

# VARIATION IN INSECT PEST AND VIRUS RESISTANCE AMONG HABANERO PEPPERS (*Capsicum chinense* JACQ.) IN YUCATÁN, MÉXICO

## VARIACIÓN EN RESISTENCIA A INSECTOS HERBÍVOROS Y VIROSIS EN LÍNEAS DE CHILE HABANERO (*Capsicum chinense* JACQ.) EN YUCATÁN, MÉXICO

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### ABSTRACT

The evaluation of crop genetic variation for herbivore resistance is a relevant tool that can inform plant breeding strategies for resistance and biological control. The objective of this study was to provide a field-based assessment of pest resistance in five lines of habanero pepper, *Capsicum chinense* Jacq. Weekly surveys were conducted at an experimental site in Mocochoá (Yucatán, México) from July 2010 to December 2010, including incidence of *Bemisia tabaci* nymphs and *Liriomyza trifolii* leafminers, fruit infestation by the pepper weevil (*Anthonomus eugenii*), and the presence and severity of symptoms of viral infection. To this end, we used a completely randomized design with five 5×5 m replicate plots, each containing an equal number of plants of each *C. chinense* line. Results showed significant differences ( $p \leq 0.05$ ) among *C. chinense* lines for the number of mines per leaf and the proportion of fruits infested by the pepper weevil. Interestingly, genotype 36 (a South American habanero) exhibited the highest incidence of leaf mines but the lowest incidence of fruit attack by the weevil, while genotype 110 (Antillean yellow habanero) showed a reverse pattern. In addition, evidence of among-line differences was found in the severity of virosis symptoms, suggesting differential susceptibility to viruses. Overall, these results provide novel evidence of pest resistance variation in *C. chinense* lines under field conditions, which will inform future efforts to select for pest resistance in this crop.

**Key words:** *Capsicum chinense*, plant resistance, plant genetic variation.

### INTRODUCTION

The use of insecticides is the most common method for pest control in horticultural crops such as peppers (*Capsicum* spp.) (Soria-Fregoso *et al.*, 1996; Bosland and Votava, 2000). However, it is widely recognized that insecticides negatively affect populations of natural enemies (Theiling and Croft, 1988), lead to resistance of target insect pests (Nauen and Denholm, 2005), and have harmful impacts on human health and the environment (Eskenazi *et al.*, 1999). A viable strategy to reduce pest damage and minimize insecticide application is the use of pest-resistant crops (Cuartero *et al.*, 1999; Cortesero *et al.*, 2000), which can serve as a complementary tool to other methods targeted for integrated pest management (Eigenbrode and Trumble, 1994). Accordingly, evaluations of pest resistance across plant genotypes represent a fundamental step towards the study of crop pest resistance (Smith, 2005). Although studies by Kim *et al.* (2010) and Fridaus *et al.* (2011) as well as multinational efforts (Sarath Babu *et al.*, 2011) address plant genotypic variation in resistance to arthropod pests and pathogens in the genus *Capsicum*, evaluations are scarce for Latin America (Morales, 2011) and lacking for some cultivated peppers such as the habanero pepper (*Capsicum chinense* Jacq.).

Habanero pepper is one of the main horticultural

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crops in southeast México owing to its cultural, culinary and economic value, as well as its high potential for exportation and industrialization (Soria-Fregoso *et al.*, 1996; Tun-Dzul, 2001). In Yucatán, the state in México with the greatest production of *C. chinense*, the total area planted with this crop has progressively increased during the last decade (SIAP, 2011). However, *C. chinense* yields remain low and this is largely due to the negative impact of insect pests and pathogens. The main pests of peppers in México's lowland tropics are the whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae), the pepper weevil *Anthonomus eugeni* Cano (Coleoptera: Curculionidae), leafminers of the genus *Liriomyza* (Diptera: Agromyzidae), as well as some species of mites (*Tetranychus* sp., *Polyphagotarsonemus latus*) (Soria-Fregoso *et al.*, 1996; Tun-Dzul, 2001). Among these pests, *B. tabaci* is typically the most damaging because it is a vector of several species of *Begomovirus* (Geminiviridae) (Torres-Pacheco *et al.*, 1996; Morales and Anderson, 2001) which cause yellowing and deformation in leaves, as well as plant stunting, reduced fruit-set and fruit deformation (Polston and Anderson, 1997).

