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Life history and temperature-dependence of cassava-colonising populations of *Bemisia tabaci*

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Abstract

The whiteflies belonging to the species group *Bemisia tabaci* transmit viruses that are the greatest constraint to the production of cassava, Africa's most important food security crop. We studied the life history of an endemic African population of *B. tabaci* SSA-ESA at six constant temperatures (16, 20, 24, 28, 32, 36 °C) in controlled environment chambers, and for 10 generations in the field. Oviposition occurred between 20 and 28 °C, with highest fecundity (114.5 ± 88.2) eggs per female at 20 °C. Similarly, *B. tabaci* adult females average survival time was longest (19.7 days) at 24 °C, and shortest (8.5 days) at 36 °C. Immature development time decreased with increasing temperature from 59.3 days at 16 °C to 16.3 days at 28 °C, and increased above 28 °C. A constant temperature of 36 °C was lethal to eggs and first instars and no immature stage developed further to adults at this temperature. Several temperature-driven models were fitted for describing the species development, survival and reproduction using Insect Life Cycle Modelling (ILCYM®) software. Median temperature-dependent development rates in individual immature life stages were statistically described by Taylor, Brière 1 and Tb (Logan) models. Temperature-dependent mortality and senescence rates in immature stages were described by using parabolic nonlinear models. The longevity of adult females and oviposition time was best described by the Weibull distribution. Maximum population growth was predicted between 26 and 28 °C. These results will be useful for spatio-temporal analysis of climate change impacts on the distribution and abundance of this pest.

Keywords *B. tabaci* · Life history · Africa · Temperature-dependence · Cassava · ILCYM

Key message

- We present a comprehensive study on temperature-dependence of life history traits of a cassava-colonising and endemic African population of *Bemisia tabaci* combining laboratory and field experiments.
- Maximum growth for *B. tabaci* SSA-ESA was predicted to be between 26 °C and 28 °C, meaning that although climate change associated temperature increase may lead to increase abundance in some regions, extreme temperatures will be unfavourable.
- The results will be useful for pest risk mapping, epidemiological modelling of transmitted viruses and climate change adaptation planning.

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Introduction

Bemisia tabaci (Hemiptera: Aleyrodidae) is a cosmopolitan insect pest that causes crop losses through phloem feeding and induction of sooty moulds that reduce photosynthesis (Oliviera et al. 2001). However, the most important economic damage caused by *B. tabaci* results from its capacity to transmit several debilitating plant viruses, which drive plant disease epidemics globally. Annual losses due to viruses transmitted by *B. tabaci* on cassava in Africa are more than $US 1 billion (Legg et al. 2006).

Bemisia tabaci is a species complex with at least 34 morphologically indistinguishable species that occur on several host crops (Dinsdale et al. 2010; De Barro et al. 2011; Firdaus et al. 2013; Lee et al. 2013; Legg et al. 2014). Two distinct categories of *B. tabaci* occur widely in sub-Saharan Africa, the cassava-colonising and the non-cassava-colonising species (Wosula et al. 2017). Cassava-colonising *B. tabaci* in Africa comprises six major genetic groups, namely sub-Saharan Africa 2 (SSA2), SSA4, SSA-Central Africa (SSA-CA), SSA-East and Central Africa (SSA-ECA), SSA-East and Southern Africa (SSA-ESA) and SSA-West Africa (SSA-WA) (Wosula et al. 2017). Although several of these groups have been thought to comprise distinct species, evidence obtained from > 7000 SNP markers occurring throughout the genome demonstrates that all are linked together through gene transfer (Wosula et al. 2017; Chen et al. 2019). This suggests that although these groups may be in the process of evolutionary divergence, they are currently not reproductively isolated.

Projections from all assessed climate change scenarios indicate that global surface temperature will rise over the twenty-first century (IPCC 2013), with consequences for pest management (Porter et al. 1991; Bale et al. 2002; Gilioli et al. 2014). Temperature-dependent impacts on the life history of members of the *B. tabaci* species complex have been reported, especially for *B. tabaci* MEAM1 (Wang and Tsai 1996; Qui et al. 2003; Yang and Chi 2006; Bayhan et al. 2006; Xie et al. 2011; Guo et al. 2013) and MED (Bonato et al. 2007; Tsueda and Tsuchida 2011; Han et al. 2013). A review of the climate impacts literature by Aregbesola et al. (2019) suggested that these would differ depending on the life history traits of the *B. tabaci* genotype, host plants and geographical locations (Nava-Camberos et al. 2001; De Barro et al. 2011; Tsueda and Tsuchida 2011).

Precise knowledge of the life history and temperature-dependence of *B. tabaci* is necessary for us to understand its population dynamics under current and future climate change scenarios. Furthermore, development of robust pest management programmes and climate change adaptation planning for *B. tabaci* must be based on a detailed understanding of the biology of the species. Despite the amount of available information on some *B. tabaci* species, there is almost no published information about temperature effects on endemic African populations. The objectives of this study were therefore to determine the effects of temperature on the reproductive performance and developmental characteristics of *B. tabaci* SSA-ESA, through natural and controlled temperature experiments. The results of the study were compared to data published on *B. tabaci* temperature-dependent development, and dissimilarities among *B. tabaci* genotypes feeding on different host plants are discussed. The results will provide essential baseline data for predicting the potential population change of field populations as well as their seasonal variation in different agroecologies in Africa.

Materials and methods

Whitefly culture

The *B. tabaci* colony used in these experiments was initiated with whiteflies collected from cassava at the Agricultural Research Station of the Tanzania Ministry of Agriculture at Chambezi, Bagamoyo, Tanzania. The colony was maintained on cassava for > 8 generations in screen-cages in the screen-house facility at IITA, Dar es Salaam, Tanzania. The *B. tabaci* colony was shown to have the mtDNA haplotype of SSA1-SG3 by sequencing the mitochondria cytochrome oxidase I gene (*mtCOI*) of adult females, as described by Frohlich et al. (1999). All individuals of SSA1-SG3 from the colony were subsequently shown to belong to genotype SSA-ESA, based on genome-wide SNPs analysis (Wosula et al. 2017).

Host plants

Virus-free cassava material (cv. Albert) collected from IITA's cassava seed programme was used in the experiments. The material was tested for *Ugandan cassava brown streak virus* (UCBSV) and *Cassava brown streak virus* (CBSV) using the method described by Shirima et al. (2017), and for *East African cassava mosaic virus* (EACMV) using the method described by Firaol (2013) and were confirmed virus-free. Cassava plants for the experiments were raised in plastic pots for about 4–5 weeks in the screen-house.

Development and survival of *B. tabaci* at constant temperatures in the laboratory

For this experiment, two clip-cages (height 3.6 cm and diameter 3.4 cm) were used per plant, and 6–10 pairs of adult *B.*

tabaci were confined in each clip-cage on 6 potted cassava plants for oviposition to take place at ambient conditions. After 24 h of oviposition, the pairs of *B. tabaci* were carefully removed from the leaves and plants were transferred to climatic chambers (Percival® PGC-6L) set at six constant temperatures of 16 °C, 20 °C, 24 °C, 28 °C, 32 °C and 36 °C, with RH of 65 ± 5%, and a 12L: 12D diurnal light regime.

