



Potential impact of climate change on whiteflies and implications for the spread of vectored viruses

[with correction]

Aregbesola, Oluwatosin Z.; Legg, James P.; Sigsgaard, Lene; Lund, Ole S.; Rapisarda, Carmelo

Published in:
Journal of Pest Science

DOI:
[10.1007/s10340-018-1059-9](https://doi.org/10.1007/s10340-018-1059-9)

Publication date:
2019

Citation for published version (APA):
Aregbesola, O. Z., Legg, J. P., Sigsgaard, L., Lund, O. S., & Rapisarda, C. (2019). Potential impact of climate change on whiteflies and implications for the spread of vectored viruses: [with correction]. *Journal of Pest Science*, 92(2), 381–392. <https://doi.org/10.1007/s10340-018-1059-9>

[Click here to view linked References](#)

1 **Potential impact of climate change on whiteflies and implications for the spread of vectored viruses**

2 Oluwatosin Z. Aregbesola^{1,2,3,4*}, James P. Legg³, Lene Sigsgaard², Ole S. Lund², and Carmelo Rapisarda¹

3 ¹Dipartimento di Agricoltura, Alimentazione e Ambiente, Università degli Studi di Catania, Italy.

4 ²Department of Plant and Environmental Sciences, University of Copenhagen, Denmark

5 ³International Institute of Tropical Agriculture, Dar es Salaam, Tanzania

6 ⁴Wesley University Ondo, Ife-Road, Ondo State, Nigeria

7 *corresponding author:

8 Oluwatosin Zacheus Aregbesola

9 Dipartimento di Agricoltura, Alimentazione e Ambiente, Università degli Studi di Catania, Via Santa Sofia n.
10 100, 95123 Catania, Italy.

11 tosinaregbs@yahoo.com

12 **KEY MESSAGE**

- 13
- 14 • An in-depth review was conducted to address the weak current understanding of the potential influence of climate change on whiteflies.
 - 15 • Our study highlights the dynamism of the interactions between vector, natural enemies and transmitted viruses, and confirms that the impacts of climate change will vary widely depending on local
16 circumstances.
 - 17 • Future efforts to manage whiteflies must be cognisant of the complex effects of climate on the agro-
18 ecological systems inhabited by these globally important insects.
- 19

20

21 **ABSTRACT**

22 Whiteflies (Hemiptera: Aleyrodidae) are important insect pests causing serious damage to plants and
23 transmitting hundreds of plant viruses. Climate change is expected to influence life history and trophic
24 interactions among plants, whiteflies, and their natural enemies. Here, we review the potential impacts of
25 climate change on whiteflies and the likely consequences for agricultural systems. This review concludes that
26 while climatic stress tends to negatively affect life history traits, the effects differ with the tolerance of the
27 whiteflies and the amount of stress experienced. Whiteflies also differ in their adaptability. Better adapted
28 species will likely experience increased distribution and abundance provided their tolerance limits are not
29 exceeded, while species with lower tolerance and adaptation limits will suffer reduced fitness, which will have
30 overall effects on their distribution and abundance in space and time. The majority of methods used to control
31 whiteflies will still be useful especially if complementary methods are combined for maximum efficacy.
32 Parasitism and predation rates of whitefly natural enemies could increase with temperature within the optimum
33 ranges of the natural enemies, although life history traits and population growth potential are generally
34 maximised below 30 °C. Changes in climatic suitability modifying the distribution and abundance of whiteflies,
35 and environmental suitability for plant viruses, will likely affect epidemics of viral diseases. Greater efforts are
36 required to improve understanding of the complex effects of climate change on multi-species and multi-trophic
37 interactions in the agro-ecological systems inhabited by whiteflies, and to use this new knowledge to develop
38 robust and climate-smart management strategies.

39 **Keywords:** whiteflies, population dynamics, begomoviruses, pest management, species interaction

40

41

42 **INTRODUCTION**

43 Whiteflies are important global agricultural pests (Oliveira et al. 2001). They have a wide host range and are
44 very adaptive to different environmental conditions (Oliveira et al. 2001; CABI 2017). The *Bemisia tabaci*
45 (Gennadius) species group is the most economically important whitefly (Lowe et al. 2000; Navas-Castillo et al.

46 2011). It causes damage to crops directly through phloem feeding as well as the excretion of honeydew leading
47 to the growth of sooty moulds that reduce photosynthesis. Whiteflies also cause indirect damage through the
48 transmission of economically important viral plant pathogens (Navas-Castillo et al. 2011; Tzanetakis et al. 2013;
49 Polston et al. 2014). Crop damage due to plant viruses transmitted by whiteflies globally results in losses worth
50 more than \$US 1 billion (Gonzalez et al. 1992; Legg et al. 2006).

51 The Intergovernmental Panel on Climate Change (IPCC) fifth assessment report predicted a 1.5 °C increase in
52 global surface temperature, and an increasing contrast in precipitation between wet and dry regions over the 21st
53 century (IPCC 2013). Independent observations by the National Oceanic and Atmospheric Administration
54 (NOAA) and the National Aeronautics and Space Administration (NASA) showed that globally, temperatures in
55 2016 were 0.99 °C warmer compared to records from the 20th century, and the third year in a row to set a new
56 record high temperature (NASA 2017). Global CO₂ concentration is the primary driver of the recent
57 anthropogenic climate change. While the global concentration of CO₂ in the atmosphere reached 400 parts per
58 million (ppm) for the first time in recorded history in 2013, the trend has continued, with the 2016 estimate at
59 404.4 ppm (NASA 2013, 2016).

60 Climatic change is affecting agricultural and natural ecosystems, and directly affects the development,
61 reproduction, survival, population dynamics, potential distribution and abundance of whitefly species (Muñiz
62 and Nombela 2001; Bonato et al. 2007; Bellotti et al. 2012; Gilioli et al. 2014). Some studies have reported
63 direct effects of temperature (Xie et al. 2011; Guo et al. 2013; Han et al. 2013), CO₂ (Koivisto et al. 2011;
64 Curnutte et al. 2014), and O₃ (Cui et al. 2012, 2014) on life history traits. Others have discussed effects of
65 rainfall (Castle et al. 1996; Naranjo and Ellsworth 2005; Naranjo et al. 2009; Sharma and Yogesh 2014) on
66 whiteflies.

67 At the present time, information on the potential influence of climate change on whiteflies is limited and effects
68 of climate change on several biological parameters of whiteflies are poorly understood. New research initiatives
69 aim to deepen insights into the influence of climate change on whiteflies, and on the tri-trophic interactions
70 within the agricultural systems in which they cause so much damage. This review explores the influence of
71 climate change on the life history, distribution, population dynamics and efficacy of management strategies of
72 whiteflies. Through this analysis, we have been able to identify important trends for some whitefly species and
73 biological parameters, and based on these, we highlight needs for further research.

74

75 **HOW WILL WHITEFLIES RESPOND TO CLIMATE CHANGE?**

76

77 **Life history traits**

78 There are differences in response of whiteflies to climate change resulting from differences in whitefly species,
79 host plants, climatic zones and climate factors. The response of different whiteflies and host plants to changes in
80 climatic factors are summarised in Table 1. Temperature and host-plant effects have been identified as important
81 factors affecting development, mortality and fecundity rates in whitefly populations. Temperature increase
82 within the thermal optimum leads to a decrease in developmental time (Madueke and Coaker 1984; Sengonca
83 and Liu 1999; Muñiz and Nombela 2001; Nava-Camberos et al. 2001; Bayhan et al. 2006; Bonato et al. 2007;
84 Xie et al. 2011; Han et al. 2013). These trends are commonly observed in insects due to the influence of
85 temperature on their physiology. Other effects of temperature increase (especially above the optimum threshold)
86 on life history traits include decreasing fecundity (Bonato et al. 2007; Xie et al. 2011; Guo et al. 2013) and
87 decreasing longevity (Sengonca and Liu 1999; Bonato et al. 2007; Guo et al. 2013). Elevated CO₂ and O₃
88 increased developmental time of whiteflies (Cui et al. 2012; Wang et al. 2014), but elevated CO₂ did not affect
89 adult longevity (Koivisto et al. 2011; Curnutte et al. 2014) and fecundity of whiteflies (Curnutte et al. 2014;
90 Wang et al. 2014). There is a dearth of information regarding the effects of elevated O₃ on whitefly longevity
91 and fecundity (Table 1).

