REVIEW

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

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

Received: 5 January 2018 / Revised: 24 October 2018 / Accepted: 27 October 2018 © Springer-Verlag GmbH Germany, part of Springer Nature 2018

Abstract

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

Keywords Whitefies · Population dynamics · Begomoviruses · Pest management · Species interaction

Communicated by N. Desneux.

 \boxtimes Oluwatosin Z. Aregbesola tosinaregbs@yahoo.com

- ¹ Dipartimento di Agricoltura, Alimentazione e Ambiente, Università degli Studi di Catania, Via Santa Sofa n. 100, 95123 Catania, Italy
- ² Department of Plant and Environmental Sciences, University of Copenhagen, Copenhagen, Denmark
- ³ International Institute of Tropical Agriculture, Dar es Salaam, Tanzania
- ⁴ Wesley University Ondo, Ife-Road, Ondo, Ondo State, Nigeria

Key message

- An in-depth review was conducted to address the weak current understanding of the potential infuence of climate change on whitefies.
- Our study highlights the dynamism of the interactions between vector, natural enemies and transmitted viruses, and confrms that the impacts of climate change will vary widely depending on local circumstances.
- Future eforts to manage whitefies must be cognisant of the complex efects of climate on the agro-ecological systems inhabited by these globally important insects.

Introduction

Whitefies are important global agricultural pests (Oliveira et al. [2001](#page-10-0)). They have a wide host range and are very adaptive to diferent environmental conditions (Oliveira et al. [2001](#page-10-0); CABI [2017\)](#page-8-0). The *Bemisia tabaci* (Gennadius) species group is the most economically important whitefy (Lowe et al. [2000](#page-10-1); Navas-Castillo et al. [2011\)](#page-10-2). It causes damage to crops directly through phloem feeding as well as the excretion of honeydew leading to the growth of sooty moulds that reduce photosynthesis. Whiteflies also cause indirect damage through the transmission of economically important viral plant pathogens (Navas-Castillo et al. [2011](#page-10-2); Tzanetakis et al. [2013;](#page-11-0) Polston et al. [2014](#page-10-3)). Crop damage due to plant viruses transmitted by whitefies globally results in losses worth more than \$US 1 billion (Gonzalez et al. [1992](#page-9-0); Legg et al. [2006](#page-10-4)).

The Intergovernmental Panel on Climate Change (IPCC) ffth assessment report predicted a 1.5 °C increase in global surface temperature, and an increasing contrast in precipitation between wet and dry regions over the twenty-first century (IPCC [2013](#page-9-1)). Independent observations by the National Oceanic and Atmospheric Administration (NOAA) and the National Aeronautics and Space Administration (NASA) showed that globally, temperatures in 2016 were 0.99 °C warmer compared to records from the twentieth century, and the third year in a row to set a new record high temperature (NASA [2017\)](#page-10-5). Global $CO₂$ concentration is the primary driver of the recent anthropogenic climate change. While the global concentration of $CO₂$ in the atmosphere reached 400 parts per million (ppm) for the frst time in recorded history in 2013, the trend has continued, with the 2016 estimate at 404.4 ppm (NASA [2013](#page-10-6), [2016](#page-10-7)).

Climatic change is afecting agricultural and natural ecosystems and directly affects the development, reproduction, survival, population dynamics, potential distribution and abundance of whitefy species (Muñiz and Nombela [2001](#page-10-8); Bonato et al. [2007;](#page-8-1) Bellotti et al. [2012;](#page-8-2) Gilioli et al. [2014\)](#page-9-2). Some studies have reported direct efects of temperature (Xie et al. [2011;](#page-11-1) Guo et al. [2013](#page-9-3); Han et al. [2013](#page-9-4)), CO_2 (Koivisto et al. [2011](#page-10-9); Curnutte et al. [2014](#page-9-5)), and O_3 (Cui et al. [2012,](#page-9-6) [2014](#page-9-7)) on life history traits. Others have discussed efects of rainfall (Castle et al. [1996](#page-9-8); Naranjo and Ellsworth [2005;](#page-10-10) Naranjo et al. [2009](#page-10-11); Sharma and Yogesh [2014\)](#page-11-2) on whitefies.

