

TIAGO AMARAL TRINDADE

**HIGH VIRULENCE OF A PLANT-PATHOGENIC VIRUS (*Cowpea mild mottle virus*, BETAFLEXIVIRIDAE) LEADS TO REDUCED PERFORMANCE OF ITS INSECT VECTOR (*Bemisia tabaci*, HEMIPTERA: ALEYRODIDAE)**

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para a obtenção do título de *Magister Scientiae*.

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Orientador

“Talvez não tenha conseguido fazer o melhor, mas lutei para que o melhor fosse feito. Não sou o que eu deveria ser, mas Graças a Deus, não sou o que eu era antes”.

Martin Luther King

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## RESUMO

TRINDADE, Tiago Amaral, M.Sc., Universidade Federal de Viçosa, março de 2016. **Alta virulência de um vírus patogênico de planta (*Cowpea mild mottle virus*, Betaflexiviridae) leva à redução da performance de seu inseto vetor (*Bemisia tabaci*, Hemiptera: Aleyrodidae).** Orientador: Simon Luke Elliot. Coorientador: Claudine Márcia Carvalho.

Infecção por vírus induz mudanças nas plantas que podem afetar a performance do vetor do vírus. Aqui, nós avaliamos os efeitos da infecção em plantas de soja por duas estirpes e uma variante de CPMMV (*Cowpea mild mottle virus*) na sobrevivência e desenvolvimento da mosca-branca (*Bemisia tabaci* MEAM1). Nós desejávamos saber como a virulência desse patógeno afetaria o inseto vetor. Assim, nós usamos um isolado brando da estirpe CPMMV-BR1 e um isolado virulento da estirpe CPMMV-BR2. Nós hipotetizamos que a estirpe CPMMV-BR1 (referida como 'estirpe mosaica') tem um efeito positivo na performance da mosca-branca, enquanto que a estirpe CPMMV-BR2 (referida como 'estirpe necrótica') tem um efeito negativo na performance da mosca-branca. Além disso, nós testamos os efeitos de uma variante branda da estirpe CPMMV-BR2 (o mesmo isolado da estirpe CPMMV-BR2, mas após perder a capacidade de causar sintomas de necrose) na sobrevivência e desenvolvimento do vetor. Nós também hipotetizamos que a perda da virulência tem um efeito positivo na performance da mosca-branca. Em acordo com nossa hipótese, a sobrevivência de ninfas de mosca-branca foi significativamente reduzida em plantas infectadas com a estirpe necrótica, mas a sobrevivência e desenvolvimento de ninfas de mosca-branca em plantas infectadas com a estirpe mosaica e em plantas infectadas com a variante branda não foram afetados. Portanto, a alta virulência da estirpe necrótica tem um efeito negativo não somente na performance da mosca-branca, mas também no fitness do vírus, uma vez que ele depende de adultos de mosca-branca para dispersão.

## ABSTRACT

TRINDADE, Tiago Amaral, M.Sc., Universidade Federal de Viçosa, March, 2016. **High virulence of a plant-pathogenic virus (*Cowpea mild mottle virus*, *Betaflexiviridae*) leads to reduced performance of its insect vector (*Bemisia tabaci*, Hemiptera: *Aleyrodidae*).** Adviser: Simon Luke Elliot. Co-adviser: Claudine Márcia Carvalho.

Viral infection induces changes in host plants that can then affect performance of the vector of the virus. Here we assess the effects of the infection of soybean plants by two strains and a variant of CPMMV (*Cowpea mild mottle virus*) on survival and development of the whitefly (*Bemisia tabaci* MEAM1). We wished to know how the virulence of this pathogen would affect the insect vector. Thus, we used a mild isolate of strain CPMMV-BR1 and a virulent isolate of strain CPMMV-BR2. We hypothesized that the mild CPMMV-BR1 (referred to as the 'mosaic strain') has a positive effect on the performance of the whitefly, whereas the virulent CPMMV-BR2 (referred to as the 'necrotic strain') has a negative effect on the performance of the whitefly. Additionally, we tested the effects of a mild variant of the CPMMV-BR2 (the same isolate of the CPMMV-BR2, but after losing the capacity to cause necrosis symptoms) on survival and development of the vector. We also hypothesized that a loss of virulence has a positive effect on the performance of the whitefly. In agreement with our hypothesis, survival of whitefly nymphs was significantly reduced on plants infected with the necrotic strain, but survival and development on plants infected with the mosaic strain and plants infected with the mild variant were not affected. Therefore, high virulence of the CPMMV-BR2 strain in soybean plants has a negative effect not only on the performance of the vector but also on viral fitness since the virus depends on adult whiteflies for dispersal.