On each leaf, six eggs were marked (twelve eggs were marked on two leaves) with a fine tip non-toxic Sharpie® marker and all unmarked eggs were removed. Immature life stages were identified using the illustrative guides provided by J. P. Legg (unpublished work), and as described by Gill (1990) and Gelman et al. (2002). In brief, eggs were identified as creamy and ovoid which gradually turn dark brown over time. First to fourth nymphal instars were identified based on their relative shapes and sizes, while the pupa stage (sometimes referred to as the fourth nymphal instar) was identified by the characteristic red eye. Change from one nymphal instar to the next is characterised by a moult, which is coupled with a sudden change in size and shape compared to the previous assessment. Adult emergence was confirmed by viewing an empty pupal case with a T-shaped slit.

Development and survival of *B. tabaci* under field conditions

In order to compare *B. tabaci* development and survivorship under field conditions with those recorded in the laboratory, *B. tabaci* life stages were monitored on field-planted cassava at the IITA station in Dar es Salaam. About 30–45 pairs of adult *B. tabaci* were confined on one of the top four cassava leaves with glass clip-cages for oviposition to take place. *B. tabaci* were removed after a 24-h-oviposition period to provide an even-aged cohort. About 20–30 eggs were marked per plant with a fine tip non-toxic Sharpie® marker, and 10–14 plants were used in each generation. A fine camel brush was used to remove all unmarked eggs. All marked individuals were monitored daily using a × 60 hand lens. Plants bearing marked eggs were tagged for ease of subsequent data collection. In the field experiments, *B. tabaci* was monitored over 10 generations from May, 2016 to April, 2017. Individuals of each single cohort were monitored through all life stages (egg to adult emergence) and data on development and survival were recorded for each individual daily. Weather data (temperature and RH) were monitored at hourly intervals using a Hobo data logger (Onset data logger, USA) positioned on the study site.

Fecundity and longevity under laboratory and field conditions

Sub-colonies of *B. tabaci,* reared under the same conditions described above, provided a steady supply of newly emerged adult whiteflies. The peak period of *B. tabaci* emergence is in the morning. Newly emerged *B. tabaci* were collected in the morning between 0800 and 1000 h. They were identified by the creamy colour which is apparent before the deposition of the whitish wax on their wings. Newly emerged whiteflies were collected from older cassava leaves towards the base of plants where these whiteflies are more abundant. The sexes of the whiteflies were identified in the laboratory using a stereo microscope. Females are slightly bigger than males and have a blunt rounded abdomen, whilst males have a pointed abdomen (Byrne and Bellows 1991).

A pair (one male and one female) of newly emerged *B. tabaci* were confined on cassava plants using glass clip-cages at ambient conditions before transferring the cassava plants with the clip-cages either to the climatic chambers, which were set at six constant temperatures, or to the field. To reduce the influence of leaf ageing on egg production and accumulation of sooty moulds, whiteflies were moved with the clip-cages every 2 days to a new leaf until their death. Both field and temperature-controlled experiments were conducted with 30–45 pairs of *B. tabaci* (replicates). Data on number of eggs laid per female and longevity of both males and females were collected daily.

Data analysis and modelling

Data analysis and modelling studies were conducted using the ILCYM software package (version 4), which is an open-source software developed by the International Potato Center (CIP), Lima, Peru. It is available for download at https://research.cip.cgiar.org. Life-table data collected at constant temperatures including data on developmental time of all immature stages, adult longevity of both males and females, and fecundity of adults were used for studying temperature-dependence using the modelling module of ILCYM version 4.0. The package uses R-statistics (R Development Core Team 2011) for all statistical calculations.

Development time, adult longevity and oviposition time

Data on immature development, adult male and female senescence and oviposition time were subjected to survival analyses. ILCYM uses the survreg procedure which fits a parameter to survival regression model. These are location-scale models for arbitrary transformation of the time variable; the most common cases use a log transformation, leading to accelerated failure time models (Therneau 2020). A distribution link function, either log-normal, log-logistic or Weibull, was selected for each life stage based on maximum likelihood.

The models were fitted at different levels of complexity; that is, data were grouped by (1) temperature (default model),

and (2) insect batches (replications per temperature in time). These models were evaluated using a likelihood ratio test and by comparing Akaike's information criterion (AIC) (Akaike 1973).

Development, immature mortality and oviposition rates

The relationships between temperature and development, mortality, oviposition rates and total fecundity per female were analysed with nonlinear regression using the values of median immature development time, adult longevity and fecundity that resulted from the AFT models for each insect batch (replications at different temperatures). Several in-built nonlinear models that describe the influence of temperature on each life history trait were tested. For a list of temperature-dependent models used by ILCYM, see the user manual at https://research.cip.cgiar.org/confluence/display/ilcym/ILCYM+manual. Immature survivorship was computed from the relative proportion of surviving test insects for each batch per temperature treatment. The best models describing temperature effects on these processes were selected according to AIC.

Estimation of life-table parameters

The method of Sporleder et al. (2016) that employs an approximate estimate for mean generation time (T) was used to simulate life-table parameters from the established phenology model considering a range of constant temperatures. An initial number of 100 individuals was used, and the "simulation" module of ILCYM was used to simulate life-table parameters. Life-table parameters evaluated included: mean generation time (T), doubling time (D_t), net reproduction rate (Ro), intrinsic rate of natural increase (r_m) and finite rate of increase (k). The simulations used a cohort updating algorithm in 1-day time steps in which within-day temperature variability was taken into consideration using a 15-min discrete time increment. A cosine-wave function describing the minimum and maximum temperature input data was used to predict temperature at each interval (Sporleder et al. 2013). A combination of temperature-dependent development rate functions selected for each life stage and the distribution link function with its shape parameter revealed by the AFT model was used to calculate the proportion of insects within each cohort that developed to the next life stage. Details of equations used are also presented in Sporleder et al. (2016).

Results

Development time at constant temperatures

Variations in development times among individuals of *B. tabaci* without considering the effect of temperature (henceforth referred to as fixed variation) were best described by log-logistic distribution functions in all immature life stages and instars (revealed by AFT model, see Tables 1, 2). *B. tabaci* SSA-ESA successfully developed from the egg to adult stage between 16 and 32 °C. Development duration was longest in the egg stage. Development rates in immature life instars increased with increasing temperature between the ranges of 16–28 °C. Above 28 °C, development rates decreased with increasing temperature in most nymphal instars (Tables 1, 2, Fig. 1). The total development duration from egg to adult emergence was 59.3 (± 1.32) days at 16 °C, 38.9 ± 0.47 days at 20 °C, 28.2 ± 0.22 days at 24 °C, 16.3 ± 0.6 at 28 °C and 25.1 ± 0.3 days at 32 °C. At 36 °C, the whitefly did not complete development; all test insects died during the first and second nymphal instars.

The relationship between temperature and median development rates in individual immature life stages were statistically best described by the Taylor model (Taylor 1981) (egg stage), the Brière model (Brière et al. 1999) (first, second and pupal instars) and the Logan Tb model (Logan et al. 1976) (third and fourth nymphal instars) (Table 3, Fig. 1). These models suggest an upper temperature threshold for development at around 35 °C and an lower temperature threshold in the range between 8 and 10 °C (see Fig. 1). The temperature thresholds revealed by the parameter T_{max} and T_0 in the Brière model are also in these temperature ranges.

Development time under field conditions

For field experiments, increasing average temperature reduced immature development time across *B. tabaci* generations ($r = -0.840$, $p = 0.009$). Immature development was slowest at the egg stage where the eggs needed an average of 5.5–8.2 days to hatch. In contrast, development at the second instar stage was fastest where it took 2.0–2.9 days for the insects to complete development. Overall, development duration ranged from 18 days (one of the hottest months—March) to 25 days (the coolest month—July). *B. tabaci* SSA-ESA required an average of 21.3 days to complete development from egg to adult under field conditions in Dar es Salaam, Tanzania, where average temperature and relative humidity were 28 °C and 78%, respectively (Supplementary 2).

