

Bionomics of the sweet potato weevil, *Cylas puncticollis* (Coleoptera: Brentidae) on four different sweet potato varieties in sub-Saharan Africa

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Abstract

Sweet potato (*Ipomoea batatas* (L.) Lam.) is an important staple food crop in sub-Saharan Africa. A limiting production factor is infestation by the sweet potato weevil *Cylas puncticollis* (Boheman) (Coleoptera: Brentidae). The use of host plant resistance is an essential component of Integrated Pest Management (IPM). Therefore, the bionomic parameters of *C. puncticollis* were studied under laboratory conditions (30 ± 1 °C and 75 ± 5 % RH) on four sweet potato varieties commonly grown in Ghana (Apumoden, Ligri, Bohye, and Okumkom) to determine their susceptibility to the pest. There were significant varietal differences between some of the parameters. Egg to adult development time was highest on Okumkom while larval survival, emergence rate, intrinsic rate of increase, and the net reproductive rate were lowest on Bohye. The results of this study indicate that Bohye was the least susceptible variety compared to the other varieties tested and can be used in host plant resistance as part of an IPM programme against *C. puncticollis* in Ghana.

Keywords: host plant resistance, integrated pest management, life table parameters, susceptibility

1 Introduction

Sweet potato (*Ipomoea batatas* [L.] Lam.) is a staple food for a large proportion of the population in many parts of sub-Saharan Africa (Bouwkamp, 1985). Recent projections by the International Food Policy Research Institute indicate that sweet potato production in Africa will be doubled by 2020. However, productivity in sub-Saharan Africa has remained static at around 5.1 t ha^{-1} compared to a world average of 12.2 t ha^{-1} (FAOSTAT, 2016). It is a tolerant crop that, once established, will reliably produce adequate

yield under marginal conditions with no inputs and minimum or intermittent care under a wide range of rainfall patterns (Ewell, 2002). The most important production constraint worldwide is plant damage caused by sweet potato weevils, viz. *Cylas* spp. (Rees *et al.*, 2003). *Cylas* spp. can damage every harvestable part of the crop, with devastating consequences especially for poor farmers (Chalfant *et al.*, 1990; Nottingham & Kays, 2002) leading to lower income and reduced food security (Smit, 1997; Magira, 2003).

In Africa, the three *Cylas* species, *C. formicarius* (Fabricius), *C. puncticollis* Boheman and *C. brenneus* (Fabricius) (Coleoptera: Apionidae) (Talekar, 1987; Ames *et al.*, 1997) are known to attack sweet potato in the field and in storage. In Ghana, *C. puncticollis* can cause yield losses of up

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to 50 % (Darko, 2000). Infestation on stored tubers not only reduces quantity, but also reduces the marketability of the commodity because of the unpalatable terpenoids produced by the plant in response to infestation caused by the weevil (Ndunguru *et al.*, 1998; Stathers *et al.*, 2003a). Presently, no viable technology exists to combat sweet potato weevil in Africa. However, host plant resistance could be an essential component of Integrated Pest Management (IPM) against sweet potato weevil (Kabi *et al.*, 2001; Stathers *et al.*, 2003a; Stevenson *et al.*, 2009).

Life table parameters are important to draw more reliable conclusions on susceptibility status of a given crop plant to a specific insect pest (Braendle *et al.*, 2006; Mirmohammadi *et al.*, 2009; Goodarzi *et al.*, 2015; Mahmoudi *et al.*, 2015). This work assessed the susceptibility of four different sweet potato varieties commonly grown in Ghana to *C. puncticollis*.

2 Materials and methods

This work was carried out at the entomology laboratory of the African Regional Postgraduate Programme in Insect Science (ARPPIS), University of Ghana, Accra.

2.1 Insect culture

A colony of sweet potato weevils was established in the laboratory ($30 \pm 1^\circ\text{C}$ and $75 \pm 5\%$ RH) from infested stored tubers collected from farmers in Akatsi located at $06^\circ07'29.10''\text{N}$, $00^\circ47'33.21''\text{E}$ (Volta region, Ghana). The tubers were incubated in rectangular $17.0 \times 17.0 \times 9.5$ cm plastic containers fitted with a mesh cover at the top to allow ventilation and placed a paper towel at the bottom to suck excessive moisture resulting from transpiration or putrefaction of stored tubers. Upon emergence, male and female adults were removed from the containers and were kept in rectangular $40 \times 26 \times 26$ cm plastic containers where they were provided with un-infested tubers for infestation. The infested tubers were removed and replaced weekly with new ones. The infested tubers were kept in incubation boxes for adult emergence.

2.2 Determination of developmental period and survival rate of *C. puncticollis* immature stages

Four un-infested stored tubers of each sweet potato variety were washed, wiped dry and offered to gravid naive female weevils for 24 h for oviposition. Twenty cubes each containing one egg were cut from each of the infested stored tubers. A small slit was made on each cube just to make the egg visible inside the oviposition hole. The experiment was

set up as a completely randomized design with four replications where cubes from one storage root represented one replication. The cubes were kept in containers and were observed daily under stereomicroscope until all eggs hatched or collapsed to determine the egg incubation period and egg survival.