## Introduction

Viral infection induces changes in host plants that can then affect performance of the vector of the virus (Castle & Berger, 1993; McKenzie, 2002; Maris *et al.* 2004; Hodge & Powell, 2008; Sidhu *et al.* 2009; Mauck *et al.* 2010). These changes involve alteration of the nutritional composition of the host plant (Blua *et al.* 1994; Mauck *et al.* 2014), reduced anti-herbivore defences (Belliere *et al.* 2005; Zhang *et al.* 2012; Luan *et al.* 2013) or a combination of the two (Su *et al.* 2015), with positive or negative effects on the performance of the vector. Thus, some vectors perform better on infected plants than healthy plants (Maris *et al.* 2004; Belliere *et al.* 2005; Jiu *et al.* 2007; Wang *et al.* 2012; Zheng *et al.* 2014), whereas others do better on healthy plants than infected plants (Donaldson & Gratton, 2007; Mauck *et al.* 2010; Ren *et al.* 2015).

Meanwhile, the consequences of such virus-induced changes on the performance of the vector have also been received attention in terms of consequences for virus spread. This is because the effects of virus infection on plants on the performance of the vector will reflect on the virus' fitness (Hodge & Powell, 2008; Zheng *et al.* 2014; Legarrea *et al.* 2015). For example, virus-induced changes on host plant that benefit the vector may enhance the virus transmission to new hosts. This was clearly demonstrated by Jiu *et al.* (2007), who documented increased fecundity and longevity of whiteflies on infected plants. The rapid population growth of whiteflies on infected plants would lead to crowding and consequently dispersal of the vectors carrying the virus.

Whitefly, *Bemisia tabaci*, is a complex consisting of 11 groups containing 24 species (Dinsdale *et al.* 2010). The biotype B, now classified as

Middle East-Asia Minor 1 (MEAM1), is one of the most widely distributed and invasive group/species of that complex (Liu *et al.* 2013). These insects cause damage to plants by sap-sucking, excretion of honeydew and transmission of viruses (Byrne & Bellows, 1991) – Whiteflies are vectors of more than 200 viruses, mainly begomoviruses (Navas-Castillo *et al.* 2011; Polston *et al.* 2014).

Three transmission modes are reported for viruses transmitted by whiteflies: nonpersistent, semipersistent and persistent circulative (Polston *et al.* 2014). In nonpersistent transmission, the insect can acquire and inoculate the virus within seconds to minutes. There is no latent period, and the virus is lost within a few minutes after acquisition. In semipersistent transmission, acquisition and inoculation periods are long (minutes to hours). There is also no latent period, and the virus is lost within a few hours after acquisition. In both cases, the viruses are retained in the stylet and foregut of the insects, so they are lost after molting. In persistent circulative transmission, acquisition and inoculation periods are longer (hours to days). Within the insect, the virus crosses the gut wall and reaches the hemolymph, in which it circulates until it reaches the salivary glands, being transmitted when the insects secrete saliva during feeding. Thus, the insect is only able to inoculate the virus after a latent period that ranges from hours to days. The virus is not lost after molting, and the insect can inoculate it for long periods (days to weeks) (Gray & Banerjee, 1999; Hogenhout *et al.* 2008).

*Cowpea mild mottle virus* (CPMMV, family Betaflexiviridae, genus *Carlavirus*) is transmitted by whiteflies in a nonpersistent manner (Munipaya & Reddy, 1983; Marubayashi *et al.* 2010). The virus was first identified in 1973 infecting cowpea (*Vigna unguiculata*) in Ghana (Brunt & Kenten, 1973). Since

then, it has been reported in several regions of the world (Iwaki *et al.* 1982; Thouvenel *et al.* 1982; Costa *et al.* 1983; Mink & Keswani, 1987; El-Hassan *et al.* 1997; Rodriguez-Padina *et al.* 2004; Brito *et al.* 2012). Symptoms caused by CPMMV infection are variable. In soybean, the virus may cause mild symptoms such as mosaic, vein clearing, blistering and crinkled leaves or severe symptoms such as dwarfism, bud blight and stem and leaf necrosis (Zanardo *et al.* 2013a).

