International Journal of Natural Sciences Research
2014 Vol. 2, No. 11, pp. 263-277
ISSN(e): 2311-4746
ISSN(p): 2311-7435

DEVELOPMENT AND DEMOGRAPHIC PARAMETERS OF BACTROCERA INVADENS (DIPTERA: TEPHRITIDAE) IN GUINEAN CLIMATIC ZONE OF TOGO

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ABSTRACT

Among the 35 Tephritidae species recorded in Togo, only Bactrocera invadens Drew, Tsuruta and White had high prevalence throughout the year and infested fruits of commercial importance. In perspective for control of B. invadens, a wild strain of this pest was reared in an open room conditions similar to those of the external medium (27.5 ± 1 ° C, 79.5 ± 3% RH and approximately 12: 12 L: D). It was fed on local diet consisting of a mixture of soya flour and superfine sugar, and water in the presence of a mango (cultivar Eldon). These conditions allowed us to determine it biological and growth parameters. Ovariole number per ovary in B. invadens was 41. The total mean development time was 21.71 ± 0.99 days. Egg incubation, larval development and puparia-adult periods were respectively 1.28 ± 0.02, 11.35 ± 1.13 and 9.37 ± 0.19 days. About 68.50 ± 5.13% of the eggs developed to the adult stage. Life expectancy at pupal eclosion was 55.03 ± 30.75 days in males and 51.94 ± 21.03 in females. Average fecundity and fertility rates were respectively 535.74 ± 235.70 eggs and 92.67 ± 4.68%. Net reproductive rate and intrinsic rate of population increase were respectively 98.50 females per female and 10% per day. These results summarized the life-history of B. invadens in Guinean zone condition and are useful for assessment of demographic parameters of natural enemies of this insect in perspective of an efficient and sustainable management of its populations.

Keywords: Bactrocera invadens, Mango, Life-history, Growth parameters.

Contribution/ Originality

This study is one of very few studies which have investigated reproductive and development of an invasive alien species *B. invadens* in a local condition in Africa. Then, the demographic parameters that are important for control strategies were determined.

1. INTRODUCTION

Fruit and vegetable production is an income-earning activity in Togo. These fruits and vegetables coming from production areas were intended for local and export trade.

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Unfortunately, the sustainability of this lucrative business is threatened by infestation of fruit flies [1].

Studies on fruit fly diversity in southern Togo (Lomé and Kpalimé) carried out by Amevoin, et al. [2] and Gomina, et al. [3] reported 35 species including 2 Asian invasive alien species: *Bactrocera invadens* Drew, Tsuruta and White and *Bactrocera cucurbitae* Coquillett. The follow up of the capture of these fruit flies in the same area showed that *B. invadens* was the most abundant and frequent species, and was maintained throughout the year. Identified for the first time in Togo in 2004, *B. invadens* belongs to *Bactrocera dorsalis* complex Drew, et al. [4]. This complex includes about 75 described species [5]. The species of this complex, such as *B. invadens*, *Bactrocera dorsalis* sensu stricto Hendel, *Bactrocera papayae* Drew & Hancock, *Bactrocera philippinensis* Drew & Hancock and *Bactrocera carambolae* Drew & Hancock are notoriously difficult to discriminate from each other using either morphological or molecular characters [6]. According to the same author, the taxonomic status of *B. invadens*, closely related to *B. dorsalis* sensu stricto, is presently under revision through new morphological, molecular, and behavioural data. These species belonging to *B. dorsalis* complex mentioned above are polyphagous [6]. Especially *B. invadens* is able to infest wild and cultivated fruits of at least 46 species from 23 plant families in West and Central Africa [7]. In southern Togo, *B. invadens* infested sweet orange (*Citrus sinensis* Osbeck, Rutaceae), grapefruit (*Citrus grandis* (Berman) Merr, Rutaceae), avocado (*Persea americana* M., Lauraceae), cashew nut (*Anacardium occidentale* L., Anacardiaceae), African wild mango (*Irvingia gabonensis* (Aubry-Lecomte) Baill., Irvingiaceae), Indian almond (*Terminalia catappa* L., Combretaceae) and especially mango (*Mangifera indica* L., Anacardiaceae) which is its main host plant. In addition, ecological studies showed that the new invasive species is able to quickly dominate the indigenous species belonging genus *Ceratitis* [8]. The polyphagous status of *B. invadens* combined with the significance of its populations, its ecological impact to native species and the damage it causes on fruits, make the species of great economic importance in Togo.

