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

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KEY MESSAGE

- An in-depth review was conducted to address the weak current understanding of the potential influence of climate change on whiteflies.
- 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 circumstances.
- Future efforts to manage whiteflies must be cognisant of the complex effects of climate on the agro-ecological systems inhabited by these globally important insects.

ABSTRACT

Whiteflies (Hemiptera: Aleyrodidae) are important insect pests causing serious damage to plants and transmitting hundreds of plant viruses. Climate change is expected to influence life history and trophic interactions among plants, whiteflies, and their natural enemies. Here, we review the potential impacts of climate change on whiteflies and the likely consequences for agricultural systems. This review concludes that while climatic stress tends to negatively affect life history traits, the effects differ with the tolerance of the whiteflies and the amount of stress experienced. Whiteflies also differ 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 suffer reduced fitness, which will have overall effects on their distribution and abundance in space and time. The majority of methods used to control whiteflies 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 whiteflies, and environmental suitability for plant viruses, will likely affect epidemics of viral diseases. Greater efforts are required to improve understanding of the complex effects of climate change on multi-species and multi-trophic interactions in the agro-ecological systems inhabited by whiteflies, and to use this new knowledge to develop robust and climate-smart management strategies.

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

INTRODUCTION

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

2011). 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; Tzanetakis et al. 2013; Polston et al. 2014). Crop damage due to plant viruses transmitted by whiteflies globally results in losses worth more than $US 1 billion (Gonzalez et al. 1992; Legg et al. 2006).

The Intergovernmental Panel on Climate Change (IPCC) fifth 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 21st century (IPCC 2013). 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 20th century, and the third year in a row to set a new record high temperature (NASA 2017). Global CO_2 concentration is the primary driver of the recent anthropogenic climate change. While the global concentration of CO_2 in the atmosphere reached 400 parts per million (ppm) for the first time in recorded history in 2013, the trend has continued, with the 2016 estimate at 404.4 ppm (NASA 2013, 2016).

Climatic change is affecting agricultural and natural ecosystems, and directly affects the development, reproduction, survival, population dynamics, potential distribution and abundance of whitefly species (Muñiz and Nombela 2001; Bonato et al. 2007; Bellotti et al. 2012; Gilioli et al. 2014). Some studies have reported direct effects of temperature (Xie et al. 2011; Guo et al. 2013; Han et al. 2013), CO_2 (Koivisto et al. 2011; Curnutte et al. 2014), and O_3 (Cui et al. 2012, 2014) on life history traits. Others have discussed effects of rainfall (Castle et al. 1996; Naranjo and Ellsworth 2005; Naranjo et al. 2009; Sharma and Yogesh 2014) on whiteflies.

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

HOW WILL WHITEFLIES 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 different whiteflies and host plants to changes in climatic factors are summarised in Table 1. Temperature and host-plant effects have been identified as important factors affecting development, mortality and fecundity rates in whitefly populations. Temperature increase within the thermal optimum leads to a decrease in developmental time (Madueke and Coaker 1984; Sengonca and Liu 1999; Muñiz and Nombela 2001; Nava-Camberos et al. 2001; Bayhan et al. 2006; Bonato et al. 2007; Xie et al. 2011; Han et al. 2013). 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; Xie et al. 2011; Guo et al. 2013) and decreasing longevity (Sengonca and Liu 1999; Bonato et al. 2007; Guo et al. 2013). Elevated CO_2 and O_3 increased developmental time of whiteflies (Cui et al. 2012; Wang et al. 2014), but elevated CO_2 did not affect adult longevity (Koivisto et al. 2011; Curnutte et al. 2014) and fecundity of whiteflies (Curnutte et al. 2014; Wang et al. 2014). There is a dearth of information regarding the effects of elevated O_3 on whitefly longevity and fecundity (Table 1).

In nature, insects often experience stressful temperatures (high and low) that may affect not only their life history, but also their distribution and abundance (Cui et al. 2008; Lü et al. 2014b). 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 defining the distribution of most insects, which may have further implications in the face of global climate change (Bowler and Terblanche 2008; Cui et al. 2008; Ma et al. 2014). There is an increasing number of empirical studies on thermotolerance and its associated evolutionary implications in whiteflies. Traits commonly investigated are survival, fecundity and viability of the offspring after heat shock.