Recently, Zanardo *et al.* (2013b) identified two CPMMV strains (CPMMV-BR1 and CPMMV-BR2) infecting soybean in Brazil. The identification was based on pairwise comparisons and phylogenetic analysis of seventeen isolates from different regions of Brazil and different years. The same strain was found in geographically distant locations, and isolates of both strains can cause either mild or severe symptoms (Zanardo *et al.* 2013b). Curiously, after successive mechanical inoculations, all necrotic isolates lost symptoms of necrosis and started mosaic symptoms (Zanardo, personal communication). Isolates that cause severe symptoms such as necrosis will kill the plant, and a negative effect on the performance of the vector is expected. For both virus and vector, the loss of virulence on the plant observed in these isolates is expected to be beneficial.

Here we assess the effects of the infection of soybean plants by the two CPMMV strains and a variant on survival and development of the whitefly. We wished to know how the virulence of this pathogen would affect the insect vector. Thus, we used a mild isolate of strain CPMMV-BR1 and a virulent isolate of strain CPMMV-BR2. We hypothesized that the mild CPMMV-BR1 has a positive effect on the performance of the whitefly, whereas the virulent

CPMMV-BR2 has a negative effect on the performance of the whitefly. Additionally, we tested the effects of a variant of the CPMMV-BR2 (the same isolate of the CPMMV-BR2, but after losing the capacity to cause necrosis symptoms) on survival and development of the vector. We also hypothesized that a loss of virulence has a positive effect on the performance of the whitefly.

## **Material and methods**

### **Insects and plants**

*Bemisia tabaci* were obtained from a colony established in 2008 at the Federal University of Viçosa, Minas Gerais, Brazil. The insects were reared on cabbage plants (*Brassica oleracea* var. capitata) in gauze cages under greenhouse conditions. The whiteflies were identified as *B. tabaci* MEAM1 by partial sequencing of the mitochondrial cytochrome oxidase 1 gene (mtCOI) and comparison with three reference sequences of this species/group in GenBank (access numbers AF340215, AJ510071 and AJ510079).

The soybean used in experiments was cultivar CD206. Soybean seeds were germinated in Petri dishes on moistened filter paper. Subsequently, the seedlings were transferred to plastic pots (1L) containing a mix of soil and commercial substrate (2:1). The plants were maintained in a greenhouse with average temperatures of 26±4 °C and watered once a day. Plants were used for mechanical inoculation 2 weeks after planting.

### **Virus strains and inoculation**

The CPMMV strains used were CPMMV-BR1 and CPMMV-BR2, described from soybean plants cv. CD206 (Zanardo *et al.* 2013b). One isolate of each strain was chosen based on different patterns of symptoms induced in this cultivar: CPMMV:BR:GO:01:1 isolate (CPMMV-BR1 strain) causes mosaic, blistering and crinkled leaf symptoms, whereas CPMMV:BR:GO:10:5 isolate (CPMMV-BR2 strain) causes dwarfism, bud blight and stem and leaf necrosis symptoms (Zanardo *et al.* 2013b). Thus, these two strains are henceforth

referred to as the 'mosaic strain' and 'necrotic strain', respectively. The variant was obtained after successive mechanical inoculations of the CPMMV:BR:GO:10:5 isolate which led to loss of necrosis symptoms and the development of mosaic symptoms. This was referred to as the 'mild variant'.

The isolates and variant were mechanically inoculated into plants using inoculum obtained by grinding infected leaves in 0.1M phosphate buffer with sodium sulfite (pH 7.2). The first pair of true leaves was mechanically damaged by dusting with carborundum, and the inoculum was applied with gauze previously embedded in it. The control plants were treated only with carborundum and buffer (free of virus). Plants showing symptoms were used 8-11 days after inoculation. The virus infection was confirmed by RT-PCR after the end of the experiments as below.

