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9    **TYLCV Infection Alters *Bemisia tabaci* MED (Hemiptera: Aleyrodidae) Vulnerability to**

10    **Flupyradifurone**

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23 **Abstract**

24 The whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae) is a major phloem-feeding pest of

25 agricultural crops that is also an important vector of many plant diseases. The *B. tabaci*

26 Mediterranean ('MED') biotype is a particularly effective vector of *Tomato yellow leaf curl virus*

27 (TYLCV), a devastating plant pathogen. While insecticides play an important role in the control

28 of MED and TYLCV, little is known about how TYLCV infection affects MED susceptibility to

29 insecticides. We conducted research addressing how MED susceptibility to flupyradifurone, the

30 first commercially available systemic control agent derived from the butenolide class of

31 insecticides, was affected by TYLCV infection. We first conducted bioassays determining the

32 $LC_{15}$ and $LC_{50}$ for control and viruliferous MED feeding on either water- or insecticide-treated

33 plants. We next measured several demographic parameters of control and viruliferous MED

34 exposed to either insecticide- or water-treated plants. TYLCV infection increased MED tolerance

35 of flupyradifurone: the $LC_{15}$ and $LC_{50}$ of viruliferous MED were double that of uninfected MED.

36 Viral infection also altered MED demographic responses to flupyradifurone, but in an

37 inconsistent manner. While the ability of TYLCV and other persistently-transmitted viruses to

38 benefit *Bemisia* via manipulation of host plant defense is well-known, this appears to be the first

39 example of virally-mediated changes in vector susceptibility to an insecticide.

40 **Key Words**

41 Insecticide, Sivanto, tolerance, *Bemisia*, TYLCV

42  **Introduction**

43  The whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) is a major phloem-feeding

44  pest of both field and greenhouse crops worldwide (Stansly and Naranjo 2010). Its management

45  is complicated by the fact that *B. tabaci* contains over 30 phenotypically identical but genetically

46  distinct cryptic species (Liu et al. 2012, Hadjistylli et al. 2016) that vary widely in traits such as

47  insecticide resistance (Chen et al. 2016, Xie et al. 2017). *Bemisia tabaci* Mediterranean (MED)

48  poses a particular threat to agriculture due to its invasiveness. Since its arrival in China in 2003

49  (Chu et al. 2006), it has displaced both native and invasive *B. tabaci* throughout the country

50  (Teng et al. 2010).

51  Although *Bemisia* feeding can itself reduce plant growth, its primary threat to agriculture

52  occurs via its ability to transmit a wide variety of plant viruses. MED is particularly effective at

53  transmitting such viruses, and its invasion is often associated with plant disease outbreaks (Ning

54  et al. 2015). The *Tomato yellow leaf curl virus* (TYLCV) is a particularly damaging pathogen

55  that has caused significant damage worldwide (Jones 2003). TYLCV relies on *B. tabaci* as a

56  vector to spread among plants (Fereres and Moreno 2009). As a result, *Bemisia-* plant-TYLCV

57  interactions have been the subject of intense interest and researchers have confirmed the

58  mutualistic relationship between *B. tabaci* and the virus. It is now known, for instance, that

59  TYLCV can increase *Bemisia* fitness via its suppression of plant defense (Zhang et al. 2012,

60  Luan et al. 2013) and that MED benefits from feeding on TYLCV-infected hosts (Pan et al.

61  2013a, Shi et al. 2019).

62  Insecticides play an important role in an integrated pest management approach to

63  controlling *Bemisia* and viral outbreaks in agricultural systems. Because the whitefly can rapidly

64  develop insecticide resistance, the continued development and deployment of novel compounds

65   is essential for effective pest control. One such compound is flupyradifurone, the first

66   commercially available systemic control agent derived from the butenolide class of insecticides

67   (Nauen et al. 2015). This compound, an agonist on insect nicotinic acetylcholine receptors,

68   differs structurally from other chemicals that target these receptors. As a result, it is effective

69   against neonicotinoid- and pymetrozine-resistant *Bemisia* populations (Nauen et al. 2015).

70        A recent assessment of MED survival and TYLCV transmission found that while

71   flupyradifurone rapidly killed MED and reduced TYLCV transmission by 85%, treatment with

72   the neonicotinoid thiomethoxam only reduced viral transmission by 25% (Roditakis et al. 2017).

