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EFFECT OF TEMPERATURE AND CASSAVA GENOTYPE ON THE DEVELOPMENT, FECUNDITY AND REPRODUCTION OF *Bemisia tabaci* SSA1

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ABSTRACT

The *Bemisia tabaci* complex is currently recognised as key agricultural pests that cause economic damage globally. Temperature is the most important driver of changes in behaviour, abundance and distribution of insect pests, including the whitefly (*Bemisia tabaci*). The objective of this study was to evaluate the development, fecundity and reproduction of *B. tabaci* SSA1 on cassava genotypes under a range of temperatures. A laboratory study was conducted using three cassava genotypes (Alado alado, NAROCASS 1 and NASE 14) at five constant temperatures (16, 20, 24, 28 and 32 °C). The parameters assessed included development duration, survival, fecundity and population parameters for *B. tabaci* SSA1. Temperature had significant effects ($P<0.001$) on development time, survival and fecundity of *B. tabaci*; while cassava genotype had no effect ($P>0.05$). An inverse relationship was observed between development time and temperature for all stages across all cassava genotypes. The total life cycle was 63.8 days at 16 °C and 17.9 days at 32 °C on NAROCASS 1. Survival for each stage throughout the entire life cycle increased with temperature and was highest at 32 °C, although this was not significantly different from that at 28 °C. Fecundity increased with temperature and was highest at 32 °C on all cassava genotypes. For all cassava genotypes, the intrinsic rate of increase (r_m), finite rate of increase (λ) and net reproductive rate (R_o) increased with temperature, while mean generation time (T) reduced following a similar pattern. At 32 °C, r_m, R_o, λ and T were 0.2, 48.7, 1.2 and 22.6 days, respectively; compared to 0.01, 1.9, 1.0 and 71.2 days at 16 °C on Alado alado. Therefore, the ideal development temperature for *B. tabaci* SSA1 is 32 °C. Thus, there is a risk of accelerated future expansion of *B. tabaci* SSA1 populations globally, with global warming and climate variability.

Key Words: Climate change, net reproductive rate

RÉSUMÉ

Le complexe *Bemisia tabaci* est actuellement reconnu comme un ravageur agricole clé causant des dommages économiques à l'échelle mondiale. La température est le facteur le plus important des changements de comportement, d'abondance et de répartition des insectes ravageurs, y compris l'aleurode (*Bemisia tabaci*). L'objectif de cette étude était d'évaluer le développement, la fécondité et la reproduction de B. *tabaci* SSA1 sur des génotypes de manioc sous une gamme de températures. Une étude en laboratoire a été menée en utilisant trois génotypes de manioc (Alado alado, NAROCASS 1 et NASE 14) à cinq températures constantes (16, 20, 24, 28 et 32 °C). Les paramètres évalués comprenaient la durée du développement, la survie, la fécondité et les paramètres de population pour B. *tabaci* SSA1. La température a eu des effets significatifs (P<0,001) sur le temps de développement, la survie et la fécondité de B. *tabaci*, tandis que le génotype du manioc n'a eu aucun effet (p>0,05). Une relation inverse a été observée entre le temps de développement et la température pour tous les stades dans tous les génotypes de manioc. Le cycle de vie total était de 63,8 jours à 16 °C et de 17,9 jours à 32 °C sur NAROCASS 1. La survie pour chaque étape tout au long du cycle de vie entier augmentait avec la température et était maximale à 32 °C. Cependant, la survie à 28 °C n'était pas significativement différente de celle observée à 32 °C. La fécondité augmentait avec la température et était maximale à 32 °C sur tous les génotypes de manioc. Pour tous les génotypes de manioc, le taux d'accroissement intrinsèque (rm), le taux d'accroissement fini (λ) et le taux net de reproduction (R_o) ont augmenté avec la température, tandis que le temps de génération moyen (T) a diminué selon un schéma similaire. A 32 °C, r_m, R_o, λ et T étaient respectivement de 0,2, 48,7, 1,2 et 22,6 jours ; contre 0,01, 1,9, 1,0 et 71,2 jours à 16 °C sur Alado alado. Par conséquent, d'après cette étude, la température de développement idéale pour B. *tabaci* SSA1 est de 32 °C. Ainsi, il existe un risque d'expansion future accélérée des populations de B. *tabaci* SSA1 à l'échelle mondiale, avec le réchauffement climatique et la variabilité climatique.

Mots Clés : changement climatique, taux net de reproduction

INTRODUCTION

The *Bemisia tabaci* complex is currently recognised as key agricultural pests that cause economic damage globally (Oliveira *et al*., 2001; Park *et al*., 2019). *Bemisia tabaci* has increased in population unprecedentedly since the 1990s, especially in the cassava growing regions of East and Central Africa (Colvin *et al*., 2004; Ally *et al*., 2019). The rapid increase in *B. tabaci* populations has heightened concern as a direct pest of cassava (FAO, 2015) and vector of two economically important diseases of cassava; namely, Cassava Mosaic Disease (CMD) and Cassava Brown Streak Disease (CBSD) (Colvin *et al*., 2004; Maruthi *et al*., 2005). This has affected cassava production in Africa (Nweke *et al*., 2002; Maruthi *et al*., 2017), resulting in reduced food and income security, and overall livelihood benefits of cassava. This is so, especially in sub-Saharan Africa, where cassava is a staple crop (Jarvis *et al*., 2012; Maruthi *et al*., 2017).