Table 1 Median development times resulting from accelerated failure time modelling and observed survival rates (egg to second instar)

Temp (°C)	Egg				First instar				Second instar			
	N[1]	Median dev. time (days)[3]		Survival (%)	N	Median dev. time (days)[C]		Survival (%)	N	Median dev. time (days)[C]		Survival (%)
16	399 (5)	19.2 (±0.47)	a	54.9 (±2.5)	219	10.5 (±0.62)	a	43.8 (±3.4)	96	7.8 (±0.44)	a	76 (±4.4)
20	399 (5)	12.2 (±0.38)	b	77.2 (±2.1)	308	5.4 (±0.38)	b	71.1 (±2.6)	219	4.7 (±0.31)	b	82.6 (±2.6)
24	343 (3)	8.9 (±0.28)	c	83.1 (±2)	285	4.3 (±0.3)	b	84.9 (±2.1)	242	3 (±0.19)	c	97.5 (±1)
28	344 (3)	6.5 (±0.2)	d	83.7 (±2)	288	3 (±0.22)	c	68.4 (±2.7)	197	2.3 (±0.16)	c	96.4 (±1.3)
32	422 (5)	5.5 (±0.16)	e	88.4 (±1.6)	373	3 (±0.21)	c	82 (±2)	306	2.7 (±0.18)	c	85.3 (±2)
36	221 (2)	5.6 (±0.46)	de	8.1 (±1.8)	18	5.7 (±2.77)	abcd	5.6 (±5.4)	1	–		
Scale[2]	$\delta =$	0.0659 (±0.0043)***			$\delta =$	0.138 (±0.0091)***			$\delta =$	0.1595 (±0.0084)***		
Model[4]		Likelihood ratio test				Likelihood ratio test				Likelihood ratio test		
		ln L	df	F (df_x, df_{x-1})		ln L	df	F (df_x,df_{x-1})		ln L	df	F (df_x,df_{x-1})
Intercept only		− 4221.4	123			− 2223.4	122			− 1731.3	113	
λ per temp		− 2247.6	118	101.6 ($P<0.001$)		− 1637.8	117	41.7 ($P<0.001$)		− 1334.8	109	37.2 ($P=0.001$)
λ per batch		− 2033.6	101	5.2 ($P<0.001$)		− 1430.5	101	10.8 ($P<0.001$)		− 1184.8	93	6.2 ($P<0.001$)
Saturated		− 1789.1	($n=125$)			− 1309.1	($n=124$)			− 1044.5	($n=115$)	

[1] N is the number of individuals evaluated at a given temperature; the number in parenthesis is the number of batches (replications in time)

[2] δ is the scale of the log-logistic link function used in the analysis because the link function revealed a lower AIC compared to the log-normal and Weibull link function; the figure in () is the SE of ln(δ) followed by asterisks indicating the parameter value significance level (*$P<0.05$; **$P<0.01$; ***$P<0.001$). The accumulated development frequency in relation to normalised age (time/median time) is calculated according to the log-logistic link function: accu. dev. freq. $=1(1/(1+x^{\alpha}))$, where x is the normalised age (determined through rate summation), and $\alpha=1/\delta$

[3] Numbers in parenthesis are 95% confidence limits. Medians followed by different letters in the same columns are significantly different ($P<0.05$) according to the AFT model

[4] For each life stage, 3 models of different complexity were evaluated: (1) with λ and ln(δ) only (intercept only), (2) with individual λ_i for each temperature i, (3) λ_j for each batch j (i.e. replication in time for each temperature). Each higher level model reduced the deviance significantly (see P values); for all stage both models with temperature-dependent λ and common scale parameter resulted significant. For further modelling, we used the scale parameter δ of model 2 (presented in the table) for simplicity

Table 2 Median development times resulting from accelerated failure time modelling and observed survival rates (third instar to pupa)

Temp (°C)	Third instar				Fourth instar				Pupa			
	N[1]	Median dev. time (days)[3]		Survival (%)	N	Median dev. time (days)[C]		Survival (%)	N	Median dev. time (days)[C]		Survival (%)
16	73	8.4 (±0.62)	a	89 (±3.7)	65	9.3 (±0.71)	a	80 (±5)	52	7.5 (±0.4)	a	90.4 (±4.1)
20	181	5.1 (±0.45)	b	89 (±2.3)	161	5.6 (±0.5)	b	96.3 (±1.5)	155	5 (±0.31)	b	96.8 (±1.4)
24	236	3.2 (±0.27)	c	94.5 (±1.5)	223	3.5 (±0.3)	c	96.4 (±1.2)	215	4.4 (±0.26)	bc	97.2 (±1.1)
28	190	2.3 (±0.2)	c	95.8 (±1.5)	182	2.3 (±0.2)	c	97.8 (±1.1)	178	3.4 (±0.21)	c	97.8 (±1.1)
32	261	4.6 (±0.4)	bc	87 (±2.1)	227	5.7 (±0.57)	b	40.5 (±3.3)	92	3.4 (±0.23)	c	88 (±3.4)
36	0	–		0	0	–		–	0	0		
Scale[2]	$\delta =$	0.1944 (±0.0107)***			$\delta =$	0.2064 (±0.011)***			$\delta =$	0.1512 (±0.0072)***		
Model[4]		Likelihood ratio test				Likelihood ratio test				Likelihood ratio test		
		ln L	df	F (df_x,df_{x-1})		ln L	df	F (df_x,df_{x-1})		ln L	df	F (df_x,df_{x-1})
Intercept only		− 1832.9	138			− 1567.7	151			− 1212.6	115	
λ per temp		− 1509.1	134	36.2 ($P=0.001$)		− 1277.1	148	66.4 ($P=0.003$)		− 1053.0	111	36.6 ($P=0.001$)
λ per batch		− 1406.2	118	3.9 ($P=0.002$)		− 1226.1	131	2.4 ($P=0.021$)		− 1021.4	95	2.1 ($P=0.046$)
Saturated		− 1209.3	($n=140$)	− 1061.3		($n=153$)	− 932.0	($n=117$)				