Pest demographic parameter determination require establishment of fertility and life tables which are appropriate for animal population dynamics study mainly those on arthropods [9]. The establishment of fertility and life tables under field conditions can be helpful in revealing the differences between the values of demographic parameters in the field and in the laboratory [10]. The calculation of these demographic parameters is based on the evaluation of survival rates, offspring number and fertility. In the Dacine group (Tephritidae : Dacinae : Dacini), after egg-laying started, females lay continuously in small batches due to asynchronous oocytes development in different ovarioles [11] because they are synovigenic species. For species of the same Tephritidae group, potential variation in fecundity is related to the number of ovarioles [12]. Consequently, the reproductive rate of Dacine species depends on their ovariole number per ovary [13]. The combined determination of ovariole number and demographic parameters of the wild strain of *B. invadens* in Togo will allow to assess the threat level faced by the promotion of the fruit sector and predict the speed of settlement of ecological zones which are favorable to its development and therefore the potential significance of damage in these areas. Furthermore, temperature and relative humidity are environmental determinants of abundance in Tephritidae

through their effects on rates of development, mortality and fertility [14, 15]. Thus, the study of reproductive biology and development of *B. invadens* on its favorite hosts in uncontrolled and local environmental conditions is a prelude to the establishment of biological control methods for this fruit pest.

For the management of wild populations of *B. invadens*, a preliminary study on the biology of development has been done in Kenya [16] and allowed to assess biological and growth parameters of the laboratory strain of this pest on artificial diet and in controlled conditions. Likewise, in Tanzania, demographic parameters of *B. invadens* were determined on artificial diet at variable temperature in environmental growth chamber and in an open rearing room [15]. In addition, similar studies have been carried out in Côte d'Ivoire on the mango and orange [17] and in Sudan on guava [18] without being able to determine the growth parameters of *B. invadens*. However, determination of the population growth parameters of the wild strain of *B. invadens* on mango which is the main cultivated host and in different local conditions is undoubtedly essential to establishing effective strategies to control this species. The objectives of this study are to assess the fecundity of the wild strain of *B. invadens* on mango after determining the ovariole number in females of this species; to study its life-history on the same fruit and determine its growth parameters from its fertility and life tables in ambient conditions similar to those of the external environment in Togo.

2. MATERIALS AND METHODS

2.1. Environmental Conditions of the Experiments

The experiments were carried out at the University of Lomé (06°11'12.2"N and 01°12'41.6"E) in southern Togo in a Guinean climatic zone. This agro-ecological zone is characterized by two rainy seasons (April-July and September-October) separated by short and long dry seasons respectively (August and November-March). The monthly average temperatures vary from 26 to 30°C during the year and the annual mean precipitations were close to 932 mm with high relative humidity throughout the year (67-90% RH). The photoperiod is approximately 12:12 L:D. The study was carried out in an open rearing room from May to September. The climatic conditions that prevailed in the rearing room were similar to those of Guinean zone at the moment of the experiments (27.5 ± 1°C, 79.5 ± 3% RH).

2.2. Evaluation of the Reproductive Capacities and Development of B. Invadens

Rearing of wild strain of B. invadens

The wild strain of *B. invadens* was obtained by incubation of naturally infested mangoes collected in March, 2013 in Lomé (06°10'08.5"N and 01°13'05.1"E). After emergence, 50 pairs of newly emerged adults from mangoes were held in transparent plastic cages (19×19×21 cm) with a diet consisting of 4 parts of soya flour mixed with 1 part of superfine sugar, water and mango (cultivar Eldon) with minor broken surfaces to facilitate egg-laying. Mangoes in cages were changed every 5 days. After this period, mangoes in contact with flies in the cages were incubated.

Adults obtained were the first generation. Individuals obtained at the second generation (F_2) were used for further experiments.

2.3. Determination of Ovariole Number in Females

Fifty pairs of flies from the second generation were introduced in three different rearing cages containing the same diet and mango cultivar. After 15 days, the females were removed from the cages with aspirator and dissected under a stereo microscope in a Petri dish containing a physiological fluid (Ringer). The reproductive tract was isolated and stained with methylene blue. Then the left and right ovaries were plated after separation of the germarium of different ovarioles. Finally, the ovarioles of each ovary were recorded by isolating one after the other. In total, 100 females were dissected.