Upon hatching, each 1st instar larva (≤ 24 h old) was transferred to an about 3 mm deep well made on a new fresh sweet potato cube ($1.5 \times 1.5 \times 2.0$ cm) of the same variety from which the egg hatched. This was done by using a needle nosed forceps and a fine brush. The well was then covered with a glass slide and the cube held between two slides with rubber bands. On the second day, dead larvae which didn't show any sign of feeding before they died were discarded; it was assumed that death was caused by the transfer procedure and not due to varietal effect. The remaining cubes were observed daily to determine larval and pupal developmental period and survival until adult emergence. Cubes were changed every week to avoid contamination by fungi or drying out till adult emergence. The sex of emerged adults was also determined.

2.3 Survival and fecundity of *C. puncticollis* adult

Newly emerged (< 24 h old) adults obtained from incubated pupae were paired (sexed by the shape of distal antennal segments, as described by Smit *et al.*, 2001) and kept in a transparent plastic jar ($\varnothing = 6.3$ cm; $h = 10.5$ cm). A fresh piece of un-infested tuber was cut almost flat (5 cm by 2 cm) and placed in the plastic jar with the periderm facing upwards until the last individual died. The jar was closed with muslin cloth. For each variety, fifteen pairs of weevils were daily monitored and continued until all adults died. The pre-oviposition period, oviposition period, post-oviposition period, and adult longevity and fecundity were determined.

2.4 Data analysis

Time from oviposition to adult emergence, survival, daily fecundity, and sex ratio (proportion of females) of *C. puncticollis* on different sweet potato varieties were used to construct the net female maternity, $l_x m_x$ (where l_x is the fraction of females alive at age x and m_x is the number of daughters born to surviving females at age x) life tables from which demographic growth parameters were calculated. The effects of sweet potato variety on developmental period and survival of immature life stages, sex-ratio, adult longevity and fecundity were analysed with one-way analysis of variance (ANOVA) and the means were separated by Student–Newman–Keuls (SNK) test. Survival of all immature stages was arcsine $\sqrt{(p/100)}$ transformed prior to analysis. Life table parameters including the intrinsic rate of increase (r_m),

the net reproductive rate (R_0), the finite rate of increase (λ), the mean generation time (G) and the doubling time (t) were calculated according to Hulting *et al.* (1990), using the jack-knife programme and subjected to ANOVA, using the general linear model (GLM) procedure of SAS for PC (SAS Institute, 1997). Differences in intrinsic rate of increase (r_m) values among populations were calculated following the protocol by Dixon (1987) and compared with Newman–Keuls sequential tests (Sokal & Rohlf, 1995) based on jack-knife estimates of variance for r_m values (Meyer *et al.*, 1986).

3 Results

3.1 Developmental time, survival of immature life stages and sex-ratio of *C. puncticollis*

Eggs were laid singly in holes and covered with a root plug. The egg incubation period did not vary significantly with sweet potato variety ($F_{3,15} = 0.44$; $P = 0.726$) (Table 1). On all the varieties, egg hatching reached its peak on 4th day with about 60% of total number of eggs laid. Larval developmental time ($F_{3,15} = 3.33$; $P = 0.056$) and the pupal developmental time ($F_{3,15} = 1.56$; $P = 0.251$) also did not vary among the varieties. The total developmental period of *C. puncticollis* was significantly longest ($F_{3,15} = 4.90$; $P = 0.019$) on Okumkom.

The egg and pupal survival rate did not differ significantly among the varieties ($F_{3,15} = 0.21$; $P = 0.888$; $F_{3,15} = 0.95$; $P = 0.251$, respectively). Whereas the larval survival was lowest on Bohye ($F_{3,15} = 7.18$; $P = 0.005$). Adult emergence varied significantly ($F_{3,15} = 4.90$; $P = 0.019$) among

the varieties. The sex ratio at emergence was similar on all the tested varieties ($F_{3,15} = 0.20$; $P = 0.897$) (Table 1).