At the present time, information on the potential infuence of climate change on whitefies is limited and efects of climate change on several biological parameters of whitefies are poorly understood. New research initiatives aim to deepen insights into the infuence of climate change on whitefies, and on the tri-trophic interactions within the

agricultural systems in which they cause so much damage. This review explores the infuence of climate change on the life history, distribution, population dynamics and efficacy of management strategies of whitefies. Through this analysis, we have been able to identify important trends for some whitefy species and biological parameters, and based on these, we highlight needs for further research.

How will whitefies respond to climate change?

Life history traits

There are differences in response of whiteflies to climate change resulting from differences in whitefly species, host plants, climatic zones and climate factors. The response of diferent whitefies and host plants to changes in climatic factors are summarised in Table [1](#page-2-0). Temperature and hostplant effects have been identified as important factors affecting development, mortality and fecundity rates in whitefy populations. Temperature increase within the thermal optimum leads to a decrease in developmental time (Madueke and Coaker [1984;](#page-10-12) Sengonca and Liu [1999](#page-11-3); Muñiz and Nombela [2001;](#page-10-8) Nava-Camberos et al. [2001;](#page-10-13) Bayhan et al. [2006](#page-8-3); Bonato et al. [2007](#page-8-1); Xie et al. [2011](#page-11-1); Han et al. [2013](#page-9-4)). These trends are commonly observed in insects due to the influence of temperature on their physiology. Other effects of temperature increase (especially above the optimum threshold) on life history traits include decreasing fecundity (Bonato et al. [2007](#page-8-1); Xie et al. [2011](#page-11-1); Guo et al. [2013](#page-9-3)) and decreasing longevity (Sengonca and Liu [1999;](#page-11-3) Bonato et al. 2007 ; Guo et al. 2013). Elevated CO₂ and O₃ increased developmental time of whitefies (Cui et al. [2012](#page-9-6); Wang et al. 2014), but elevated $CO₂$ did not affect adult longevity (Koivisto et al. [2011](#page-10-9); Curnutte et al. [2014](#page-9-5)) and fecundity of whiteflies (Curnutte et al. [2014;](#page-9-5) Wang et al. [2014\)](#page-11-4). There is a dearth of information regarding the effects of elevated O_3 on whitefy longevity and fecundity (Table [1](#page-2-0)).

In nature, insects often experience stressful temperatures (high and low) that may afect not only their life history, but also their distribution and abundance (Cui et al. [2008](#page-9-9); Lü et al. [2014b\)](#page-10-14). Research on the thermal biology of insects has revealed that the ability of insects to tolerate extreme temperatures is one of the most crucial biotic factors defning the distribution of most insects, which may have further implications in the face of global climate change (Bowler and Terblanche [2008;](#page-8-4) Cui et al. [2008;](#page-9-9) Ma et al. [2014\)](#page-10-15). There is an increasing number of empirical studies on thermotolerance and its associated evolutionary implications in whitefies. Traits commonly investigated are survival, fecundity and viability of the ofspring after heat shock.

Table 1 (continued)

White fly spp.	Host plant	Climatic variable	Effects on life history trait	$Range**$	Geographic loca- tions	Key references
B. tabaci MEAM1	\cot _c	Elevated $CO2$		$375 - 750$	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 ${}^{\circ}C$, CO_2 and ozone levels are in ppm except where otherwise stated

***Measured in nmol/mol

^aWang and Tsai ([1996\)](#page-11-5) and Guo et al. [\(2013](#page-9-3)) reported up to 35 °C and 37 °C, respectively

^bYang and Chi ([2006\)](#page-11-6) reported a range comprising from 15 °C and 35 °C

^cGuo et al. [\(2013](#page-9-3)) reported 27–37 °C, while Wang and Tsai [\(1996](#page-11-5)) reported up to 35 °C