The stages of its life cycle (growth, development, survival, distribution and abundance) are affected by climatic factors; particularly temperature since insects are poikilothermic (Robinson and Partridge, 2001; Sharma and Dhillon, 2020). It has been projected that temperature increase in the wake of climate change will profoundly affect the biology and development of the insects and may lead to greater outbreaks of insect populations (Bale *et al*., 2002). High temperatures have also often been linked with faster development rate; leading to increased insect populations (Zeshan *et al*., 2015; Ezeakacha and Yee, 2019).

For *B. tabaci* population dynamics, temperature and host plant effects have been singled out as the primary factors affecting its development, fecundity and mortality (Nava-Camberos *et al*., 2001; Naranjo *et al*., 2010). With the expected rise in global surface temperatures of up to 11 °C by the year 2100 (Githeko *et al*., 2000; United States Global Climate Research Program, 2009) and a projected 2 °C rise in mean annual temperature in Africa (Giesen *et al.*, 2020), momentous temporal and spatial distribution shifts are expected among organisms with continued global warming (Parmesan, 2006). However, for phloem feeders (e.g. whiteflies), inconsistent responses due to global warming (Bezemer and Jones, 1998) for different insect species and host plants (Bezemer *et al*., 1999) have been reported. It is, therefore, imperative that the behavior of *B. tabaci* populations are investigated along its life cycle against temperature, cassava genotype and their interactions (temperature *versus* cassava genotypes) and how these affect whitefly population dynamics, with special attention to the currently known *B. tabaci* species.

Recent literature revealed that a combination of moderate temperature, relative humidity and use of broad leaf cassava genotypes of short stature supports high *B. tabaci* populations (Katono *et al*., 2021). The objective of this study was to evaluate the development, fecundity, survival and reproduction *B. tabaci* sub-Saharan Africa 1 (SSA1) species on cassava genotypes under a range of temperatures.

MATERIALS AND METHODS

Plant materials. Three cassava genotypes namely; NAROCASS 1 and NASE 14 (improved genotypes that support high *B. tabaci* SSA1 populations) and Alado alado (a local genotype that supports low *B. tabaci* SSA1 populations) were used in the study. Ten centimeter long stem cuttings of cassava test genotypes were grown placed vertically in 10 cm-diameter plastic pots containing sterilised black soil in insect proof cube cages (50 cm x 50 cm x 50 cm) in a screenhouse at the National Crops Resources Research institute (NaCRRI), Uganda.

***Bemisia tabaci* SSA1 pure colony.** *Bemisia tabaci* SSA1 species pure colonies in cube cages were raised from a single mated female on the cassava genotype NAROCASS 1 grown in 10 cm-diameter plastic cups in a screenhouse at NaCRRI. The colonies were maintained under natural fluctuating conditions; with temperatures ranging from 16-32.5 °C and relative humidity ranged from 38-100%, and a photoperiod of 12:12 (L:D).

Experimental conditions and design. The experiment was conducted under controlled environmental conditions in separate temperature-humidity controlled rooms. The three test cassava genotypes were placed under five different study temperatures (16, 20, 24, 28 and 32±2 °C), with relative humidity (RH) maintained at 70±5% and a photoperiod of 12 h light: 12 h darkness. These temperatures and RH range are typical of the prevailing environmental conditions of Uganda (World Climate Guide, 2021).

The experiment was set in a randomised complete block design (because of a temperature and RH gradient in the controlled rooms) with replications depending on parameter under study. For all studies, temperature was the main plot factor, while cassava genotype was the sub plot factor.

Immature development duration and survival. Fifty pairs of 24 hr old *B. tabaci* (50 males and 50 females) were clipped in cages (5.5 cm in diameter and 3 cm in length with a nylon cloth at the base) on the first and second fully expanded leaves of cassava plants and allowed to oviposit for 24 hours at 24 °C (the study temperatures closest to room temperature of 25 °C). The test plants were then transferred to temperature-controlled

rooms set at the various study temperatures. Plants were watered two to three times a week.

Fifty eggs were then selected for observation, and all other eggs on the leaves were removed by gently brushing them off using the edge of soft tissue paper (Asiimwe *et al.*, 2007). Daily observations were recorded on survival and the transition from one stage to another (Eggs, 1st, 2nd, 3rd and 4th nymphal instars and the pupal stage) using a 10× hand lens until adult emergence according to (Gangwar and Gangwar, 2018).

Survival during each immature stage was recorded as the number of individuals developing to the subsequent stage, and this was converted into percentage of survivorship for each stage. The experiment was set in six replicates (3 plants per genotype per temperature) using a randomised complete block design and was repeated three times.

Longevity, fecundity and population parameters. Five newly emerged adults pairs were confined on the underside of the 1st, 2nd, 3rd and 4th fully expanded cassava leaves of each genotype (each leaf was treated as a replicate) and allowed to oviposit for 24 hr. The five mating pairs were transferred daily to a new leaf, until death of all the females. The number of eggs laid was recorded daily and used to calculate fecundity; while lifespan of the females was used to calculate longevity. The eggs were observed until adult emergence and the number of males and females was identified according to Kedar *et al*. (2014). The experiment was also set in four replicates using a randomised complete block design, and was repeated twice.

Data analysis. All data collected were analysed using R statistical software (R Core Team, 2017). Prior to analysis, all data were tested for normality and where skewness occurred, the data were subjected to the Box Cox procedure (Venables and Ripley, 2002) in order to determine the most appropriate transformation based on the lambda value. The data were then subjected to fixed model analysis of variance (ANOVA) for temperature and genotype effects.