3.2 Adult longevity and female fecundity

The pre-oviposition period did not vary significantly with variety ($F_{3,59} = 0.54$; $P = 0.656$) but the oviposition and post-oviposition periods varied significantly among varieties ($F_{3,59} = 12.73$; $P < 0.0001$ and $F_{3,59} = 3.75$; $P = 0.016$, respectively). The shortest oviposition periods were recorded on Bohye and Okumkom while the shortest post-oviposition period was recorded only on Okumkom (Table 2). During the oviposition period, the female fecundity differed significantly ($F_{3,59} = 14.85$; $P < 0.0001$) among the varieties with the lowest recorded on Bohye. Female longevity was higher on Apumoden and Ligri than on Bohye and Okumkom ($F_{3,59} = 17.00$; $P < 0.0001$) but male longevity did not vary significantly ($F_{3,59} = 0.46$; $P = 0.709$) among the varieties. Generally, *C. puncticollis* females tended to live longer than the male. The differences were however significant only on Apumoden ($t_{28} = 5.6$; $P < 0.0001$) and Ligri ($t_{28} = 3.99$; $P < 0.0001$) and statistically similar on Bohye ($t_{28} = 0.87$; $P = 0.390$) and Okumkom ($t_{28} = 0.44$; $P = 0.208$). The female age specific survival (Fig. 1) showed that all females lived up to 10 weeks on Ligri and Apumoden but only 6 and 5 weeks on Okumkom and Bohye, respectively. The age-specific reproduction of the females followed almost a similar pattern with the lowest rate at the early time of oviposition period and increased to reach at peak between 3 and 5 weeks, and decreased gradually.

Table 1: Developmental period and survival rate of immature life stages (mean \pm SEM) of *Cylas puncticollis* on different sweet potato varieties.

Life stages	Sweet potato variety			
	Apumoden	Ligri	Bohye	Okumkom
<i>Development period (days)</i>				
Egg – larva	4.0 \pm 0.00 ^a	3.8 \pm 0.13 ^a	3.7 \pm 0.14 ^a	3.9 \pm 0.24 ^a
Larva – pupa	14.8 \pm 0.33 ^a	15.1 \pm 0.42 ^a	15.5 \pm 0.38 ^a	16.6 \pm 0.23 ^a
Pupa – adult	4.1 \pm 1.87 ^a	3.7 \pm 0.27 ^a	4.4 \pm 0.33 ^a	3.9 \pm 0.18 ^a
Developmental period	22.8 \pm 0.54 ^a	22.6 \pm 0.35 ^a	23.2 \pm 0.25 ^a	24.7 \pm 0.46 ^b
<i>Survival rate (%)</i>				
Egg	93.8 \pm 4.73 ^a	96.3 \pm 3.70 ^a	92.5 \pm 4.78 ^a	90.0 \pm 7.07 ^a
Larva	79.7 \pm 2.24 ^a	82.7 \pm 1.20 ^a	66.7 \pm 4.04 ^b	72.3 \pm 2.92 ^{ab}
Pupa	94.7 \pm 3.25 ^a	93.7 \pm 4.18 ^a	94.1 \pm 3.71 ^a	100.0 \pm 0.00 ^a
Emergence rate (%)	70.8 \pm 3.24 ^a	74.9 \pm 3.40 ^a	57.9 \pm 1.69 ^b	64.5 \pm 4.11 ^{ab}
Female sex – ratio	0.49 \pm 0.22 ^a	0.47 \pm 0.24 ^a	0.49 \pm 0.24 ^a	0.51 \pm 0.51 ^a

Means within a row followed by the same letter are not significantly different (Student–Newman–Keuls, $P < 0.05$).

Table 2: Mean (\pm SE) pre-oviposition, oviposition, post-oviposition periods, fecundity and longevity of *Cylas puncticollis* on the different sweet potato varieties.

Variables	Sweet potato variety			
	Apumoden	Ligri	Bohye	Okumkom
Pre-oviposition period (day)	5.0 \pm 0.37 ^a	6.0 \pm 0.70 ^a	5.3 \pm 0.63 ^a	5.2 \pm 0.51 ^a
Oviposition period (day)	88.8 \pm 4.22 ^a	81.4 \pm 4.56 ^a	57.7 \pm 4.40 ^b	63.4 \pm 3.09 ^b
Post-oviposition period (day)	12.9 \pm 1.58 ^a	13.2 \pm 2.31 ^a	8.6 \pm 1.74 ^{ab}	6.6 \pm 0.72 ^b
Fecundity (egg/ female)	233.3 \pm 13.90 ^a	242.1 \pm 17.72 ^a	125.7 \pm 11.69 ^b	194.1 \pm 10.65 ^{ab}
<i>Longevity (day)[†]</i>				
Female	106.8 \pm 4.48 ^{Aa}	100.6 \pm 4.38 ^{Aa}	71.6 \pm 5.00 ^{Ab}	75.2 \pm 3.07 ^{Ab}
Male	73.8 \pm 4.03 ^B	69.4 \pm 6.46 ^B	66.2 \pm 3.77 ^A	68.9 \pm 3.83 ^A

Means within the same row followed by the same lower case letter ([†] and within the same column followed by the same upper case letter) differ significantly (Student–Newman–Keuls, $P < 0.05$).