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

In some cases, significant differences in thermotolerance have been reported among populations experiencing different levels of environmental stress, pointing towards adaptive divergence (Diaz et al. 2014; Ma et al. 2014). For instance, Diaz et al. (2014) 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) also demonstrated that differences in habitat temperature resulted in significant differences 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). Elbaz et al. (2011) showed that *B. tabaci* MEAM1 and MED deploy different 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 beneficial to somatic maintenance. In another interesting study, Lü et al. (2014b) highlighted the significance 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) 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 fitness and thermal stress could influence 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 influence the life history and response of whiteflies to climate change. For instance, adaptation to one environmental stress (insecticides like thiamethoxam) increased thermotolerance in *B. tabaci* MEAM1 (Su et al. 2017) which could be beneficial to *B. tabaci* MEAM1 in the light of climate change. Absence of secondary endosymbionts in cassava-colonising whiteflies increased their fitness and vector abilities, and a possible ecosystem service in suppressing populations of cassava-colonising whiteflies has been proposed (Ghosh et al. 2018). Nutrition and defensive chemistry of host plants (Jiao et al. 2018) could also influence the response of whiteflies 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). Generally, rainfall has been noted to negatively affect populations of *B. tabaci* (Naranjo and Ellsworth 2005; Sharma and Yogesh 2014). Using sprinkler irrigation to simulate rainfall, Castle et al. (1996) found a consistent reduction in densities of immature whiteflies. 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). Experiments considering prolonged exposure to constant temperatures and brief exposure to heat shock agree that elevated temperatures (above the optimum threshold of whiteflies) negatively affect life history of whiteflies. However with climate change, high thermotolerance and the polyphagous nature of some whiteflies (*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; EFSA 2013; Gilioli et al. 2014; Gamarra et al. 2016b). By combining general circulation models (GCMs) with a stochastic weather generator and population dynamics models, Zidon et al. (2016) 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 sub-tropical regions respectively, under current temperature conditions, while *T. vaporariorum* can have up to 11 generations per year (Gamarra et al. 2016a, c). 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 sub-tropical 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). 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).

Increases in the number of generations do not necessarily translate into range expansion or elevated whitefly 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 affected (Qui et al. 2003; Bonato et al. 2007). 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, b, c) 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 finite 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 sub-tropical regions. However, the abundance of *B. afer* will potentially increase in southern sub-tropical and temperate zones (Gamarra et al. 2016a). For *B. tabaci* MEAM1, a small increase in potential growth is predicted for most tropical and sub-tropical regions. *B. tabaci* MEAM1 populations will possibly reduce along the Equator as temperature increases (Gamarra et al. 2016c). Furthermore, based on the activity index and generation index available in the Insect Life Cycle Modelling software used by Gamarra et al. (2016a, b, c), 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). Using the Physiologically Based Demographic Model, Gilioli et al. (2014) 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 whiteflies 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). 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 whitefly species. Ecological niche models which generate maps of a species' environmental suitability based on its current distribution (e.g Campos et al. 2011; Jarvis et al. 2012; Bellotti et al. 2012), and insect physiology based models (e.g Gilioli et al. 2014; Gamarra et al. 2016a, b, c; Aregbesola 2018) 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 whiteflies. 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). *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) 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). A similar trend is predicted for Central African Republic, Ethiopia and Cameroon (Jarvis et al. 2012) and southern India (Campos et al. 2011). There will also be more *B. tabaci* further south, in regions where there is a cool and dry winter (Bellotti et al. 2012; Aregbesola 2018). According to Gamarra et al. (2016a, b), 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 sub-tropical 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, b).

Since virus transmission by whiteflies is mainly mediated by *B. tabaci* and *T. vaporariorum*, any change in the distribution of these vectors may affect the overall geography of viral diseases. Populations of *B. tabaci* are distributed in tropical and sub-tropical 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) although local patterns of seasonal temperature, precipitation and altitude appear to play an important role (Morales and Jones 2004). Sporadic records of viruses from greenhouse plants in cooler climates most likely reflect the importation of infected plant material and not *per se* the natural spread of viruses (Botermans et al. 2009). 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). 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 field-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). The same regions are characterised by year-round outdoor cultivation of tomato (main virus host) and the presence of populations of *B. tabaci* (EFSA 2013; Gilioli et al. 2014). 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 significant local variations due to local topography. The spread of TYLCV in open fields is expected to follow the same pattern.