Means were separated using the Least Significant Difference (LSD) test at 5% probability level. Development rate was calculated as a reciprocal of development duration in days (Nava-Camberos *et al*., 2001). The effect of temperature on immature development rate was then subjected to linear regression. Population parameters; net reproductive rate (R_O), mean generation time (T) in days, finite rate of increase (λ) and the intrinsic rate of increase (r_m) were calculated according to (Birch, 1948; Islam and Ren, 2007).

RESULTS

***Bemisia tabaci* SSA1 development duration.** Cassava genotype and the genotype* temperature interaction had no effect development duration ($P>0.05$) (Table 1). However, the effect of temperature variation was significant ($P<0.001$) on development duration of all stages and total development duration of *B. tabaci* SSA1. Developmental duration reduced by a factor of 3 to 5.6 with increase in temperature, for the lowest and highest temperature values depending on the development stage (Table 2).

Generally, the effect of temperature on development duration was more pronounced on the eggs, and first, second and third nymph instars. The egg stage was 20 days at 16 °C, while it only lasted for 5.5 days at 32 °C (Table 2). The shortest development time was observed at 32 °C; while the longest time occurred at 16 °C (Table 2). Mean egg development time ranged from 5.52 days at 32 °C to 19.99 days at 16 °C; while mean total developmental duration for all immature *B. tabaci* SSA1 growth stages ranged from 17.93 days at 32 °C to 65.33 days at 16 °C. However, there were no significant differences ($P>0.05$) in development times for the first, second, fourth instar; and pupal stages for 28

TABLE 1. F-statistics for the effects of temperature and cassava genotype on *B. tabaci* SSA1 development duration, immature survival, female fecundity and longevity

SOV	DF	Development duration	Survival	Fecundity	Female longevity	Total duration
Temperature (A)	4	284.31***	156.69***	687.99***	703.71***	3583.54***
Cassava genotype (B)	2	0.16ns	8.44***	2.68ns	2.98ns	2.10ns
A x B	8	0.18ns	3.00**	0.79ns	0.37ns	2.12*
CV (%)		53.50	10.11	59.27	22.9	13.97

Significance: ns, not significant; *P< 0.05; ** P< 0.01; and *** P < 0.001

TABLE 2. Development duration of *B. tabaci* SSA1 at five constant temperatures on cassava in the laboratory in 2019

Temperature (°C)	Development duration (days) of different *B. tabaci* SSA1 growth stages						All stages
	Egg	1st instar	2nd instar	3rd instar	4th instar	Pupa	
16°C	19.99a	9.02a	12.68a	12.76a	5.63a	6.24a	65.33a
20°C	9.63b	3.02c	4.00b	6.18b	1.69b	3.02b	27.54b
24°C	7.30c	3.39b	3.48c	5.37c	1.24c	2.61c	23.39c
28°C	7.15c	3.13bc	2.94d	3.94d	1.06cd	2.28d	20.50d
32°C	5.52d	3.06c	2.80d	3.41e	1.00d	2.15d	17.93e
SD	5.11	2.49	3.86	3.57	1.88	1.66	17.7

Means within a stage followed by the different letters are significantly different at 5% significance level. Means poled over all cassava genotypes

and 32 °C (Table 2). The egg stage had the longest development period at all temperatures (Table 2).

***Bemisia tabaci* SSA1 development rate.** Developmental rates generally increased with temperature for all growth stages and total life cycle (Fig. 1), with the exception of the first nymph instar where the development rate of observed at 20 °C was similar to the development rate observed at 28 and 32 °C (Fig. 1). The lowest and highest development rates were observed at 16 and 32 °C, respectively (Fig. 1).

Simple linear regression analysis of developmental rates and temperature for each growth stage and the total life cycle further revealed a strong and significant positive relationship between development rate and temperature, with temperature accounting for between 47% (1st instar) to 82% (eggs) of the variation observed in development rate (Table 3).

Survival of immature stages of *B. tabaci* SSA1. There were significant genotype* temperature (P<0.05) effects on the survival of all immature *B. tabaci* growth stages (Table 1). For all growth stages in all genotypes, survival was lowest at 16 °C; e.g. survival ranged from 63.7 to 88.9% on Alado alado (Table 4). *Bemisia tabaci* SSA1 survival from