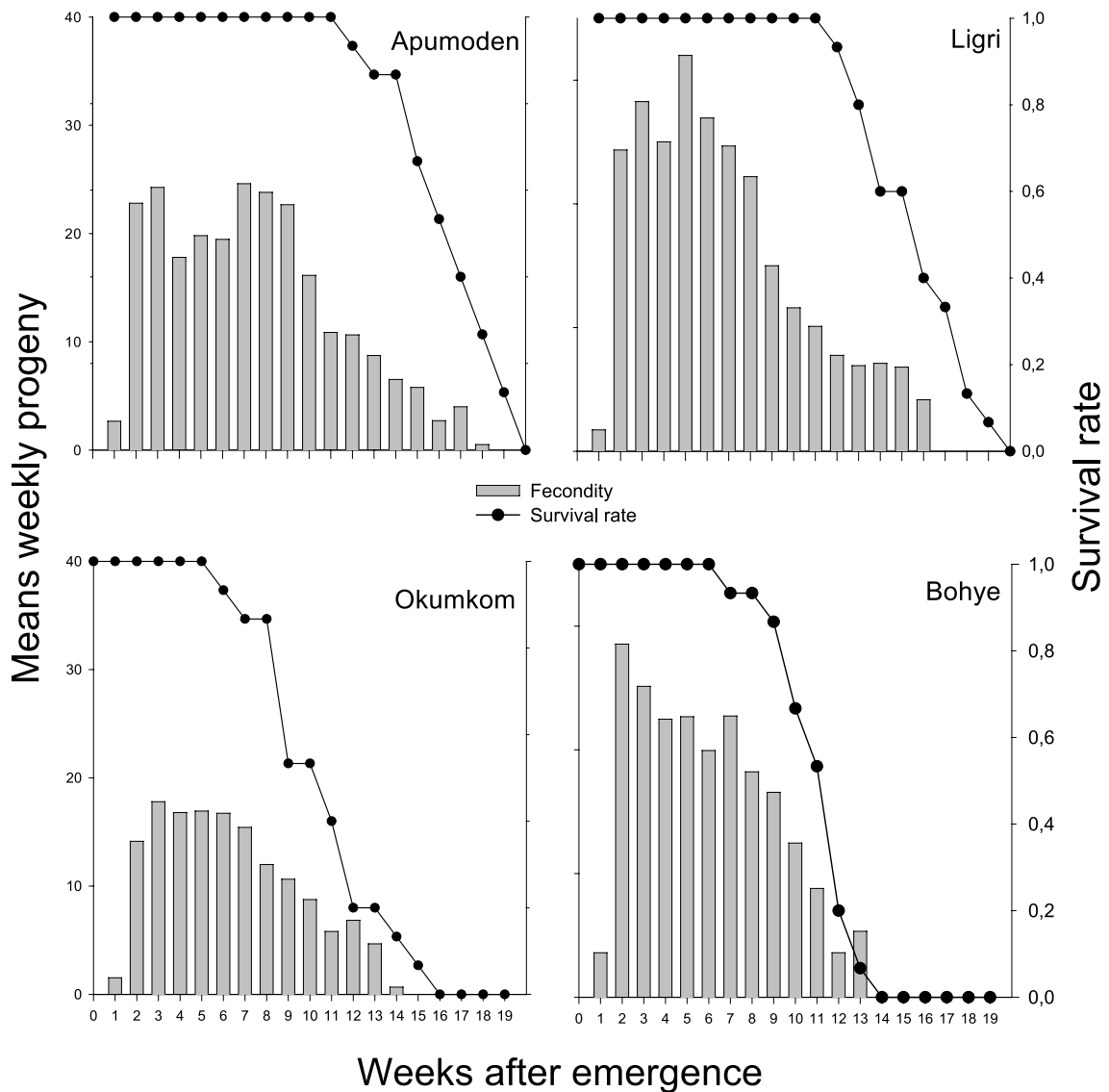


Fig. 1: Survival and age-specific reproduction of females of *Cylas puncticollis* adults on different sweet potato varieties.

Table 3: Life table parameters (mean \pm SEM) of *Cylas puncticollis* on different sweet potato varieties.

Variety	Parameter				
	r_m	R_0	G (days)	T (days)	λ
Apumoden	0.082 \pm 0.002 ^a	90.5 \pm 5.39 ^a	54.7 \pm 1.70 ^a	8.4 \pm 0.23 ^a	1.08 \pm 0.002 ^{ab}
Ligri	0.087 \pm 0.002 ^a	86.1 \pm 6.27 ^a	50.9 \pm 1.32 ^{ab}	7.9 \pm 0.18 ^{ab}	1.09 \pm 0.002 ^a
Bohye	0.077 \pm 0.004 ^b	34.7 \pm 6.27 ^c	45.9 \pm 2.22 ^b	8.9 \pm 0.64 ^a	1.08 \pm 0.004 ^b
Okumkom	0.089 \pm 0.002 ^a	64.0 \pm 7.54 ^b	46.7 \pm 1.26 ^{ab}	7.8 \pm 0.17 ^b	1.09 \pm 0.020 ^a

Means within a column followed by different letters are significantly different (Student–Newman–Keuls sequential test; $P < 0.05$). r_m = intrinsic rate of increase, R_0 = net reproductive rate, G = mean generation time, T = doubling time, λ = finite rate of increase.