92 In nature, insects often experience stressful temperatures (high and low) that may affect not only their life
93 history, but also their distribution and abundance (Cui et al. 2008; Lü et al. 2014b). Research on the thermal
94 biology of insects has revealed that the ability of insects to tolerate extreme temperatures is one of the most
95 crucial biotic factors defining the distribution of most insects, which may have further implications in the face of
96 global climate change (Bowler and Terblanche 2008; Cui et al. 2008; Ma et al. 2014). There is an increasing
97 number of empirical studies on thermotolerance and its associated evolutionary implications in whiteflies. Traits
98 commonly investigated are survival, fecundity and viability of the offspring after heat shock.

99 Comparing both *B. tabaci* MEAM1 and MED, Mahadav et al. (2009); Elbaz et al. (2011) and Xiao et al. (2016)
100 showed that survival of both species reduced as temperature increased, and that *B. tabaci* MED performed better
101 than MEAM1 after brief exposure to higher temperatures (41 – 45 °C). Similarly, Cui et al. (2008) showed that
102 survival rates drop after brief exposure to higher temperatures (39 – 45 °C), and *B. tabaci* MEAM1 is more
103 thermotolerant than *Trialeurodes vaporariorum* (Westwood). A similar decline in survival after exposure to
104 high temperatures was also reported for *B. tabaci* MED (Zhu et al. 2010; Lü et al. 2014a) and *B. tabaci* MEAM1
105 (Muñoz-Valencia et al. 2013; Diaz et al. 2015). Fecundity of whiteflies after brief exposure to heat shock
106 generally reduces with temperature increase (Elbaz et al. 2011; Xiao et al. 2016). However, other studies have
107 shown no significant effect (Cui et al. 2008; Zhu et al. 2010; Lü et al. 2014a). Furthermore, progeny viability
108 post-heat shock could either decrease (Cui et al. 2008; Diaz et al. 2015) or show an inconsistent pattern (Muñoz-
109 Valencia et al. 2013; Xiao et al. 2016) with temperature increase. Several studies on thermotolerance and life
110 history of whiteflies suggest that female *B. tabaci* are more thermotolerant than males (Cui et al. 2008; Muñoz-
111 Valencia et al. 2013; Ma et al. 2014).

112
113 In some cases, significant differences in thermotolerance have been reported among populations experiencing
114 different levels of environmental stress, pointing towards adaptive divergence (Diaz et al. 2014; Ma et al. 2014).
115 For instance, Diaz et al. (2014) associated significant differences in survival and fecundity among populations
116 with mean temperature and temperature variation in the local environment respectively. Similarly, Ma et al.
117 (2014) also demonstrated that differences in habitat temperature resulted in significant differences in the
118 adaptive strategies to heat stress between the Harbin and Turpan *B. tabaci* MED populations from China. Their
119 work suggests that adaptive microevolution of *B. tabaci* is directly related to its high narrow-sense heritability
120 for both heat and cold resistance. These potential evolutionary changes could be used by *B. tabaci* to maintain
121 its populations with climate change (Ma et al. 2014). Elbaz et al. (2011) showed that *B. tabaci* MEAM1 and
122 MED deploy different adaptation strategies when experiencing heat stress. *B. tabaci* MEAM1 achieves
123 maximum reproduction at the expense of soma protection, while *B. tabaci* MED invests more of its resources on
124 processes beneficial to somatic maintenance. In another interesting study, Lü et al. (2014b) highlighted the
125 significance of stress-inducing conditions on the ecological adaptations and distribution of insects in the context
126 of climate change. Their work demonstrated that thermotolerance and longevity were more important than
127 reproductive traits, and that enhanced thermotolerance and prolonged longevity were essential adaptive
128 strategies that contributed to the survival of MEAM1 under the hot and harsh desert climate reported in the
129 study. Pusag et al. (2012) showed that acquisition of *Tomato yellow leaf curl virus* (TYLCV) by *B. tabaci* MED
130 resulted in increased development rate and increased susceptibility to thermal stress which may result in a
131 decline in vector longevity. This highlights how the complex interactions between vector fitness and thermal
132 stress could influence the ability of the vector to acquire and transmit plant viruses especially with climate
133 change.

134
135 Apart from temperature and other environmental factors, other important factors could influence the life history
136 and response of whiteflies to climate change. For instance, adaptation to one environmental stress (insecticides
137 like thiamethoxam) increased thermotolerance in *B. tabaci* MEAM1 (Su et al. 2017) which could be beneficial
138 to *B. tabaci* MEAM1 in the light of climate change. Absence of secondary endosymbionts in cassava-colonising
139 whiteflies increased their fitness and vector abilities, and a possible ecosystem service in suppressing
140 populations of cassava-colonising whiteflies has been proposed (Ghosh et al. 2018). Nutrition and defensive
141 chemistry of host plants (Jiao et al. 2018) could also influence the response of whiteflies to climate change.

142 **Population dynamics**

143
144 The major factors that regulate population dynamics are climate, natural enemies, initial population size, host-
145 plant suitability, farming systems and management practices (Price et al. 2011). Generally, rainfall has been
146 noted to negatively affect populations of *B. tabaci* (Naranjo and Ellsworth 2005; Sharma and Yogesh 2014).
147 Using sprinkler irrigation to simulate rainfall, Castle et al. (1996) found a consistent reduction in densities of
148 immature whiteflies. Some of the most abundant populations of *B. tabaci* in history were from irrigated desert
149 cropping systems where consistently high temperatures shorten generation times and rainfall is infrequent
150 (Naranjo et al. 2009). Experiments considering prolonged exposure to constant temperatures and brief exposure
151 to heat shock agree that elevated temperatures (above the optimum threshold of whiteflies) negatively affect life
152 history of whiteflies. However with climate change, high thermotolerance and the polyphagous nature of some
153 whiteflies (*B. tabaci* MEAM1 and MED) which contribute to their invasion success, could possibly facilitate
154 their population increase in some locations depending on the amount of heat stress experienced (Bellotti et al.
155 2012; EFSA 2013; Gilioli et al. 2014; Gamarra et al. 2016b). By combining general circulation models (GCMs)
156 with a stochastic weather generator and population dynamics models, Zidon et al. (2016) studied population

157 dynamics of *B. tabaci* in three locations in the Mediterranean region under two future scenarios. Their study
158 suggests that temperature increase will increase population size and average number of generations completed
159 by *B. tabaci* yearly, and a lengthening of growing season in the three locations.

160
161 *Bemisia afer* (Priesner and Hosny) can go through 8 – 10 and 4 – 8 generations per year in tropical and sub-
162 tropical regions respectively, under current temperature conditions, while *T. vaporariorum* can have up to 11
163 generations per year (Gamarra et al. 2016a, c). Considering the effects of climatic change up to 2050, *B. afer* is
164 predicted to increase by only 1 generation per year in temperate regions of Europe, North America, and parts of
165 Asia. An increase of 1 – 2 generations per year is predicted for tropical and sub-tropical regions in Asia
166 (Malaysia, Philippines, Indonesia); Europe (Portugal); South America (southern Brazil, central Colombia,
167 Peruvian coast); Central, East, and Southern Africa; the Caribbean; central and southern China; and Oceania
168 (Papua New Guinea) (Gamarra et al. 2016a). Furthermore, an increase of 1 – 2 generations per year is predicted
169 for *T. vaporariorum* in most tropical regions. *T. vaporariorum* will likely have a small increase in temperate
170 regions (mainly Europe and North America), while increasing temperatures around the Equator will possibly
171 reduce *T. vaporariorum* activity (Gamarra et al. 2016c).

172
173 Increases in the number of generations do not necessarily translate into range expansion or elevated whitefly
174 populations. Generally, increasing temperature within developmental thresholds leads to an increase in insect
175 population by reducing development time and hastening metabolic and physiologic activities. However, at
176 extreme temperatures (above optimum), other important life history traits are negatively affected (Qui et al.
177 2003; Bonato et al. 2007). Hence, with a high number of generations per year due to faster development rate,
178 there is also an increased possibility of lower population increase over time. Nevertheless, these same studies
179 that indicated increased number of generations based on generation index (which measures mean number of
180 generations that can be produced by an insect within a given year) (Gamarra et al. 2016a, b, c) also presented a
181 more robust estimate of changes in abundance of insects called activity index, which accounts for the whole life
182 history traits, measures the rate of finite increase and also indicates the severity of the pest problem. Based on
183 this additional estimate, climate change is predicted to cause a small increase in the population of *T.*
184 *vaporariorum* in the temperate regions of Europe and America, while *T. vaporariorum* populations along the
185 Equator will likely reduce with increasing temperature. Similarly, due to climate change, the population growth
186 potential of *B. afer* is predicted to decrease in most of the sweet potato growing areas in tropical and sub-
187 tropical regions. However, the abundance of *B. afer* will potentially increase in southern sub-tropical and
188 temperate zones (Gamarra et al. 2016a). For *B. tabaci* MEAM1, a small increase in potential growth is
189 predicted for most tropical and sub-tropical regions. *B. tabaci* MEAM1 populations will possibly reduce along
190 the Equator as temperature increases (Gamarra et al. 2016c). Furthermore, based on the activity index and
191 generation index available in the Insect Life Cycle Modelling software used by Gamarra et al. (2016a, b, c),
192 populations of cassava-colonising *B. tabaci* sub-Saharan Africa 1 – Sub-group 3 (SSA1-SG3) have been
193 predicted to increase in East, Central and Southern Africa (Aregbesola 2018). Using the Physiologically Based
194 Demographic Model, Gilioli et al. (2014) simulated changes in distribution and population of *B. tabaci* MED in
195 Europe considering a worst-case scenario (upper threshold for development, survival and fecundity), and
196 indicated that climate change resulted in increased population density and infestation of *B. tabaci* MED which is
197 highly consistent with the high thermotolerance previously reported for *B. tabaci* MED.