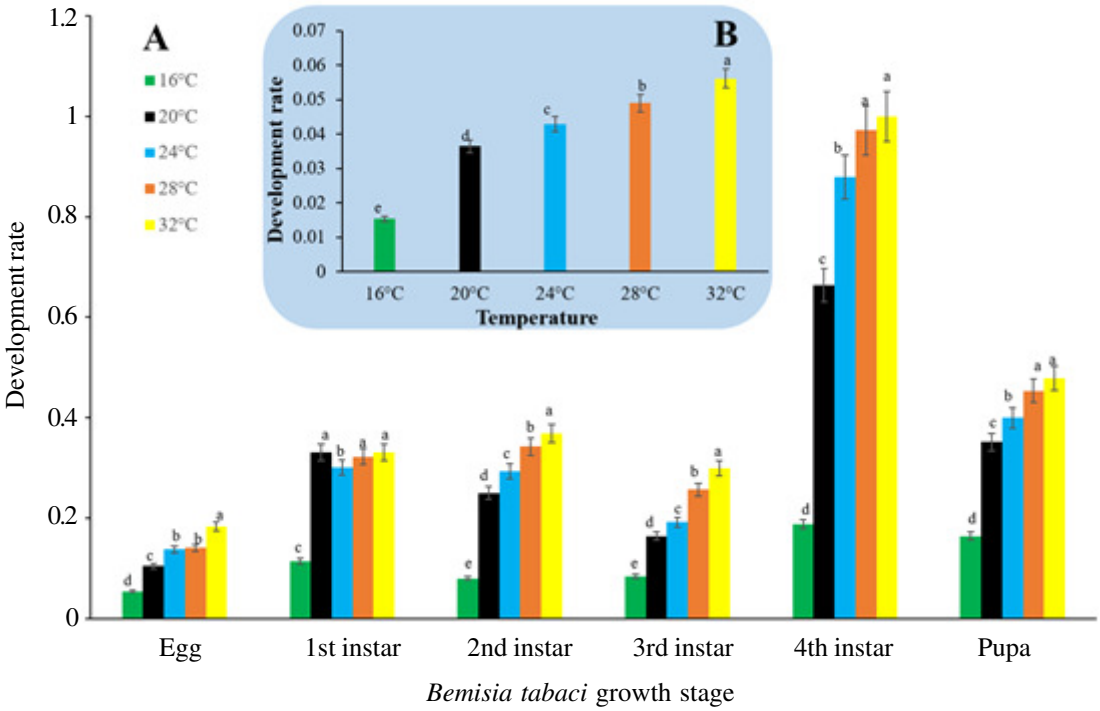

Figure 1. Developmental rates for different *B. tabaci* SSA1 growth stages (A) and all growth stages combined (B) at five constant temperatures, pooled over all cassava genotypes in the Laboratory in 2019.

TABLE 3. Linear regression parameters of temperature versus developmental rates of *B. tabaci* SSA1 on cassava

Stage	Intercept	Slope	R^2
Egg	-3.818	0.069	0.815***
1st instar	-2.618	0.053	0.47***
2nd instar	-3.459	0.084	0.688***
3rd instar	-3.554	0.077	0.802***
4th instar	-2.775	0.096	0.64***
Pupa	-2.524	0.06	0.62***
Total life cycle	-5.039	0.072	0.781***

Significance: *** $P < 0.001$; R^2, coefficient of determination

egg to adult in all genotypes at all temperatures was generally over 80%; although survival varied from 82.1% at 16 °C in Alado alado to 98.7% at 28 °C on NAROCASS 1. There were no significant survival differences between 28 and 32 °C, which recorded the highest survival for all growth stages in all genotypes. At all temperatures, over 85% of the eggs were able to reach the first instar in all genotypes (Table 4). The significant genotype effects were most pronounced in the 2nd instar stage at 16 °C where survival of 63.7% was observed for

TABLE 4. Survival of *B. tabaci* SSA1 immature stages at five constant temperatures on three cassava genotypes

Genotype	Temperature	Survival (%) of *B. tabaci* growth stage stages						All stages
		Egg	1st instar	2nd instar	3rd instar	4th instar	Pupa	
Alado alado	16°C	86.78c	87.16c	63.71c	80.26c	88.90c	85.51c	82.05d
	20°C	92.78b	90.88bc	88.84b	87.22b	89.93c	90.79bc	90.07c
	24°C	95.78ab	94.41ab	93.72ab	94.24a	95.20b	93.86ab	94.53b
	28°C	97.78ab	98.52a	96.44a	99.10a	99.24a	99.30a	98.40a
	32°C	100.00a	98.56a	97.48a	97.51a	96.64ab	98.93a	98.19a
NAROCASS 1	16°C	94.56b	94.12ab	88.94c	87.34c	79.51c	80.70b	87.53c
	20°C	93.00b	91.72b	92.00bc	92.68b	89.07b	93.05a	91.92b
	24°C	98.56a	96.88a	96.76ab	96.18ab	95.93a	97.56a	96.98a
	28°C	100.00a	96.67a	97.12a	100.00a	98.92a	99.29a	98.67a
	32°C	100.00a	97.56a	96.77ab	97.83ab	96.90a	99.41a	98.08a
NASE 14	16°C	88.33c	87.93c	81.47c	84.90c	80.76b	88.25b	85.27c
	20°C	92.44bc	93.78b	91.28b	91.80b	92.74a	94.01a	92.68b
	24°C	95.33ab	97.50ab	96.34ab	96.66a	96.41a	96.93a	96.53a
	28°C	98.44a	97.51ab	96.97a	95.68ab	95.45a	96.94a	96.83a
	32°C	100.00a	99.11a	96.63a	97.17a	96.23a	98.12a	97.88a

Means within the same stage followed by the same letter are not significantly different at 5% significance level

Alado alado, compared with 81.5% on NASE 14 and 88.9% on NAROCASS 1 (Table 5). In general, inconsistent differences in survival were noted among genotypes at temperatures of 16 to 24 °C where differences were observed. While Alado alado recorded the lowest survival of 63.7% in the 2nd nymph stage, it recorded the highest survival of 88.9% in the 4th nymph stage (Table 5). At 32 °C, survival across the different growth stages was similar in all genotypes.

Fecundity and female longevity of *B. tabaci* SSA1. Cassava genotype and their interaction with temperature did not significantly affect fecundity and female longevity ($P > 0.05$) (Table 1). However, fecundity increased significantly ($P<0.001$) with temperature, with the highest value observed at 32 °C and the lowest at 16 °C for all genotypes (Fig. 2A). The median number of eggs laid daily at 16 °C was 1 egg for Alado alado and 2 eggs for NAROCASS 1 and NASE 14 each per five females for all genotypes. This was in contrast with 35.5, 34 and 37 eggs laid daily for Alado alado, NAROCASS 1 and NASE 14, respectively at 32 °C (Fig. 2A). The reverse was true for female longevity with the highest lifespan recorded at 16 °C and the shortest at 32°C (Fig. 2B). Female *B. tabaci* SSA1 lived for 28, 29 and 27 days on Alado alado, NAROCASS 1 and NASE 14, respectively at 16 °C (Fig. 3).