Clarifications indicated in Table 1 also apply

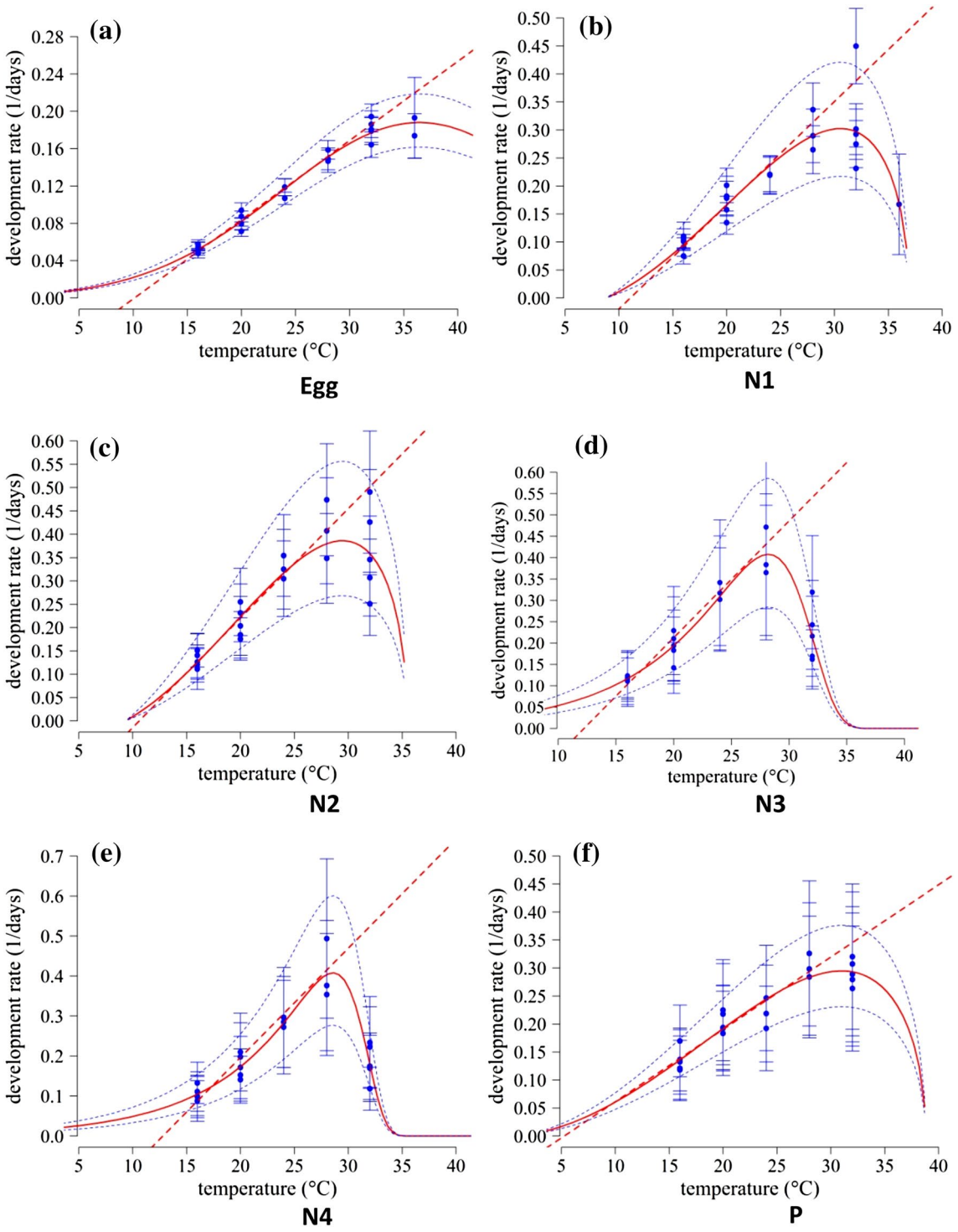

Fig. 1 The relationship between temperature and median development rates for immature life stages of *B. tabaci* (**a** eggs, **b** 1st nymphal instar N1, **c** N2, **d** N3, **e** N4, **f** pupae). The models, in a: Taylor model (Taylor 1981), in **b**, **c**, **f**: Brière model (Brière et al. 1999), **d**; and **e** Logan Tb model (Logan et al. 1976), model were fitted in terms of ln development time instead of development rate. Broken lines represent 95% confidence limits for the fitted model. Markers are observed median development rates (batches). Bars represent 95% confidence limits of observed data points.

Table 3 Models and parameters fitted to describe effects of temperature on median development rates of *B. tabaci* SSA-ESA

Life stage	Model		Parameters[1]	*F* value	*df* 1, 2	*P* value	Adj R^2
Egg	Taylor	r_m	0.188 (±0.008)***	497.6	2, 20	< 0.001	0.978
		T_{opt}	36.44 (±1.58)***				
		T_σ	12.76 (±0.88)***				
First instar	Brière 1	aa	0.0002 (±0.00)***	83.2	2, 19	< 0.001	0.887
		T_0	8.7808 (±0.00)***				
		T_{max}	36.9153 (±0.00)***				
Second instar	Brière 1	aa	0.0003 (±0.00)***	63.7	2, 18	< 0.001	0.862
		T_0	9.3041 (±0.00)***				
		T_{max}	35.448 (±0.00)***				
Third instar	Tb model (Logan)	ψ	0.82 (±0.172)***	40.04	3, 17	< 0.001	0.854
		b	0.1296 (±0.026)***				
		T_b	31.0194(±1.143) ***				
		ΔT	0.3318 (±0.232) ***				
Fourth instar	Tb model (Logan)	$S\psi$	0.7226 (±0.133) ***	39.74	3, 17	< 0.001	0.853
		b	0.1265 (±0.021) ***				
		T_b	31.267 (±0.776)***				
		ΔT	0.232 (±0.173)***				
Pupa	Brière 1	aa	0.0001 (±0.00)***	69.19	2, 18	< 0.001	0.872
		T_0	−0.4385 (±0.00)***				
		T_{max}	38.7971 (±0.00)***				

[1]Numbers in parenthesis are standard errors. Parameter values significantly different from zero are indicated by asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)

Model: Taylor used to describe development rates of egg stage is given by the equation:

$$r(T) = r_m \exp\left(-\frac{1}{2}\left[-\frac{(T-T_{opt})}{T_\sigma}\right]^2\right) \quad (1)$$

where r_m is is the maximum achievable developmental rate at optimum temperature T_{opt} and T_σ measures the rate at which development slows beyond the rate at T_{opt}.

Model: Brière 1 used to describe development rates of first, second and pupa nymphal stages is given by the equation:

$$r(T) = aT(T - T_0)(T_L - T)^{\frac{1}{2}} \quad (2)$$

where a is an empirical constant, T_0 is the low temperature development threshold, T_L (or T_{max}) is the lethal temperature threshold.

Model: Tb Model (Logan) used to describe development rates of third and fourth nypmphal stage is given by the equation:

$$r(T) = \psi \exp\left(b[T - T_b]\right) - \exp\left(b\frac{[T-T_b]}{\Delta T}\right) \quad (3)$$

where ψ, b, T_b, ΔT are parameters.

Mortality of immature stages and adult senescence rate at constant temperatures

Mortality in eggs and first instar nymphs was higher than in other nymphal instars, and lowest mortality was observed in the pupal stage (Fig. 2, Tables 1, 2). Egg to adult mean survival peaked at 24 °C (62.5%) but was very low at 16 °C (14.9%) and 32 °C (20.3%). It was 43.3% at 20 °C and 48.4% at 28 °C. At 36 °C, survival in eggs was only 8.1%, and none of the insects survived to the adult stage (Table 1). Overall, mortality of immature stages was relatively low between 20 and 28 °C (Tables 1, 2, Fig. 2). Temperature-dependent mortality in all immature stages was described by a parabolic model (Supplementary material 4). Adult senescence rates also followed a similar pattern as mortality rate of immature stages. Adult senescence rate was lower between 20 and 24 °C and high at temperature extremes (Fig. 3a). Adult senescence rate was best described by the Stinner 4 model.

Mortality under field conditions

Mortality rates in field populations of *B. tabaci* SSA-ESA in Dar es Salaam, Tanzania was lower in the first, second and third instars compared to other stages (Supplementary 3). Fewer whitefly survived through the fourth instar and pupal stages where the impact of predators and parasitoids was greatest (Supplementary 3). Overall, egg to adult mortality was very high since natural enemies and other mortality factors which were absent in the constant temperature experiments caused severe mortality.