Efficacy of management strategies

Evidence from Wang et al. (2014) indicates that the biological control of *B. tabaci* by *Encarsia formosa* (Gahan) would not be influenced by transgenic Bt cotton and/or elevated CO_2. Cui et al. (2014) suggest that elevated O_3 enhanced the attraction of *En. formosa* to whiteflies 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 whiteflies. Furthermore, it has been experimentally confirmed that parasitism and predation rates of whitefly natural enemies could increase with temperature within the optimum ranges of the natural enemies as in the case of *En. formosa* (Burnett 1949; Enkegaard 1994; Qui et al. 2004; Zilahi-Balogh et al. 2006), *Eretmocerus eremicus* (Rose & Zolnerowich) (Qui et al. 2004), *Er. mundus* (Mercet) (Qui et al. 2004), *Eretmocerus* spp. (McCutcheon and Simmons 2001), *Delphastus catalinae* (Horn) (Simmons and Legaspi 2004) and *Nesidiocoris tenuis* (Reuter) (Madbouni et al. 2017). Similarly, walking speed, walking activity and flight activity of whitefly natural enemies have been shown to be positively correlated with temperature (van Roermund and van Lenteren 1995; Bonsignore 2016), while handling time decreases with temperature increase (Enkegaard 1994; Madbouni et al. 2017). Comparable studies on the impact of temperature on walking pattern and flight activity of whitefly are very scarce; however, Reader and Southwood (1984) suggest that temperature did not strongly affect flight 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 significantly (Table 3). Of course, the effects of diurnal temperature regimes could increase adaptability of these insects (Kingsolver et al. 2015). 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 (Qui et al. 2004; Qui et al 2006; Zandi-Sohani and Shishehbor 2011; Malekmohammadi et al. 2012), which could either favour population build up or decline (Deutsch et al. 2008; Youngsteadt et al. 2016). In line with this, biocontrol companies recommend temperatures between 21 – 29 °C for optimal performance of commercially available natural enemies. To ensure efficacy of their products, commercial producers of whitefly 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).

Host-natural enemy interactions are not linear or directly predictable due to complex species and environment interactions. Greenberg et al. (2000) compared the life history of *Er. eremicus* and two host whiteflies (*T. vaporariorum* and *B. tabaci* MEAM1), while Burnett (1949) 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 whiteflies at higher temperatures (24 – 32 °C) for most of the traits tested. Similarly, Youngsteadt et al. (2016) compared the changes in abundance of whiteflies, predators and parasitoids, and reported that parasitoids had higher abundance per °C urban warming compared to whiteflies, while predators show lower response to warming compared to parasitoids and whiteflies 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 influenced by temperature (Sparks et al. 1983; Boina et al. 2009; Glunt et al. 2014), 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 CO_2 levels would increase the consumption of insecticide (Coviella and Trumble 2000) and could therefore increase the efficacy of insecticides. However, climate change and faster population growth of whiteflies may also increase insecticide application rates and associated costs of management with insecticides (Chen and McCarl 2001; Koleva and Schneider 2009). 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).

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 effective 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 greenhouse strategy (physical barrier) is to a large extent already in place in the new areas that might be invaded by whiteflies, 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 affected by climatic change due to changes in C:N ratio, which could in turn affect both synthesis and functioning of defence compounds (Zavala et al. 2013), there is insufficient evidence as to how this will influence resistance to whiteflies. Even under current production conditions, insect pests and pathogens often develop mechanisms for breaking down host resistance. How climate change will affect whitefly resistance is unknown, although it will most probably be host-whitefly specific. This topic presents an important opportunity for additional research.