Total RNA was extracted from 100mg of leaf tissue with the RNeasy Plant Mini Kit (QIAGEN) according to the manufacturer's recommendations. The cDNA was synthesized with the Superscript III Reverse Transcriptase (Invitrogen) according to the manufacturer's recommendations, using the primer ORF 6 (Zanardo *et al.* 2013a). The cDNA obtained was amplified with the Platinum Taq DNA polymerase (Invitrogen) according to the manufacturer's recommendations, using the forward primer carla up (Nicolaisen & Nielsen, 2001) and the reverse primer ORF 6 (Zanardo *et al.* 2013a). PCR amplification consisted of 35 cycles of denaturation at 94°C for 1 minute, annealing at 45°C for 1 minute, elongation at 72°C for 2 minutes and extension at 72°C for 10 minutes. PCR products were separated in 1% agarose gel for 60 minutes.

### **Survival and developmental time experiment**

We used newly emerged nymphs (<24h after emergence) to evaluate survival and developmental times of whiteflies. Nymphs were obtained by allowing adults to oviposit on healthy soybean plants. They were collected with a fine paint brush and placed on the abaxial surface of the first and second trifoliolate leaves. Nymphs that died after 24h were replaced by the others of the same age. Each treatment consisted of 30-40 nymphs placed on 3-4 plants (replicates). The experiment was carried out in a room at  $26\pm 2^{\circ}\text{C}$  and photoperiod of 12h light/12h dark. Survival and development were recorded daily under the stereomicroscope until emergence of adults or death of nymphs. Dead nymphs were identified by their dark-color and dried appearance.

In order to eliminate handling effects on mortality, only nymphs that survived more than 3 days after placing them on the plants were used for survival analysis. Survival on plants infected with the necrotic strain was very low: no individual reached the adult stage. Thus, this treatment was excluded from the development analysis.

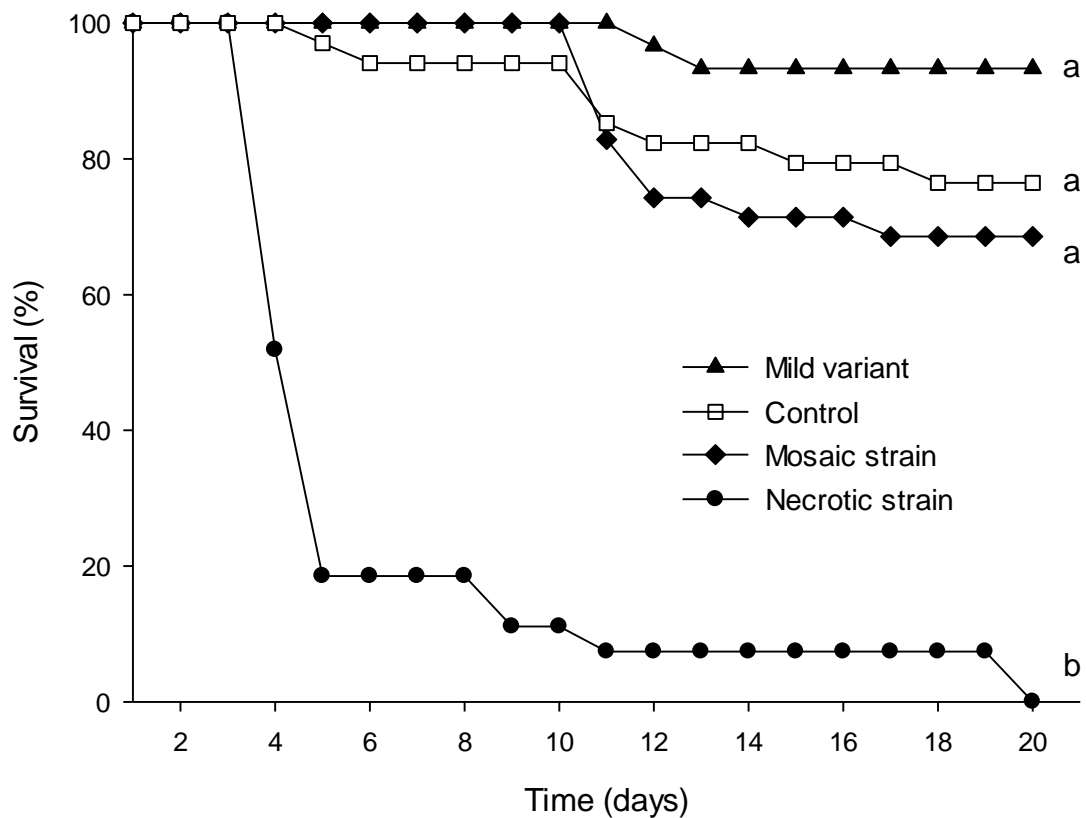
### **Data analysis**

Survival and development data were analysed using a linear mixed effects model (nlme package of R, R Development Core, 2014). Replicates were used as random factor and the treatments as fixed factor. We started the analyses by including interactions of factors and checking residual distributions. Non-significant interactions and factors were removed from the full model using the anova function. Contrasts among treatments were assessed with the glht function (lsmeans package of R).