73   Other work confirming the general efficacy of flupyradifurone against *B. tabaci* Middle East-

74   Asia Minor 1 (MEAM1) nonetheless found a few field populations with high levels of

75   flupyradifurone tolerance (Smith et al. 2016). While increasing insecticide tolerance in its vector

76   would clearly benefit TYLCV and similar viruses, there is no published research assessing

77   whether viruses can provide such benefits. Alternately, TYLCV could affect MED in a manner

78   similar to Rickettsia, which is correlated with increased *Bemisia* sensitivity to a range of

79   different insecticides (Kontsedalov et al. 2008, but see Pan et al. 2013b). Understanding how

80   TYLCV affects the flupyradifurone tolerance of its vector is important to maximize the effective

81   use of this important insecticide.

82        We report the results of two experiments exploring how TYLCV infection affected MED

83   susceptibility to flupyradifurone (trade name Sivanto). We first determined the $LC_{15}$ and $LC_{50}$ for

84   control and viruliferous MED feeding on plants treated with either Sivanto or distilled water. We

85   calculated both $LC_{15}$ and $LC_{50}$ because chemical degradation and dilution gradually reduce

86   insecticide concentrations following application (e.g., Roditakis et al. 2017),. We next measured

87   several demographic parameters of control and viruliferous MED exposed to either insecticide-

88  or water-treated plants. Although TYLCV infection has little direct effect on MED fitness (Pan et

89  al. 2013a, Su et al. 2015), recent work found a net downregulation of detoxification enzymes in

90  TYLCV-infected MED (Ding et al. 2019); we hypothesized that viruliferous MED would be

91  more sensitive to Sivanto than uninfected individuals.

92  **Materials and Methods**

93  <u>Plants:</u> Tomato plants (*Solanum lycopersicum* L, cv. Zhongza 9) were grown individually in two-

94  liter pots in a greenhouse with natural lighting and controlled temperature (26±2℃). All plants

95  were grown in a 10:5:1 (by volume) mixture of peat moss, vermiculite, and organic 8-8-8

96  fertilizer. TYLCV-infected plants were produced with injection of *Agrobacterium tumefaciens*-

97  mediated TYLCV clones (Shanghai isolate) at the 3-4 true leaf stage (Zhang et al. 2009). The

98  plants were grown for four weeks post-injection to give them time to display infection-associated

99  pathological symptoms.

100  <u>Insects:</u> The whitefly *Bemisia tabaci* MED (Q) was first collected in 2009 from

101  poinsettia, *Euphorbia pulcherrima* Wild. (ex Klotz.), in Beijing, China. It was reared on

102  poinsettia. In 2015, a portion of the population (~300 adults) was transferred to the Tianjin

103  Institute of Plant Protection and reared on cotton plants (*Gossypium herbaceum* L., cv DP99B) in

104  80 mesh nylon insect cages (45×45×60 cm) under 26±2℃, 60±10% RH, 14L:10D photoperiod.

105  A viruliferous MED population was produced by transferring ~300 whiteflies into a cage with

106  four TYLCV-infected tomato plants; a parallel uninfected MED population was produced by

107  transferring >300 whiteflies into a cage with four healthy tomato plants. Both viruliferous and

108  uninfected MED were reared for two generations on their respective plants before being used for

109  experiments. Colony purity was monitored every 2-3 generations using a DNA marker (Khasdan

110  et al. 2005), and TYLCV infection was confirmed via PCR validation (Ghanim et al. 2007).

111    Flupyradifurone bioassay of viruliferous and uninfected MED: Sivanto 200SL (17.09%

112    flupyradifurone) was provided by Bayer Crop Science (China) Company Ltd. and diluted with

113    distilled water to five different concentrations: 200 mg[AI]kg$^{-1}$, 100 mg[AI]kg$^{-1}$, 50 mg[AI]kg$^{-1}$,

114    25 mg[AI]kg$^{-1}$, and 12.5 mg[AI]kg$^{-1}$. For each of the five concentrations and an additional

115    distilled water control (a total of six treatments), 200 mL was added to a 500 mL plastic spray

116    bottle. For each concentration, one spray bottle was used to spray four tomato plants that were

117    each at the 6-7 true leaf stage; plants were sprayed until drip-off. One day after spraying, 100

118    newly-emerged (within 24 hours) adult MED per plant were placed in clip cages attached to the

119    abaxial side of both the third and fourth leaves of each sprayed plant. Clip cages were kept on for

120    two days; the number of living and dead MED were then counted. This work was conducted in a

121    climate-controlled chamber at 26±1℃ and 60±10% RH with 14L:10D photoperiod.