Comparing both *B. tabaci* MEAM1 and MED, Mahadav et al. ([2009\)](#page-10-18), Elbaz et al. ([2011](#page-9-11)) and Xiao et al. ([2016\)](#page-11-7) showed that survival of both species reduced as temperature increased, and that *B. tabaci* MED performed better than MEAM1 after brief exposure to higher temperatures $(41-45 \degree C)$. Similarly, Cui et al. ([2008\)](#page-9-9) showed that survival rates drop after brief exposure to higher temperatures (39–45 °C), and *B. tabaci* MEAM1 is more thermotolerant than *T. vaporariorum*. A similar decline in survival after exposure to high temperatures was also reported for *B. tabaci* MED (Zhu et al. [2010](#page-11-8); Lü et al. [2014a\)](#page-10-19) and *B. tabaci* MEAM1 (Muñoz-Valencia et al. [2013;](#page-10-20) Díaz et al. [2015](#page-9-12)). Fecundity of whitefies after brief exposure to heat shock generally reduces with temperature increase (Elbaz et al. [2011](#page-9-11); Xiao et al. [2016\)](#page-11-7). However, other studies have shown no signifcant efect (Cui et al. [2008](#page-9-9); Zhu et al. [2010;](#page-11-8) Lü et al. [2014a](#page-10-19)). Furthermore, progeny viability post-heat shock could either decrease (Cui et al. [2008;](#page-9-9) Díaz et al. [2015\)](#page-9-12) or show an inconsistent pattern (Muñoz-Valencia et al. [2013](#page-10-20); Xiao et al. [2016\)](#page-11-7) with temperature increase. Several studies on thermotolerance and life history of whitefies suggest that female *B. tabaci* are more thermotolerant than males (Cui et al. [2008](#page-9-9); Muñoz-Valencia et al. [2013](#page-10-20); Ma et al. [2014\)](#page-10-15).

In some cases, signifcant diferences in thermotolerance have been reported among populations experiencing diferent levels of environmental stress, pointing towards adaptive divergence (Díaz et al. [2014](#page-9-13); Ma et al. [2014\)](#page-10-15). For instance, Díaz et al. ([2014\)](#page-9-13) associated significant differences in survival and fecundity among populations with mean temperature and temperature variation in the local environment, respectively. Similarly, Ma et al. ([2014](#page-10-15)) also demonstrated that diferences in habitat temperature resulted in signifcant diferences in the adaptive strategies to heat stress between the Harbin and Turpan *B. tabaci* MED populations from China. Their work suggests that adaptive microevolution of *B. tabaci* is directly related to its high narrow-sense heritability for both heat and cold resistance. These potential evolutionary changes could be used by *B. tabaci* to maintain its populations with climate change (Ma et al. [2014](#page-10-15)). Elbaz et al. [\(2011](#page-9-11)) showed that *B. tabaci* MEAM1 and MED deploy diferent adaptation strategies when experiencing heat stress. *B. tabaci* MEAM1 achieves maximum reproduction at the expense of soma protection, while *B. tabaci* MED invests more of its resources on processes benefcial to somatic maintenance. In another interesting study, Lü et al. ([2014b\)](#page-10-14) highlighted the signifcance of stress-inducing conditions on the ecological adaptations and distribution of insects in the context of climate change. Their work demonstrated that thermotolerance and longevity were more important than reproductive traits, and that enhanced thermotolerance and prolonged longevity were essential adaptive strategies that contributed to the survival of MEAM1 under the hot and harsh desert climate reported in the study. Pusag et al. ([2012](#page-10-21)) showed that acquisition of *Tomato yellow leaf curl virus* (TYLCV) by *B. tabaci* MED resulted in increased development rate and increased susceptibility to thermal stress which may result in a decline in vector longevity. This highlights how the complex interactions between vector ftness and thermal stress could infuence the ability of the vector to acquire and transmit plant viruses especially with climate change.

Apart from temperature and other environmental factors, other important factors could infuence the life history and response of whitefies to climate change. For instance, adaptation to one environmental stress (insecticides like thiamethoxam) increased thermotolerance in *B. tabaci* MEAM1 (Su et al. [2018\)](#page-11-9) which could be benefcial to *B. tabaci* MEAM1 in the light of climate change. Absence of secondary endosymbionts in cassava-colonising whitefies increased their ftness and vector abilities, and a possible ecosystem service in suppressing populations of cassavacolonising whitefies has been proposed (Ghosh et al. [2018](#page-9-14)). Nutrition and defensive chemistry of host plants (Jiao et al.

