 1.89 wk; this value can be used for making any pairwise comparison of means.

we do agree with them, as well as with Chen and Liao (3) and Williamson and Whitcomb (30) that CSS is pathogenic to *D. elimatus*. High mortality in *D. elimatus*, as well as other species, precluded higher transmission rates. For example, in one test only three of 58 *D. gelbus* survived a 1-wk IAP compared to 18 of 20 *D. maidis*. The median survival times for most infected, susceptible leafhopper species are only slightly longer than the mean latent period of CSS in *D. maidis* (17). Thus, in many instances a potential vector would have died before it could transmit. The median survival time for all leafhoppers exposed to MBSM exceeds by several weeks the mean latent period of MBSM in *D. maidis* (17). Therefore, transmission rates of MBSM are less likely to be affected by mortality than transmission rates of CSS.

A long association between a vector and plant pathogen should result in a selection of vector biotypes and pathogen strains that are highly compatible, ie, plant pathogens not pathogenic to their insect vectors. Our results are consistent with this hypothesis. Consider first the two maize specialists, *D. maidis* and *D. elimatus*, that appear best adapted for transmitting CSS and MBSM, respectively, based on differential pathogenicity of the mollicutes. This is consistent with known distributions of pathogens and vectors; *D. maidis* and CSS are most prevalent at mid-to-low elevations in Mexico, whereas *D. elimatus* and MBSM are more common at high elevations (1,6,7,18). On the other hand, *D. tripsacoides*, *D. quinquenotatus*, and *B. tripsaci* are highly susceptible to CSS and MBSM. These species occur solely on

Tripsacum spp. and are unlikely to encounter CSS or MBSM in nature because, so far as is known, *Tripsacum* spp. are immune to both mollicutes (17,22). The other two species, *D. guevarai* and *D. gelbus*, are susceptible to CSS and occur on maize; however, they are both considered best adapted to *Tripsacum* (22). The lack of pathogenicity of MBSM to *D. gelbus* suggests that this species may occur more commonly on maize at high elevations than is currently

TABLE 2. Transmission rates of corn stunt spiroplasma (CSS) and maize bushy stunt mycoplasma (MBSM) by adult leafhoppers in six *Dalbulus* and one *Baldulus* species after an acquisition access period of 1 wk

Species	CSS			MBSM		
	n^x	p^y	s.e. ^z	n^x	p^y	s.e. ^z
<i>D. maidis</i>	71	0.80	0.08	76	0.64	0.09
<i>D. elimatus</i>	37	0.38	0.08	37	0.57	0.23
<i>D. gelbus</i>	96	0.34	0.13	69	0.35	0.15
<i>D. guevarai</i>	46	0.22	0.02	86	0.69	0.10
<i>D. quinquenotatus</i>	68	0.29	0.09	75	0.35	0.06
<i>D. tripsacoides</i>	11	0.09	0.09	20	0.55	0.13
<i>B. tripsaci</i>	14	0.21	0.11	35	0.71	0.11

^x n equals number of leafhoppers alive at end of a total of a 1-wk acquisition access period, 2-wk incubation period, and 5-7 day inoculation access period. Transmission rate calculations based on this number.

^yRate of transmission; p equals the number of plants showing symptoms divided by the number of plants exposed to leafhoppers.

^zs.e. equals standard error of estimated p calculated by using the method described in Cochran (4) for proportions obtained from independent tests ("clusters") with unequal numbers of observations.

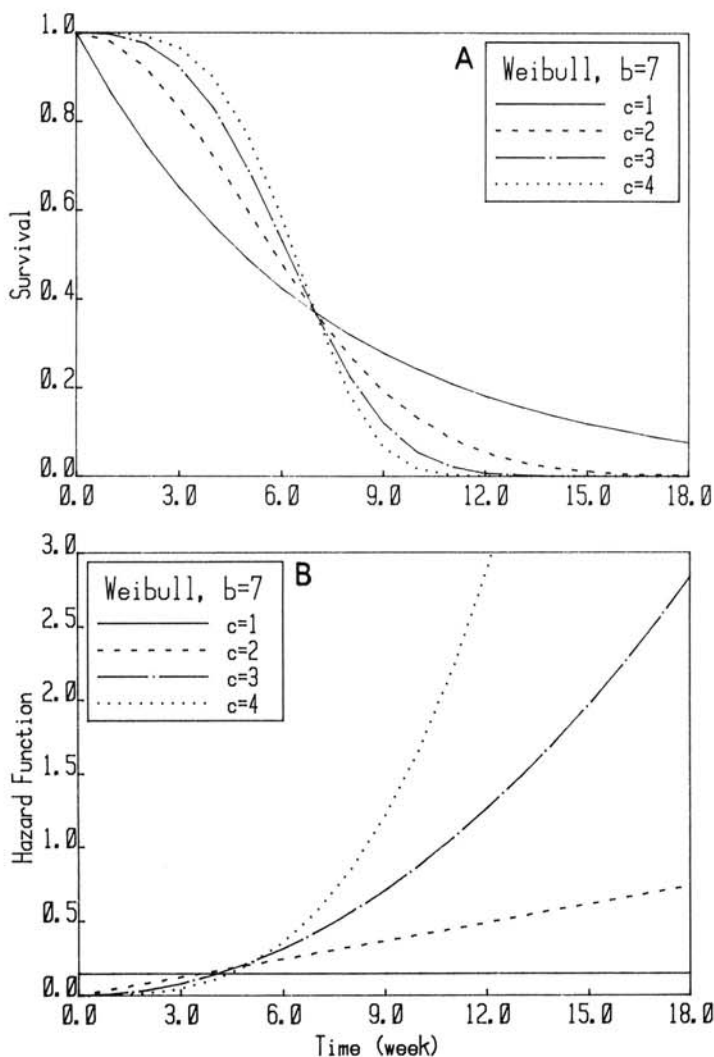


Fig. 4. Effect of four values of the shape parameter (c) on the: A, survival distribution; and B, hazard rate of the Weibull model. Data were generated from t equals 0 to 18 wk. The scale parameter (b) was fixed at $b = 7$ wk. When $c = 1$, the Weibull model reduces to the exponential. For $c = 4$, hazard rate equals 9.7 at $t = 18$ wk.