The goal of this study is to provide a field assessment of resistance to multiple pests in five lines of *C. chinense* in southeast México (Yucatán). To this end, we conducted detailed surveys of abundance and damage by three major pests of habanero pepper, as well as recorded the onset and severity of symptoms of virosis. In doing so, we show genetic variation for pest resistance in habanero pepper which will serve as baseline information for the selection and breeding of genotypes with enhanced pest resistance.

## MATERIALS AND METHODS

The study was conducted from July 2010 to November 2010 at the Mococho Research Station of the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), in Yucatán, México (21° 6' 40" N, 89° 26' 35" W). A 30×50-m area was used to establish five 5×5-m plots of *C. chinense*, each of which included an equal number of plants of all five lines. Within each plot we randomly assigned positions to plants of each line. Distance between plots was 2.5 m, and within each plot the planting design was 30 cm between plants within rows, and 1.25 m between rows within plots. Planting density was 2.64 plants m<sup>-2</sup> (66 plants per plot), for a total of 330 plants.

Of these, eight plants per line, per plot, were randomly chosen and monitored throughout the growing season, resulting in 40 sampled plants per line, and a total of 200 sampled plants. The fertilization and irrigation regime was the same across all plots and followed standard agricultural practices used for *C. chinense* in the region (Tun-Dzul, 2001), with the only exception being that insecticides were not used.

*Capsicum chinense* lines were selected *a priori* to include a wide range of phenotypic variation in vegetative and reproductive traits. We used a typical orange habanero (G84), a Belizean red habanero (G149), an Antillean yellow habanero (G110), a South American habanero of small fruits (G36), and the Cuban habanero (G37). These lines have been previously shown to differ in vegetative (*e.g.*, plant size, architecture) and reproductive traits (flowering phenology, fruit size and yield) (Trujillo-Aguirre and Pérez-Llanes, 2004).

The response variables measured for each plant were: 1) number of leaf mines of *L. trifolii* on six randomly chosen leaves, and this survey was conducted on different leaves every two weeks from July 2010 to September 2010; 2) presence of whitefly *B. tabaci* nymphs on the abaxial surface of four leaves, recorded once every two weeks (on different leaves each survey) from July 2010 to September 2010, as well as an additional survey in November 2010; both leafminer and whitefly nymph data were recorded on young, fully-expanded leaves; 3) the number of weeks until the appearance of symptoms of virosis based on weekly surveys from July 2010 to November 2010; 4) severity of virosis, scored from one (low severity) to nine (high severity) based on infection symptoms (Gonzalez-Perez *et al.*, 2011) at the end of the experiment (November 2010); and 5) fruit infestation by the pepper weevil *A. eugeni* based on weekly harvests of all fruits per plant from late September 2010 to mid November 2010. Infested fruits were identified based on the presence of yellowing of the fruit petiole which is a reliable indicator of weevil presence (>95 % of the cases based on a random subsample; data from this study).

Surveys of *B. tabaci* at the study site confirmed the presence of whitefly biotypes A and B during the sampling season through barcoding mitochondrial cytochrome c oxidase subunit I (Papayiannis *et al.*, 2009) and sequence similarity in the GenBank database (Benson *et al.*, 2013). However, we did not discern between these two biotypes when recording nymph presence (although resistance to both is frequently positively related; Wilhoit, 1992; Nombela *et al.*, 2001). In the case of virus infection transmitted by *B. tabaci*, although a wide range of symptoms were observed in the field and co-infections by begomoviruses are common in cultivated Solanaceae plantations (Mendez-Lozano *et al.*, 2001; Anaya-Lopez *et al.*, 2003; Mendez-Lozano *et al.*, 2003), we do not have evidence to support the presence of mixed

infections in this study. Thus our documentation of virosis in the field represented a measure of resistance to either one and/or multiple virus species (e.g. resistance to the *Begomovirus* complex or *Tospovirus*).

