

# Life-table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda

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## Abstract

A study was set up to determine the sources and rates of mortality of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) on field-grown cassava in Uganda. Using a cohort-based approach, daily direct observations were used to construct partial life tables for 12 generations of egg and nymph populations which were studied over a 1-year period. Mortality was categorized as dislodgement, predation, parasitism (for nymphs only), unknown death, and inviability (for eggs only). The highest mean rate of marginal mortality across all stages was attributed to parasitism, with dislodgement and predation following, respectively. Across all factors, the highest mean rate of marginal mortality was observed in the fourth instar followed by the eggs, first-, second-, and third-instars, respectively. Key factor analysis revealed that dislodgement was the major mortality factor contributing to generational mortality in eggs while for nymphs, parasitism in the fourth instar was the main driving force behind the observed generational mortality. Highest irreplaceable mortality in both the egg and nymph stages was attributed to dislodgement followed by parasitism and predation, and least was due to unknown death. Across stages, highest irreplaceable mortality rates were observed in the eggs and the fourth-instar nymphs. The other stages had relatively low rates of irreplaceable mortality. Rain-protection experiments revealed no significant differences in marginal mortality rates when compared to the open field situation.

## Introduction

*Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) is a key pest of both field and greenhouse crops in many parts of the world. It causes both direct and indirect damage through feeding on plant sap. Direct feeding damage is shown by leaf chlorosis, a mottled appearance, reduction in plant vigour, general plant stunting, and induction of various phytotoxic disorders in several plants (Brown & Bird, 1992). Indirect damage is mainly through transmission of plant viruses, and to a lesser extent through encouraging development of sooty mould (Bedford et al., 1994; Schuster et al., 1996). Transmission of plant viruses in many tropical and subtropical countries represents the most economically important role of this pest (Basu,

1995). At least seven genera of whitefly-transmitted viruses have so far been described, of which the most economically important are the begomoviruses (Cohen, 1990; Brown & Bird, 1992). In Uganda, cassava is the main host of this pest, where it is the vector of cassava mosaic geminiviruses (CMGs) (Geminiviridae; genus *Begomovirus*) that cause cassava mosaic disease (CMD). An epidemic of an unusually severe form of the disease spread throughout northern and central Uganda during the 1990s (Otim-Nape et al., 1997). More recently this epidemic has spread further into neighboring countries in East and Central Africa (Legg, 1999).

Several control options have been developed for CMD, the most important of which has been the use of CMD-resistant varieties. These varieties have been widely effective in controlling the CMD epidemic in Uganda (Otim-Nape et al., 1994; Thresh et al., 1994; Legg et al., 1999), but have recently been shown to support high *B. tabaci* populations (JP Legg, unpubl.). This poses a threat to the

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future effectiveness of CMD control because of the ability of these whiteflies to migrate and spread CMGs to susceptible varieties grown nearby and the increased likelihood of the appearance of more virulent virus strains through new virus–vector interactions.

Many of the biological characteristics of *B. tabaci* such as multivoltinism, high reproductive rate, broad host range, ability to migrate great distances, and vectoring of plant viruses have increased the difficulty of developing sustainable management options for this pest (Gerling & Mayer, 1996). Outbreaks of large *B. tabaci* populations have raised the need to obtain information as to their possible causes and cures. Despite major advances having been made in understanding the biology and behaviour of *B. tabaci* and in developing pest-management systems, there is a need to develop a better understanding of the factors affecting *B. tabaci* population dynamics on cassava. One approach is to develop age-specific/cohort-based life tables of *B. tabaci* under field conditions. These involve studying the population dynamics of a known number of individuals of the same developmental stage and using this information to determine the relevance and importance of the different mortality factors affecting the pest. Life tables have previously been used to study population dynamics of many insects, especially pests and their natural enemies (Carey, 1989; Cornell & Hawkins, 1995; Hawkins et al., 1999; Naranjo & Ellsworth, 2005). The current study therefore aims to use a comparable approach to determine the mortality factors affecting immature *B. tabaci* populations on CMD-resistant cassava in the field. This will provide essential background information for developing effective management options to control the current super-abundant *B. tabaci* populations on CMD-resistant varieties.