Population parameters of *B. tabaci* SSA1. The population parameters, namely net reproductive rate (R_o), innate capacity for increase (r_m) and the finite rate of increase (ë) also increased with temperature; being lowest at 16 °C and highest at 32 °C in all cassava

TABLE 5. Survival of *B. tabaci* SSA1 immature stages at five constant temperatures on three cassava genotypes

Temperature	Genotype	Survival (%) of *B. tabaci* growth stage stages						All stages
		Egg	1st instar	2nd instar	3rd instar	4th instar	Pupa	
16°C	Alado alado	86.78a	87.16a	63.71b	80.26a	88.90a	85.51a	82.05b
	NAROCASS 1	94.56a	94.14a	88.94a	87.34a	79.51b	80.70a	87.53a
	NASE 14	88.33a	87.93a	81.47a	84.90a	80.75ab	88.25a	85.27ab
20°C	Alado alado	92.78a	90.88a	88.84a	87.22b	89.93ab	90.79b	90.07b
	NAROCASS 1	93.00a	91.72a	92.00a	92.68a	89.07b	93.05ab	91.92a
	NASE 14	92.44a	93.78a	91.28a	91.80ab	92.74a	94.01a	92.68a
24°C	Alado alado	95.78a	94.41a	93.72b	94.24a	95.19a	93.86b	94.53b
	NAROCASS 1	98.56a	96.88a	96.76a	96.18a	95.93a	97.56a	96.98s
	NASE 14	95.33a	97.49a	96.34ab	96.66a	96.41a	96.93ab	96.53a
28°C	Alado alado	97.78a	98.52a	96.44a	99.10a	99.23a	99.30a	98.40a
	NAROCASS 1	100.00a	96.67a	97.12a	100.00a	98.92a	99.29a	98.67a
	NASE 14	98.44a	97.51a	96.97a	95.68b	95.45b	96.94b	96.83b
32°C	Alado alado	100.00a	98.56a	97.48a	97.51a	96.65a	98.93a	98.19a
	NAROCASS 1	100.00a	97.56a	96.77a	97.83a	96.90a	99.41a	98.08a
	NASE 14	100.00a	99.11a	96.63a	97.17a	96.23a	98.12a	97.88a

Column means with dissimilar letter(s) per temperature differ significantly at $P < 0.05$

genotypes (Table 6). Generation time (T) on the other hand was inversely related to temperature with the longest and shortest T-values recorded at 16 °C and the shortest at 32 °C on all cassava genotypes (Table 6).

Sex ratio of *B. tabaci* SSA1. Cassava genotypes and their interaction with temperature had no significant effect on sex ratios ($P > 0.05$) of progeny. In contrast, temperature had significant effects on sex ratio ($P < 0.001$). From 20 to 32 °C, the proportion of male off springs reduced with temperature: with 38 males per 100 females produced at 20 °C and 9 males produced at 32 °C (Table 7). In general, fewer males were produced at all temperatures with the highest being 38 males produced per 100 females at 20 °C.

DISCUSSION

***Bemisia tabaci* SSA1 development duration.** The successful development of *B. tabaci* SSA1 at all study temperatures (Table 2) suggests that the chosen temperature range supports the development of this pest as reported earlier for temperatures between 15 and 35 °C (Muniz and Nombela, 2001; Yang and Chi, 2006). The observed decrease in development time with increase in temperature is because *B. tabaci* SSA1 is ectothermic in nature (Neven, 2000; Sgolastra *et al.*, 2011) and is known to exhibit a thermophilic tendency (Gerling *et al.*, 1986). This implies that *B. tabaci* SSA1 will thrive and reproduce rapidly as temperature increases, thus enhanced population abundance (Shrestha, 2019;