198 199 **Movement and distribution**

200
201 Spread of whiteflies is facilitated partly by human transportation of infested plant materials, but there is
202 increasing concern that climate change allows establishment in hitherto unsuitable regions (Bebber et al. 2013).
203 Climate change will also have additional implications for the invasion success of whitefly species as climatic
204 suitability and overall community interaction will play a key role in the establishment and geographical
205 expansion of the introduced whitefly species. Ecological niche models which generate maps of a species'
206 environmental suitability based on its current distribution (e.g Campos et al. 2011; Jarvis et al. 2012; Bellotti et
207 al. 2012), and insect physiology based models (e.g Gilioli et al. 2014; Gamarra et al. 2016a, b, c; Aregbesola
208 2018) which utilise detailed descriptions of the life history of the insect, provide very powerful tools to assess
209 the potential impact of climate change on the distribution of whiteflies. Both ecological niche modelling and
210 physiology-based modelling are commonly used, and our review considers research relating to both approaches.

211 In Europe, expansion of *B. tabaci* northwards is expected to be limited by low temperatures, reducing the risk of
212 *B. tabaci* establishment because of climatic limitations (Gilioli et al. 2014). *B. tabaci* could possibly expand its
213 range in some of the Mediterranean countries (Spain, France, Italy, and Greece) and in countries along the
214 Adriatic coast line (Gilioli et al. 2014) as a consequence of climate change. Increased climatic suitability for *B.*

215 *tabaci* has been predicted to occur in northern Argentina, south-central Bolivia, north-eastern Brazil, south-west
216 Peru, northern Australia, southern China, as well as parts of the USA (Bellotti et al. 2012). A similar trend is
217 predicted for Central African Republic, Ethiopia and Cameroon (Jarvis et al. 2012) and southern India (Campos
218 et al. 2011). There will also be more *B. tabaci* further south, in regions where there is a cool and dry winter
219 (Bellotti et al. 2012; Aregbesola 2018). According to Gamarra et al. (2016a, b), in 2050, temperature will
220 potentially reduce *B. afer* and *T. vaporariorum* establishment in current high-risk areas of the tropics globally.
221 By contrast, the risk of establishment of *B. afer* will increase in the sub-tropical sweet potato growing areas of
222 South Africa, southern Brazil, Peru, Uruguay, Chile, and Argentina. The temperate regions of Europe, North
223 America and Asia will become increasingly suitable for *T. vaporariorum*, although the risk of establishment will
224 still be very low (Gamarra et al. 2016a, b).

225
226 Since virus transmission by whiteflies is mainly mediated by *B. tabaci* and *T. vaporariorum*, any change in the
227 distribution of these vectors may affect the overall geography of viral diseases. Populations of *B. tabaci* are
228 distributed in tropical and sub-tropical zones all around the globe and viruses transmitted by *B. tabaci* are found
229 – as a group – roughly within the same areas (Navas-Castillo et al. 2011) although local patterns of seasonal
230 temperature, precipitation and altitude appear to play an important role (Morales and Jones 2004). Sporadic
231 records of viruses from greenhouse plants in cooler climates most likely reflect the importation of infected plant
232 material and not *per se* the natural spread of viruses (Botermans et al. 2009). However, any future increase in
233 temperature will allow populations of *B. tabaci* to expand towards the poles and the epidemic areas of the
234 viruses vectored will most likely follow (Bebber et al. 2013). A scenario of climate change has been outlined for
235 *B. tabaci* and begomoviruses using TYLCV in Europe as an example. Manifest and frequent infection of field-
236 grown tomato by TYLCV in Europe is restricted to the most southern, coastal/lowland regions, particularly the
237 islands of Cyprus, Crete, Sicily, Sardinia and the southern parts of Spain and Portugal (Khan et al. 2013). The
238 same regions are characterised by year-round outdoor cultivation of tomato (main virus host) and the presence
239 of populations of *B. tabaci* (EFSA 2013; Gilioli et al. 2014). In case of a temperature increase of 2 °C, both
240 studies predict a movement of established populations of *B. tabaci* approximately 300 – 500 km northwards,
241 taking into account significant local variations due to local topography. The spread of TYLCV in open fields is
242 expected to follow the same pattern.
243

244 **Efficacy of management strategies**

245
246 Evidence from Wang et al. (2014) indicates that the biological control of *B. tabaci* by *Encarsia formosa* (Gahan)
247 would not be influenced by transgenic Bt cotton and/or elevated CO₂. Cui et al. (2014) suggest that elevated O₃
248 enhanced the attraction of *En. formosa* to whiteflies with resulting augmented biological control. This probably
249 relates to the enhanced production of volatile organic compounds by the host plant, which indirectly increased
250 the attraction of *En. formosa* to whiteflies. Furthermore, it has been experimentally confirmed that parasitism
251 and predation rates of whitefly natural enemies could increase with temperature within the optimum ranges of
252 the natural enemies as in the case of *En. formosa* (Burnett 1949; Enkegaard 1994; Qui et al. 2004; Zilahi-
253 Balogh et al. 2006), *Eretmocerus eremicus* (Rose & Zolnerowich) (Qui et al. 2004), *Er. mundus* (Mercet) (Qui
254 et al. 2004), *Eretmocerus* spp. (McCutcheon and Simmons 2001), *Delphastus catalinae* (Horn) (Simmons and
255 Legaspi 2004) and *Nesidiocoris tenuis* (Reuter) (Madbouni et al. 2017). Similarly, walking speed, walking
256 activity and flight activity of whitefly natural enemies have been shown to be positively correlated with
257 temperature (van Roermund and van Lenteren 1995; Bonsignore 2016), while handling time decreases with
258 temperature increase (Enkegaard 1994; Madbouni et al. 2017). Comparable studies on the impact of temperature
259 on walking pattern and flight activity of whitefly are very scarce; however, Reader and Southwood (1984)
260 suggest that temperature did not strongly affect flight activity of *Aleurotuba jelinekii* (Frauenfeld). For most
261 natural enemies, however, immature survival, fecundity, adult longevity and intrinsic rate of natural increase are
262 maximised below 30 °C, and above this temperature the chance of population expansion drops significantly
263 (Table 3). Of course, the effects of diurnal temperature regimes could increase adaptability of these insects
264 (Kingsolver et al. 2015). Hence, how a natural enemy responds to temperature increase will be a function of its
265 life history traits in relation to the amount of environmental stress experienced (Qui et al. 2004; Qui et al 2006;
266 Zandi-Sohani and Shishehbor 2011; Malekmohammadi et al. 2012), which could either favour population build
267 up or decline (Deutsch et al. 2008; Youngsteadt et al. 2016). In line with this, biocontrol companies recommend
268 temperatures between 21 – 29 °C for optimal performance of commercially available natural enemies. To ensure
269 efficacy of their products, commercial producers of whitefly biocontrol products now combine more than one

270 natural enemy. For instance, *En. formosa* is combined with *Er. eremicus* to harness the rapid population growth
271 potential of *En. formosa* and high temperature tolerance of *Er. eremicus* (Biobest, 2017).

272 Host-natural enemy interactions are not linear or directly predictable due to complex species and environment
273 interactions. Greenberg et al. (2000) compared the life history of *Er. eremicus* and two host whiteflies (*T.*
274 *vaporariorum* and *B. tabaci* MEAM1), while Burnett (1949) compared the life history of *T. vaporariorum* and
275 *En. formosa* under the same experimental conditions respectively. Their results show that the parasitoids
276 perform better than the whiteflies at higher temperatures (24 – 32 °C) for most of the traits tested. Similarly,
277 Youngsteadt et al. (2016) compared the changes in abundance of whiteflies, predators and parasitoids, and
278 reported that parasitoids had higher abundance per °C urban warming compared to whiteflies, while predators
279 show lower response to warming compared to parasitoids and whiteflies respectively.