3.3 Life table parameters of *C. puncticollis*

All life table parameters of *C. puncticollis* were affected by the sweet potato variety. The r_m and R_0 were lower on Bohye than on the other three varieties. For the other parameters, there were no clear trends (Table 3).

4 Discussion

The determination of factors on which the fitness of an insect pest depends is the cornerstone for developing an environmentally friendly pest management strategy (Golizadeh & Razmjou, 2010; Reddy & Chi, 2015). In this study, the developmental period of *C. puncticollis* was affected by the sweet potato variety. The effects of sweet potato variety on the developmental period of *C. puncticollis* were reported earlier by Darko (2000) with two different Ghanaian varieties. The adult emergence rate differed significantly among tested varieties which collaborates with the findings of Kabi *et al.* (2001) and Stathers *et al.* (2003b). Several secondary metabolites occur in the sweet potato stored tubers and some of these possess diverse biological activities. Resin glycosides and caffeic acid in the latex of sweet potato may have an insecticidal effect on sweet potato weevil and affect survival and development of certain insects such as *Plutella xylostella* (Lepidoptera: Plutellidae) (Jackson & Peterson, 2000). In Tanzania, Stevenson *et al.* (2009) found that the resistance in sweet potato was governed by levels of hydroxycinnamic acid esters in the latex of one of the sweet potato varieties. Since these compounds occur in the latex and this latex occurs throughout the plant, these compounds may be responsible for the resistance effects. The same authors hypothesized that the reduction of *Cylas* spp. infestation is active, quantifiable and manageable through breeding. Variation in the content of these metabolites may explain the difference in developmental period and adult emergence rate found among the varieties in this study.

In addition, nutritional quality of an insect host plant can also affect growth and development of the insect (Das *et*

al., 1993; Golizadeh & Razmjou, 2010). In Nigeria, Anota & Odebiyi (1984) identified carotene as a major factor in tuber resistance to the sweet potato weevil. There was a lower survival rate in all life stages, smaller body weights and a longer developmental period of *C. puncticollis* raised on resistant cultivars (*ibid.*). The proportion of females of *C. puncticollis* population emerged from all varieties in this study was close to 50%, which corroborate results from other studies like Smit & Van Huis (1999), and Mohamed (2005). It appears that the environmental conditions coupled with the sweet potato varieties do not have any effect on the weevil sex-ratio. Insects regulate the sex ratio of its progeny based on the total number of eggs laid and the clutch size (Yu *et al.*, 2003).

Various studies found different pre-oviposition periods in female *C. puncticollis* and this could be attributed to differences in experimental conditions (Moyer *et al.*, 1989; Smit & Van Huis, 1999). However pre-oviposition period recorded in the current study on different sweet potato varieties are not far from the findings of Mohamed (2005). The oviposition period found varied from 88.8 on Apumoden to 54.6 days on Bohye. This range of mean fecundity values among varieties correlates with previous studies (Anota & Leuschner, 1983; Smit & Van Huis, 1999; Darko, 2000). Smit & Van Huis (1999), for instance, reported an oviposition period of 110 days on one Kenyan variety “Kalamba Nyerere” while Darko (2000) found 42 days less. Two secondary metabolites boehmeryl acetate and boehmerol, occurring in the periderm of sweet potato stored tuber were identified to act as ovipositional stimulants for *C. formicarius* and the content of these chemicals differs among sweet potato varieties (Wilson *et al.*, 1988; Mao *et al.*, 2001). Wang & Kays (2002) identified three oxygenated monoterpenes especially: nerol, Z-citral, and methyl geranate in the storage roots known as the primary site of oviposition, but not in another part of the plant, and these compounds were shown to be attractants to the female weevils.

On the other hand, the identification of resistance mechanisms in African sweet potato to *C. puncticollis* is not well understood, particularly since it can affect early development of larvae and may also affect oviposition behaviour. Therefore, varieties with higher quantities of hexadecylcaffeic and hexadecyl-p-coumaric acids are less suitable for oviposition and larval development of *C. puncticollis* weevil (Stevenson *et al.*, 2009). Although not tested in the current study, the level of these chemicals may therefore vary among the investigated varieties, and may have contributed to different levels of fecundity in *C. puncticollis*. The highest female fecundity was observed with females that had the highest oviposition period. This suggests that the stimulation of oviposition in the female *C. puncticollis*, may also lengthen the oviposition period and even the post-oviposition period as hypothesized by Darko (2000). Moreover, previous experiments found that, the susceptible varieties upon which the highest numbers of eggs are laid are also in most of the cases the most consumed by the female weevil (Mao *et al.*, 2001; Parr *et al.*, 2016). Thus, increased female longevity on the varieties which were most susceptible for egg laying as observed in this study may also be attributed to the abundance of food obtained by the female weevil.