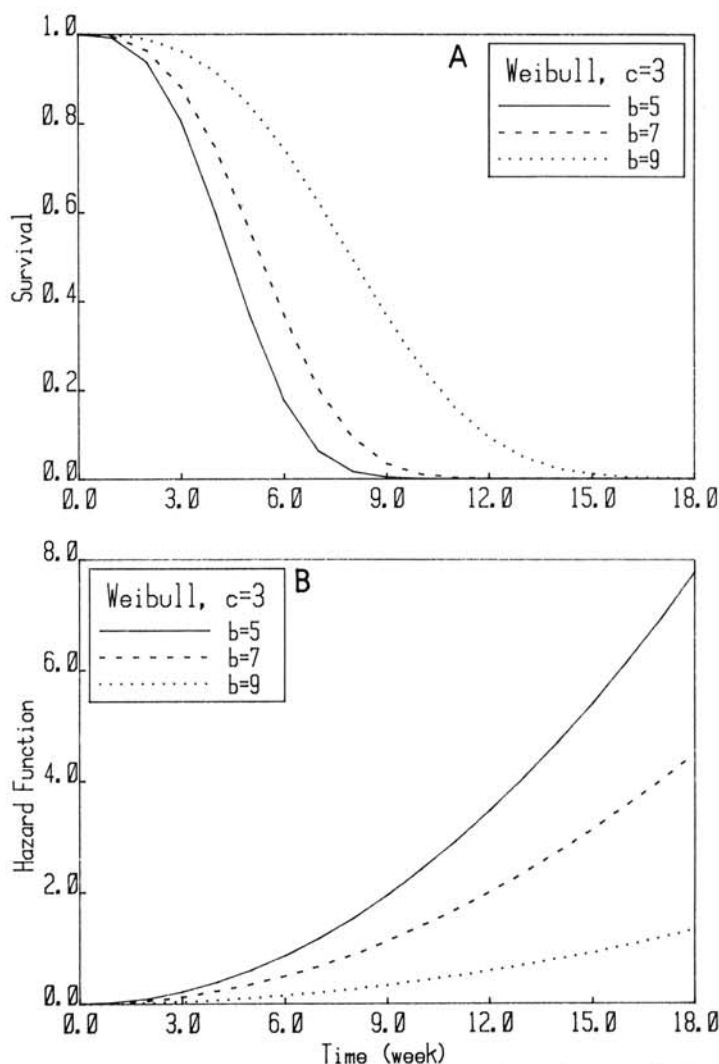


Fig. 5. Effect of three values of the scale parameter (b) on the: A, survival distribution; and B, hazard rate of the Weibull model. Data were generated from t equals 0 to 18 wk. The shape parameter (c) was fixed at $c = 3$.

known. Its efficiency as an MBSM vector equals that of *D. elimatus*.

Given time, the development of a mutualistic vector-pathogen association in which both partners would benefit seems possible. The benefit derived by the obligately transmitted pathogen is obvious; however, potential benefits accrued to the vector are more difficult to demonstrate. The possible broadening of the host range of *D. maidis* is one possibility. For example, Maramorosch (15) noted that *D. maidis* can utilize aster (a dicot) as a feeding host only if it is infected with the aster yellows mycoplasma (AYM). Such previously exposed leafhoppers can then feed on healthy asters. However, the association is non-adaptive since *D. maidis* is not an AYM vector. Perhaps MBSM or CSS has a similar effect on *D. maidis* or *D. elimatus*, by broadening their range of feeding hosts during the dry winter season in Mexico when maize and the annual teosintes are not available. Another possibility is that *D. maidis* could benefit from reduced competition from its congeners by transmitting CSS to its maize host. Similarly, *D. elimatus* or *D. gelbus* could benefit from MBSM.

Recently, Maramorosch (16) speculated that "plant pathogenic prokaryotes may have originated as insect pathogens and gradually became less harmful to their original hosts. Their ability to infect plants in which they cause severe and sometimes fatal diseases might be of more recent origin." While we do not debate the possibility that plant pathogenic prokaryotes may have originated in their insect vectors, our evidence does not agree with Maramorosch's (16) generalization of low pathogenicity of mycoplasmas to their vectors. Low pathogenicity or its absence likely occurs only with certain well-adapted vectors. We predict that close relatives of vector species of other plant pathogenic mollicutes will, as happened in this study, also succumb to these pathogens. We further disagree with the inference that plant pathogenic mollicutes usually cause severe plant disease. Although this may be true for highly selected cultivars of crop species, it is not necessarily true for their better-adapted wild relatives. For example, the perennial relatives of maize among *Zea* and *Tripsacum* spp. generally are tolerant or immune to MBSM and CSS (17). We suggest that a high level of pathogenicity of a plant pathogenic mollicute to its plant host or insect vector should alert investigators to search for *native* hosts and vectors. Their discovery could be vital to understanding disease epidemiology and developing effective control measures.

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