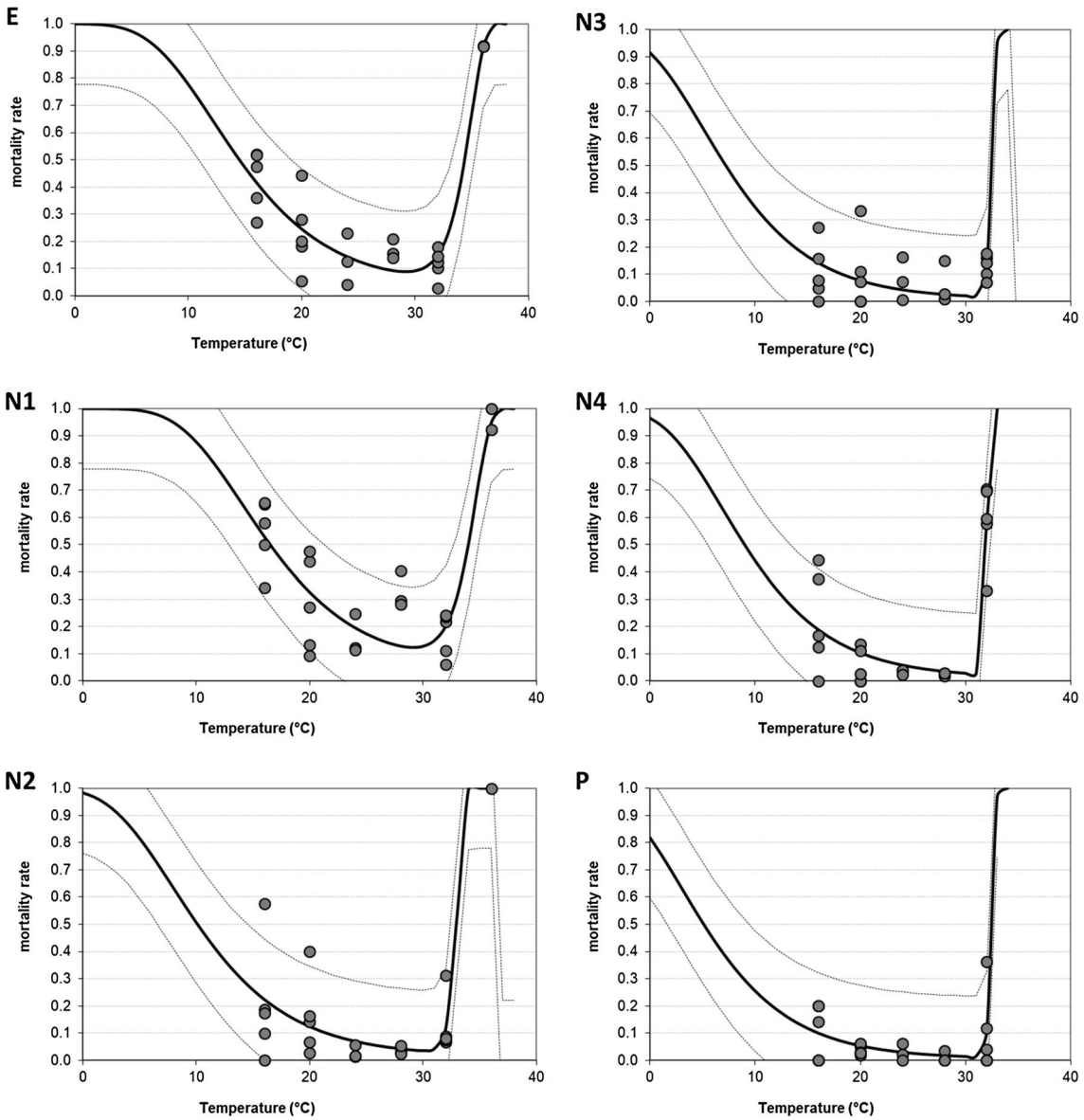

Fig 2 Mortality of *B. tabaci* SSA-ESA egg to pupa stage (E–P) under constant temperature treatments. The black shaped curve is the mortality percentage predicted by the model(s), the faint curve above and below the black curve represents the 95 % confidence intervals, the black dots are experimental data points.

Adult longevity and fecundity at constant temperatures

In all treatments, females lived longer than males. The longevity of adult females varied markedly with temperature, it was low at the extremes of 16 °C, 32 °C and 36 °C. The insects lived longer at 24 °C and 20 °C (Table 4). The maximum longevity of a single whitefly observed in this study was 47 days and was recorded for both the 20 °C and 24 °C treatments. The longevity of adult females at 20 °C and 24 °C was significantly different from longevity at 32 °C and 36 °C, whilst other treatment combinations were not significantly different ($p < 0.001$) (Table 4). Life span of adult males was in the range of 6–11 days across the temperature treatments.

Total fecundity per female observed was highest at 20 °C and least at 16 °C. The Weibull link function best described survival time and median oviposition times of adult females. The maximum number of eggs laid by a single individual in its entire life was 387 eggs at 20 °C, and only a few individuals laid eggs at 16 °C.

Median oviposition time decreased linearly from 20 to 36 °C was highest at 20 °C and least at 36 °C. The median

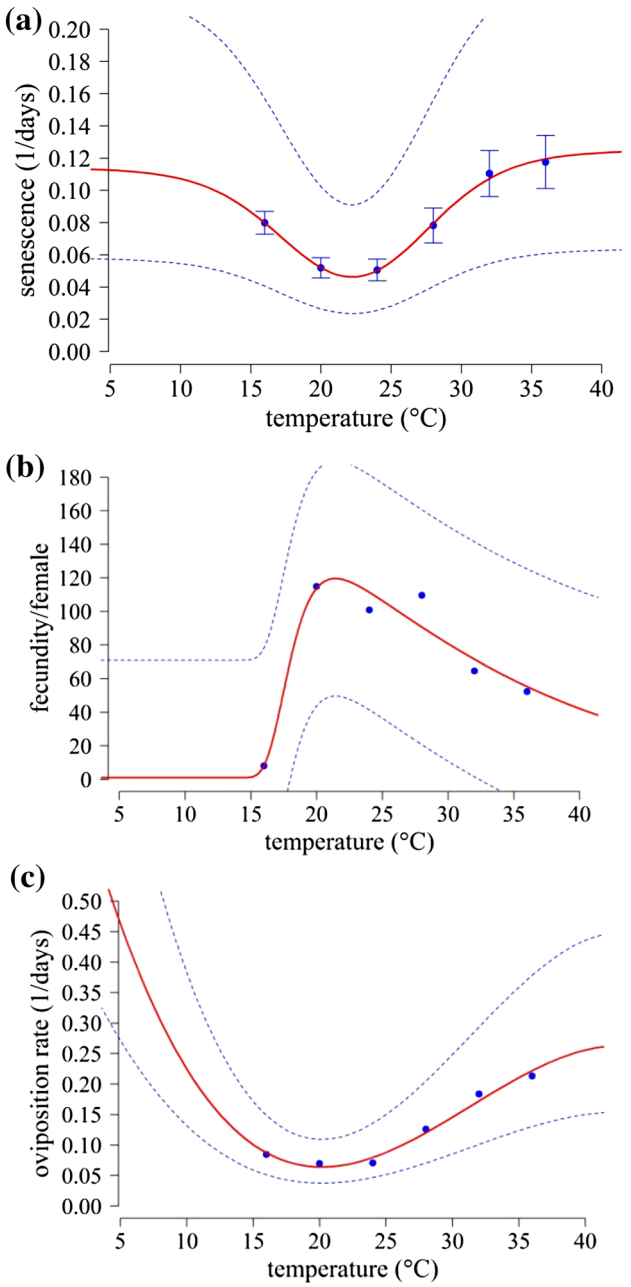

Fig 3 Temperature-dependent: **a** senescence rates (day^{-1}) for *B. tabaci* adult (**b**). Total fecundity per female (**c**). Oviposition rate. Dots are observed data; solid lines are fitted curves, in **a**: Stinner-4 model, in **b**: parabolic model, in **c**: Tanigoshi model. Broken lines: 95% confidence limits for the fitted model (for parameters and statistical regression results, see Supplementary Table 5). Bars represent standard deviation in observed data.

oviposition time for the 16 °C, 20 °C and 24 °C treatments differed significantly ($p < 0.05$) from the 32 °C and 36 °C treatments. Median oviposition time at 20 °C and 24 °C also differed significantly from that at 28 °C (Table 4).