On all varieties, female *C. puncticollis* lived longer than the corresponding male. This is in agreement with Darko (2000). Difference in longevity between males and females is commonly observed across many insect species, depending on the genetic make-up of insect species and also on the environmental effects especially quality composition of diets (Partridge *et al.*, 2005; Tower & Arbeitman, 2009). For instance, females of the African wild silkworm, *Gonometa postica* Walker (Lepidoptera: Lasiocampidae) live significantly longer than the males, to offer ample time for egg laying (Fening *et al.*, 2011). Accordingly, the difference between female and male longevity may be attributed to some of the above reasons.

Significant difference in the developmental period, fecundity and survivorship among tested sweet potato varieties was reflected in life table parameters of the *C. puncticollis* including the intrinsic rate of population increase (r_m), net reproductive rate (R_0), mean generation time (G), population doubling time (T) and finite rate of natural increase (λ). Life table parameters of phytophagous insect pest are inherently tied to the host plant characteristics such as nutritional value, secondary chemical compounds and morphology (Norris & Kogan, 1980; Yamaguchi *et al.*, 2006). Reddy & Chi (2015) found that the growth rate of *C. formicarius* differed depending on whether it exploits its major host *Ipomea batatas* or the alternative host *I. triloba*. Das *et al.* (1993) reported Irish potato varietal effect on the life

table parameters of *Phthorimaea oprecullela* (Lepidoptera: Gelechiidae).

Life table parameters, particularly r_m are used as indices for host plant susceptibility (Razmjou *et al.*, 2006). Intrinsic rate of population increase is actually a reflective of many biological traits, including survival, fecundity, development and sex ratio and adequately summarizes the physiological qualities of an animal in relation to its capacity to increase; it would be a more appropriate index to evaluate performance of an insect on different host plants (Southwood & Henderson, 2000; Jha *et al.*, 2012). In the current study, the r_m varied significantly from 0.077 ± 0.004 on Bohye to 0.089 ± 0.002 on Okumkom. This suggests different levels of susceptibility of investigated sweet potato varieties to *C. puncticollis* due to different levels of antibiosis mechanisms which affect the development of the insect pests (Dent, 2000; Golizadeh & Razmjou, 2010).

5 Conclusion

This study showed the importance of sweet potato variety in the population build-up of *C. puncticollis*. It is therefore possible to reduce the infestation level by choosing variety in which weevil population grows less rapidly. The lowest intrinsic rate of population increase of *C. puncticollis* on Bohye tubers indicates the relatively lower susceptibility of this variety and can therefore be used in breeding programs as part of IPM of *C. puncticollis*.

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References

- Ames, T., Smith, N. E. J. M., Braun, A. R., O'Sullivan, J. N. & Skoglund, L. G. (1997). *Sweetpotato: Major pests, diseases, and nutritional disorders*. International Potato Centre, Lima, Peru.
- Anota, T. & Leuschner, K. (1983). *Survival of sweet potato weevil on some promising sweet potato clones*. International Institute of Tropical Agriculture, Ibadan, Nigeria.