## Materials and methods

### Study site and plants used

The experiments were set up at Namulonge Agricultural and Animal Production Research Institute, Kampala, Uganda. The CMD-resistant variety, Nase 4 (Ssemakula et al., 1997), was planted in two fields in August and November 2003. Each field measured 14 × 9 m, and consisted of 150 plants planted in rows 1 m apart. The study was carried out over 6 months in each field, which represented half of the normal growing period of cassava.

### Cohort establishment

Ten plants were randomly chosen from each field and monthly cohorts of both eggs and nymphs were established separately. Cohorts of eggs were selected from naturally established populations on the underside of the

top-most expanded plant leaf. Eggs used were freshly laid and these were identified by their creamy white colour and location on the youngest leaves at the top of the plant. The leaves were turned over and a 10× hand lens was used to locate the eggs. Using a nontoxic fine marker, a circle was drawn around each selected egg. All other eggs on the leaf were removed by gently rubbing them off the underside of the leaf with the edge of a soft paper. This ensured that every leaf chosen only remained with a specific number of eggs, all of which had been marked. A single leaf was used per plant and 10–20 eggs were marked depending on the populations on the plant at the time of marking. A small numbered tag was tied around the petiole of the leaf bearing the marked eggs.

Settled first-instar nymphs were identified and marked on separate leaves and plants. The leaves and nymphs were marked using the same procedure as above. Settled first-instar nymphs were identified by their translucent colour, small size, and characteristic ovoid shape. Marked nymphs were revisited after 1 h to ensure that they had settled. Any nymph that had crawled out of the circle was replaced by marking another one. A minimum of 30 nymphs were marked per plant for 10 plants, to give a total of 300 nymphs per cohort. The precise number per plant varied depending on the season and stage of growth of the plant but always approximated 30. All cohorts in each plot were established on the same day, and were marked between 09:00 and 11:00 hours. The cohorts were established monthly for 6 months, in each of the plots.

### Determination of mortality factors

After cohorts had been established, each marked egg and nymph was observed daily using a 10× hand lens. Each nymph was observed for 30 days unless it died or disappeared. This time period was sufficient to allow for both adult whitefly and parasitoid emergence. For the eggs, each was observed for a total of 15 days, substantially in excess of the previously reported average egg hatching period of 11 days for *B. tabaci* on cassava (Legg, 1995). Based on the establishment of separate cohorts of eggs and nymphs, mortality in the crawler stage is missed and thus is not accounted for in this study.

Each day, the instar and state of each nymph were recorded and categorized as alive, missing, dead, predated, or parasitized. A nymph was categorized as ‘alive’ based on its size, shape, and the symmetrical position of mycetomes; predation observed was mainly due to sucking, leaving the nymphs empty and translucent or, in some cases, partially empty, while parasitism was distinguished by the displacement of mycetomes or presence of parasitoid larvae in the third or pupae within the fourth-instar nymphs. A sample of 25 parasitized nymphs was collected and, basing on the methods

of Otim et al. (2005), were identified. Nymphs that were missing were assumed to have been displaced or eaten. The stage of missing was determined based on its appearance on the previous day. To maintain uniformity in determining causes of mortality, only three people carried out all field observations throughout the duration of the experiment.

The daily counts disclosed the continuous disappearance of marked individuals, either eggs or nymphs. The presence of these individuals had been accounted for on 1 day and they were absent without leaving a trace on the next. Naranjo & Ellsworth (2005) noted this phenomenon as 'dislodgement', a term subsequently adopted as a distinct mortality source in this experiment.

A parallel study conducted on the same fields to catalogue the predators of *B. tabaci* was done. All insects in the field were collected and fed on *B. tabaci* eggs and nymphs in the laboratory, and those found to be predators were sent to the US Department of Agriculture insect museum and identified (Asiimwe, 2006). A study to monitor the activity of these predators was carried out on the same fields. During this time, 24-h checks done at 3-h intervals over a 1-month period were carried out (Asiimwe, 2006).

#### Rain-protection experiments

Following the observation that heavy rains were able to dislodge whitefly nymphs from the leaves (Naranjo & Ellsworth, 2005), an experiment to determine the contribution of rain and direct wind was carried out on the same plots. Two plants were selected per field and protected from rain and wind by placing large umbrellas, covering the entire canopy of the plants. Two monthly cohorts, each consisting of 25 eggs and 50 nymphs, were marked on each plant. Each individual egg and nymph was followed for 15 and 30 days, respectively, or until it hatched, emerged or disappeared. During this time, the umbrellas were removed before each observation and replaced immediately after data collection.