### Statistical analyses

Generalized linear models in Proc GLIMMIX, SAS version 9.1 (SAS Institute, 2002, Cary, NC) were used to test for differences among *C. chinense* lines in the number of mines per leaf (number of mines per plant/number of leaves sampled per plant), the proportion of fruits attacked by the pepper weevil (number of weevils per plant/number of fruits sampled per plant), and number of weeks until the appearance of symptoms of virosis and severity of virosis. In all three cases, data were not normally distributed even after transformation; therefore, we selected alternative error distributions which best fitted the raw data. The model number of leaf mines assumed a gamma distribution (log link), the weevil attack model assumed an exponential distribution (log link), and models for number of weeks until appearance of symptoms and severity of virosis both assumed a Poisson distribution (log link) which is appropriate for count data. The gamma and exponential distributions are appropriate for continuous data and handle different types of non-normal distributions (Zuur *et al.* 2009). In addition, Proc LOGISTIC was used to test for pepper line differences in the likelihood of whitefly nymph presence based on presence/absence data.

Proc GLIMMIX was used to test for differences among *C. chinense* lines in the number of fruits produced, total yield (g) and mean fruit weight (g; number of fruits/total yield). Fruit number and total yield models assumed a Poisson distribution (log link), while the fruit weight model assumed a Gamma distribution (log link).

For all statistical models, the effect of plot in the model was included to account for spatial variation in insect attack and spread of virosis. Previously, the plot×line interaction was removed owing to its non-significance. The only exception was the model for number of weeks until appearance of symptoms of virosis. For all models results for type 3 analysis are reported. Whenever the line effect was significant, tests were run for differences among line least-square means (using corrected P-values). In all cases, back-transformed least-square means and 95 % confidence limits as descriptive statistics are shown. All models treated *C. chinense* line as fixed effect given that this study was based on the a priori selection and examination of resistance of pepper lines of interest in breeding programs at INIFAP as well as for commercial purposes.

## RESULTS AND DISCUSSION

### Fruit number, yield, and fruit weight

There were significant differences among habanero lines for fruit number (Table 1); G36 produced the greatest number of fruits and differed significantly from all other lines ( $p \leq 0.05$ ). Then followed G110 and G37 with intermediate values similar between them ( $p > 0.05$ ). Finally, G84 and G149 produced the lowest number of fruits and differed significantly from G37 and G110 ( $p \leq 0.05$ ), but not among each other ( $p > 0.05$ ) (Table 2).

Fruit weight also differed significantly among habanero lines (Table 1), with G149 showing the greatest mean fruit weight, differing significantly from all other lines ( $p \leq 0.05$ ). G110 and G84 had the following greatest mean fruit weights, differing significantly from G37 and G36 ( $p < 0.05$ ), but not among each other ( $p > 0.05$ ). G37 had the following lowest mean fruit weight and differed significantly from G36 with the lowest mean value of all lines ( $p \leq 0.05$ ) (Table 2).

Lastly, there were weaker differences (marginal) for total yield among habanero lines (Table 1) with genotype G110 and G37 showing the highest and lowest average yield, while G149, G37, and G36 showed intermediate values (Table 2). These findings show how G84 by having an intermediate mean fruit weight, but one of the lowest fruit outputs, exhibited the lowest yield of all five lines. In contrast, line G36, despite producing the smallest fruits, had the highest fruit output and achieved an intermediate yield. Line G110 exhibited the highest yield by producing the second largest amount of fruits and having intermediate-size fruits.