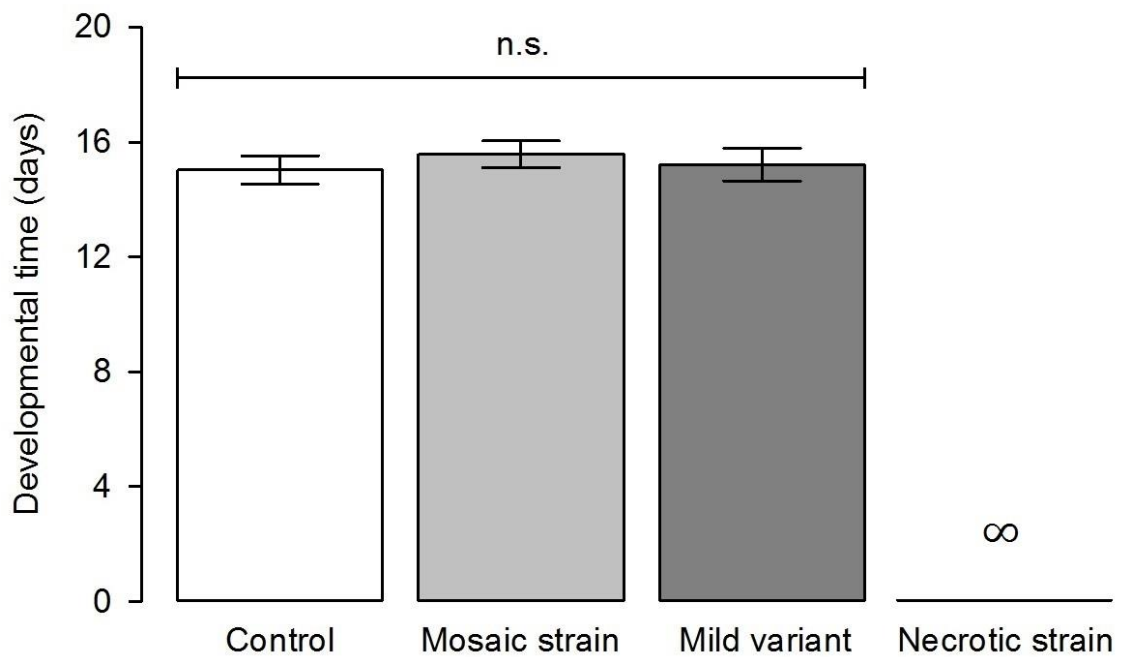
## Results

There were significant differences in survival of whitefly nymphs among treatments (LME, Likelihood ratio test = 24.2, d.f = 3,  $P < 0.0001$ ; Figure 1). Survival on plants infected with the mosaic strain, plants infected with the mild variant and control plants did not differ statistically from one another. However, survival on plants infected with the necrotic strain was significantly lower compared to survival on plants infected with the mosaic strain, plants infected with the mild variant and control plants.

The developmental time from newly emerged nymphs to adult was not affected by treatment (LME, Likelihood ratio test = 5.62, d.f = 3,  $P = 0.06$ ; Figure 2).



**Figure 1.** Survival of whitefly nymphs on control soybean plants, plants infected with the mosaic strain of CPMMV, plants infected with the mild variant and plants infected with the necrotic strain of this virus. Newly emerged nymphs were placed on the abaxial surface of the first and second trifoliolate leaves and recorded daily. Curves followed by the same letter were not significantly different,  $P < 0.05$ ).



**Figure 2.** Mean developmental times of whiteflies from newly emerged nymphs to adults on control soybean plants, plants infected with the mosaic strain of CPMMV and plants infected with the mild variant of this virus. Newly emerged nymphs were placed on the abaxial surface of the first and second trifoliolate leaves and recorded daily. *n.s.* = not significant.  $\infty$  = no data from plants infected with the necrotic strain of the virus – see text for explanation.