#### Data analysis

*Determination of mortality rates.* The methods proposed by Buonaccorsi & Elkinton (1990), Elkinton et al. (1992), and Naranjo & Ellsworth (2005) were used to determine

age-specific marginal rates of mortality for each factor based on observed (apparent) rates of mortality. The marginal rate estimates the level of mortality arising from a single factor assuming that factor was the only one operating at the time. A mortality factor may be obscured by another factor because these factors operate in a contemporaneous fashion with no obvious sequence of events. Dislodgement is the only factor for which the apparent rate of mortality is equal to the marginal rate because it can not be obscured by any other factor. The general equation for determining marginal rate of mortality was derived from Naranjo & Ellsworth (2005) and it is:

$$M_A = d_A / (1 - d_B),$$

where  $M_A$  is the marginal rate of mortality for factor A,  $d_A$  is the apparent (observed) rate of mortality from factor A, while  $d_B$  is the sum of apparent mortalities from all other relevant contemporaneous factors. The apparent rates of mortality needed to estimate marginal rates of mortality for each factor within each stage are outlined in Table 1.

*Irreplaceable mortality.* Following the methods of Carey (1989) and Naranjo & Ellsworth (2005), irreplaceable mortality was calculated for each mortality factor and each developmental stage. Irreplaceable mortality is that portion of total generational mortality that would not occur if a given mortality factor was eliminated (Southwood, 1978; Naranjo & Ellsworth, 2005). The general equation for its determination is:

$$I_C = [D - (1 - M_A)(1 - M_B)], \text{ and}$$

$$D = [1 - (1 - M_A)(1 - M_B)(1 - M_C)],$$

where  $M_A$  is the marginal mortality for factor or stage A, B, or C.  $I_C$  is the irreplaceable mortality for factor or stage C and excludes marginal mortality of the factor or stage of interest (which in this case is C).

*Key-factor analysis.* Data were transformed to natural logarithms for key-factor analysis. The method of Varley &

**Table 1** Matrix for determining marginal rates of mortality of *Bemisia tabaci* from apparent rates of relevant competing contemporaneous factors, based on the methods of Naranjo & Ellsworth (2005)

Marginal rate ( $M_A$ )	Apparent rate ( $d_A$ )	Other apparent rates ( $d_B$ )	Stage
Inviability	Inviability	Predation + dislodgement	Egg
Parasitism	Parasitism	Predation + dislodgement	Third and fourth instars
Predation	Predation	Dislodgement	Egg and all nymph stages
Unknown	Unknown	Predation + dislodgement	Egg and all nymph stages

Gradwell (1960) was used to calculate individual sources of mortality ( $k$ ) and therefore total mortality ( $K$ ) for each generation, where  $k = \log$  number before mortality minus  $\log$  number after mortality, and represents a proportion of the number dying due to the observed mortality factor. The method of Podoler & Rogers (1975) was then used to quantitatively evaluate key factors by regressing individual  $k$ -values on total  $K$ . This method identifies the key factor as that associated with the largest regression coefficient (slope). The method of Smith (1973) was then used to determine the relative importance of all factors by sequentially eliminating each key factor based on the regression coefficient until all but the final two factors were eliminated. Partial life tables were then constructed using the above values.

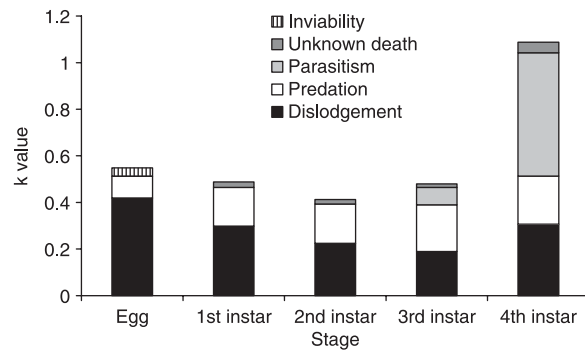
## Results

### Mortality experiments

*Sources and levels of mortality.* Partial life tables were developed for all 12 generations of eggs and nymphs separately with considerable variation in marginal mortality rates for each factor across all the generations ( $P < 0.001$ ,  $n = 12$ ). The highest mean rates of marginal mortality across all stages were associated with parasitism ( $0.30 \pm 0.127$ ) (mean  $\pm$  SE), followed by dislodgement ( $0.29 \pm 0.039$ ), predation ( $0.17 \pm 0.020$ ), inviable eggs ( $0.04 \pm 0.009$ ), and unknown death being the least ( $0.03 \pm 0.009$ ). Holm-Sidak pairwise comparisons (Hochberg & Tamhane, 1987) revealed significant differences between dislodgement and the other mortality factors affecting the egg population ( $P < 0.001$ ,  $n = 3$ ) but no significant difference was observed between mortality due to predation and that due to inviability (Table 2).