2.4. Egg Stage Duration and Larval Development

B. invadens eggs were collected from 5 different rearing cages each containing 50 pairs of flies. It was introduced in each cage a Petri dish (5 cm in diameter and 1.2 cm in height) containing three mango slices (Eldon cultivar) from 1 to 2 mm thick. Females could also lay eggs between the first slice and second or between the second slice and third using method developed by Vayssières, et al. [19]. Mango slices covered the entire surface of the Petri dishes. After 1 hour, the Petri dishes were removed from the different cages. Then, 100 randomly selected eggs were collected under a stereo microscope using a small camel hair brush and deposited on the surfaces of 24 different mango slices each 8 mm thick contained in 24 Petri dishes (9 cm in diameter and 1.2 cm in height) numbered from 1 to 24. Slices also covered the entire surface of the Petri dishes. At the 24th hour after egg-laying, observation of the contents of the 24 different Petri dishes under a stereo microscope showed no hatching eggs. So, from that moment, the contents of the 24 boxes were observed successively every 3 hours under a stereo microscope to identify the state of egg development and count the number of dead or live larvae from a development stage to another. The larvae sizes, the presence or absence of spiracle and the structure of their cephalo-pharyngeal skeleton were criteria that allowed accurate identification of the different larval stages according to Frias, et al. [20] method. This protocol was repeated 6 times to get statistically reliable data.

2.5. Pupal Development and Obtaining Adults

Likewise, 100 eggs were counted and deposited on the surface of a mango slice about 1cm thick sitting in the middle of a grid support with 16 cm diameter and about 3 mm mesh. The rest of the grid surface was covered with mango slices. The total amount of mango pulp used was 100 g. After hatching of the eggs (after 48 hours), 30 g of mango pulp was added every two days to prevent intraspecific resource competition. The grid support has been deposited on a translucent pipe (5 cm in diameter and 6 cm in height) in a rearing cage containing moistened sterilized sand allowing third instar larva to fall easily. The role of the pipe was to prevent direct contact between the grid support and sand. The third instar larvae were collected every 12 hours and

followed until emergence in the plastic and translucent drinking glasses (5 cm in diameter and 10 cm in height) covered with muslin, and containing sterilized moistened sand. Adults emerging from the boxes were recovered every 24 hours and counted. The process was repeated six times.

2.6. Evaluation of Fecundity

Thirty four pairs of flies (F_2) were isolated individually in cylindrical and translucent plastic pots (16cm in diameter and 14cm in height) to assess the fecundity of *B. invadens*. The upper part of the pot was covered with muslin knotted at its end to prevent flies from escaping from the pot and facilitate handling. These flies have stayed five days in the cage to allow contact between individuals and especially to allow the full development of body color [16] before being isolated in couples in rearing pots. The mango contained in the cage was observed under a stereo microscope to ensure that no female has laid eggs before isolation. A mango with minor broken surfaces was added to each pot and renewed every 24 hours until the death of the female. The mangoes removed daily from different pots were dissected under a binocular microscope and the number of eggs laid per puncture was recorded. In addition, the number of dead females or males every 24 hours was recorded to calculate the percentage of surviving females or males versus time (survival).

2.7. Determination of Demographic Parameters

At the end of the experiments, the survival rate of adult males and females, mean fecundity, fertility rate, emergence rate, sex-ratio and duration of developing male and female offspring were calculated and allow establish the fertility and life tables [21]. Growth parameters (net reproductive rate (R_0), mean generation time (G), intrinsic rate of population increase (r_m) and doubling time of the population (DT) of *B. invadens* were calculated from survival and fertility tables [9].

2.8. Statistical Analyses

The SPSS.16.0 software was used to analyze the different results obtained in our experiment. Comparisons of the mean numbers were made using analysis of variance (ANOVA-1) followed by Student-Newman-Keuls (SNK) comparison tests when F from the analysis of variance was significant at the 5% level.

3. RESULTS

3.1. Structure of the Ovary and Variation of Ovariole Number in the Ovaries of Females

The ovary of *B. invadens* is composed of meroistic polytrophic ovarioles (fig. 1). Their observation showed that the number of ovarioles per ovary varies depending on the individual. The number of ovarioles in the left and right ovaries respectively ranged from 22 to 50 and from 22 to 51 with an average number equal to 41.06 ± 4.99 and 40.87 ± 5.22 respectively (table 1). The number of ovarioles per ovary of a female ranged from 26 to 50.5 with an average number equal to 40.97 ± 4.72. There was no significant difference between the number of ovarioles in the

right and left ovaries, and the number of ovarioles per ovary of a female (F = 0.36; df = 2; P = 0.964) (table 1).