### Pest incidence and virosis among *C. chinense* lines

There were significant differences among lines for the number of mines per leaf, the proportion of fruits attacked by the pepper weevil, the degree of severity of virosis, and the number of weeks up to appearance of symptoms of virosis (Table 1). Differences among genotypes were not significant for the likelihood of presence of whitefly nymphs (logistic regression:  $\chi^2 = 7.59$ , d.f. = 4, 197,  $p = 0.06$ ).

**Table 1. Results from generalized linear models testing for the effects of *Capsicum chinense* line and plot on fruit number, yield (g), fruit weight (g), number of mines per leaf of *Liriomyza trifolii*, proportion of fruits attacked by the weevil *Anthonomus eugenii*, number weeks until the appearance of symptoms of virosis, and severity of virosis at the end of the experiment.**

Response variable	Source of variation	D. F.	F-value	P-value
Fruit number	Line	4,189	58.8	<0.0001
	Plot	4,189	6.3	<0.0001
Yield	Line	4,181	2.06	0.08
	Plot	4,181	7.91	<0.001
Fruit weight	Line	4,181	704.5	<0.0001
	Plot	4,181	2.2	0.07
Mines per leaf	Line	4,182	4.6	0.001
	Plot	4,182	4.2	0.002
Proportion of attacked fruits	Line	4,185	13.7	<0.0001
	Plot	4,185	7.2	<0.0001
Weeks for symptoms	Line	4,173	3.0	0.02
	Plot	4,173	6.8	<0.0001
	Line*plot	16,173	2.3	0.004
Severity of virosis	Line	4,172	9.6	<0.0001
	Plot	4,172	6.1	0.0001

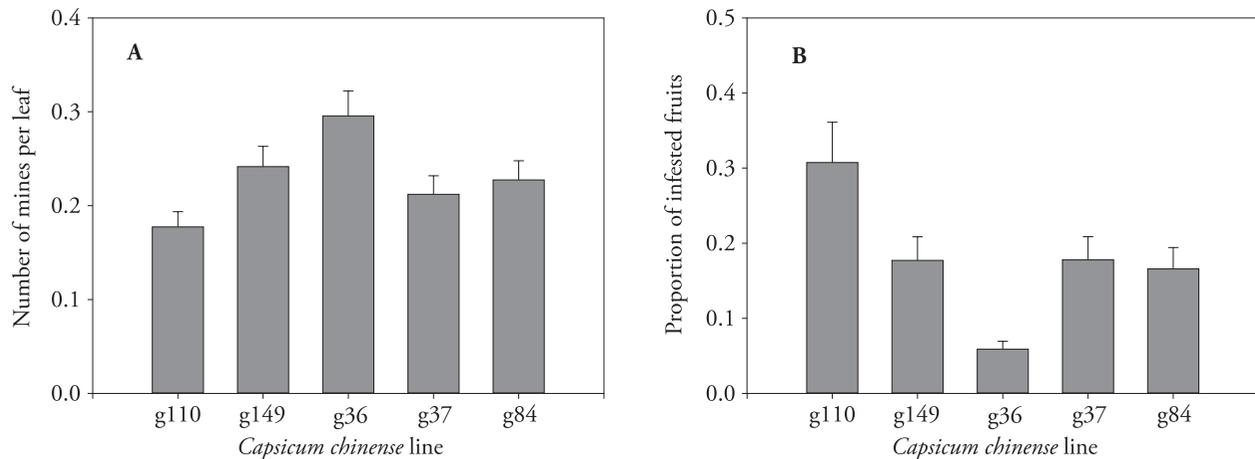
D.F.=degrees of freedom.