Life-table parameters from constant temperatures and field experiments

An estimation of life-table parameters showed that at constant temperatures, *B. tabaci* SSA-ESA populations would be maximised between 26 and 28 °C as the intrinsic rate of natural increase peaked around 26 °C and 28 °C. Net reproductive rate was also maximal between 24 and 28 °C. Similarly, the finite rate of increase also peaked between 26 and 28 °C. Gross reproductive rate was low at the extremes of 16 °C and 32 °C, and maximal between 24 and 26 °C. Generation time was highest (76.6 days) at 16 °C, also high (26.2 days) at 30 °C, but least between 28 and 30 °C. The doubling was highest at the cold extreme (16 °C) and least between 28 and 30 °C. Life-table parameters could not be estimated for the 36 °C treatment because immatures did not complete their development to the adult stage at this temperature (Fig. 4).

Longevity of field populations of *B. tabaci* SSA-ESA

Under field conditions, adult males in clip-cages lived up to 28 days, although the mean longevity was 9.2 days. Under the same conditions, adult females lived up to 31 days although the mean longevity was 13.1 days. The pattern of longevity for the two sexes was therefore similar to that observed in the experiments with constant temperature treatments. The highest number of eggs laid by an individual *B. tabaci* was 287 eggs and mean fecundity per female was 94.5 eggs.

Discussion

Development and development duration

This study investigated temperature-dependent effects on the life history traits of *B. tabaci* SSA-ESA over a range of temperatures in climatic chambers and under field conditions. The immature development time of 25.1 days for *B. tabaci* SSA-ESA on cassava at 32 °C is comparable to values for *B. tabaci* MEAM1 on broad beans (23.0 days) (Bosco and Caciagli 1998) and cotton (23.1 days) (Nava-Camberos et al. 2001), but differs substantially from that of *B. tabaci* MEAM1 on cantaloupe (19.5 days) at 32 °C. In this study, no individual completed development from egg to adult at 36 °C. This is likely to be because the 36 °C treatment exceeds the maximum temperature for development of *B. tabaci* SSA-ESA. Similar observations were made by Nava-Camberos et al. (2001) and Butler et al. (1983). However, several studies on the developmental time for *B. tabaci* MED and MEAM1 showed that both species are able to complete development at 35 °C or even higher (Wang and Tsai 1996;

Table 4 Median survival times, median oviposition times and total fecundity per female of *Bemisa tabaci* adults at different constant temperatures

Temp (°C)	Females			Males			Oviposition			
	N^1 (f/m)	Median survival time (days)[3]		Median survival time (days)[C]			n	Median ovi. time (days)[C]		Mean Oviposition per female eggs (STD)
16	41/37	15.7 (±1.52)	ab	9.5 (±1.59)		a	96	14.8 (±1.63)	ab	8.4 (±12.53)
20	45/46	24.2 (±3.19)	a	14.9 (±3.33)		a	219	17.9 (±2.03)	a	114.9 (±88.22)
24	31/33	24.8 (±3.61)	a	16 (±3.87)		a	242	17.7 (±2.05)	a	100.9 (±65.03)
28	28/29	16.1 (±2.41)	ab	9.6 (±2.41)		a	197	9.9 (±1.15)	bc	109.6 (±63.63)
32	36/35	11.4 (±1.59)	b	10.5 (±2.5)		a	306	6.8 (±0.8)	cd	64.6 (±50.52)
36	27/27	10.7 (±1.62)	b	8.6 (±2.2)		a	1	5.9 (±0.72)	d	52.3 (±34.52)
Scale[2]	δ =	0.6215 (±0.0351)***		δ =	0.7272 (±0.0549)***		δ =	0.6084 (±0.0126)***		
Model[4]	Likelihood ratio test			Likelihood ratio test			Likelihood ratio test			
	ln L	df	F (df_x,df_{x-1})	ln L	df	F (df_x,df_{x-1})	ln L	df	F (df_x,df_{x-1})	
Intercept only	−652.6	110		−689.2	113		−43,362.5	1381		
λ per temp	−628.5	105	10 (P=0.008)	−679.1	108	2.1 (P=0.207)	−40,634.3	1376	98 (P<0.001)	
Saturated	−577.8	(n=112)		−575.2	(n=115)		−32,972.7	(n=1383)		