3.2. Survival of Adults

The mean longevity of *B. invadens* adult males and females was 55.03 ± 30.75 and 51.94 ± 21.03 days respectively. However, there is no significant difference between the longevity of both sexes (F = 0.234; df = 1; P = 0.630). Survival was high when the age of males and females was respectively between 1 and 16, and between 1 and 20 days. From the 16th day, the surviving males decrease significantly until the 111th day when all of the males had died (fig. 2). Whereas in females, the mortalities had occurred from the 20th day until the 106th day.

3.3. Fecundity

In our experimental conditions, all of the 34 females of *B. invadens* have laid 18215 eggs with 2149 punctures. Almost all punctures (99.86%) were observed in mango wounds. The mean number of punctures per female was 63.21 ± 28.04 (table 2). However, the average of punctures with oviposition and no oviposition was respectively 59.21 ± 26.78 and 4 ± 3.95. The females laid eggs in clutches and the clutch size was 1-64 eggs per oviposition. Furthermore, the total number of eggs laid per day by each female varied between 1 and 134. During its life time, the female laid an average of 535.74 ± 235.70 eggs; while the mean number of eggs per female per day was 15.22 ± 5.59 (table 2). The mean number of eggs per female per puncture was 8.83 ± 2.24. The total number of eggs laid by each of 34 females until death varied between 309 and 1168.

Different periods of reproductive activity of *B. invadens* namely periods of pre-oviposition, oviposition and post-oviposition were respectively 9.85 ± 2.93, 39.38 ± 20.48 and 2.71 ± 2.58 days (fig. 3). There was a significant difference between the three values (F = 88.691, df = 2, P < 0.001). The oviposition period was the longest period and the post-oviposition the shortest. The number of eggs laid by the females of *B. invadens* during the oviposition period fluctuated depending on its age (fig. 3). The females have deposited the maximum number of eggs (11-28 eggs) between the 11th and the 28th day after emergence with an average of 16.56 ± 5.42 eggs per day and a peak on the 15th day. From the 29th to the 105th day after emergence, the fecundity was low (0-10 eggs) with an average of 2.81 ± 2.78 eggs per day.

3.4. Development and Survival of Immature Stages

The average duration of egg development varied from 1 to 2 days and the mean fertility rate was 92.67 ± 4.68% (table 3). Three larval stages (L_1, L_2 and L_3) and one pupal stage were identified. The larvae of the first (L_1) and second (L_2) stages appeared respectively 1.28 ± 0.02 (incubation period of eggs) and 2.43 ± 0.04 days after egg-laying with respective survival rates of 89.86 ± 2.82% and 95.18 ± 1.12% (table 3). The development times of L_1 and L_2 stages were respectively 1.14 ± 0.03 and 1.10 ± 0.05 days. However, third stage larvae (L_3) appeared 3.52 ± 0.04 days after egg-laying and spent 6.44 ± 1.15 days on the natural diet (mango pulp) with a mean survival rate of 92.33 ± 4.02%. After leaving the mesh support, the L_3 stage needed an

average of 1.90 ± 0.19 days to give puparia with a mean survival rate of 97.98 ± 1.01%. Thus, the total development time of the L_3 stage was 8.34 ± 1.13 days and the average duration of the three larval stages combined was 11.35 ± 1.13 days. The duration of pupal development varied between 9 and 10 days (9.37 ± 0.19 days) with a mean survival rate of 95.56 ± 1.95%. There was no significant difference between the average duration of the pupal development and the mean development times of males and females (table 4). The total development time of males and females varied between 20 and 23 days (21.71 ± 0.99 days).

3.5. Sex-Ratio

The emergence period of the adult *B. invadens* was between the 16th and 33rd day after egg-laying. An average of 34.67 ± 5.68 males and 33.67 ± 2.66 females was obtained from eggs (100 eggs × 6 repetitions) monitored until emergence. The sex-ratio (number of emerged females divided by the number of emerged males) and the rate of emergence (egg to adult) were 1 ± 0.20 and 68.50 ± 5.13% respectively.