Line G36 was the most heavily attacked by the leafminer, followed by G149 from which it did not, however, differ significantly, these two lines showed a greater amount of leaf mines relative to lines G110, G37 and G84, the latter three lines did not differ significantly (Figure 1A). In contrast, G36 exhibited the lowest proportion of attacked fruits by the pepper weevil, the following line with the lowest proportion of attacked fruits showed more than a three-fold difference relative to G36. Line G110 showed the highest proportion of attacked fruits, followed by lines G149, G37 and G84, which

were similar between them ( $p>0.05$ ; Figure 1B). Interestingly, by showing the highest incidence of fruit infestation but a tendency for the lowest number of mines per leaf, line G110 showed a reverse pattern of attack for these two pests relative to G36. Such reverse patterns of attack by leaf miners relative to the weevil may suggest trade-offs in resistance against pests for these two lines (Koricheva *et al.*, 2004; Lankau, 2007). Indeed, although of preliminary nature due to the limited number of lines used in this study, a significant negative correlation was observed between the number of leaf mines and the

**Table 2. Back-transformed least-square means for fruit production, yield and fruit weight for five lines of habanero pepper (*Capsicum chinense*) in a field experiment in Yucatán, México from July to December 2010. Values in parentheses are lower and upper 95 % confidence limits.**

Line	Fruit number	Yield (g)	Fruit weight (g)
G110	61.1 (53.7, 69.4)	348.1 (308.7, 392.5)	6.9 (6.7, 7.1)
G149	31.8 (26.6, 38.2)	245.7 (215.3, 280.4)	8.7 (8.4, 8.9)
G36	233.5 (217.3, 251.0)	235.9 (206.3, 269.7)	1.0 (1.0, 1.1)
G37	54.7 (47.9, 62.4)	237.3 (209.2, 269.2)	5.3 (5.4, 5.1)
G84	31.0 (26.0, 37.0)	196.8 (170.4, 227.3)	6.5 (6.8, 6.3)

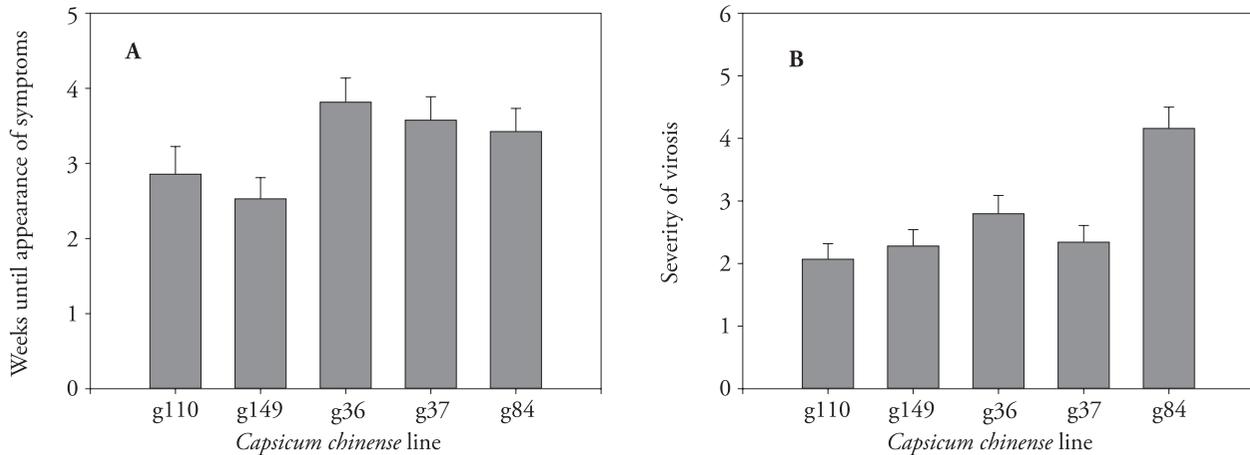


**Figure 1.** Differences between *Capsicum chinense* lines for (A) the number of mines per leaf (*Liriomyza trifolii*), and (B) the proportion of fruits attacked by the pepper weevil (*Anthonomus eugenii*). Values are back-transformed least-square means and 95 % confidence limits.

proportion of weevil-attacked fruits using pepper line means ( $r = -0.89$ ,  $p = 0.03$ ). Nonetheless, to formally test this hypothesis, further experiments are needed using prescribed levels of infestation rates of each pest (including control plants), comparing results at several sites and across two or more years.