280 Insecticides have long been applied successfully in diverse environments from hot, irrigated desert regions to
281 cool temperate regions. Although the toxicity of insecticides may be influenced by temperature (Sparks et al.
282 1983; Boina et al. 2009; Glunt et al. 2014), diurnal variations in temperature will still permit insecticide
283 applications to be made within temperature ranges relevant to the functionality of the compounds. Moreover,
284 compensatory feeding at elevated CO₂ levels would increase the consumption of insecticide (Coviella and
285 Trumble 2000) and could therefore increase the efficacy of insecticides. However, climate change and faster
286 population growth of whiteflies may also increase insecticide application rates and associated costs of
287 management with insecticides (Chen and McCarl 2001; Koleva and Schneider 2009). Climate change may also
288 indirectly affect the efficacy of insecticides since periods suitable for spraying will likely increase with drier
289 locations and decrease where it is wetter (Harrington et al. 2001).

290
291 Cultural practices are commonly used as part of an overall strategy for whitefly management. Where efficient
292 weather forecasting systems are available to farmers, changing planting date will remain an easy and effective
293 tool to reduce pest pressure. However, climatic uncertainties may render this practice less useful (especially for
294 small-holder farmers because of their limited use of weather information). The greenhouse strategy (physical
295 barrier) is to a large extent already in place in the new areas that might be invaded by whiteflies, and will
296 continue to be useful especially in intensive production systems if well managed and combined with other
297 control methods. Phytosanitary measures, such as quarantine and the removal of weeds and crop residues, are
298 widely used today and will continue to be useful since there are no indications that climate change will affect
299 their effectiveness. Although constitutive and induced plant defences can be affected by climatic change due to
300 changes in C:N ratio, which could in turn affect both synthesis and functioning of defence compounds (Zavala
301 et al. 2013), there is insufficient evidence as to how this will influence resistance to whiteflies. Even under
302 current production conditions, insect pests and pathogens often develop mechanisms for breaking down host
303 resistance. How climate change will affect whitefly resistance is unknown, although it will most probably be
304 host-whitefly specific. This topic presents an important opportunity for additional research.

305

306

307 **CONCLUSION AND FUTURE PROSPECTS**

308

309 The study reviewed the impact of climate change on whiteflies with the primary goal of identifying important
310 trends for biological parameters. Among the new insights from our study is that while environmental stress
311 tends to negatively affect life history, the effects differ with tolerance of the whiteflies, amount of stress
312 experienced (which is often related to habitat characteristics) and the host plant. Whiteflies differ in their
313 adaptability and adaptive strategies, and these will influence their eventual response in terms of distribution and
314 abundance with climate change. With climate change, better adapted species will likely experience increased
315 distribution and abundance provided their tolerance limits are not exceeded, while species with lower tolerance
316 and adaptation limits will suffer reduced fitness, which will have overall effects on their distribution and
317 abundance in space and time. Most methods used to control whiteflies will still be effective, especially if
318 complementary methods are combined for maximum efficacy. Changes in climatic suitability modifying the
319 distribution and abundance of whiteflies and the environmental suitability for plant viruses will likely affect

320 epidemics of viral diseases. Overall, the impacts of climate change on whiteflies will show latitudinal or
321 location specificity, as reported for other insect species (Deutsch et al. 2008; Bebber et al. 2013; Youngsteadt et
322 al. 2016). Although reduced climatic suitability and establishment risk of whiteflies is predicted for some parts
323 of the tropics, and temperature will remain a limiting factor to the distribution and abundance of whiteflies in
324 temperate regions (outside greenhouses), some regions will see population increases and whiteflies will still
325 continue to pose a threat to crop production (Gamarra et al. 2016a, b, c). However, there are uncertainties
326 associated with predicting the effects of climate change when considered locally in space and in time. Effects of
327 single climatic factors on whiteflies species are often not complementary and may be antagonistic (Table 1). The
328 study also shows that the influence of temperature (in comparison to other environmental variables) on
329 whiteflies has been given overwhelming attention probably due to its established importance in the biology of
330 whiteflies and other insects. Studying the influence of multiple climatic factors simultaneously (Curnutte et al.
331 2014) is an important further step in elucidating how climate change is likely to affect whiteflies. Additionally,
332 there is very little information currently available on how climate change will affect trophic interactions
333 involving whiteflies. The limited research that has been done suggests that climate change impacts may be
334 significant or negligible depending on the host, whitefly and factors considered (Tripp et al. 1992; Cui et al.
335 2012; Wang et al. 2014). More research insights addressing the effect of single or multiple factors on trophic
336 interactions of whiteflies will significantly contribute to our knowledge of whitefly biology and will help in the
337 design of robust future management guidelines.

338 Our key message here is that developing effective responses to the additional whitefly threat that may result
339 from climate change will depend heavily on improving understanding of the complex interactions between
340 whitefly species, host plants, natural enemies and the components of climate change that will affect them in each
341 of the world's major agro-ecological zones. A varied set of control tactics for whiteflies and the viruses that they
342 transmit are already being applied. The challenge will be working out, through research, how to apply this
343 basket of technologies most effectively in the dynamic new agricultural environment that is emerging as humans
344 continue to modify the world. This is a challenge of global significance, but certainly one that can be resolved if
345 addressed with appropriate levels of investment, leading to a more sustainable, food secure future.

346
347

348 **CONTRIBUTIONS**

349 CR, OSL, JPL secured the funding for the study, AOZ, CR, JPL, OLS, LS designed the study, AOZ, JPL, OSL,
350 LS wrote the manuscript, all authors read and approved the manuscript.

351

352 **ACKNOWLEDGEMENTS**

353 The study was funded by the Education, Audio-visual and Culture Executive Agency of the European
354 Commission through the Erasmus Mundus Joint Doctorate Fellowship (Agricultural Transformation by
355 Innovation programme) awarded to AOZ. The contribution of Dr. James Legg was supported through the Roots,
356 Tubers and Bananas (RTB) Programme of the CGIAR.

357

358 **COMPLIANCE WITH ETHICAL STANDARDS**

359 Conflict of interest: The authors (AOZ, CR, JPL, OLS, LS) declare that there is no conflict of interest.

360 Ethical approval: This article does not contain any studies with human participants or animals performed by any
361 of the authors.

362 Informed consent: The study does not concern any human subject, thus informed consent was not applicable.

363

364

365 **REFERENCES**

366 Aregbesola OZ (2018) Understanding the potential impact of climate change on cassava-colonising whitefly,
367 *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae). PhD Thesis University of Catania (Italy) and University
368 of Copenhagen (Denmark).

369

370 Bayhan E, Ulusoy MR, Brown JK (2006) Effects of different cucurbit species and temperature on selected life
371 history traits of the 'B' biotype of *Bemisia tabaci*. *Phytoparasitica* 34(3): 235-242.

372
373 Biobest (2017) Eretmix. Available at [http://www.biobestgroup.com/en/biobest/products/biological-control-](http://www.biobestgroup.com/en/biobest/products/biological-control-4463/beneficial-insects-and-mites-4479/eretmix-system-4658/)
374 [4463/beneficial-insects-and-mites-4479/eretmix-system-4658/](http://www.biobestgroup.com/en/biobest/products/biological-control-4463/beneficial-insects-and-mites-4479/eretmix-system-4658/). Accessed on November 14, 2017.
375
376 Bebbler DP, Ramotowski MA, Gurr SJ (2013) Crop pests and pathogens move polewards in a warming
377 world. *Nature Clim Change* 3(11): 985-988.
378
379 Bellotti A, Campo BVH, Hyman G (2012) Cassava production and pest management: present and potential
380 threats in a changing environment. *Trop Plant Biol* 5(1): 39-72.
381
382 Boina DR, Onagbola EO, Salyani M, Stelinski LL (2009) Influence of post-treatment temperature on the
383 toxicity of insecticides against *Diaphorina citri* (Hemiptera: Psyllidae). *J Econ Entomol* 102(2): 685-691.
384
385 Bonato O, Lurette A, Vidal C, Fargues J (2007) Modelling temperature-dependent bionomics of *Bemisia tabaci*
386 (Q-biotype). *Physiol Entomol* 32(1): 50-55.
387
388 Bonsignore CP (2016) Environmental factors affecting the behavior of *Coenosia attenuata*, a predator of
389 *Trialeurodes vaporariorum* in tomato greenhouses. *Entomol Exp et Appl* 158(1): 87-96.