Part of clarifications indicated in Table 1 also apply

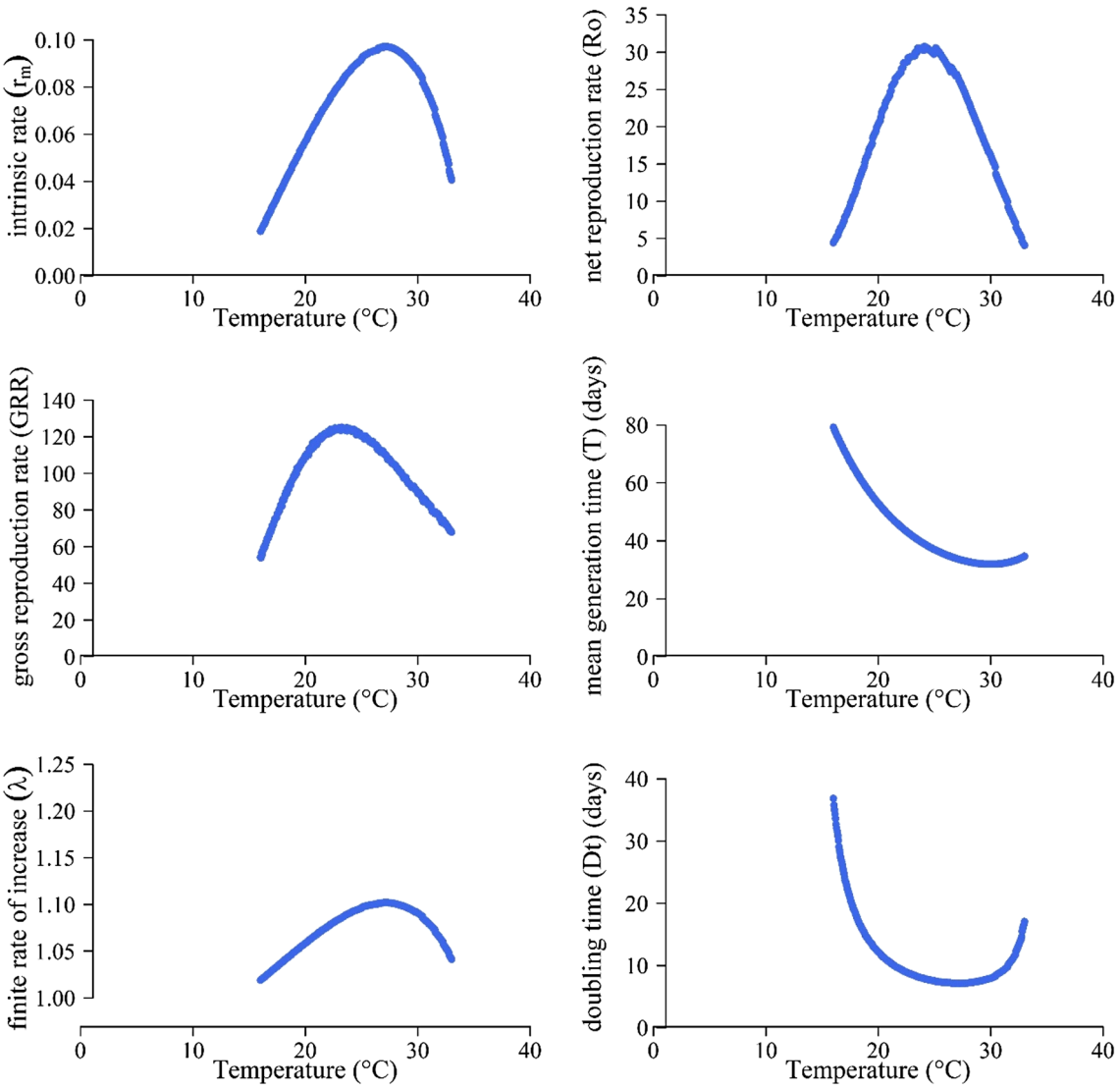

Fig 4 Life-table parameters of *B. tabaci* SSA-ESA estimated for the constant temperature treatments

Muñiz and Nombela 2001; Qui et al. 2003; Bonato et al. 2007; Delatte et al. 2009; Guo et al. 2013; Han et al. 2013). Peak development of *B. tabaci* SSA-ESA on cassava was observed at 28 °C. Curnutte et al. (2014) reported a similar value (28 °C) for *B. tabaci* MEAM1 on collard. Qui et al. (2003), Delatte et al. (2009), Guo et al. (2013), Tsueda and Tsuchida (2011) and Wang and Tsai (1996) observed optimum development temperature of *B. tabaci* MEAM1 on tomato to be between 29 and 32 °C. However, Yang and Chi (2006) reported up to 35 °C on tomato. An optimum development temperature of 30 °C has been reported for both *B. tabaci* MEAM1 and MED on cucurbits (Nava-Camberos et al. 2001; Muñiz and Nombela, 2001; Bayhan et al. 2006; Tsueda and Tsuchida 2011) and cotton (Butler et al. 1983; Nava-Camberos et al. 2001). The works of Bonato et al. (2007), Tsueda and Tsuchida (2011) and Han et al. (2013) show that the optimal development time of *B. tabaci* MED on solanaceous crops varied from 27.5 (sweet pepper and eggplant) to 33 °C (tomato).

Mortality

Mortality under constant temperature conditions at the egg and first instar stages is relatively higher than all other stages within the range of temperatures tested. This is an observation that has been widely reported for other members of the *B. tabaci* species complex (Wang and Tsai 1996; Muñiz and Nombela 2001; Qui et al. 2003; Bonato et al. 2007; Delatte et al. 2009; Guo et al. 2013; Han et al. 2013). First instars are known to be mobile for the first few hours after egg hatching, during which time they are more vulnerable to environmental stress factors. Additionally, thermal

sensitivity of each life stage may differ, leading to differences in mortality (Kingsolver et al. 2011). Immature survival of *B. tabaci* SSA-ESA on cassava was highest at 24 °C. Wang and Tsai (1996), Qui et al. (2003), Nava-Camberos et al. (2001), Bonato et al. (2007) and Han et al. (2013) observed optimum immature survival of *B. tabaci* MEAM1 on solanaceous crops (pepper and eggplant) between 25 and 27.5 °C. However, higher values (32.5 °C) were reported for *B. tabaci* MED on oriental melon (Han et al. 2013), *B. tabaci* MEAM1 on tomato (31 °C) (Guo et al. 2013) and cotton (Nava-Camberos et al. 2001). Percentage survival from egg to adult emergence of *B. tabaci* MEAM1 on eggplant reported by Qui et al. (2003) (27–67%) is also similar to our result (14–62%). However, results of Bonato et al. (2007) (48–85%) for *B. tabaci* MED, Nava-Camberos et al. (2001) (76.5–100%) for *B. tabaci* MEAM1 on cantaloupe, Butler et al. (1983) (37–89%) for *B. tabaci* MEAM1 on eggplant, and Wang and Tsai (1996) (36.8–88.7%) on eggplant are far higher than what was recorded on cassava in this study. *B. tabaci* SSA-ESA individuals were more tolerant to moderate temperatures (20–28 °C) than higher (32–36 °C) or lower (16 °C) temperature extremes because mortality rates were lower within this range. In contrast, Qui et al. (2003), Bonato et al. (2007) and Guo et al. (2013) suggest that both *B. tabaci* MEAM1 and MED appear to be better adapted to higher temperatures because they are still able to survive relatively well at these extremes.

Fecundity

Total fecundity per female decreased as temperature increased with a maximum at 20 °C (114.9 eggs/female). Wang and Tsai (1996) and Qui et al. (2003) reported a similar optimum fecundity temperature of 20 °C for *B. tabaci* MEAM1 on tomato and eggplant, while Guo et al. (2013) and Tsueda and Tsuchida (2011) reported 30–31 °C on tomato. Yang and Chi (2006), Butler et al. (1983) and Curnutte et al. (2014) recorded optimum fecundity at 25 °C, 26.7 °C and 28–33 °C on tomato, cotton and collard, respectively. Additionally, optimum fecundity for *B. tabaci* MED on tomato was obtained at 20 °C (Bonato et al. 2007) and 30 °C (Tsueda and Tsuchida 2011). Unlike the trend in whitefly development and survival, where development and survival is greatly impaired above 30 °C, our results show that females are still able to lay relatively large numbers of eggs (64.6 eggs per female at 32 °C and 52.3 eggs per female at 36 °C). In contrast to this study, where fecundity was higher in the range of 20–28 °C, Tsueda and Tsuchida (2011) reported much higher fecundities up to 135 eggs/female for *B. tabaci* MEAM1 and 81 eggs/female and MED species at 30 °C. Total fecundity per female in this study is also closely related with those reported for *B. tabaci* MED species by Bonato et al. (2007), although fecundity observed in our study was much lower at 16 °C, and relatively higher at 36 °C compared to similar temperatures in their study. Qui et al. (2003) reported much higher fecundity for *B. tabaci* MEAM1 than that observed for *B. tabaci* SSA-ESA at comparable temperatures, and Wang and Tsai (1996) showed that *B. tabaci* MEAM1 could lay up to 324 eggs per female at 20 °C, which greatly exceeds the 115 eggs per female observed for *B. tabaci* SSA-ESA tested at the same temperature in this study. A similar pattern was also reported within the range of 20–27 °C by the same study; however, total fecundity at 30 °C and 35 °C was less than what was observed in this study.