CONCLUSION AND FUTURE PROSPECTS

The study reviewed the impact of climate change on whiteflies 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 affect life history, the effects differ with tolerance of the whiteflies, amount of stress experienced (which is often related to habitat characteristics) and the host plant. Whiteflies differ in their adaptability and adaptive strategies, and these will influence 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 suffer reduced fitness, which will have overall effects on their distribution and abundance in space and time. Most methods used to control whiteflies will still be effective, especially if complementary methods are combined for maximum efficacy. Changes in climatic suitability modifying the distribution and abundance of whiteflies and the environmental suitability for plant viruses will likely affect epidemics of viral diseases. Overall, the impacts of climate change on whiteflies will show latitudinal or location specificity, as reported for other insect species (Deutsch et al. 2008; Bebber et al. 2013; Youngsteadt et al. 2016). Although reduced climatic suitability and establishment risk of whiteflies is predicted for some parts of the tropics, and temperature will remain a limiting factor to the distribution and abundance of whiteflies in temperate regions (outside greenhouses), some regions will see population increases and whiteflies will still continue to pose a threat to crop production (Gamarra et al. 2016a, b, c). However, there are uncertainties associated with predicting the effects of climate change when considered locally in space and in time. Effects of single climatic factors on whiteflies species are often not complementary and may be antagonistic (Table 1). The study also shows that the influence of temperature (in comparison to other environmental variables) on whiteflies has been given overwhelming attention probably due to its established importance in the biology of whiteflies and other insects. Studying the influence of multiple climatic factors simultaneously (Curnutte et al. 2014) is an important further step in elucidating how climate change is likely to affect whiteflies. Additionally, there is very little information currently available on how climate change will affect trophic interactions involving whiteflies. The limited research that has been done suggests that climate change impacts may be significant or negligible depending on the host, whitefly and factors considered (Tripp et al. 1992; Cui et al. 2012; Wang et al. 2014). More research insights addressing the effect of single or multiple factors on trophic interactions of whiteflies 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 whitefly threat that may result from climate change will depend heavily on improving understanding of the complex interactions between whitefly species, host plants, natural enemies and the components of climate change that will affect them in each of the world's major agro-ecological zones. A varied set of control tactics for whiteflies 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 effectively in the dynamic new agricultural environment that is emerging as humans continue to modify the world. This is a challenge of global significance, but certainly one that can be resolved if addressed with appropriate levels of investment, leading to a more sustainable, food secure future.