Because G36 produced the smallest fruits of all five lines and showed the lowest proportion of attacked fruits by *A. eugenii*, it is possible that fruit selection by ovipositing female weevils is dictated by plant traits such as fruit size. Indeed, female beetles may prefer to oviposit on larger fruits for two reasons: greater resource availability or decreased risk of predation. Supporting the latter idea, G36 showed higher parasitism rates of weevils (1.2-fold to 6.3-fold greater relative to the other lines), presumably due to easier access of the female parasitoid to weevil larvae during oviposition. Nonetheless, contrary to our findings, Porter *et al.* (2007) report that weevils preferred smaller fruits of a Jalapeño cultivar, which could be due to differences in fruit developmental time. Indeed, other fruit traits such as pericarp thickness were proposed as important predictors of parasitism risk of pepper weevil in bell pepper (Riley and Schuster, 1992) and remain to be tested in *C. chinense*. Finally, in addition to fruit traits *per se*, high fruit production may cause an effect of satiation on the pepper weevil (Elzinga *et al.*, 2007), which may have influenced results in this study. These and other plant traits influencing weevil attack deserve further examination.

The mean number of weeks until the appearance of symptoms of virosis was similar among most lines, with the exception of G149, which was the earliest to show symptoms of infection but not significantly different from G110 (Figure 2A). In contrast, line G110 showed the highest mean score for severity of virosis by the end of the experiment, but there were no differences ( $p > 0.05$ ) among all other lines (Figure 2B). Considering that lines appeared to show similar levels of antibiosis or antixenosis or both to whitefly (*i.e.* weak differences in nymph presence/absence), the fact that g84 showed a much higher mean score of severity suggests a lower degree of virus resistance by this line. It should be noted that whitefly nymphs were present at very low abundances during the first half of the sampling period (July to September), and that higher abundances of this pest may uncover stronger among-line differences in female oviposition choice and feeding. Hence, additional research is warranted to distinguish between *B. tabaci* antixenosis and antibiosis patterns, as well as how this relates to incidence and susceptibility to virosis in habanero peppers. To our knowledge, only Godinez-Hernandez *et al.* (2001) and Anaya-Lopez *et al.* (2003) have reported differences in virus susceptibility among habanero lines. Unfortunately, we do not have evidence to support single virus species or co-infections in the field. Regardless of this limitation, however, we believe that providing a field-based assessment of habanero resistance to viruses transmitted by *B. tabaci* is important even when



**Figure 2.** Differences between *Capsicum chinense* lines for (A) weeks until the appearance of first symptoms of virosis and (B) severity of virosis infection at the end of the experiment. Values are back-transformed least-square means and 95 % confidence limits.

symptoms of infection cannot be linked to particular species of virus as in co-infection patterns frequently observed in the field (Janick and Jansky, 2000).

Finally, there was significant variation among plots for attack rates by several of the studied pests, which may be partly due to limited dispersal ability of these insects across the agricultural landscape, leading to spatially-aggregated attack patterns (Parella, 1987; Riley *et al.*, 1992). It is likely that pests will disperse more readily across a continuous agricultural landscape (relative to plots as in this study) with this influencing the observed pest incidence levels among lines, and that responses by each pest species will vary depending on their degree of mobility. Moreover, decisions on planting design such as plot size and the establishment of line mixtures or monocultures, will likely have an influence on attack levels (Peacock *et al.*, 2001; Mundt, 2002).

## CONCLUSIONS

Results from this study provide evidence of field-based variation for pest attack levels as well as virus susceptibility among the studied *Capsicum chinense* lines. In particular, variation among habanero lines for incidence of *L. trifolii* and *A. eugenii* represents novel information for this crop species. Thus, these results provide baseline information for the selection of *C. chinense* lines for cultivar development purposes as well as research on crop traits associated with insect resistance and their inheritance.

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