[2018](#page-9-15)) could also infuence the response of whitefies to climate change.

Population dynamics

The major factors that regulate population dynamics are climate, natural enemies, initial population size, host-plant suitability, farming systems and management practices (Price et al. [2011\)](#page-10-22). Generally, rainfall has been noted to negatively afect populations of *B. tabaci* (Naranjo and Ellsworth [2005](#page-10-10); Sharma and Yogesh [2014\)](#page-11-2). Using sprinkler irrigation to simulate rainfall, Castle et al. ([1996\)](#page-9-8) found a consistent reduction in densities of immature whitefies. Some of the most abundant populations of *B. tabaci* in history were from irrigated desert cropping systems where consistently high temperatures shorten generation times and rainfall is infrequent (Naranjo et al. [2009\)](#page-10-11). Experiments considering prolonged exposure to constant temperatures and brief exposure to heat shock agree that elevated temperatures (above the optimum threshold of whitefies) negatively afect life history of whitefies. However with climate change, high thermotolerance and the polyphagous nature of some whitefies (*B. tabaci* MEAM1 and MED) which contribute to their invasion success could possibly facilitate their population increase in some locations depending on the amount of heat stress experienced (Bellotti et al. [2012](#page-8-2); EFSA [2013](#page-9-16); Gilioli et al. [2014;](#page-9-2) Gamarra et al. [2016b\)](#page-9-10). By combining general circulation models (GCMs) with a stochastic weather generator and population dynamics models, Zidon et al. ([2016\)](#page-11-10) studied population dynamics of *B. tabaci* in three locations in the Mediterranean region under two future scenarios. Their study suggests that temperature increase will increase population size and average number of generations completed by *B. tabaci* yearly, and a lengthening of growing season in the three locations.

Bemisia afer (Priesner and Hosny) can go through 8–10 and 4–8 generations per year in tropical and subtropical regions respectively, under current temperature conditions, while *T. vaporariorum* can have up to 11 generations per year (Gamarra et al. [2016a,](#page-9-17) [c\)](#page-9-18). Considering the effects of climatic change up to 2050, *B. afer* is predicted to increase by only 1 generation per year in temperate regions of Europe, North America and parts of Asia. An increase of 1–2 generations per year is predicted for tropical and subtropical regions in Asia (Malaysia, Philippines, Indonesia); Europe (Portugal); South America (southern Brazil, central Colombia, Peruvian coast); Central, East, and Southern Africa; the Caribbean; central and southern China; and Oceania (Papua New Guinea) (Gamarra et al. [2016a](#page-9-17)). Furthermore, an increase of 1–2 generations per year is predicted for *T. vaporariorum* in most tropical regions. *T. vaporariorum* will likely have a small increase in temperate regions (mainly Europe and North America), while increasing temperatures around the Equator will possibly reduce *T. vaporariorum* activity (Gamarra et al. [2016c\)](#page-9-18).