## Discussion

Our results show that survival of whitefly nymphs was far lower on plants infected with the necrotic strain of CPMMV when compared with all other treatments. The high mortality of nymphs would be expected to occur as consequence of high virulence of this strain on soybean plants. The infection leads to death of the tissues and then of the plant, resulting in a lack of nutritional resources for development of the nymphs. The early stages of development were extended for those nymphs surviving for longer time on plants infected with this strain.

Survival and development of whitefly nymphs on plants infected with the mosaic strain and plants infected with the mild variant were similar to survival and development on control plants. Because soybean is a good host for whiteflies, the infection by the mosaic strain and mild variant on soybean plants could not further improve their performance. Viral infection improving the performance of the vector is mainly observed on plants of poor quality or on plants that have strong induced defences (Belliere *et al.* 2005; Jiu *et al.* 2007; Luan *et al.* 2013). Thus, it is expected that the virus infection, when mild, has neither positive nor negative effects on the performance of the vector (Belliere *et al.* 2005).

Previous studies have shown positive and negative effects of viral infection of host plants on the performance of *B. tabaci* MEAM1 (Mckenzie, 2002; Jiu *et al.* 2007; Mann *et al.* 2008; Sidhu *et al.* 2009; Wang *et al.* 2012; Su *et al.* 2015). All of these studies used plants that were infected with persistent viruses, so direct effects (from the virus circulating within the vector) and

indirect effects (mediated via the plant) can affect the performance of the whitefly.

Nonpersistent viruses represent the majority of known insect-transmitted viruses. However, studies describing the effects of infection by these viruses on the performance of their vectors are scarce (Blua & Perring, 1992; Donaldson & Gratton, 2007; Hodge & Powell, 2008; Mauck *et al.* 2010; Kersch-Becker & Thaler, 2014). Outcomes of these studies show mainly negative effects of virus infection on host plant on the performance of the vector.

Infection of plants with nonpersistent viruses is predicted to have negative effects on the performance of the vector when compared to uninfected plants (Mauck *et al.* 2010; Mauck *et al.* 2012). Because these viruses are quickly acquired, they are effectively transmitted when vectors spread soon after virus acquisition. Also, these viruses could be lost after long-term feeding and molting (Gray & Banerjee, 1999; Hogenhout *et al.* 2006). Our results support partially this prediction since survival and development of whitefly nymphs on plants infected with the mosaic strain and plants infected with the mild variant showed no difference from survival and development from control plants.

Kersch-Becker & Thaler (2014) investigated the effects of three PYV strains on tomato plants and found no difference in the abundances of aphids, but aphid fecundity varied significantly according to virus strains infecting the plants. In the present study, we also found significant differences in survival of whitefly nymphs between CPMMV strains. It is important to point out

that the strains tested here differ from each other in terms of virulence from those used by these authors.

Effects of viral infection of plants on vector performance have been found to vary according to the stage of the infection process. Blua & Perring (1992a) documented a population increase of aphids on plants that were infested at different times after virus inoculation. When plants were inoculated and infested at the same time, more aphids were produced than on plants that showed advanced symptoms, i.e. severe stunting and chlorosis and leaf necrosis. Considering the necrotic strain in our study, we placed the nymphs on plants that showed advanced stem and leaf necrosis symptoms. Consequently, 80% of the nymphs died during the first five days of evaluation (Figure 1). We believe that response of the vector to virus infection is best detected on symptomatic leaves. As such, symptoms are more apparent on the leaves that will appear after virus inoculation, that is, on leaves in which the nymphs were placed.

A question which emerges in this system is why the necrotic strain is so virulent to the point to kill the offspring of the whitefly. A hypothesis is that rapid deterioration of the plant would discourage the colonization of them and promote the migration of the vector to new host plants, thereby enhancing virus transmission (Blua & Perring, 1992a, 1992b; Hodge & Powell, 2008). However, the preference of whiteflies for plants infected with the necrotic strain would not be beneficial if this strain killed the infected plant before the offspring reached adulthood. On the other hand, although there was no difference in survival and development on plants infected with the mosaic strain or the mild variant, when

compared with whitefly on control plants, this certainly would result in large numbers of adults that could transmit the virus.

Based on the results, we conclude that high virulence of the necrotic strain has a negative effect not only on the performance of the vector but also on viral fitness since the virus depends on adult whiteflies for dispersal.

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