- Anota, T. & Odebiyi, J. A. (1984). Resistance in sweet potato to *Cylas puncticollis* Boh. (Coleoptera: Curculionidae). *Biologia Africana*, 1, 21–30.
- Bouwkamp, J. C. (1985). Production requirement. In: Bouwkamp, J. C. (ed.), *Sweet potato products: a natural resource for the tropics*. pp. 9–33, Boca Raton (FL), CRC Press, Florida.
- Braendle, C., Davis, G. K., Brisson, J. A. & Stern, D. L. (2006). Wing dimorphism in aphids. *Journal of Heredity*, 97, 192–199.
- Chalfant, R. B., Jansson, R. K., Seal, D. R. & Schalk, J. M. (1990). Ecology and management of sweet potato insects. *Annual Review of Entomology*, 35, 157–180.
- Darko, Y. S. (2000). *Species composition, biology and management of sweet potato weevils (Cylas species) in Southern Ghana*. Master's thesis, University of Ghana, Ghana, Legon.
- Das, G. P., Magallona, E. D., Raman, K. V. & Adalla, C. B. (1993). Growth and development of the potato tuber moth, *Phthorimaea operculella* (Zeller), on resistant and susceptible potato genotypes in storage. *The Philippine Entomologist*, 9, 15–27.
- Dent, D. (2000). Host plant resistance. In: Dent, D. (ed.), *Insect Pest Management*, (2nd ed.). pp. 123–179, CABI Publishing, Wallingford.
- Dixon, A. F. G. (1987). Parthenogenetic reproduction and the rate of increase in aphids. In: Minks, A. K. & Harrewijn, P. (eds.), *Aphids: Their Biology, Natural Enemies and Control*. pp. 269–285, Elsevier, Amsterdam.
- Ewell, P. T. (2002). *Sweet potato production in Sub-Saharan Africa: Patterns and key issues*. International Potato Center (CIP), Lima, Peru.
- FAOSTAT (2016). Production Statistics. FAO, Rome, Italy. Available at: <http://faostat.fao.org/>
- Fening, K. O., Kioko, E. N., Mueke, J. M. & Raina, S. K. (2011). Oviposition preferences of the African wild silkworm, *Gonometa postica* Walker (Lepidoptera: Lasiocampidae) on different substrates. *Journal of Insect Behavior*, 24, 1–10.
- Golizadeh, A. & Razmjou, J. (2010). Life table parameters of *Phthorimaea operculella* (Lepidoptera: Gelechiidae), feeding on of six potato cultivars. *Journal of Economic Entomology*, 103, 966–972.
- Goodarzi, M., Fathipour, Y. & Talebi, A. A. (2015). Antibiotic resistance of ranola rultivars affecting demography of *Spodoptera exigua* (Lepidoptera: Noctuidae). *Journal of Agricultural Science and Technology*, 17, 23–33.
- Hulting, F. L., Orr, D. B. & Obrycki, J. J. (1990). A computer program for calculation and statistical comparison of intrinsic rates of increase and associated life-table parameters. *Entomologist*, 73, 601–612.
- Jackson, D. M. & Peterson, J. K. (2000). Sublethal effects of resin glycosides from the periderm of sweetpotato storage roots on *Plutella xylostella* (Lepidoptera: Plutellidae). *Journal of Economic Entomology*, 93 (2), 388–393.
- Jha, R. K., Chi, H. & Tang, L. C. (2012). A comparison of artificial diet and hybrid sweet corn for the Rearing of *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) based on life table characteristics. *Environmental Entomology*, 41, 30–39.
- Kabi, S., Ocenga-Latigo, M. W., Smit, N. E. J. M., Stathers, T. E. & Rees, D. (2001). Influence of sweetpotato rooting characteristics on infestation and damage by *Cylas* spp. *African Crop Science Journal*, 1, 165–174.
- Magira, P. (2003). *Evaluating sweet potato clones for resistance to the African sweetpotato weevils (Cylas puncticollis) Boheman and Cylas brunneus (Fab.) (Coleoptera: Apionidae)*. Master's thesis, Makerere University, Kampala, Uganda.
- Mahmoudi, M., Sahragard, A., Pezhman, H. & Ghadamyari, M. (2015). Demographic analyses of resistance of five varieties of date palm, *Phoenix dactylifera* L. to *Ommatissus lybicus* De Bergevin (Hemiptera: Tropiduchidae). *Journal of Agricultural Science and Technology*, 17, 263–273.
- Mao, L., Story, R. N., Hammond, A. M. & Labont, D. R. (2001). Effect of sweet potato genotype, storage time and production site on feeding and oviposition behavior of the sweet potato weevil, *Cylas formicarius* (Coleoptera: Apoinidae). *Florida Entomological Society*, 8, 259–264.
- Meyer, J. S., Ingersoll, C. G., McDonald, L. L. & Boyce, M. S. (1986). Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. *Ecology*, 67, 1156–1166.
- Mirmohammadi, S., Allahyari, H., Nematollahi, M. R. & Saboori, A. (2009). Effect of host plant on biology and life table parameters of *Brevicoryne brassicae* (Hemiptera: Aphididae). *Annals of the Entomological Society of America*, 102, 450–455.
- Mohamed, A. E. Z. G. (2005). *Biology, ecology and management of the sweetpotato weevil, Cylas puncticollis Boheman (Coleoptera: Brentidae)*. Ph.D. thesis, University of Khartoum; Soudan, Khartoum.