3.6. Demographic Parameters

Demographic parameters were derived from fertility and life tables. The net reproductive rate (R_0), generation time (G), intrinsic rate of population increase (r_m) and doubling time of the population (DT) were respectively 98.499 females offspring per female ; 45.635 days; 0,101 (10% per day) and 6.891 days (table 5).

4. DISCUSSION

The results related to the variation of ovariole number in *B. invadens* showed that the number of ovarioles per ovary varied intraspecifically and these results are close to those reported by Fitt [22] in species of the same genera mainly *Bactrocera tryoni* Froggatt and *Bactrocera jarvisi* Tryon. This variation is probably related to the body size of various females dissected. Indeed, Fitt [22] showed the existence of a positive correlation between the number of ovarioles per ovary and body size (size of wings) in *B. tryoni* and *B. jarvisi*. To our knowledge, the intraspecific variation of ovariole number per ovary in the wild strain of this species has not yet been reported in the literature. The average number of ovarioles per ovary in the Togo wild strain of *B. invadens* is relatively higher than that obtained in species of the same genus including *B. tryoni* (39 ovarioles/ovary) and *Bactrocera neohumeralis* Hardy (38 ovarioles/ovary) which are also polyphagous [12]. In general, Fitt [12] showed that in polyphagous Dacine (Tephritidae) the number of ovarioles per ovary varied between 35 and 40 and was higher than in oligophagous and monophagous which varied between 8 and 25. *B. invadens* being a polyphagous species, this result can be easily explained.

The longevity of adult males and females of *B. invadens* was the same in our experimental conditions and lower than that obtained in Kenya on artificial diet [16] and in Côte d'Ivoire on mango [17]. This is probably due to rearing conditions and diet used. The authors mentioned above [16, 17] have shown that males of *B. invadens* lived longer than females, probably because

of the high reproductive cost in females compared to males and hormonal as well as other behavioral and physiological differences [23, 24].

Almost all punctures and eggs laid were observed on mango wounds. The broken parts of mangoes probably facilitated the escape of volatiles, in this case carbon dioxide which seems to attract gravid females and favor oviposition in these areas [25]. Furthermore, these parts are easily accessible to female oviposition because they are less hard [14]. However, a small proportion of punctures was not accompanied by egg-laying probably because these punctured areas were not conducive to hatching of eggs and good larval development. According to Yuval and Hendrichs [26], the fate of fruit fly offspring is largely determined by the decisions made by females of where to deposit their eggs. Consequently, female behavior involved in the choice of oviposition site is of great consequence for offspring fitness [26]. The higher fecundity observed in females of the wild strain of *B. invadens* varied between 309 and 1168 eggs and probably due to temperature and relative humidity that prevailed in the Guinean zone of Togo at the moment of experiments. This fecundity is comparable to that obtained in *B. dorsalis* and *B. cucurbitae* (380 and 1428 eggs) at temperature conditions varied from 16 to 36°C [27]. On mango, clutch size was 1-64 eggs in *B. invadens* and 1 egg in *Bactrocera oleae* Gmelina which infest only the olive [28] and 1-3 eggs on tomato in *Neoceratitis cyanescens* Bezzi (Dacinae : Ceratitidini) which attack only Solanaceae [29]. Clutch size depends on the size of infested fruit; species infesting small hosts normally lay a few eggs [30]. Indeed, the number of eggs laid in a host will determine, depending on the quality of the available resources (food, space) [31], the intensity of a potential larval competition. This larval competition affects the quality and quantity of insects [32] and thus the fitness of offspring females [33].

The pre-oviposition period of the wild strain (second generation) of *B. invadens* in our experimental conditions was similar to that obtained with the tenth generation of the same species by Salum, et al. [15] in an open rearing room condition. But it was longer than that observed by Ekesi, et al. [16] in laboratory conditions. These differences are probably correlated with the type of strain used in relation to the number of generations and experimental conditions which are not the same (adult diet, temperature and relative humidity). The relation between the length of the pre-oviposition period and type of strain was determined by Arakaki, et al. [34] and Foote and Carey [35]. These authors concluded that the wild strain of *B. dorsalis* got a longer one than those of the laboratory strain.