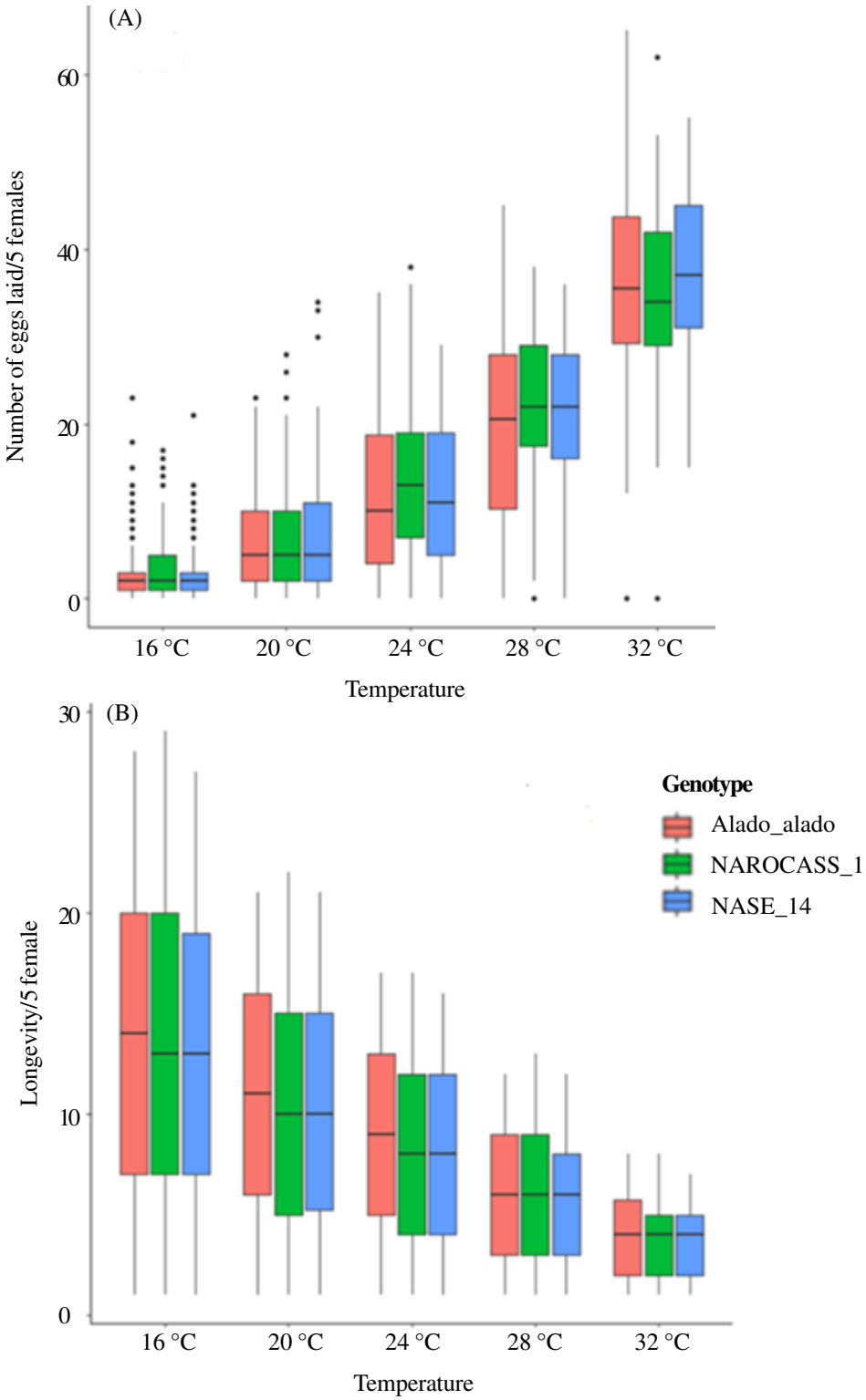

Figure 2. Box plots for the number of eggs laid daily by five females (A) and longevity of female (B) *Bemisia tabaci* SSA1 on three cassava genotypes at five constant temperatures.

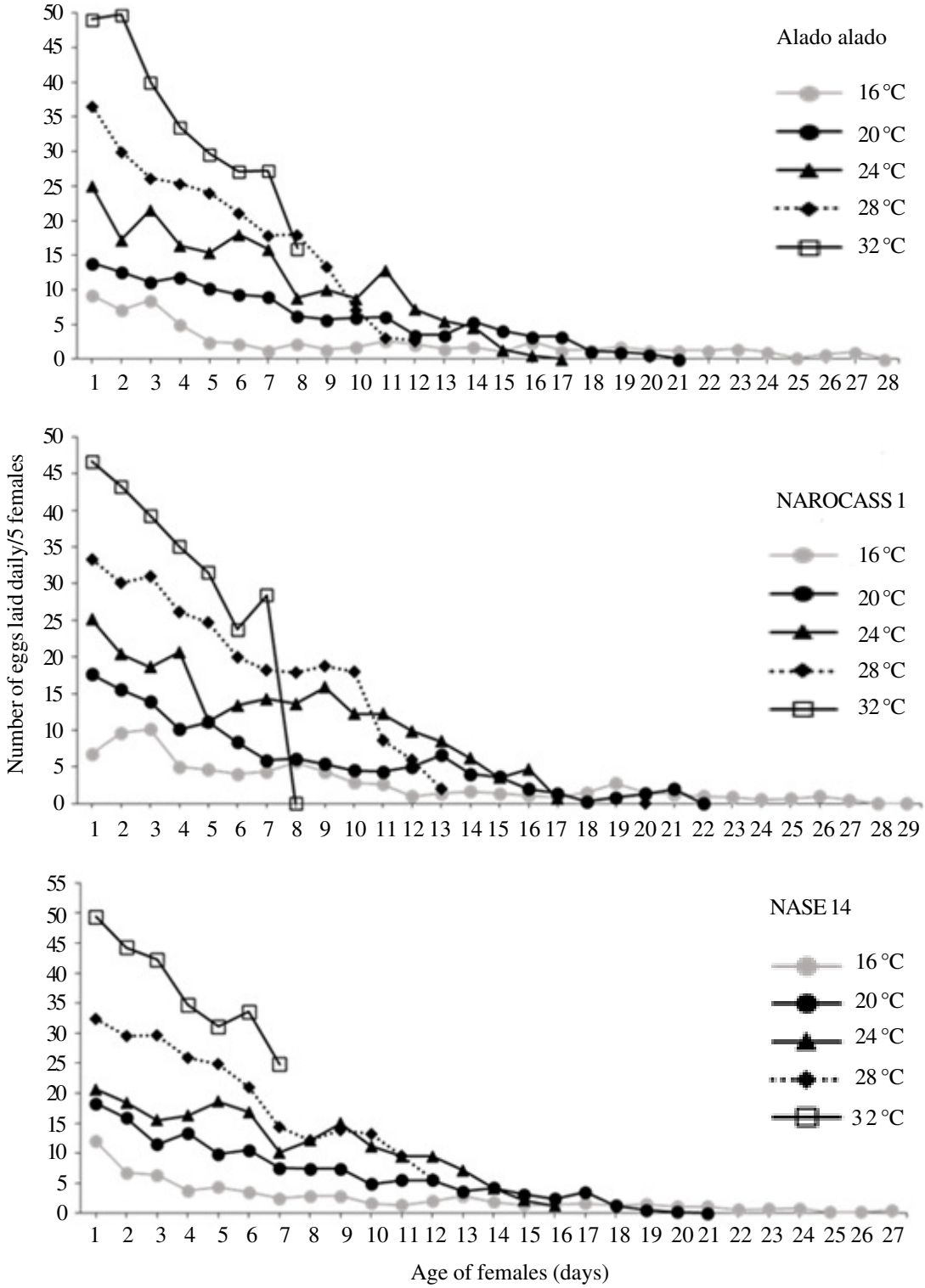

Figure 3. Number of eggs laid daily for five *B. tabaci* SSA1 females on three cassava genotypes at five constant temperatures.