Increases in the number of generations do not necessarily translate into range expansion or elevated whitefy populations. Generally, increasing temperature within developmental thresholds leads to an increase in insect population by reducing development time and hastening metabolic and physiologic activities. However, at extreme temperatures (above optimum), other important life history traits are negatively afected (Qiu et al. [2003](#page-10-16); Bonato et al. [2007\)](#page-8-1). Hence, with a high number of generations per year due to faster development rate, there is also an increased possibility of lower population increase over time. Nevertheless, these same studies that indicated increased number of generations based on generation index (which measures mean number of generations that can be produced by an insect within a given year) (Gamarra et al. [2016a,](#page-9-17) [b](#page-9-10), [c\)](#page-9-18) also presented a more robust estimate of changes in abundance of insects called activity index, which accounts for the whole life history traits, measures the rate of fnite increase and also indicates the severity of the pest problem. Based on this additional estimate, climate change is predicted to cause a small increase in the population of *T. vaporariorum* in the temperate regions of Europe and America, while *T. vaporariorum* populations along the Equator will likely reduce with increasing temperature. Similarly, due to climate change, the population growth potential of *B. afer* is predicted to decrease in most of the sweet potato growing areas in tropical and subtropical regions. However, the abundance of *B. afer* will potentially increase in southern subtropical and temperate zones (Gamarra et al. [2016a\)](#page-9-17). For *B. tabaci* MEAM1, a small increase in potential growth is predicted for most tropical and subtropical regions. *B. tabaci* MEAM1 populations will possibly reduce along the Equator as temperature increases (Gamarra et al. [2016b](#page-9-10)). Furthermore, based on the activity index and generation index available in the Insect Life Cycle Modelling software used by Gamarra et al. [\(2016a,](#page-9-17) [2b](#page-9-10), [c](#page-9-18)), populations of cassava-colonising *B. tabaci* sub-Saharan Africa 1—Sub-Group 3 (SSA1-SG3) have been predicted to increase in East, Central and Southern Africa (Aregbesola [2018](#page-8-5)). Using the Physiologically Based Demographic Model, Gilioli et al. ([2014](#page-9-2)) simulated changes in distribution and population of *B. tabaci* MED in Europe considering a worst-case scenario (upper threshold for development, survival and fecundity) and indicated that climate change resulted in increased population density and infestation of *B. tabaci* MED which is highly consistent with the high thermotolerance previously reported for *B. tabaci* MED.

Movement and distribution

Spread of whitefies is facilitated partly by human transportation of infested plant materials, but there is increasing concern that climate change allows establishment in hitherto unsuitable regions (Bebber et al. [2013\)](#page-8-6). Climate change will also have additional implications for the invasion success of whitefly species as climatic suitability and overall community interaction will play a key role in the establishment and geographical expansion of the introduced whitefy species. Ecological niche models which generate maps of a species' environmental suitability based on its current distribution (e.g. Campo et al. [2011;](#page-9-19) Jarvis et al. [2012;](#page-9-20) Bellotti et al. [2012\)](#page-8-2), and insect physiology-based models (e.g. Gilioli et al. [2014](#page-9-2); Gamarra et al. [2016a](#page-9-17), [b,](#page-9-10) [c](#page-9-18); Aregbesola [2018](#page-8-5)) which utilise detailed descriptions of the life history of the insect, provide very powerful tools to assess the potential impact of climate change on the distribution of whitefies. Both ecological niche modelling and physiology-based modelling are commonly used, and our review considers research relating to both approaches.

In Europe, expansion of *B. tabaci* northwards is expected to be limited by low temperatures, reducing the risk of *B. tabaci* establishment because of climatic limitations (Gilioli et al. [2014\)](#page-9-2). *B. tabaci* could possibly expand its range in some of the Mediterranean countries (Spain, France, Italy and Greece) and in countries along the Adriatic coast line (Gilioli et al. [2014\)](#page-9-2) as a consequence of climate change. Increased climatic suitability for *B. tabaci* has been predicted to occur in northern Argentina, south-central Bolivia, north-eastern Brazil, south-west Peru, northern Australia, southern China, as well as parts of the USA (Bellotti et al. [2012](#page-8-2)). A similar trend is predicted for Central African Republic, Ethiopia and Cameroon (Jarvis et al. [2012](#page-9-20)) and southern India (Campo et al. [2011\)](#page-9-19). There will also be more *B. tabaci* further south, in regions where there is a cool and dry winter (Bellotti et al. [2012;](#page-8-2) Aregbesola [2018\)](#page-8-5). According to Gamarra et al. [\(2016a,](#page-9-17) [b](#page-9-10)), in 2050, temperature will potentially reduce *B. afer and T. vaporariorum* establishment in current high-risk areas of the tropics globally. By contrast, the risk of establishment of *B. afer* will increase in the subtropical sweet potato growing areas of South Africa, southern Brazil, Peru, Uruguay, Chile and Argentina. The temperate regions of Europe, North America and Asia will become increasingly suitable for *T. vaporariorum*, although the risk of establishment will still be very low (Gamarra et al. [2016a,](#page-9-17) [c](#page-9-18)).