Daily fecundity and therefore average fecundity of *B. invadens* in our experimental conditions were closed to that obtained by Salum, et al. [15] but lower with Ekesi, et al. [16]. The average duration of egg development varied between 1 and 2 days while it was 2 to 3 days on the mango (variety mango), 3 to 4 days on the orange [17] and 1 and 4 days on guava [18]. Our result is similar to that of Ekesi, et al. [16] and Salum, et al. [15]. These differences observed compared to the result of N'Guessan, et al. [17] and Magid, et al. [18] would be linked to the methodology used in the follow up of egg hatching, the plant host and the experimental conditions that were different from ours. These authors have followed up egg-hatching in the pulp of the different fruits mentioned above after egg-laying rather than on fruit slices in open air. The survival rate

from a development stage to the other varied between 89 and 98%. This showed a low mortality rate from one development stage to another compared to that of Salum, et al. [15] which noted higher mortality rate. The low mortality rate of different immature stages in our conditions is linked to the availability of nutrients in mango (larval diet) necessary for their development. Indeed, the nutritional elements, texture of the fruit pulp and chemical composition determined the suitability of a host for larval development [36]. Furthermore, the additions of mango pulp every 48 hours to diet containing developing larvae in our experiments probably annihilated intraspecific competition between larvae. Nevertheless, the low mortality observed is linked to the physiological state of individuals in these stages. The total larval and pupal development time in our experimental condition was lower than that obtained by Salum, et al. [15] on artificial diet in the open rearing room. These differences seem related to rearing conditions. The mean longevity for males and females in this study were lower than experiments of Ekesi, et al. [16].

The total development time of males and females of *B. invadens* is close to that obtained on mango (21 days) and less than that obtained on orange (23 days) [17]. This can be explained by the availability of nutrients and acidity of the fruit pulp in which larval development takes place. Mango which is rich in carbohydrates and less acidic constitutes a better diet for the rapid development of the larvae of fruit flies [37], while the orange is more acidic [38] and slows down their development. Likewise, Ibrahim and Rahman [39] had shown that different host fruits affected the development of *B. dorsalis* larvae in terms of the weight of the puparia and duration of the life cycle. These authors reported that in general, the mango is better suited to larval development of fruit flies than Citrus.

The evolution of a population can be predicted by the analysis of fertility and life tables. The net reproductive rate (R_0) of the wild strain of *B. invadens* in our study condition was lower than that obtained on artificial diet [15, 16]. This low rate is probably due to low daily fecundity obtained during the period of high egg-laying of females. Indeed, during the experiment, the high number of eggs laid by the female daily during the period of high egg-laying, varied between 11 and 28; whereas this number has fluctuated between 30 and 80 on artificial diet [16]. Thus, the daily low fecundity in *B. invadens* in the experiments is linked to female diet (mixture of sugar and soya flour) which is probably less rich in protein. In Dacinae species, females need a protein source to enable egg production [14, 40]. This protein source in the diet of females is consequently essential to maintain a high reproductive rate [13]. At 25 °C, net reproductive rate was respectively 456 and 154 in *B. cucurbitae* and *D. ciliatus* on cucumber [19]. The intrinsic rate of increase (r_m) allows to compare the reproductive potential of the species under various biotic and abiotic conditions [21]. This growth rate is slightly lower than that obtained in the laboratory at 28 °C and in open rearing room at 23-28°C [15, 16]. Furthermore, generation time is reduced. The difference is probably due to the generation of the strain [15, 16, 23]. Reproductive value (Vx) of *B. invadens* has shown that females in age classes 4-12 (9-36 days after emergence) produced more offspring than females in other age classes. Our results have shown that *B. invadens* is capable of doubling the size of its population in seven days. This duration is

close to that obtained by Ekesi, et al. [16] in the same species (6 days). It is equal to that observed in *D. ciliates* [19].

5. CONCLUSION

The dissections of sexually mature females of *B. invadens* allowed determine the number of ovarioles per ovary (41 ovarioles) of this economically important species. The number of ovarioles suggests high fecundity. This high potential of fecundity combined with low mortality of larval stages observed in our experiments and low doubling time of the population, with a relatively high growth rate predispose this species to rapidly and easily colonize different ecological zones favorable to its development thus causing enormous damage to fruits. Furthermore, the short duration of development cycle of *B. invadens* would permit to obtain many generations during the year (multivoltine species) and their maintenance in Guinean zone through its polyphagous status. Although the female punctures are not always accompanied by egg-laying, the oviposition scars left over fruit depreciate their market value and are gateways to other parasites (bacteria, fungi). The different results obtained constitute a complement of database on life-history of *B. invadens* on its favorite host (mango) with a less expensive local diet (soya bean flour and castor sugar) under ambient laboratory conditions, similar to those of the external environment. This is an undeniable asset for the study of interactions between this pest and native or introduced parasitoids with a view to its efficient and sustainable biological control in Togo in particular and in and West Africa in general.