Longevity

Longevity of adult stages differed with temperature. High longevity at 20 °C and 24 °C, and low longevity at temperature extremes (16 °C, 32 °C, 36 °C) mirrored patterns observed for other life history traits in this study and for many other insects (Qui et al. 2003; Bonato et al. 2007; Khadioli et al. 2014). However, unlike most studies, where adult longevity was highest at the lowest temperature (Wang and Tsai 1996; Qui et al. 2003; Bonato et al. 2007), adult *B. tabaci* SSA-ESA longevity was not highest at the lowest temperature. Peak longevity at 20 °C and 24 °C observed for *B. tabaci* SSA-ESA on cassava was similar to the observations of Yang and Chi (2006), Qui et al (2003) and Wang and Tsai (1996) who reported an optimum longevity of adult *B. tabaci* MEAM1 at 20 °C on eggplant and tomato. An optimum temperature (17 °C) was reported by Bonato et al. (2007) for *B. tabaci* MED on tomato. Butler et al. (1983) and Tsueda and Tsuchida (2011) reported maximum longevity at 30–32.2 °C for *B. tabaci* MEAM1 and MED on tomato, cucumber and cotton. Damage to leaves and retarded growth of cassava plants during studies of immature development on cassava at 16 °C provided evidence for strong host plant effects on the survival of whiteflies at this temperature, and also explains the low longevity of adults. In all cases, females lived longer than males, a trend that has been reported in other insects (Khadioli et al. 2014; Sporleder et al. 2016).

Population increase

Our work suggests that *B. tabaci* SSA-ESA populations on cassava would be maximised between 26 and 28 °C as the intrinsic rate of natural increase peaked around these temperatures. Qui et al. (2003) and Wang and Tsai (1996) suggest that the rate of population increase of *B. tabaci* MEAM1 on eggplant is maximised at temperatures between 25 and 29 °C. Intrinsic rate of natural increase of *B. tabaci* MEAM1 and MED on tomato is optimum between 30 and

31 °C (Tsueda and Tsuchida 2011; Delatte et al. 2009; Guo et al. 2013; Yang and Chi 2006; Bonato et al. 2007).

Development, mortality, fecundity and longevity under field conditions

Development and mortality recorded from field experiments were comparable to results from laboratory experiments. The 18–28 days required for immature development under field conditions is similar to results for immature development time at the 28 °C and 24 °C constant temperature treatments, using the same cassava variety and whiteflies from the same colony.

Legg (1995) reported a higher development duration (27–39 days) on cassava under field conditions, although this was in southern Uganda, which is on average about 4 °C cooler than coastal Tanzania. Fishpool et al. (1995), working in hot lowland Ivory Coast, reported a development duration of 21 days, while Chant (1958) obtained a development duration of 12 days under glasshouse conditions in Nigeria. Survival under field conditions (0.7–18.6%) was much lower than the peak survival of 62.5% observed for the 24 °C constant temperature treatment. Several factors, including predators and parasitoids that were active in the field, accounted for this wide difference between survival under field and laboratory conditions. Very similar low survival of *B. tabaci* (5.2–22.4%) on cassava under field conditions was also reported by Legg (1995). Even under screen house conditions, free of the influence of natural enemies, Boni et al. (2017) observed mortality of the coastal population (*B. tabaci* SSA-ESA) up to 77.8% and 76.1% for two of the three virus-free cassava varieties tested. Other than natural enemies, one of the most important sources of mortality for *B. tabaci* on cassava has been shown to be dislodgement, presumed to occur as first instars emerge from eggs (Asiimwe et al. 2007).

The average fecundity per female of 94.5 eggs obtained under field conditions is comparable to the 100.9 eggs observed in the 24 °C constant temperature treatment. The total fecundity per female recorded during the field experiments was higher than values reported by Avidov (1956), Azab et al. (1971) and Gameel (1978), but very similar to the 108 eggs/female reported by Khalifa and El Khidir (1964).

In comparison with this study, Tsai and Wang (1996) reported greater adult longevity (24 days) for MEAM1 on eggplant. Similarly, Chaubey et al. (2015) showed that *B. tabaci* Asia II-1 and Asia II-2 could live up to an average of 16.7 and 16.5 days, respectively, on cotton. The results of Musa and Ren (2005) for *B. tabaci* MEAM1 on several crops are similar to what we report here. In contrast, the longevity of *B. tabaci* ZHJ-I from China was much lower than the observations from this study (Zang et al. 2006).

The difference between our results and those of others can possibly be attributed to differences in thermal tolerance of *B. tabaci* and other traits related to their response to climate (Kingsolver et al. 2011; Aregbesola 2018; Aregbesola et al. 2019). Other important factors are genetic differences among the host plants, for example, differences in plant defence strategies or secondary metabolites. In some cases, differences in performance among varieties of the same host plant has been recorded (Nava-Camberos et al. 2001; Boni et al. 2017), and differences in the ability of *B. tabaci* to manipulate host plant defences (Aregbesola 2018).

Modelling temperature responses of *B. tabaci*

A log-logistic link function was used in the accelerated failure time modelling of median development times because the link function revealed a lower AIC compared to the log-normal and Weibull link function. The AFT model determines the distribution link function and its shape parameter, and tests if this distribution curve is expected to be the same across all temperatures. A similar approach has been used by Sporleder et al. (2004), Khadioli et al. (2014), Sporleder et al. (2016) and Mujica et al. (2017). A combination of nonlinear models was used to describe development, adult senescence, total oviposition rates, fecundity per female and mortality of *B. tabaci* SSA-ESA. These models and other related models have been used to describe temperature-dependence in whiteflies (Bonato et al. 2007; Han et al. 2013) and other insects (Logan et al. 1976; Sharpe and DeMichele 1977).

Our modelling of development, mortality and oviposition rates gave a very good fit and is comparable to the reports of Wang and Tsai (1996), Muñiz and Nombela (2001), Nava-Camberos et al. (2001), Bonato et al. (2007) and Han et al. (2013). The model used to describe adult senescence rate predicted an optimum temperature of 22.4 °C which provides an accurate reflection of the experimental observations. The optimum temperature for fecundity was predicted to be 17.2 °C which appears lower than the observed data. However, other models that predicted total fecundity per female in the range closer to observed data were not significant, so they were not selected.

Conclusions

The study described here was the first in which both laboratory (constant temperatures) and field experiments were combined to describe temperature-dependent effects on life history traits of an African population of cassava-colonising *B. tabaci*. Informative data were generated on temperature-dependence models, demographic parameters of adult females and life-table parameters for immature stages and

adult males and females. The study confirms that reproductive performance, developmental characteristics and thermal requirements of cassava-colonising *B. tabaci* SSA-ESA differ from non-cassava types in terms of the influence of temperature, which is critical to predicting the optimum temperature for their population increase. The study also suggests that *B. tabaci* SSA-ESA may not be as fit on cassava as the highly invasive species MEAM1 and MED are on some of the many host plants which they are able to colonise. These essential baseline data gathered from field and constant temperature studies have been developed into a phenology model for the pest which can be used for pest risk mapping and assessing the potential impact of climate change on the distribution and abundance of *B. tabaci* SSA-ESA. Though we have compared the performance of *B. tabaci* SSA-ESA in coastal Tanzania to other whiteflies tested in different locations, a useful topic of future study would be the simultaneous comparison in the same location of distinct *B. tabaci* species groups. This would help to determine whether the temperature responses of different cassava-colonising *B. tabaci* genotypes are the same or whether they differ. If they differ, the consequence would be that separate phenology models would be required for each of the six currently recognised major genotype groups of cassava-colonising *B. tabaci* (Wosula et al. 2017). Risk maps based on phenology models that would indicate anticipated future threats from whiteflies and whitefly-transmitted viruses affecting cassava will be of great future value in improving the targeting of control measures.

Author contributions

CR, OSL, JL and LS secured funding and supervised the research; CR, AOZ, JL, OSL, LS, MS and PC designed the study; AOZ collected the data; AOZ, MS and PC handled the modelling and data analysis in ILCYM; AOZ, CR, JL, OSL, LS, PC and MS wrote the manuscript. All authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest.

Ethical approval This article does not contain any studies with human or animal subjects that require ethical approval.

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

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