Since virus transmission by whitefies is mainly mediated by *B. tabaci* and *T. vaporariorum*, any change in the distribution of these vectors may afect the overall geography of viral diseases. Populations of *B. tabaci* are distributed in tropical and subtropical zones all around the globe and viruses transmitted by *B. tabaci* are found—as a group—roughly within the same areas (Navas-Castillo et al. [2011](#page-10-2)) although local patterns of seasonal temperature, precipitation and altitude appear to play an important role (Morales and Jones [2004](#page-10-23)). Sporadic records of viruses from greenhouse plants in cooler climates most likely refect the importation of infected plant material and not per se the natural spread of viruses (Botermans et al. [2009](#page-8-7)). However, any future increase in temperature will allow populations of *B. tabaci* to expand towards the poles and the epidemic areas of the viruses vectored will most likely follow (Bebber et al. [2013](#page-8-6)). A scenario of climate change has been outlined for *B. tabaci* and begomoviruses using TYLCV in Europe as an example. Manifest and frequent infection of feld-grown tomato by TYLCV in Europe is restricted to the most southern, coastal/lowland regions, particularly the islands of Cyprus, Crete, Sicily, Sardinia and the southern parts of Spain and Portugal (Khan et al. [2013\)](#page-10-24). The same regions are characterised by yearround outdoor cultivation of tomato (main virus host) and the presence of populations of *B. tabaci* (EFSA [2013](#page-9-16); Gilioli et al. [2014](#page-9-2)). In case of a temperature increase of 2 °C, both studies predict a movement of established populations of *B. tabaci* approximately 300–500 km northwards, taking into account signifcant local variations due to local topography. The spread of TYLCV in open felds is expected to follow the same pattern (Table [2](#page-6-0)).

Efcacy of management strategies

Evidence from Wang et al. [\(2014](#page-11-4)) indicates that the biological control of *B*. *tabaci* by *Encarsia formosa* (Gahan) would not be infuenced by transgenic Bt cotton and/or elevated CO₂. Cui et al. ([2014](#page-9-7)) suggest that elevated O_3 enhanced the attraction of *En. formosa* to whitefies with resulting augmented biological control. This probably relates to the enhanced production of volatile organic compounds by the host plant, which indirectly increased the attraction of *En. formosa* to whitefies. Furthermore, it has been experimentally confrmed that parasitism and predation rates of whitefy natural enemies could increase with temperature within the optimum ranges of the natural enemies as in the case of *En. formosa* (Burnett [1949](#page-8-8); Enkegaard [1994](#page-9-21); Qiu et al. [2004;](#page-10-25) Zilahi-Balogh et al. [2006](#page-11-11)), *Eretmocerus eremicus* (Rose & Zolnerowich) (Qiu et al. [2004\)](#page-10-25), *Er. mundus* (Mercet) (Qiu et al. [2004\)](#page-10-25), *Eretmocerus* spp. (McCutcheon and Simmons [2001](#page-10-26)), *Delphastus catalinae* (Horn) (Simmons and Legaspi [2004\)](#page-11-12) and *Nesidiocoris tenuis* (Reuter) (Madbouni et al. [2017\)](#page-10-27). Similarly, walking speed, walking activity and fight activity of whitefy natural enemies have been shown to be positively correlated with temperature (van Roermund and van Lenteren [1995;](#page-11-13) Bonsignore [2016\)](#page-8-9), while handling time decreases with temperature increase (Enkegaard [1994](#page-9-21); Madbouni et al. [2017\)](#page-10-27). Comparable studies on the impact of temperature on walking pattern and fight activity of whitefy