122    Demographic responses of viruliferous and uninfected MED to flupyradifurone (LC$_{15}$):

123    Data from the above-mentioned experiment was used to calculate the LC$_{15}$ for viruliferous MED.

124    a solution of this concentration was sprayed on healthy tomato plants at the 6-7 true leaf stage

125    until drip-off. Another group of healthy tomato plants was sprayed to drip-off with distilled

126    water. After 24 hours, approximately 100 newly emerged (within one day) viruliferous or

127    uninfected MED were attached in separate clip cages to the abaxial side of the third and fourth

128    leaves of either a Sivanto-treated or control plant. This produced four treatments: TYLCV

129    (uninfected, viruliferous) crossed with insecticide (dH$_2$O, Sivanto). This work were conducted in

130    a climate-controlled chamber at 26±1℃ and 60±10% RH with 14L:10D photoperiod. Clip cages

131    were removed after two days and the living and dead adult MED collected and counted.

132    Female adult longevity and first-week fecundity: Thirty female MED from each of the

133    four treatments (=120 total) were placed individually in clip cages. Each cage was then clipped

134  on the abaxial side of a middle leaf of an unsprayed healthy tomato plant (6-7 true leaf stage). A

135  total of two MED were clipped onto each plant, one per leaf, and both MED on a given plant had

136  the same infection status (i.e., they were both either uninfected or viruliferous). The clip cages

137  were checked each day for MED mortality; after one week, all surviving adults were individually

138  transferred to new unsprayed healthy tomato plants and the number of eggs laid during the first

139  week counted.

140  Egg-to-adult survival and developmental time: Five pairs of newly-emerged MED

141  (within one day; 1:1 sex ratio) from a given treatment were placed into a single clip cage and

142  clipped onto the abaxial side of a middle leaf of an unsprayed healthy tomato plant (6-7 true leaf

143  stage). Only one clip cage was attached to each plant. This was replicated 10 times in each of the

144  four treatments, for a total of 40 replicates. After one day, each clip cage was opened and the

145  adults were removed, leaving only the eggs and nymphs. Each clip cage was then inspected daily

146  and the number of nymphs and adults recorded. Daily inspections continued until the last nymph

147  had either entered adulthood or died.

148  Statistical analysis: Probit parameter estimation of the concentration-mortality response

149  for viruliferous and uninfected MED in the six concentrations were calculated using POLO-PC

150  (Russell et al. 1977, LeOra 1987). These parameters included $LC_{15}$ and $LC_{50}$ values expressed in

151  mg[AI]kg-1 and their corresponding 95% confidence limit (CL) along with the slopes of the

152  probit regressions. Between-treatment differences in the mortality of viruliferous and uninfected

153  MED were calculated using 95% CLs; $LC_{15}$ or $LC_{50}$ values for viruliferous and uninfected MED

154  were considered significantly different if their corresponding 95% CLs did not overlap.

155  Data on each of the demographic responses was analyzed using two-way ANOVA to

156  assess the main effects of TYLCV (uninfected, viruliferous) and insecticide (dH2O, Sivanto) as

157   well as their interaction. When one or more main effects or their interaction was significant at p

158   = 0.05, Tukeys' HSD was used for means separation tests. Data on adult longevity and survival

159   was sqrt transformed before analysis. All analyses were conducted using JMP 9.0.0 (SAS 2010).

160   **Results**

161   Viruliferous MED were more tolerant of Sivanto than uninfected MED (Table 1). The

162   $LC_{15}$ of viruliferous MED was more than twice that of uninfected MED (11.8 versus 5.8,

163   respectively), and the $LC_{50}$ of viruliferous MED was almost twice as high (31.3 versus 17.3).

164   The 95% CLs of viruliferous and uninfected MED did not overlap, meaning that the two groups

165   differed significantly in both their $LC_{15}$ and $LC_{50}$ values (Table 1).

166   Exposure to Sivanto (at $LC_{15}$ concentration determined for viruliferous MED) marginally

167   increased adult female longevity (Fig. 1A), increased first-week fecundity (Fig. 1B) and

168   decreased egg-adult development time (Fig. 1C) in both MED groups (Table 2). In contrast, the

169   only significant main effect of TYLCV was a 28% decrease in first-week fecundity (Fig. 1B).