**Table 2** One-way analysis of variance of marginal rates of *Bemisia tabaci* egg and nymph mortalities across 12 generations on cassava in Uganda

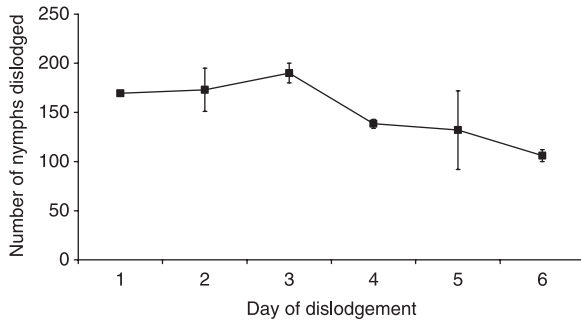
Sources of mortality	Eggs (P-values)	Nymphs (P-values)
All sources	0.001	0.001
Dislodgement vs. inviable	0.001	–
Predation vs. inviable	0.121	–
Dislodgement vs. predation	0.001	0.133
Dislodgement vs. unknown death	–	0.001
Parasitism vs. unknown death	–	0.001
Predation vs. unknown death	–	0.001
Dislodgement vs. parasitism	–	0.444
Parasitism vs. predation	–	0.452



**Figure 1** Mean levels of mortality factors within each immature *Bemisia tabaci* stage expressed as  $k$  values, across all generations on cassava in Uganda.

Pooled over all developmental stages, the highest marginal mortality rate was observed in the fourth instars ( $0.27 \pm 0.101$ ) followed by the eggs ( $0.18 \pm 0.119$ ), first ( $0.16 \pm 0.079$ ) and second instar ( $0.14 \pm 0.062$ ), with the least in the third instar ( $0.12 \pm 0.045$ ). Across generations, the highest levels of mortality were associated with parasitism, dislodgement, and unknown factors (Figure 1). There were no significant differences ( $P = 0.340$ ,  $n = 12$ ) in marginal rates of mortality across generations. Pooled over all instars, there was significant variation in the rates of marginal mortality acting on the nymph population ( $P < 0.001$ ,  $n = 4$ ) and pairwise comparison (Holm-Sidak) revealed significant differences ( $P < 0.001$ ,  $n = 4$ ) between all mortality factors except between predation and dislodgement, dislodgement and parasitism, and parasitism and predation (Table 2). Basing on the methods of Otim et al. (2005), parasitism was mainly due to *Encarsia sophia* (Girault and Dodd) and *Eretmocerus mundus* (Mercet), which are the most commonly occurring *B. tabaci* parasitoids in Uganda (Otim et al., 2005). A parallel study (Asiimwe, 2006) showed that predation was mainly due to *Serangium* spec. nov. (Coleoptera: Coccinellidae). Pooled over all instars, highest levels of dislodgement were observed on the first 3 days of the instar, with the numbers gradually rising until they peaked on the third day of a new instar (Figure 2).

*Key-factor analysis.* Using the methods of Smith (1973) and Podoler & Rogers (1975), multiple regressions were performed to determine the key factor for each stage. This was carried out for all mortality factors in each stage. Results revealed dislodgement as the major factor contributing to overall mortality in the egg populations ( $P < 0.001$ ,  $R^2 = 0.66$ ). No other factor was found to significantly contribute to generational mortality in the egg populations. In the



**Figure 2** Mean ( $\pm$  SE) rates of dislodgement of *Bemisia tabaci* instars pooled over all generations and all instars on cassava in Uganda.

nymph populations, parasitism in the fourth instar was most closely associated with overall generational mortality ( $P < 0.001$ ,  $R^2 = 0.74$ ). On removal of this mortality factor, predation in the second instar was the most important factor ( $P = 0.003$ ,  $R^2 = 0.61$ ). No factor was found to significantly contribute to overall generational mortality in either the first or third instars (Table 3).