Whitefly species	Development time $(^{\circ}C)$	Immature survival $(^{\circ}C)$	Adult longevity $(^{\circ}C)$	Fecundity $(^{\circ}C)$	Intrinsic rate of increase $(^{\circ}C)$	Geographic location	References
B. tabaci MEAM 1	29	26	20	20	29	China	Qiu et al. (2003)
B. tabaci MEAM 1	35	NA.	20	25	30	China	Yang and Chi (2006)
B. tabaci MED	30	25	17	21	30	France	Bonato et al. (2007)
B. tabaci MED	27.5 and 30°	$27.5 - 32.5^{\mathrm{a}}$	NA	NA	NA	Korea	Han et al. (2013)
T. vaporariorum	24	NA.	18	18	NA.	China	Xie et al. (2011)
T. vaporariorum	26	19	19	22	19 and 22^a	Colombia	Manzano and Len- teren (2009)
A. takahashi	35	15	15	25	NA	China	Sengonca and Liu (1999)
Parabemisia myri- cae (Kuwana)	30	25 ± 1	15 ± 1	25 ± 1	NA	Turkey	Uygun et al. (1993)
Singhiella simplex (Singh)	30	15	15	27	27	USA	Legaspi et al. (2011)

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

NA not available

a Multiple host plants

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are very scarce; however, Reader and Southwood ([1984\)](#page-10-28) suggest that temperature did not strongly afect fight activity of *Aleurotuba jelinekii* (Frauenfeld). For most natural enemies, however, immature survival, fecundity, adult longevity and intrinsic rate of natural increase are maximised below 30 °C, and above this temperature the chance of population expansion drops signifcantly (Table [3\)](#page-7-0). Of course, the effects of diurnal temperature regimes could increase adaptability of these insects (Kingsolver et al. [2015](#page-10-29)). Hence, how a natural enemy responds to temperature increase will be a function of its life history traits in relation to the amount of environmental stress experienced (Qiu et al. [2004;](#page-10-25) Qiu et al. [2006](#page-10-30); Zandi-Sohani and Shishehbor [2011;](#page-11-14) Malekmohammadi et al. [2012\)](#page-10-31), which could either favour population build up or decline (Deutsch et al. [2008](#page-9-22); Youngsteadt et al. [2017](#page-11-15)). In line with this, biocontrol companies recommend temperatures between 21 and 29 °C for optimal performance of commercially available natural enemies. To ensure efficacy of their products, commercial producers of whitefy biocontrol products now combine more than one natural enemy. For instance, *En. formosa* is combined with *Er. eremicus* to harness the rapid population growth potential of *En. formosa* and high temperature tolerance of *Er. eremicus* (Biobest [2017\)](#page-8-10).

Host-natural enemy interactions are not linear or directly predictable due to complex species and environment interactions. Greenberg et al. [\(2000\)](#page-9-23) compared the life history of *Er. eremicus* and two host whitefies (*T. vaporariorum* and *B. tabaci* MEAM1), while Burnett [\(1949](#page-8-8)) compared the life history of *T. vaporariorum* and *En. formosa* under the same experimental conditions, respectively. Their results show that the parasitoids perform better than the whitefies at

higher temperatures (24–32 °C) for most of the traits tested. Similarly, Youngsteadt et al. ([2017\)](#page-11-15) compared the changes in abundance of whitefies, predators and parasitoids, and reported that parasitoids had higher abundance per °C urban warming compared to whitefies, while predators show lower response to warming compared to parasitoids and whitefies, respectively.

Insecticides have long been applied successfully in diverse environments from hot, irrigated desert regions to cool temperate regions. Although the toxicity of insecticides may be infuenced by temperature (Sparks et al. [1983;](#page-11-16) Boina et al. [2009;](#page-8-11) Glunt et al. [2014\)](#page-9-24), diurnal variations in temperature will still permit insecticide applications to be made within temperature ranges relevant to the functionality of the compounds. Moreover, compensatory feeding at elevated $CO₂$ levels would increase the consumption of insecticide (Coviella and Trumble [2000](#page-9-25)) and could therefore increase the efficacy of insecticides. However, climate change and faster population growth of whitefies may also increase insecticide application rates and associated costs of management with insecticides (Chen and McCarl [2001;](#page-9-26) Koleva and Schneider [2009](#page-10-32)). Climate change may also indirectly affect the efficacy of insecticides since periods suitable for spraying will likely increase with drier locations and decrease where it is wetter (Harrington et al. [2001\)](#page-9-27).