- Moyer, J. W., Jackson, G. V. H. & Frison, E. A. (1989). FAO/IBPGR Technical guidelines for the safe movement of sweet potato germplasm. Food and Agricultural Organization of the United Nation/International Board for Plant Genetic Resources, Rome. 29 pp.
- Ndunguru, G., Thomson, M., Waida, R., Rwiza, E. & Westby, A. (1998). Methods for examining the relationship between quality characteristics and economic values of marketed fresh sweet potato. *Tropical Agriculture*, 75, 129–133.
- Norris, D. M. & Kogan, M. (1980). Biochemical and morphological basis of resistance. In: Maxwell, F. G. & Jennings, P. R. (eds.), *Breeding Plants Resistant to Insects*. pp. 23–61, Wiley, New York.
- Nottingham, S. F. & Kays, S. J. (2002). Sweet potato weevil control. In: Ames, T. (ed.), *Proceedings of the 1st International Conference on Sweetpotato. Food and Health for the Future*. Vol. 583, pp. 155–161, Acta Horticulturae.
- Parr, M. C., Ntonifor, N. N. & Jackai, L. E. (2016). Evaluation of sweet potato cultivars for differences in *Cylas puncticollis* (Curculionidae: Brentidae) damage in South Western Cameroon. *International Journal of Research in Agricultural Sciences*, 3, 1–8.
- Partridge, L., Gems, D. & Withers, D. J. (2005). Sex and death: what is the connection? *Cell*, 120, 461–472.
- Razmjou, J., Moharramipour, S., Fathipour, Y. & Mirhoseini, S. Z. (2006). Effect of cotton cultivar on performance of *Aphis gossypii* (Homoptera: Aphididae) in Iran. *Journal Economic Entomology*, 99, 1820–1825.
- Reddy, G. V. & Chi, H. (2015). Demographic comparison of sweet potato weevil reared on a major host *Ipomoea batatas*, and an alternative host, *I. triofoli*. *Scientific Reports*, 5, 11871. doi:10.1038/srep1187.
- Rees, D., Van Oirschot, Q. E. A., Kapinga, R. E., Mtunda, K., Chilosa, D., Mbilinyi, L. B., Rwiza, E. J., Kilima, M., Kiozya, H., Amour, R., Ndoni, T., Chottah, M., Mayona, C. M., Mende, D., Tomlins, K. I., Aked, J. & Carey, E. E. (2003). Extending root shelf-life during marketing by cultivar selection. In: Rees, D., Quirien, O. & Kapinga, R. (eds.), *Sweet potato post-harvest assessment. Experiences from East Africa*. pp. 51–56, University of Greenwich, London, UK.
- SAS Institute (1997). SAS/STAT Software: changes and enhancements through Release, 6–12. Cary, North Carolina.
- Smit, N. E. J. & Van Huis, A. (1999). Biology of the African Sweetpotato Weevil Species *Cylas Puncticollis* (Boheman) and *C. Brunneus* (Fabricius) (Coleoptera: Apionidae). *The Journal of Food Technology in Africa*, 4 (3), 103–107.
- Smit, N. E. J. M. (1997). *Integrated pest management for sweet potato in Eastern Africa*. Ph.D. thesis, Wageningen University, Wageningen, The Netherlands.
- Smit, N. E. J. M., Downham, M. C. A., Laboke, P. O., Hall, D. R. & Odongo, B. (2001). Mass-trapping male *Cylas* spp. with sex pheromones; a potential IPM component in sweetpotato production in Uganda. *Crop Protection*, 20, 643–651.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*. (3rd ed.). W. H. Freeman and Company, San Francisco, CA. 880 pp.
- Southwood, T. R. E. & Henderson, P. A. (2000). *Ecological methods*. (3rd ed.). Blackwell, Oxford, United Kingdom.
- Stathers, T. E., Rees, D., Kabi, S., Mbilinyi, L., Smith, N., Kiozya, H., Jeremiah, S., Nyango, A. & Jeffries, D. (2003a). Sweet potato infestation by *Cylas* spp. in East Africa: I. Cultivar differences in field infestation and the role of plant factors. *International Journal of Pest Management*, 49, 131–140.
- Stathers, T. E., Rees, D., Nyango, A., Kiozya, H. & Mbilinyi, L. (2003b). Sweet potato infestation by *Cylas* spp. in East Africa: II. Investigating the role of tuber characteristics. *International Journal of Pest Management*, 49, 141–146.
- Stevenson, P. C., Muyinza, H., Hall, D. R., Porter, E. A., Farman, D. I., Talwana, H. & Mwanga, R. O. M. (2009). Chemical basis for resistance in sweetpotato *Ipomoea batatas* to the sweetpotato weevil *Cylas puncticollis*. *Pure and Applied Chemistry*, 81 (1), 141–151. doi: 10.1351/PAC-CON-08-02-10.
- Talekar, N. S. (1987). Feasibility of the use of resistant cultivars in sweet potato weevil control. *Insect Science and its Application*, 8, 815–817.
- Tower, J. & Arbeitman, M. (2009). The genetics of gender and life span. *Journal of Biology*, 8, 38. doi: 10.1186/jbiol141.
- Wang, Y. & Kays, S. J. (2002). Sweet potato volatile chemistry in relation to sweet potato weevil (*Cylas formicarius*) behavior. *Journal of the American Society for Horticulture Science*, 127, 656–662.
- Wilson, D. D., Severson, R. F., Son, K. C. & Kays, S. J. (1988). Oviposition stimulant in sweet potato periderm for the sweet potato weevil, *Cylas formicarius elegantulus*. *Environmental Entomology*, 17, 691–693.

Yamaguchi, T., Tokimura, K., Hara, Y. & Atari, N. (2006). Mass-production of the Sweet potato weevil *Cylas formicarius* (Fabricius) (Coleoptera: Brentidae) using inexpensive sweet potato cultivars for starch and alcohol production. *Japanese Journal of Applied Entomology and Zoology*, 50, 157–165.

Yu, S. H., Ryoo, M. I., Na, J. H. & Choi, W. I. (2003). Effect of host density on egg dispersion and the sex ratio of progeny of *Bracon hebetor* (Hymenoptera: Braconidae). *Journal of Stored Products Research*, 39(4), 385–393. doi:10.1016/S0022-474X(02)00032-2.