390 Botermans M, Verhoeven JJ, Jansen CC, Roenhorst JW, Stijger CC, Pham KK (2009) First report of *Tomato*
391 *yellow leaf curl virus* in tomato in the Netherlands. *Plant Dis* 93(10): 1073-1073.

392 Bowler K, Terblanche JS (2008) Insect thermal tolerance: what is the role of ontogeny, ageing and senescence?.
393 *Biological Reviews* 83: 339-355.

394 Burnett T (1949) The Effect of Temperature on an Insect Host-Parasite Population. *Ecol* 30(2): 113-134.
395
396 (CABI) Centre for Agriculture and Biosciences International (2017). *Bemisia tabaci* datasheet. Available at
397 <http://www.cabi.org/isc/datasheet/8927>. Accessed on October 17, 2018.
398
399 Campo BVH, Hyman G, Bellotti A (2011) Threats to cassava production: known and potential geographic
400 distribution of four key biotic constraints. *Food Secur* 3(3): 329-345.
401
402 Castle SJ, Henneberry TJ, Toscano NC (1996) Suppression of *Bemisia tabaci* (Homoptera: Aleyrodidae)
403 infestations in cantaloupe and cotton with sprinkler irrigation. *Crop Prot* 15(7): 657-663.
404
405 Chen CC, McCarl BA (2001) An investigation of the relationship between pesticide usage and climate change.
406 *Clim Change* 50(4): 475-487.
407
408 Coviella CE, Trumble JT (2000) Effect of elevated atmospheric carbon dioxide on the use of foliar application
409 of *Bacillus thuringiensis*. *Biocontrol* 45(3): 325-336.

410 Cui H, Su J, Wei J, Hu Y, Ge F (2014) Elevated O₃ enhances the attraction of whitefly-infested tomato plants to
411 *Encarsia formosa*. *Sci Reports* DOI: 10.1038/srep05350.
412
413 Cui H, Sun Y, Su J, Ren Q, Li C, Ge F (2012) Elevated O₃ reduces the fitness of *Bemisia tabaci* via
414 enhancement of the SA-dependent defense of the tomato plant. *Arthropod-Plant Interact* 6(3): 425-437.
415
416 Cui X, Wan F, Xie M, Liu T (2008) Effects of Heat Shock on Survival and Reproduction of Two Whitefly
417 Species, *Trialeurodes vaporariorum* and *Bemisia tabaci* Biotype B. *J Insect Sci* 8(24): 1-10
418 DOI:10.1673/031.008.2401.
419
420 Curnutte LB, Simmons AM, Abd-Rabou S (2014) Climate change and *Bemisia tabaci* (Hemiptera:
421 Aleyrodidae): Impacts of temperature and carbon dioxide on life history. *Ann Entomol Soc Am* 107(5): 933-
422 943.
423
424 Deng H, Ali S, Wang XM, Chen XS, Ren SX (2016) Temperature dependence for development of *Clitostethus*
425 *brachylobus* Peng, Ren & Pang 1998 (Coleoptera: Coccinellidae), a predator of *Bemisia tabaci* (Genn.). *Egypt J*
426 *Biol Pest Control* 26(1): 139-145.

427
428 Deutsch CA., Joshua JT, Raymond BH, Kimberly SS, Cameron KG, David CH, Paul RM (2008) Impacts of
429 climate warming on terrestrial ectotherms across latitude. PNAS 105(18): 6668-6672.
430
431 Díaz F, Muñoz- Valencia V, Juvinao- Quintero DL, Manzano- Martínez MR, Toro- Perea N, Cárdenas-
432 Henao H, Hoffmann AA (2014) Evidence for adaptive divergence of thermal responses among *Bemisia*
433 *tabaci* populations from tropical Colombia following a recent invasion. J Evol Biol 27: 1160-1171.
434
435 Díaz F, Saldaña-Guzmán C, Manzano M, Toro-Perea N, Cárdenas-Henao H (2015) Thermal reaction norms
436 between populations with climatic differences of the invader silverleaf whitefly, *Bemisia tabaci* (Hemiptera:
437 Aleyrodidae) MEAM 1 clade in Colombia. Int J Trop Insect Sci 35(1):54-61.
438
439 (EFSA) European Food and Safety Authority (2013) Scientific opinion on the risks to plant health posed by
440 *Bemisia tabaci* species complex and viruses it transmits for the EU territory. EFSA J 11: 3162.
441
442 Elbaz M, Weiser M, Morin S (2011) Asymmetry in thermal tolerance trade-offs between the B and Q sibling
443 species of *Bemisia tabaci* (Hemiptera: Aleyrodidae). J Evol Biol 24: 1099-1109.
444
445 Enkegaard A (1993) *Encarsia formosa* parasitizing the Poinsettia-strain of the cotton whitefly, *Bemisia tabaci*,
446 on Poinsettia: bionomics in relation to temperature. Entomol Exp et Appl 69(3): 251-261.
447
448 Enkegaard A (1994) Temperature dependent functional response of *Encarsia formosa* parasitizing the
449 Poinsettia-strain of the cotton whitefly, *Bemisia tabaci*, on Poinsettia. Entomol Exp et Appl 73(1): 19-29.
450
451 Gamarra H, Carhuapoma P, Kreuze J, Kroschel J (2016a) Whitefly, *Bemisia afer* (Priesner & Hosny 1934). In:
452 Kroschel J, Mujica N, Carhuapoma P, Sporleder M (eds.). Pest distribution and risk atlas for Africa. Potential
453 global and regional distribution and abundance of agricultural and horticultural pests and associated biocontrol
454 agents under current and future climates. International Potato Center (CIP). DOI 10.4160/9789290604761-8. pp.
455 100-113.
456
457 Gamarra H, Mujica N, Carhuapoma P, Kreuze J, Kroschel J (2016b) Sweetpotato whitefly, *Bemisia tabaci*
458 (Gennadius 1889) (Biotype B). In: Kroschel J, Mujica N, Carhuapoma P, Sporleder M (eds.). Pest distribution
459 and risk atlas for Africa. Potential global and regional distribution and abundance of agricultural and
460 horticultural pests and associated biocontrol agents under current and future climates. International Potato
461 Center (CIP). DOI 10.4160/9789290604761-7. pp. 85-99.
462
463 Gamarra H, Carhuapoma P, Mujica N, Kreuze J, Kroschel J (2016c). Greenhouse whitefly, *Trialeurodes*
464 *vaporariorum* (Westwood 1956). In: Kroschel J, Mujica N, Carhuapoma P, Sporleder M (eds.). Pest distribution
465 and risk atlas for Africa. Potential global and regional distribution and abundance of agricultural and
466 horticultural pests and associated biocontrol agents under current and future climates. International Potato
467 Center (CIP). DOI 10.4160/9789290604761-12. pp. 154-168.
468
469 Ghosh S, Bouvaine S, Richardson SCW, Ghanim M, Maruthi MN (2018) Fitness costs associated with
470 infections of secondary endosymbionts in the cassava whitefly species *Bemisia tabaci*. J Pest Sci 91 (1): 17-28.
471
472 Gilioli G, Pasquali S, Parisi S, Winter S (2014) Modelling the potential distribution of *Bemisia tabaci* in Europe
473 in light of the climate change scenario. Pest Manag Sci 70(10): 1611-1623.
474
475 Glunt KD, Paaijmans KP, Read AF, Thomas MB (2014) Environmental temperatures significantly change the
476 impact of insecticides measured using WHOPES protocols. Malaria J 13: 350.
477
478 Gonzalez R, Goldman G, Natwick E, Rosenberg H, Grieshop J, Sutter S, Funakoshi T, Davila-Garcia S (1992)
479 Whitefly invasion in Imperial Valley costs growers, workers millions in losses. California Agric 46(5): 7-8.
480 <http://calag.ucanr.edu/Archive/?article=ca.v046n05p7>
481
482 Greenberg SM, Legaspi Jr BC, Jones WA, Enkegaard A (2000) Temperature-dependent life history of
483 *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) on two whitefly hosts (Homoptera: Aleyrodidae). Environ
484 Entomol 29(4): 851-860.
485

486 Guo JY, Cong L, Wan FH (2013) Multiple generation effects of high temperature on the development and
487 fecundity of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) biotype B. *Insect Sci* 20(4): 541-549.
488

489 Han EJ, Choi BR, Lee JH (2013) Temperature-dependent development models of *Bemisia tabaci* (Gennadius)
490 (Hemiptera: Aleyrodidae) Q biotype on three host plants. *J Asia-Pacific Entomol* 16(1): 5-10.
491

492 Harrington R, Fleming RA, Woiwod IP (2001) Climate change impacts on insect management and conservation
493 in temperate regions: can they be predicted?. *Agric Forest Entomol* 3(4): 233-240.
494

495 Huang Z, Ren S, Musa PD (2008) Effects of temperature on development, survival, longevity, and fecundity of
496 the *Bemisia tabaci* Gennadius (Homoptera: Aleyrodidae) predator, *Axinoscymnus cardilobus* (Coleoptera:
497 Coccinellidae). *Biol Control* 46(2): 209-215.