Across all developmental stages, highest rates of irreplaceable mortality were associated with dislodgement ( $0.13 \pm 0.022$ ), parasitism ( $0.07 \pm 0.017$ ), predation ( $0.06 \pm 0.011$ ), and unknown death ( $0.01 \pm 0.003$ ). No irreplaceable mortality was associated with egg inviability. Pooled over all developmental stages, the highest rates of irreplaceable mortality were associated with the egg stage ( $0.19 \pm 0.025$ ), followed by the fourth instar ( $0.17 \pm 0.025$ ), first instar ( $0.04 \pm 0.008$ ), third instar ( $0.04 \pm 0.008$ ), and second instar ( $0.03 \pm 0.004$ ) in declining order of importance.

**Rain-protection experiments**

There were no significant differences ( $P = 0.25$ ,  $n = 5$ ) in rates of marginal mortality between the rain protected and the open field experiments though generally lower rates were observed under the rain protection with dislodgement accounting for  $0.17 (\pm 0.024)$ , predation for  $0.13 (\pm 0.031)$ , and parasitism for  $0.11 (\pm 0.005)$ . Egg inviability and unknown death in nymphs were not observed in this experiment. The levels of natural enemy mortality varied between the experiments with predation occurring at a higher rate than parasitism in the rain-protected experiment, while the reverse was true in the open field experiment.

**Discussion**

The study showed that egg mortality was due to dislodgement, predation, and inviability. Sources of nymph mortality were dislodgement, predation, parasitism,

and unknown death. This is consistent with findings in most of the previous studies, which also reveal natural enemies and weather-related factors as the major sources of mortality. The rates of mortality from this study are largely consistent with previous studies showing highest mortality due to dislodgement followed by natural enemies in both the egg and nymph populations. The main source of natural enemy induced mortality was parasitism in the nymphs, which accounted for the highest levels of mortality observed in the fourth instar. These two factors, dislodgement and parasitism, were also consistently associated with highest irreplaceable mortalities indicating their importance to overall immature *B. tabaci* mortality.

In previous studies, dislodgement has largely been associated with the combined effect of wind, rain, and chewing predators. Studies by Khalifa & El-Khidir (1964) in Sudan revealed a dramatic decline in *B. tabaci* populations

**Table 3** Key-factor analysis of mortality factors affecting *Bemisia tabaci* populations over 12 generations on cassava in Uganda, based on the methods of Smith (1973) and Podoler & Rogers (1975)

Stage/factor	Step			
	1	2	3	4
<b>Egg</b>				
Predation	0.606			
Dislodgement	<b>0.879</b>			
Inviability	1.77			
<b>First instar</b>				
Predation	2.342			
Dislodgement	-0.466	-0.536	-0.326	
Unknown death	-9.892	1.250		
<b>Second instar</b>				
Predation	12.346			
Dislodgement	4.948	2.576		
Unknown death	8.362	2.465	2.208	
<b>Third instar</b>				
Predation	2.321	3.038	2.642	
Dislodgement	3.503			
Unknown death	0.982	1.036	1.776	0.643
Parasitism	2.277	4.303		
<b>Fourth instar</b>				
Predation	2.109			
Dislodgement	0.092	-0.591	-0.041	-1.741
Unknown death	0.369	1.635		
Parasitism	<b>1.014</b>			

Values represent the slope of individual k values on total K. At each subsequent step, the factor with the highest slope was eliminated to determine the relative contribution of each factor to generational mortality. The factor in bold was found to significantly ( $P < 0.001$ ,  $n = 12$ ) contribute to total K and is therefore the key factor in the stage indicated.