Cultural practices are commonly used as part of an overall strategy for whitefly management. Where efficient weather forecasting systems are available to farmers, changing planting date will remain an easy and efective tool to reduce pest pressure. However, climatic uncertainties may render this practice less useful (especially for small-holder farmers because of their limited use of weather information). The

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

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

greenhouse strategy (physical barrier) is to a large extent already in place in the new areas that might be invaded by whitefies, and will continue to be useful especially in intensive production systems if well managed and combined with other control methods. Phytosanitary measures, such as quarantine and the removal of weeds and crop residues, are widely used today and will continue to be useful since there are no indications that climate change will affect their effectiveness. Although constitutive and induced plant defences can be afected by climatic change due to changes in C:N ratio, which could in turn afect both synthesis and functioning of defence compounds (Zavala et al. [2013](#page-11-18)), there is insufficient evidence as to how this will influence resistance to whitefies. Even under current production conditions, insect pests and pathogens often develop mechanisms for breaking down host resistance. How climate change will afect whitefy resistance is unknown, although it will most probably be host-whitefy specifc. This topic presents an important opportunity for additional research.

Conclusion and future prospects

The study reviewed the impact of climate change on whitefies with the primary goal of identifying important trends for biological parameters. Among the new insights from our study is that while environmental stress tends to negatively afect life history, the efects difer with tolerance of the whitefies, amount of stress experienced (which is often related to habitat characteristics) and the host plant. Whitefies difer in their adaptability and adaptive strategies, and these will infuence their eventual response in terms of distribution and abundance with climate change. With climate change, better adapted species will likely experience increased distribution and abundance provided their tolerance limits are not exceeded, while species with lower tolerance and adaptation limits will sufer reduced ftness, which will have overall efects on their distribution and abundance in space and time. Most methods used to control whitefies will still be efective, especially if complementary methods are combined for maximum efficacy. Changes in climatic suitability modifying the distribution and abundance of whitefies and the environmental suitability for plant viruses will likely affect epidemics of viral diseases. Overall, the impacts of climate change on whitefies will show latitudinal or location specifcity, as reported for other insect species (Deutsch et al. [2008](#page-9-22); Bebber et al. [2013;](#page-8-6) Youngsteadt et al. [2017\)](#page-11-15). Although reduced climatic suitability and establishment risk of whitefies are predicted for some parts of the tropics, and temperature will remain a limiting factor to the distribution and abundance of whitefies in temperate regions (outside greenhouses), some regions will see population increases and whitefies will still continue to pose a threat to crop production (Gamarra et al. [2016a,](#page-9-17) [b](#page-9-10), [c](#page-9-18)). However, there are uncertainties associated with predicting the efects of climate change when considered locally in space and in time. Efects of single climatic factors on whitefies species are often not complementary and may be antagonistic (Table [1](#page-2-0)). The study also shows that the infuence of temperature (in comparison with other environmental variables) on whitefies has been given overwhelming attention probably due to its established importance in the biology of whitefies and other insects. Studying the infuence of multiple climatic factors simultaneously (Curnutte et al. [2014\)](#page-9-5) is an important further step in elucidating how climate change is likely to afect whitefies. Additionally, there is very little information currently available on how climate change will afect trophic interactions involving whitefies. The limited research that has been done suggests that climate change impacts may be signifcant or negligible depending on the host, whitefly and factors considered (Tripp et al. [1992](#page-11-23); Cui et al. [2012](#page-9-6); Wang et al. [2014\)](#page-11-4). More research insights addressing the effect of single or multiple factors on trophic interactions of whitefies will significantly contribute to our knowledge of whitefly biology and will help in the design of robust future management guidelines.

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

Acknowledgements The study was funded by the Education, Audiovisual and Culture Executive Agency of the European Commission through the Erasmus Mundus Joint Doctorate Fellowship (Agricultural Transformation by Innovation programme) awarded to Aregbesola Z Oluwatosin. The contribution of Dr. James Legg was supported through the Roots, Tubers and Bananas (RTB) Programme of the CGIAR.

Authors' contribution CR, OSL, JPL secured the funding for the study, AOZ, CR, JPL, OSL, LS designed the study, AOZ, JPL, OSL, LS wrote the manuscript, all authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest The authors (AOZ, CR, JPL, OSL, LS) declare that there is no confict of interest.

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

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

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