TABLE 6. Life table parameters for *B. tabaci* SSA1 on three cassava genotypes at five constant temperatures

Genotype	Temperature (°C)	Parameters			
		Net reproductive rate (R_o)	Generation time (T)	Intrinsic rate of increase (r_m)	Finite rate of increase (λ)
Alado alado	16°C	1.8945	71.2027	0.0090	1.0090
	20°C	7.4934	33.8098	0.0596	1.0614
	24°C	17.6695	28.9972	0.0990	1.1041
	28°C	37.2391	25.2057	0.1435	1.1543
	32°C	48.6990	22.6390	0.1720	1.1870
NAROCASS 1	16°C	2.5949	68.9857	0.0138	1.0139
	20°C	7.1020	32.1628	0.0610	1.0628
	24°C	17.9569	29.2684	0.0987	1.1037
	28°C	40.9130	26.0386	0.1425	1.1532
	32°C	44.1370	21.9417	0.1726	1.1884
NASE 14	16°C	1.5416	69.2605	0.0062	1.0063
	20°C	6.7543	32.7889	0.0583	1.0600
	24°C	17.4408	30.3933	0.0941	1.0986
	28°C	37.4320	25.9945	0.1394	1.1495
	32°C	45.7560	21.4434	0.1783	1.1952

TABLE 7. Sex ratio of *B. tabaci* SSA1 at different temperatures on cassava

Temperature (°C)	Number of females	Number of males	Sex ratio (%)
16°C	249	60	24.10
20°C	873	333	38.14
24°C	2164	681	31.47
28°C	4514	536	11.87
32°C	5187	450	8.68

Pathania *et al.*, 2020) due to reduced thermal constraints on population dynamics under global warming situations (Deutsch *et al.*, 2008).

The longer development period at low temperature (Table 2) might be as a result of slower metabolic processes due to reduced enzyme activity and high energy consumption for physiological repair of injuries resulting from extended cold conditions (Lalouette *et al.*, 2011; Damos and Savopoulou-soultani, 2012). These findings are consistent with other reports (Cui *et al.*, 2018; Salimi *et al.*, 2018). Hence, warmer temperatures in the range of 28 to 32 °C will result in higher *B. tabaci* SSA1 populations, thus supporting Petzoldt and Seaman (2006), who anticipated higher insect populations at warmer temperatures. The lack of significant genotype and genotype*temperature interaction effect on development time indicates that the relative effect of temperature on development was similar across the three cassava genotypes used in this study. This result rules out the existence of antibiosis resistance in cassava to *B. tabaci* SSA1 infestation, and is in

agreement with the findings of Nava-Camberos *et al*. (2001).

***Bemisia tabaci* SSA1 development rate.** The high R^2 values (>0.5) in this study for the relationship between development rate and temperature (Table 3) indicates a strong linear relationship between the two for the eggs, nymphs and the total life cycle. These results show that development rate was highest at 32 °C and lowest at 16 °C, implying that *B. tabaci* SSA1 can quickly build-up its population at higher temperatures and slowly at the lower temperatures. This result indicates that 32 °C greatly favours *B. tabaci* SSA1 development, which is within the optimum temperature range reported by several authors (Bonato *et al*., 2007; Curnutte *et al*., 2014).

Among the different stages, the egg, third and second instar stages had the longest development times, respectively. This is critical information in the choice of management option (Sohani *et al*., 2007), e.g. deployment of nymph parasitoids *Encarsia sophia* and *Eretmocerus mundus* would be appropriate since they are known to prefer the 3rd (Yang *et al*., 2012) and 2nd (Urbaneja and Stansly, 2004) instar stages, respectively.

Survival of immature stages of *B. tabaci* SSA1. The high, though similar survival for all genotypes at 32 °C shows that *B. tabaci* SSA1 is adapted to high temperatures, a result in agreement with that of Bonato *et al.* (2007) who observed high survival rates at temperatures of 21 to 30 °C. This result may be due to the expression of heat shock proteins at high temperatures, as reported earlier by Wan *et al*. (2009) and Xiao *et al*. (2016) for *B. tabaci* B-biotype. Furthermore, although high temperatures are known to cause desiccation in insects, the high RH range used in this study (a norm for East Africa) offset the desiccation ability of the high temperatures (Kreppel *et al*., 2016), thus enhanced survival as temperature increased. This confirms earlier findings (Powell and Bellows, 1992; Katono *et al*., 2021), whereby higher *B. tabaci* populations under high temperature and RH conditions are also reported to improve food quality of the host plant due to abiotic stress, which may result in increased availability of soluble nitrogen in plant sap, thereby providing better feeding sites; hence the enhancing the survival of insect immature stages (White, 1984). Generally, pest outbreaks are reported in stressed plants, as a result of a weakened plant defense system (Rhoades, 1985). This result is consistent with findings of Nava-Camberos *et al*. (2001), who reported no significant difference in survival of *B. argentifolii* between the susceptible and resistant genotypes of cotton and cantaloupe.