498 IPCC (2013) Summary for Policymakers. In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J,
499 Nauels A, Xia Y, Bex V, Midgley PM (eds.). *Climate Change 2013: The Physical Science Basis. Contribution*
500 *of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*
501 Cambridge University Press, Cambridge pp 1-28.
502

503 Jarvis A, Ramirez-Villegas J, Campo BVH, Navarro-Racines C (2012) Is cassava the answer to African climate
504 change adaptation? *Trop Plant Biol* 5(1): 9-29.
505

506 Jiao X, Xie W, Zeng Y, Wang C, Liu B, Wang S, Wu Q, Zhang Y (2018) Lack of correlation between host choice
507 and feeding efficiency for the B and Q putative species of *Bemisia tabaci* on four pepper genotypes. *J Pest Sci*
508 91(1): 133-143.
509

510 Khan MS, Tiwari AK, Khan AA, Ji SH, Chun SC (2013) Current scenario of *Tomato yellow leaf curl virus*
511 (TYLCV) and its possible management: A Review. *Vegetos* 26: 139-147.
512

513 Kingsolver JG, Higgins JK, Augustine KE (2015) Fluctuating temperatures and ectotherm growth:
514 distinguishing non-linear and time-dependent effects. *J Exp Biol* 218(14): 2218-2225.

515 Koivisto K, Nissinen A, Vänninen I (2011) Responses of the greenhouse whitefly to elevated CO₂ on tomato.
516 Integrated control in protected crops, temperate climate IOBC/wprs Bull 68: 93-96.
517

518 Koleva NG, Schneider UA (2009) The impact of climate change on the external cost of pesticide applications in
519 US agriculture. *Int J Agric Sustain* 7(3): 203-216.
520

521 Legaspi JC, Mannion C, Amalin D, Legaspi B. C. (2011) Life table analysis and development of *Singhiella*
522 *simplex* (Hemiptera: Aleyrodidae) under different constant temperatures. *Ann Entomol Soc Am* 104(3): 451-
523 458.

524 Legg JP, Owor B, Sseruwagi P, Ndunguru J (2006) Cassava mosaic virus disease in East and Central Africa:
525 epidemiology and management of a regional pandemic. *Adv Virus Res* 67: 355-418.
526

527 Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the World's Worst Invasive Alien Species: A
528 selection from the Global Invasive Species Database. Published by The Invasive Species Specialist Group
529 (ISSG) a specialist group of the Species Survival Commission of the World Conservation Union (IUCN), 12pp.
530 Available at http://www.issg.org/pdf/publications/worst_100/english_100_worst.pdf. Accessed on October 17,
531 2018.
532

533 Lü ZC, Gao QL, Wan FH, Yu H, Guo JY (2014b) Increased survival and prolonged longevity mainly contribute
534 to the temperature-adaptive evolutionary strategy in invasive *Bemisia tabaci* (Hemiptera: Aleyrodidae) Middle
535 East Asia Minor 1. *J Insect Sci* 14(143):1-5.
536

537 Lü ZC, Wang YM, Zhu SG, Yu H, Guo JY, Wan FH (2014a) Trade-offs between survival, longevity, and
538 reproduction, and variation of survival tolerance in Mediterranean *Bemisia tabaci* after temperature stress. *J*
539 *Insect Sci* 14(124): 1-14.
540

541 Ma FZ, Lu ZC, Wang R, Wang FH (2014) Heritability and evolutionary potential in thermal tolerance traits in
542 the invasive Mediterranean cryptic species of *Bemisia tabaci* (Hemiptera: Aleyrodidae). PLoS ONE 9. e103279.
543 DOI.org/10.1371/journal.pone.0103279.

544

545 Madbouni MAZ, Samih MA, Namvar P, Biondi A (2017) Temperature-dependent functional response of
546 *Nesidiocoris tenuis* (Hemiptera: Miridae) to different densities of pupae of cotton whitefly, *Bemisia tabaci*
547 (Hemiptera: Aleyrodidae). Euro J Entomol 114: 325 -331.

548

549 Madueke EDN, Coaker TH (1984) Temperature requirements of the whitefly *Trialeurodes vaporariorum*
550 (Homoptera: Aleyrodidae) and its parasitoid *Encarsia formosa* (Hymenoptera: Aphelinidae). Entomol Gen 9(3):
551 149-154.

552

553 Mahadav A, Kontsedalov S, Czosnek H, Ghanim M (2009) Thermotolerance and gene expression following
554 heat stress in the whitefly *Bemisia tabaci* B and Q biotypes. Insect Biochem Mol Biol 39: 668-676.

555

556 Malekmohammadi A, Shishehbor P, Kocheili F (2012) Influence of constant temperatures on development,
557 reproduction and life table parameters of *Encarsia inaron* (Hymenoptera: Aphelinidae) parasitizing
558 *Neomaskellia andropogonis* (Hemiptera: Aleyrodidae). Crop Prot 34: 1-5.

559

560 Manzano MR, van Lenteren JC (2009) Life history parameters of *Trialeurodes vaporariorum* (Westwood)
561 (Hemiptera: Aleyrodidae) at different environmental conditions on two bean cultivars. Neotrop Entomol 38(4):
562 452-458.

563 McCutcheon GS, Simmons AM (2001). Relationship between temperature and rate of parasitism by
564 *Eretmocerus* sp.(Hymenoptera: Aphelinidae), a parasitoid of *Bemisia tabaci* (Homoptera: Aleyrodidae). J Agric
Urban Entomol 18(2): 97-104.

565

566 Morales FJ, Jones PG (2004) The ecology and epidemiology of whitefly-transmitted viruses in Latin
567 America. Virus Res 100(1): 57-65.

568

569 Mota JA, Soares AO, Garcia PV (2008) Temperature dependence for development of the whitefly predator
Clitostethus arcuatus (Rossi). Biocontrol 53(4): 603-613.

570

571 Muñiz M, Nombela G (2001) Differential variation in development of the B-and Q-biotypes of *Bemisia tabaci*
(Homoptera: Aleyrodidae) on sweet pepper at constant temperatures. Environ Entomol 30(4): 720-727.

572

573 Muñoz-Valencia, V, Díaz-González F, Manzano-Martínez M, Toro-Perea N, Cárdenas-Henao H (2013) Basal
574 and induced thermotolerance to heat shocks in *Bemisia tabaci* biotype B (Hemiptera: Aleyrodidae). Revista
575 Colombiana de Entomol 39(1): 18-25.

576

577 Naranjo SE, Castle SJ, De Barro PJ, Liu SS (2009) Population dynamics, demography, dispersal and spread of
578 *Bemisia tabaci*. In *Bemisia: Bionomics and management of a global pest*. Springer, Netherlands, pp. 185-226.

579

580 Naranjo SE, Ellsworth PC (2005) Mortality dynamics and population regulation in *Bemisia tabaci*. Entomol Exp
581 et Appl 116(2): 93-108.

582

583 (NASA) National Aeronautics and Space Administration (2013) Graphic: The relentless rise of carbon dioxide.
584 https://climate.nasa.gov/climate_resources/24/. Accessed 21 August 2017.

585

586 (NASA) National Aeronautics and Space Administration (2016) Climate change: How do we know?
587 <http://climate.nasa.gov/evidence/>. Accessed 21 August 2017.

588

589 (NASA) National Aeronautics and Space Administration (2017) NASA, NOAA Data Show 2016 Warmest Year
590 on Record Globally. <https://www.nasa.gov/press-release/nasa-noaa-data-show-2016-warmest-year-on-record-globally/>. Accessed 21 August 2017.

591

592 Nava-Camberos U, Riley DG, Harris MK (2001) Temperature and host plant effects on development, survival,
593 and fecundity of *Bemisia argentifolii* (Homoptera: Aleyrodidae). Environ Entomol 30(1): 55-63.