CONTRIBUTIONS

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

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest: The authors (AOZ, CR, JPL, OLS, LS) declare that there is no conflict 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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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				
B. tabaci MEAM1	Eggplant, Tomatoes,	Temperature increase	-	20 – 32[a]	USA; China; China	*Wang and Tsai 1996; Qui et al. 2003; Guo et al. 2013
B. tabaci MED	Tomatoes	Temperature increase	-	21 – 35	France	Bonato et al. 2007
T. vaporariorum	Kidney bean, *Brassica* spp.	Temperature increase	-	19 – 26; 15-24	Colombia; China	Manzano and Lenteren 2009; Xie et al. 2011
B. tabaci MEAM1	*Brassica* spp.	Temperature increase	+	15 – 24	China	Xie et al. 2011
T. vaporariorum	Tomatoes	Elevated CO_2	-	400 – 1200	Finland	Koivisto et al. 2011
B. tabaci MEAM1	Collard, Cotton	Elevated CO_2	0	424 – 753; 375 – 750	USA; China	Curnutte et al. 2014; Wang et al. 2014
B. tabaci MEAM1	Tomatoes	Elevated ozone	-	37.3 – 72.2***	China	Cui et al. 2012
		Immature developmental time				
B. tabaci MEAM1 and MED	Sweet pepper	Temperature increase	-	17 – 33	Spain	Muñiz and Nombella 2001
B. tabaci MED	Tomatoes, Sweet pepper, Eggplant and Oriental melon	Temperature increase	-	15 – 30	France; Korea	Bonato et al. 2007; Han et al. 2013
T. vaporariorum	Greenhouse crops	Temperature increase	-	18 – 27	England	Madueke and Coaker 1984
B. tabaci 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
Aleurotuberculatus takahashi (David et Subramaniam)	Citrus	Temperature increase	-	15 – 35	China	Sengonca and Liu 1999
B. tabaci MEAM1 and *T. vaporariorum*	*Brassica* spp.	Temperature increase	-	15 – 24	China	Xie et al. 2011
Bemisia afer (Priesner and Hosny)	Sweet potato	Temperature increase	-	17 – 25		Gamarra et al. 2016a
B. tabaci MEAM1	Cotton	Elevated CO_2	+	375 –750	China	Wang et al. 2014
B. tabaci MEAM1	Tomatoes	Elevated ozone	+	37.3 – 72.2***	China	Cui et al. 2012
		Adult longevity				
B. tabaci MEAM1	Eggplant, Tomatoes	Temperature increase	-	20 – 32^{c}	China; USA; China	Qui et al. 2003; *Wang and Tsai 1996; Guo et al. 2013
A. takahashi	Citrus	Temperature increase	-	15 – 35	China	Sengonca and Liu 1999
B. tabaci MED	Tomatoes	Temperature increase	-	21 – 35	France	Bonato et al. 2007
T. vaporariorum	Kidney bean	Temperature increase	-	19 – 26	Colombia	Manzano and Lenteren 2009
B. afer	Sweet potato	Temperature increase	-	17 – 28	Philippines	Gamarra et al. 2016a
T. vaporariorum	Tomatoes	Elevated CO_2	0	400 – 1200	Finland	Koivisto et al. 2011
B. tabaci 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, CO_2 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
B. tabaci MEAM 1	29 °C	26 °C	20 °C	20 °C	29 °C	China	Qui et al. 2003
B. tabaci MEAM 1	35 °C	NA	20 °C	25 °C	30 °C	China	Yang and Chi 2006
B. tabaci MED	30 °C	25 °C	17 °C	21 °C	30 °C	France	Bonato et al. 2007
B. tabaci MED	27.5 &30 °C *	27.5 – 32.5 °C *	NA	NA	NA	Korea	Han et al. 2013
T. vaporariorum	24 °C	NA	18 °C	18 °C	NA	China	Xie et al. 2011
T. vaporariorum	26 °C	19 °C	19 °C	22 °C	19&22 °C *	Colombia	Manzano and Lenteren 2009
A. takahashi	35 °C	15 °C	15 °C	25 °C	NA	China	Sengonca and Liu 1999
Parabemisia myricae (Kuwana)	30 °C	25±1 °C	15±1 °C	25±1 °C	NA	Turkey	Uygun et al. 1993
Singhiella simplex (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							
En. formosa	28 °C	22 °C	16 °C	28 °C	28 °C	Germany	Enkegaard 1993
En. formosa	32 °C	NA	15 °C	NA	NA	USA	Qui et al. 2004
En. inaron (Walker)	30 °C	25 °C	20 °C	25 °C	25 °C	Iran	Malekmohammadi et al. 2012
En. bimaculatus (Heraty and Polaszek)	32 °C	26 °C	20 °C	29 °C	29 °C	China	Qui et al 2006
En. acaudaleyrodis (Hayat)	32°C	25 °C	20 °C	25 °C	25 °C	Iran	Zandi-Sohani and Shishehbor 2011
Er. eremicus (Rose & Zolnerowich)	32 °C	NA	15 °C	NA	NA	USA	Qui et al. 2004
Er. sp. Nr. furuhasii (Rose & Zolnerowich)	29 °C	26 °C	20 °C	26 °C	29°C	China	Qui et al. 2007
Er. mundus (Mercet)	30 °C	25 °C	20 °C	25 °C	30 °C	Iran	Zandi-Sohani et al. 2009
Er. mundus (Mercet)	32 °C	NA	15°C	NA	NA	Italy	Qui et al. 2004
Predators							
Serangium japonicum (Chapin)	32 °C	26 °C	20 °C	26 °C	29 °C	China	Yao et al. 2011
Axinoscymnus cardilobus (Ren and Pang)	29 – 32 °C	23 °C	17 °C	23 °C	23 °C	China	Huang et al. 2008
A. apioides (Kuznetsov and Ren)	29 °C	26 °C	20 °C	23 °C	26 °C	China	Zhou et al. 2017
Clitostethus brachylobus	29 °C	26 °C	17 °C	26 °C	26 °C	China	Deng et al. 2016
C. arcuatus (Rossi)	30 °C	25 °C	15 °C	20 °C	30 °C	Portugal	Mota et al. 2008
Nephaspis oculatus (Blatchley)	33 °C	26 °C	20 °C	26 °C	26 °C	USA	Ren et al. 2002