following heavy rains. Similarly, Avidov & Harpaz (1969) revealed delays in outbreaks of *B. tabaci* populations in the Jordan valley following low relative humidities caused by Khamsims (hot and dry winds). Results from our manipulative experiments, in which the plants were protected from heavy rain, resulted in dislodgement rates that were not significantly different from those of unprotected plants. Considering the otherwise favourable climatic field conditions in our plots, and given that the experimental area does not experience high winds or large variations in relative humidity, we ruled out the effect of weather as a major whitefly dislodging factor. Whitefly dislodgement by chewing insects was also considered. Considering that *Serangium* spec. nov. kills its host by sucking out its contents and leaving the corpse on the leaf, only sugar ants were chewing predators capable of removing whitefly nymphs from the leaf. Observations of sugar ant activity on the leaf (Asiimwe, 2006) showed that they rarely fed on *B. tabaci* nymphs, preferring to feed on honeydew. This coupled with the fact that they were only occasionally seen in the fields, yet dislodgement was consistently high in most generations rules them out as a major cause of the observed dislodgement. Thus, it appears that dislodgement is related to life history and/or physiological factors. As shown in Figure 2, most of the dislodgement occurred on the third day of each instar, indicating a possible failure of the newly formed nymph to reinsert its stylets into the phloem of the leaf after moulting as shown by Walker & Perring (1994). In addition, studies by Jiang et al. (2001) on whitefly host resistance suggested that resistance is correlated with epidermal and/or mesophyll features that inhibit whiteflies from reaching phloem sieve elements explaining that the plant develops a defence mechanism whereby on reinsertion of the mouth parts, the nymph finds the plant sap unsuitable and thus starves and drops off after a few days. This could have been the case in our study.

Our study revealed that parasitism in the fourth instar is the most important factor driving nymphal mortality, while dislodgement is the key factor determining egg mortality. The relatively high irreplaceable mortality from parasitism, coupled with parasitism being the key mortality factor, points to its importance in reducing the nymph populations. This differs from previous similar studies on *B. tabaci* where Horowitz et al. (1984) found mortality due to disappearance in the first instar to be the key factor, and the most recent study by Naranjo & Ellsworth (2005), which found predation in the fourth instar as the major factor. These studies, however, were conducted using cotton as the host plant. The differences observed in this study could be due to the different microenvironment provided by cassava. A bushy year-round semiperennial such as

cassava might provide a more favourable environment for the more specialist natural enemies such as parasitoids. The differences may have also occurred due to ecosystem variations between Uganda and Arizona, where their study was carried out. In Uganda, cassava is grown on small plots, which are never completely free of whiteflies and given that the cassava growth cycle is 1 year, the whiteflies are present all year round although the highest populations are observed at 3–4 months after planting. On harvesting the cassava, the whiteflies migrate to new cassava plants as there are no good alternative hosts for the cassava whitefly. This is in contrast with the Arizona system, where cotton has a spring and summer growth cycle (March–September), followed by a cool fall and winter during which no whitefly and parasitoid development occurs. On harvesting the cotton, the whiteflies move to other host plants where they develop until a new cotton crop is planted. Sucking predators, though observed in relatively high numbers, contributed much less to mortality compared to dislodgement and parasitism in both the eggs and nymphs. This could have been due to the fact that there was only one prominent sucking predator species, *Serangium* spec. nov. This contrasts with the cotton system described by Naranjo & Ellsworth (2005) where up to three species were found to contribute significantly to predation.

Results of this study serve to corroborate results of a similar study by Legg (1995), which found parasitism in the fourth instar and dislodgement in the eggs as the key factors. The study by Legg (1995) was carried out in a pre-CMD-epidemic situation while this study was carried out in the current post-epidemic situation. The similarity in results shows the absence of major differences in major factors causing *B. tabaci* mortality in pre- and post-epidemic situations.

The cohort-based system coupled with the daily observation of each individual in the cohort was able to give us comprehensive measurements on the rates of mortality affecting this pest. The combination of dislodgement and natural enemies causes most of the mortality observed on cassava in the field. Because parasitism is the key late stage source of mortality, enhancing the overall effect of parasitism is the most effective way of increasing overall generational mortality. Studies by Morris (1957) revealed that adding mortality to a factor that is already occurring at high levels will have a greater effect in reducing generational survival than adding it to a low level factor. In our case, addition of mortality to fourth instars and in particular to parasitism and dislodgement at this stage will bring about adequate control or even reduction of this pest on cassava. Therefore, efforts aimed at conserving and/or enhancing the levels of parasitism at this stage should be adopted for cassava. A good option in this case would be to

promote development of cassava varieties that support fewer *B. tabaci* numbers but encourage survival and oviposition of the native parasitoid species in Uganda and for this, future studies will need to concentrate on finding local land races or developing new varieties that discourage the pest while encouraging the parasitoids. An additional option for enhancing mortality could be the introduction, after careful climate matching and other suitability studies, of exotic parasitoids to complement the native species.

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