594

595 Navas-Castillo J, Fiallo-Olivé E, Sánchez-Campos S (2011) Emerging virus diseases transmitted by
596 whiteflies. *Annu Rev Phytopathol* 49: 219-248.
597

598 Oliveira MRV, Henneberry TJ, Anderson P (2001) History, current status, and collaborative research projects
599 for *Bemisia tabaci*. *Crop Prot.* 20(9): 709-723.
600

601 Polston JE, De Barro P, Boykin LM (2014) Transmission specificities of plant viruses with the newly identified
602 species of the *Bemisia tabaci* species complex. *Pest Manag Sci* 70(10): 1547-1552.
603

604 Price PW, Denno RF, Eubanks MD, Finke DL, Kaplan I (2011) *Insect ecology: behavior, populations and*
605 *communities.* Cambridge University Press, Cambridge.
606

607 Pusag JCA, Jahan SMH, Lee KS, Lee S, Lee KY (2012) Upregulation of temperature susceptibility in *Bemisia*
608 *tabaci* upon acquisition of *Tomato yellow leaf curl virus* (TYLCV). *J Insect Physiol* 58: 1343-1348
609

610 Qiu BL, De Barro PJ, Xu C, Ren S (2006) Effect of temperature on the life history of *Encarsia bimaculata*
611 (Hymenoptera: Aphelinidae), a parasitoid of *Bemisia tabaci* (Homoptera: Aleyrodidae). *Euro J Entomol* 103(4):
612 787-792.
613

614 Qiu BL, Ren S, Mandour NS, Lin L (2003) Effect of temperature on the development and reproduction of
615 *Bemisia tabaci* B biotype (Homoptera: Aleyrodidae). *Insect Sci* 10(1): 43-49.
616

617 Qiu BL, De Barro PJ, Ren S, Xu CX (2007) Effect of temperature on the life history of *Eretmocerus* sp. nr.
618 *furuhashii*, a parasitoid of *Bemisia tabaci*. *Biocontrol* 52(6): 733-746.
619

620 Qiu YT, Van Lenteren JC, Drost YC, Posthuma-Doodeman, CJ (2004) Life-history parameters of *Encarsia*
621 *formosa*, *Eretmocerus eremicus* and *E. mundus*, aphelinid parasitoids of *Bemisia argentifolii* (Homoptera:
622 Aleyrodidae). *Euro J Entomol* 101(1): 83-94.
623

624 Reader PM, Southwood TR (1984) Studies on the flight activity of the *Viburnum* whitefly, a reluctant flyer.
625 *Entomol Exp et Appl* 36: 185-191.
626

627 Ren SX, Stansly PA, Liu TX (2002) Life history of the whitefly predator *Nephaspis oculatus* (Coleoptera:
628 Coccinellidae) at six constant temperatures. *Biol Control* 23(3): 262-268.

629 Sengonca C, Liu B (1999) Laboratory studies on the effect of temperature and humidity on the life table of the
630 whitefly, *Aleurotuberculatus takahashi* David & Subramaniam (Hom., Aleyrodidae) from southeastern China. *J*
631 *Pest Sci* 72(2): 45-48.
632

633 Sharma SS, Yogesh K (2014) Influence of abiotic weather parameters on population dynamics of whitefly,
634 *Bemisia tabaci* (Genn) on cotton. *J Cotton Res Dev* 28(2): 286-288.
635

636 Simmons AM, Legaspi JC (2004) Survival and predation of *Delphastus catalinae* (Coleoptera: Coccinellidae), a
637 predator of whiteflies (Homoptera: Aleyrodidae), after exposure to a range of constant temperatures. *Environ*
638 *Entomol* 33(4): 839-843.

639 Sparks TC, Pavloff AM, Rose RL, Clower DF (1983) Temperature-toxicity relationships of pyrethroids on
640 *Heliothis virescens* (F.) (Lepidoptera: Noctuidae) and *Anthonomus grandis grandis* Boheman (Coleoptera:
641 Curculionidae). *J Econ Entomol* 76(2): 243-246.
642

643 Su Q, Li S, Shi C, Zhang J, Zhang G, Jin Z, Li C, Wang W, Zhang Y (2018) Implication of heat-shock protein
644 70 and UDP-glucuronosyltransferase in thiamethoxam-induced whitefly *Bemisia tabaci* thermotolerance *J Pest*
645 *Sci* 91(1): 469-478.
646

647 Tripp KE, Kroen WK, Peet MM, Willits DH (1992) Fewer whiteflies found on CO₂-enriched greenhouse
648 tomatoes with high C:N ratios. *HortSci* 27(10): 1079-1080.
649

650 Tzanetakis IE, Martin RR, Wintermantel WM (2013) Epidemiology of criniviruses: an emerging problem in
651 world agriculture. *Frontiers MicroBiol* 4(119): 1-15.

652
653 Uygun N, Sengonca C, Ulusoy MR (1993) Laboratory studies of the effect of temperature and humidity on
654 development and fecundity of *Parabemisia myrietae* (Kuwana) (Homoptera, Aleyrodidae). J Plant Dis and
655 Protect 100 :144-149.
656
657 van Roermund HJV, van Lenteren JP (1995) Foraging behaviour of the whitefly parasitoid *Encarsia formosa* on
658 tomato leaflets. Entomol Exp et Appl 76(3): 313-324.

659 Wang GH, Wang XX, Sun YC, Ge F (2014) Impacts of elevated CO₂ on *Bemisia tabaci* infesting Bt cotton and
660 its parasitoid *Encarsia formosa*. Entomol Expt et Appl 152(3): 228-237.
661
662 Wang K, Tsai JH (1996) Temperature effect on development and reproduction of silverleaf whitefly
663 (Homoptera: Aleyrodidae). Ann Entomol Soc Am 89(3): 375-384.
664
665 Xiao N, Pan LL, Zhang CR, Shan HW, Liu SS (2016). Differential tolerance capacity unfavourable low and
666 high temperatures between two invasive whiteflies. Sci Reports 6: 24306. DOI:10.1038/srep24306
667
668 Xie M, Wan FH, Chen YH, Wu G (2011) Effects of temperature on the growth and reproduction characteristics
669 of *Bemisia tabaci* B-biotype and *Trialeurodes vaporariorum*. J Appl Entomol 135(4): 252-257.
670
671 Yang TC, Chi H (2006) Life tables and development of *Bemisia argentifolii* (Homoptera: Aleyrodidae) at
672 different temperatures. J Econ Entomol 99(3): 691-698.
673
674 Yao S, Huang Z, Ren S, Mandour N, Ali S (2011) Effects of temperature on development, survival, longevity,
675 and fecundity of *Serangium japonicum* (Coleoptera: Coccinellidae), a predator of *Bemisia tabaci* Gennadius
676 (Homoptera: Aleyrodidae). Biocontrol Sci Technol 21(1): 23-34.
677
678 Youngsteadt E, Ernst AF, Dunn RR, Frank SD (2017) Responses of arthropod populations to warming depend
679 on latitude: evidence from urban heat islands. Global Change Biol 23(4): 1436-1447.

680 Zandi-Sohani N, Shishehbor P (2011) Temperature effects on the development and fecundity of *Encarsia*
681 *acaudaleyrodidis* (Hymenoptera: Aphelinidae), a parasitoid of *Bemisia tabaci* (Homoptera: Aleyrodidae) on
682 cucumber. Biocontrol 56(3): 257-263.
683
684 Zandi-Sohani N, Shishehbor P, Kocheili F (2009) Parasitism of cotton whitefly, *Bemisia tabaci* on cucumber by
685 *Eretmocerus mundus*: Bionomics in relation to temperature. Crop Prot 28(11): 963-967.
686
687 Zavala JA, Nability PD, DeLucia EH (2013) An emerging understanding of mechanisms governing insect
688 herbivory under elevated CO₂. Annu Rev Entomol 58: 79-97.
689
690 Zidon R, Tsueda H, Morin E, Morin S (2016) Projecting pest population dynamics under global warming: the
691 combined effect of inter-and intra-annual variations. Ecol Appl 26(4): 1198-1210.
692
693 Zhou H, Ali S, Wang X, Chen X, Ren S (2017) Temperature influences the development, survival, and life
694 history of *Axinoscymnus apioides* Kuznetsov & Ren (Coleoptera: Coccinellidae), a predator of whitefly. Turk J
695 Zoo 41(3): 495-501.
696
697 Zhu S, Li Z, Wan F (2010) Effects of brief exposure to high temperature on survival and reproductive
698 adaptation of *Bemisia tabaci* Q-biotype. Chinese Bull Entomol 47(6):1141-1144.
699
700 Zilahi-Balogh GMG, Shipp JL, Cloutier C, Brodeur J (2006) Influence of light intensity, photoperiod, and
701 temperature on the efficacy of two aphelinid parasitoids of the greenhouse whitefly. Environ Entomol 35(3):
702 581-589.