170   The TYLCV*Sivanto interaction was marginally significant (P = 0.067 – 0.085) for three of the

171   four variables: Sivanto had a greater impact on the first-week fecundity and egg-adult

172   development time of uninfected MED than viruliferous MED (Fig. 1B, 1C), but increased the

173   adult female lifespan of viruliferous MED more than for uninfected MED (Fig. 1A). Survival

174   from egg to adult (Fig. 1D) was not affected by either main effect or their interaction (Table 2).

175   **Discussion**

176   Contrary to expectations, we found that TYLCV did not increase MED vulnerability to

177   flupyradifurone. Instead, both the $LC_{15}$ and $LC_{50}$ values for viruliferous MED were significantly

178   higher than those of uninfected MED (Table 1). In three of the four demographic variables, there

179   was also a marginally significant interaction between Sivanto and TYLCV: Sivanto tended to

180   increase adult longevity only in viruliferous MED and first-week fecundity only in uninfected

181   MED, and tended to decrease egg-adult development time only in uninfected MED (Fig.

182   1A,B,C). While the ability of TYLCV and other persistently-transmitted viruses to benefit

183   *Bemisia* via manipulation of host plant defense is well-known, this appears to be the first

184   example of virally-mediated changes in vector susceptibility to an insecticide.

185         While our results were surprising, there have been other reports of microorganism-

186   mediated changes in insecticide susceptibility (Pietri and Liang 2018). Gut symbionts in both the

187   cigarette beetle *Lasioderna serricorne* (Shen and Dowd 1991) and the apple fly *Rhagoletis*

188   *pomonella* (Lauzon et al. 2003) are involved with the detoxification of natural and synthetic

189   toxins. In contrast, the symbiotic microorganism *Rickettsia* increased *Bemisia* sensitivity to a

190   range of different insecticides (Kontsedalov et al. 2008, but see Pan et al. 2013b); later research

191   linked increases in *Bemisia* symbiont diversity and density to greater insecticide susceptibility

192   (Ghanim and Kontsedalov 2009). Similar results have been reported in the psyllid *Diaphorina*

193   *citri*, where infection with *Candidatus* Liberibacter asiaticus increased its vulnerability to several

194   insecticides (Tiwari et al. 2011). A recent review (Pietri and Liang 2018) suggested these

195   variable results may partially reflect symbiont-specific effects on both host detoxification

196   enzymes and their immune/stress response. A transcriptomic analysis of gene regulation in

197   TYLCV-infected MED found that while TYLCV generally downregulated detoxification

198   enzymes, genes involved in both stress and immune responses were upregulated (Ding et al.

199   2019). It seems likely that some of these upregulated genes alter MED susceptibility to

200   flupyradifurone.

201         The negative impact of flupyradifurone revealed in the $LC_{15}$ and $LC_{50}$ bioassays appears

202   at odds with its equivocal effect on various aspects of MED demography. MED that survived one

203  day of flupyradifurone exposure had slightly higher female longevity, higher first-week

204  fecundity, and a shorter egg-adult development time than MED in the control treatment. These

205  'benefits' of flupyradifurone are almost certainly an experiment artifact: a day of insecticide

206  exposure removed the weakest and/or most susceptible MED from the population that was

207  subsequently used for our demographic work. They may also reflect hormesis, a phenomenon in

208  which sublethal dosages of insecticide improve fecundity or provide other benefits to the

209  targeted insects (Cutler 2012). It is also worth noting that both uninfected and viruliferous MED

210  were exposed to flupyradifurone at the $LC_{15}$ concentration determined for viruliferous MED.

211  Because the $LC_{15}$ value for uninfected MED was lower than for viruliferous MED, this

212  flupyradifurone concentration was more lethal to the uninfected population than to the

213  viruliferous one. Higher rates of exposure-related mortality in our uninfected group may have

214  had the unintended effect of minimizing differences between the uninfected and viruliferous

215  groups. It should also be noted that the recommended label rate of flupyradifurone, 150 mg/l,

216  was substantially higher than the concentrations we used; we chose to work with lower

217  concentrations in order to assess MED that survive initial exposure. The effect of TYLCV on

218  MED insecticide tolerance may be reduced or eliminated at these higher concentrations.

219  Pesticides can indirectly control insect-vectored plant diseases via their impact on vector

220  density. This control may be lessened, however, if vectors feeding on pesticide-sprayed plants

221  survive long enough to transmit TYLCV and other viruses. Viruliferous *Bemisia* efficiently

222  transmit TYLCV to uninfected plants. Less than two minutes of *Bemisia* salivation is necessary

223  to infect a healthy tomato plant (Jiang et al. 2000). As a result, thiamethoxam and other

224  insecticides that do not quickly kill *Bemisia* may prove inefficient at decreasing TYLCV

225  transmission (Roditakis et al. 2017). Flupyradifurone has a higher knockdown rate than

226  thiamethoxam and is more effective at reducing TYLCV transmission (Roditakis et al. 2017).