Fecundity and female longevity of *B. tabaci* SSA1. Fecundity increased with temperature, yet the reverse was true for female longevity (Fig. 2). The highest fecundity was observed at 32 °C because high temperatures were reported to shorten the pre-oviposition period and thus increase the speed of oviposition (Huang *et al*., 2021). Additionally, high temperatures cause abiotic stress to plants, which in turn provide better feeding sites for egg laying females due increased concentrations of soluble nitrogen in plant sap, hence resulting high fecundity (White, 1984). Therefore, as temperatures increase within the optimum range, *B. tabaci* SSA1 populations are likely to increase as well.

The reduced longevity as temperatures increased may be due to the fact that high temperatures affect physiological functions of insects, hence reducing the longevity (Damos and Soulopoulou, 2015). But also, high fecundity at high temperatures increases the cost of reproduction; hence reduced adult longevity owing to the costly gamete production (Bell and Koufopanou, 1986; Harshman and Zera, 2007; Tatar, 2011). Thus, the trade-off between reproduction and survival is thought to be as a result of competitive allocation of meagre resources between reproduction and adult survival (Flatt, 2011).

Population parameters of *B. tabaci* SSA1. The observed reduction in generation time with increase in temperature (Table 5) could be because insects complete their development faster at favourable temperatures (Muturi *et al*., 2012), wherby a temperature of 32 °C is within the optimum range (30-33 °C) reported for *B. tabaci* development (Drost *et al*., 1998; Bonato *et al*., 2007). Additionally, net reproductive rate (R_0), finite rate (λ) and intrinsic rate (r_m) increased with temperature from 16 to 32 °C. This implies that more generations of *B. tabaci* SSA1 are going to occur given its multivoltine nature (Asiimwe *et al*., 2007; Pöyry *et al*., 2011; Karuppaiah and Sujayanad, 2012) which will lead to larger populations (Cannon, 1998; Sharma, 2010; Ma *et al*., 2017) of this global pest in the face of continued global warming. This confirms the findings of Yamamura and Kiritani (1998), who reported that a 2 °C temperature increase may result in up to five additional life cycles of an insect in a season. Furthermore, the projected global warming (IPCC, 2013) will increase the range of favourable conditions for *B. tabaci* SSA1, which will cover niches (high altitude areas) that were previously unfavourable (Shrestha, 2019; Sharma and Dhillon, 2020). This phenomenon has also been reported by several workers (Afrane *et al*., 2012; Lehmann *et al*., 2020). Shorter development time will lead to larger populations of *B. tabaci* SSA1 since just like other insects, its niche space is mainly defined by climatic regimes (Ma *et al*., 2017; Shrestha, 2019). Although the r_m was positive at all study temperatures, it was over 0.05 at temperature between 20 and 32 °C, suggesting that *B. tabaci* SSA1 is more productive in this temperature range; although, 32 °C is the ideal temperature for *B. tabaci* SSA1.

The study elucidated the effects of different temperatures on the biological performance parameters of *B. tabaci* SSA1, and 32 °C was best for *B. tabaci* SSA1 for expressing a strong level of reproductive capacity and fitness. Therefore, the projected climate change scenarios (Marinho *et al*., 2016; Skendzic´ *et al*., 2021) are likely to advance the overall biological fitness of *B. tabaci* SSA1, and allow for continued geographical range expansion hence increased crop production losses and prevalence of *B. tabaci* SSA1 vectored diseases in parts of the world with average temperature of 32 °C and RH range of 65-75%. In Uganda, agro-ecologies like the North Eastern Savanna grassland (hot and dry environment) and Kabale-Rukungiri highlands (cold and wet environment) (Sserumaga *et al.,* 2013), which were previously unfavourable for *B. tabaci* existence are likely to witness increased populations of this pest in the near future due increased fitness and prevailing temperatures.

Sex ratio of *B. tabaci* SAA1. The female-biased sex ratio as temperature increased from 20 to 32 °C may be as a result of increased adult activity and mating success at high temperatures (Enkegaard, 1993), thus increased proportion of fertilised eggs resulting into more female progeny. Similar results were reported earlier on *B. tabaci* (Gerling *et al*., 1985; Enkegaard, 1993) and *Thrips tabaci* (Woldemelak *et al*., 2021). Furthermore, increase in temperature has been reported to increase host plant quality for insect colonisation (White, 1984), a phenomenon reported to result into female biased sex ratio (Horowitz and Gerling, 1992). The implication of this result is that *B. tabaci* SSA1 populations can effortlessly build-up at high temperatures.

CONCLUSION

Temperature has significant effect on development duration, survival, longevity and population parameters of *B. tabaci* SSA1; while casssava genotype has no significant effect on these parameters. These results have shown that at high relative humidity (RH), a temperature of range of 24 to 32 °C greatly enhances *B. tabaci* SSA1 development,

survival and fitness; hence supports higher pest populations climaxing at 32 °C. The study has also shown that at high temperatures, tolerance in genotypes such as Alado alado broke down hence confirming absence of antibiosis resistance to *B. tabaci* SSA1 in the cassava genotypes that were tested. Findings of this study provide useful data for the development of prediction models for *B. tabaci* SSA1 population dynamics and future outbreaks, as well as aid the design and development of improved integrated pest management strategies for this pest in the context of global warming. Future studies are required to understand the combined effect of temperature and RH variations on *B. tabaci* SSA1 population dynamics.

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