703

Table 1: Effects of climatic factors on life history traits that include fecundity, immature development time and adult longevity of whiteflies

Whitefly spp.	Host plant	Climatic variable	Effects on life history trait	Range **	Geographic locations	Key references
Fecundity						
<i>B. tabaci</i> MEAM1	Eggplant, Tomatoes,	Temperature increase	-	20 – 32 ^a	USA; China; China	*Wang and Tsai 1996; Qui et al. 2003; Guo et al. 2013
<i>B. tabaci</i> MED	Tomatoes	Temperature increase	-	21 – 35	France	Bonato et al. 2007
<i>T. vaporariorum</i>	Kidney bean, <i>Brassica</i> spp.	Temperature increase	-	19 – 26; 15-24	Colombia; China	Manzano and Lenteren 2009; Xie et al. 2011
<i>B. tabaci</i> MEAM1	<i>Brassica</i> spp.	Temperature increase	+	15 – 24	China	Xie et al. 2011
<i>T. vaporariorum</i>	Tomatoes	Elevated CO ₂	-	400 – 1200	Finland	Koivisto et al. 2011
<i>B. tabaci</i> MEAM1	Collard, Cotton	Elevated CO ₂	0	424 – 753;	USA; China	Curnutte et al. 2014; Wang et al. 2014
<i>B. tabaci</i> MEAM1	Tomatoes	Elevated ozone	-	375 – 750 37.3 – 72.2***	China	Cui et al. 2012
Immature developmental time						
<i>B. tabaci</i> MEAM1 and MED	Sweet pepper	Temperature increase	-	17 – 33	Spain	Muñiz and Nombella 2001
<i>B. tabaci</i> MED	Tomatoes, Sweet pepper, Eggplant and Oriental melon	Temperature increase	-	15 – 30	France; Korea	Bonato et al. 2007; Han et al. 2013
<i>T. vaporariorum</i>	Greenhouse crops	Temperature increase	-	18 – 27	England	Madueke and Coaker 1984
<i>B. tabaci</i> MEAM1	Fruits and vegetables	Temperature increase	-	20 – 30 ^b	USA; China; Turkey	*Nava-Camberos et al. 2001; *Yang and Chi 2006;

						Bayhan et al. 2006
<i>Aleurotuberculatus takahashi</i> (David et Subramaniam)	Citrus	Temperature increase	-	15 – 35	China	Sengonca and Liu 1999
<i>B. tabaci</i> MEAM1 and <i>T. vaporariorum</i>	<i>Brassica</i> spp.	Temperature increase	-	15 – 24	China	Xie et al. 2011
<i>Bemisia afer</i> (Priesner and Hosny)	Sweet potato	Temperature increase	-	17 – 25		Gamarra et al. 2016a
<i>B. tabaci</i> MEAM1	Cotton	Elevated CO ₂	+	375 – 750	China	Wang et al. 2014
<i>B. tabaci</i> MEAM1	Tomatoes	Elevated ozone	+	37.3 – 72.2***	China	Cui et al. 2012
Adult longevity						
<i>B. tabaci</i> MEAM1	Eggplant, Tomatoes	Temperature increase	-	20 – 32 ^c	China; USA; China	Qui et al. 2003; *Wang and Tsai 1996; Guo et al. 2013
<i>A. takahashi</i>	Citrus	Temperature increase	-	15 – 35	China	Sengonca and Liu 1999
<i>B. tabaci</i> MED	Tomatoes	Temperature increase	-	21 – 35	France	Bonato et al. 2007
<i>T. vaporariorum</i>	Kidney bean	Temperature increase	-	19 – 26	Colombia	Manzano and Lenteren 2009
<i>B. afer</i>	Sweet potato	Temperature increase	-	17 – 28	Philippines	Gamarra et al. 2016a
<i>T. vaporariorum</i>	Tomatoes	Elevated CO ₂	0	400 – 1200	Finland	Koivisto et al. 2011
<i>B. tabaci</i> MEAM1	Cotton	Elevated CO ₂	0	375 – 750	China	Wang et al. 2014

+ represents an increase, - represents a decrease, 0 represents no change

MEAM1 (Middle East-Asia Minor 1) = B biotype

MED (Mediterranean) = Q biotype

**B. argentifolii* = MEAM 1

**Temperatures were measured in °C, CO₂ and ozone levels are in ppm except where otherwise stated.

*** measured in nmol/mol

a. Wang and Tsai (1996) and Guo et al. (2013) reported up to 35 °C and 37 °C respectively.

b. Yang and Chi et al. (2006) reported a range from 15 – 35 °C.

c. Guo et al. (2013) reported 27 – 37 °C, while Wang and Tsai (1996) reported up to 35 °C.

Table 2: Temperature conditions at which peak performance for selected life history traits of whiteflies was reported

Whitefly species	Development time	Immature survival	Adult longevity	Fecundity	Intrinsic rate of increase	Geographic location	References
<i>B. tabaci</i> MEAM 1	29 °C	26 °C	20 °C	20 °C	29 °C	China	Qui et al. 2003
<i>B. tabaci</i> MEAM 1	35 °C	NA	20 °C	25 °C	30 °C	China	Yang and Chi 2006
<i>B. tabaci</i> MED	30 °C	25 °C	17 °C	21 °C	30 °C	France	Bonato et al. 2007
<i>B. tabaci</i> MED	27.5 & 30 °C *	27.5 – 32.5 °C *	NA	NA	NA	Korea	Han et al. 2013
<i>T. vaporariorum</i>	24 °C	NA	18 °C	18 °C	NA	China	Xie et al. 2011
<i>T. vaporariorum</i>	26 °C	19 °C	19 °C	22 °C	19&22 °C *	Colombia	Manzano and Lenterer 2009
<i>A. takahashi</i>	35 °C	15 °C	15 °C	25 °C	NA	China	Sengonca and Liu 1999
<i>Parabemisia myricae</i> (Kuwana)	30 °C	25±1 °C	15±1 °C	25±1 °C	NA	Turkey	Uygun et al. 1993
<i>Singhiella simplex</i> (Singh)	30 °C	15 °C	15 °C	27 °C	27 °C	USA	Legaspi et al. 2011

*multiple host plants

NA – not available

Table 3: Temperature conditions at which peak performance for selected life history traits of whitefly natural enemies was reported

Whitefly species	Development time	Immature survival	Adult longevity	Fecundity	Intrinsic rate of increase	Geographic origin	References
Parasitoids							
<i>En. formosa</i>	28 °C	22 °C	16 °C	28 °C	28 °C	Germany	Enkegaard 1993
<i>En. formosa</i>	32 °C	NA	15 °C	NA	NA	USA	Qui et al. 2004
<i>En. inaron</i> (Walker)	30 °C	25 °C	20 °C	25 °C	25 °C	Iran	Malekmohammadi et al. 2012
<i>En. bimaculatus</i> (Heraty and Polaszek)	32 °C	26 °C	20 °C	29 °C	29 °C	China	Qui et al 2006
<i>En. acaudaleyrodis</i> (Hayat)	32°C	25 °C	20 °C	25 °C	25 °C	Iran	Zandi-Sohani and Shishehbor 2011
<i>Er. eremicus</i> (Rose & Zolnerowich)	32 °C	NA	15 °C	NA	NA	USA	Qui et al. 2004
<i>Er. sp. Nr. furuhasii</i> (Rose & Zolnerowich)	29 °C	26 °C	20 °C	26 °C	29°C	China	Qui et al. 2007
<i>Er. mundus</i> (Mercet)	30 °C	25 °C	20 °C	25 °C	30 °C	Iran	Zandi-Sohani et al. 2009
<i>Er. mundus</i> (Mercet)	32 °C	NA	15°C	NA	NA	Italy	Qui et al. 2004
Predators							
<i>Serangium japonicum</i> (Chapin)	32 °C	26 °C	20 °C	26 °C	29 °C	China	Yao et al. 2011
<i>Axinoscymnus cardilobus</i> (Ren and Pang)	29 – 32 °C	23 °C	17 °C	23 °C	23 °C	China	Huang et al. 2008
<i>A. apioides</i> (Kuznetsov and Ren)	29 °C	26 °C	20 °C	23 °C	26 °C	China	Zhou et al. 2017
<i>Clitostethus brachylobus</i>	29 °C	26 °C	17 °C	26 °C	26 °C	China	Deng et al. 2016
<i>C. arcuatus</i> (Rossi)	30 °C	25 °C	15 °C	20 °C	30 °C	Portugal	Mota et al. 2008
<i>Nephaspis oculatus</i> (Blatchley)	33 °C	26 °C	20 °C	26 °C	26 °C	USA	Ren et al. 2002