227        Research assessing the impact of flupyradifurone on *Bemisia* feeding behavior is

228  necessary to understand the mechanism(s) underlying its effect on viral transmission. Aphids

229  feeding on thiamethoxam-treated plants, for example, spend less time in the sieve element phase

230  required for viral transmission to an uninfected plant (Cho et al. 2011, Stamm et al. 2013).

231  Although TYLCV increased MED tolerance to flupyradifurone (Table 1), it might still change

232  MED feeding behavior in ways that make this pesticide effective at reducing or eliminating viral

233  transmission. Alternately, TYLCV-linked increases in flupyradifurone tolerance may provide

234  viruliferous MED an advantage over uninfected individuals in pesticide-treated fields. If so,

235  insecticide application could, under some conditions, favor viral outbreaks in agricultural

236  systems (Pan et al. 2015).

237        In summary, our work found that infection with TYLCV altered the susceptibility of

238  *Bemisia tabaci* MED to flupyradifurone. While the mechanism underlying our results is

239  unknown, our findings suggest that viral infection may be capable of changing population-level

240  responses to current management practices. Even for novel insecticides, such interactions

241  highlight how work exploring pesticide impacts on each part of the vector-virus-plant interaction

242  can contribute to the development of effective strategies to control MED and TYLCV.

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345

**Table 1:** Median lethal concentration (LC$_{15}$ and LC$_{50}$) of flupyradifurone (Sivanto) to uninfected

and viruliferous MED. LC$_{15}$ and LC$_{50}$ followed by different upper-case letters indicate that

uninfected and viruliferous MED are significantly different based on overlap of 95% CLs.

| Treatment | N | Slope ± SE | LC$_{15}$(mg[AI]kg$^{-1}$) (95% CL) | LC$_{50}$(mg[AI]kg$^{-1}$) (95% CL) | $X^2$ (df) | P value |
|---|---|---|---|---|---|---|
| Uninfected | 478 | 3.64 ± 0.39 | 5.78 (3.72-7.82) A | 17.33 (14.08-20.48) A | 1.61 (3) | 0.66 |
| Viruliferous | 476 | 4.07 ± 0.36 | 11.75 (8.91-14.44) B | 31.33 (27.22-35.82) B | 2.4 (3) | 0.49 |

**Table 2:** Results of ANOVA assessing the impact of TYLCV infection, Sivanto exposure, and

their interaction on MED demographic variables.

| Treatment | Female longevity (d) | | | First week fecundity (# eggs) | | | Egg-adult developmental time (d) | | | Egg-adult survival (%) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | df | P | F | df | P | F | df | P | F | df | P |
| TYLCV[†] | 0.43 | 1,101 | 0.513 | 15.71 | 1,101 | <0.001 | 0.86 | 1,18 | 0.364 | 1.03 | 1,18 | 0.324 |
| Sivanto | 3.55 | 1,101 | 0.063 | 10.24 | 1,101 | 0.002 | 7.26 | 1,18 | 0.015 | 0.31 | 1,18 | 0.586 |
| TYLCV*Sivanto | 3.43 | 1,101 | 0.067 | 3.18 | 1,101 | 0.078 | 3.34 | 1,18 | 0.085 | 0.97 | 1,18 | 0.338 |

[†]*Tomato yellow leaf curl virus*

354 **Figure Legends**

355 Figure 1. *Bemisia tabaci* MED feeding on *Lycopersicon esculentum.* Mean ± SE values for the

356 demographic variables A) Female longevity (days); B) Eggs per female over one week; C) Egg-

357 adult development time (days); and D) Egg-adult survival (%). Light gray bars: uninfected MED;

358 dark gray bars: viruliferous MED. Unstriped bars (S-): plants sprayed with distilled water;

359 striped bars (S+): plants sprayed with 11.75 mg[AI]kg$^{-1}$ Sivanto (LC$_{15}$ for viruliferous MED).

360 Different upper-case letters above bars indicate significant differences (Tukeys' HSD with α =

361 0.05); in figure 1D, there were no significant between-treatment differences.

362        Figure 1.