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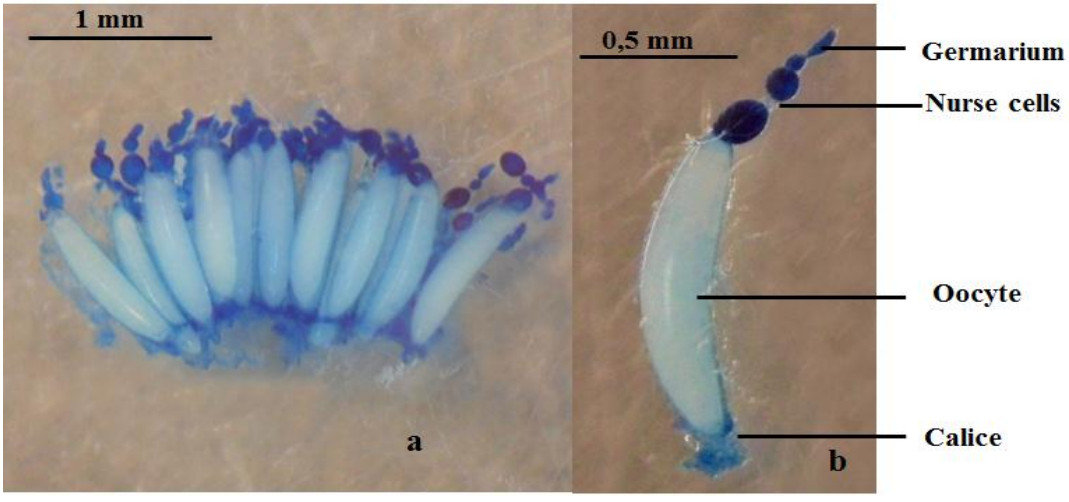

Fig-1. Left plated ovary of B. invadens (a) with a detail of an ovariole (b).

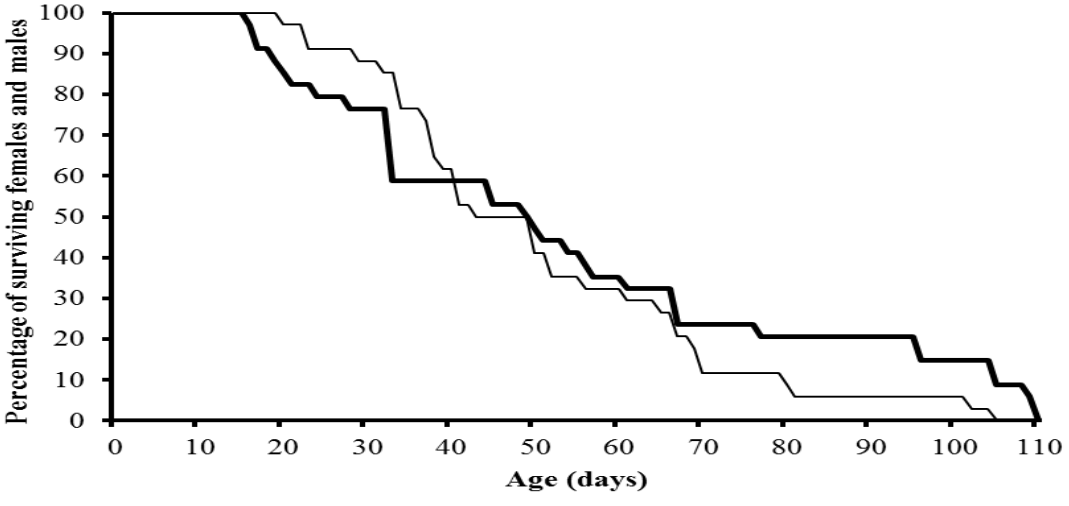

Fig-2. Survivorship of *B. invadens* (—: female ; ▬: male) at 27.5 ± 1°C; 79.5 ± 3% RH; 12:12 L:D (n= 34).

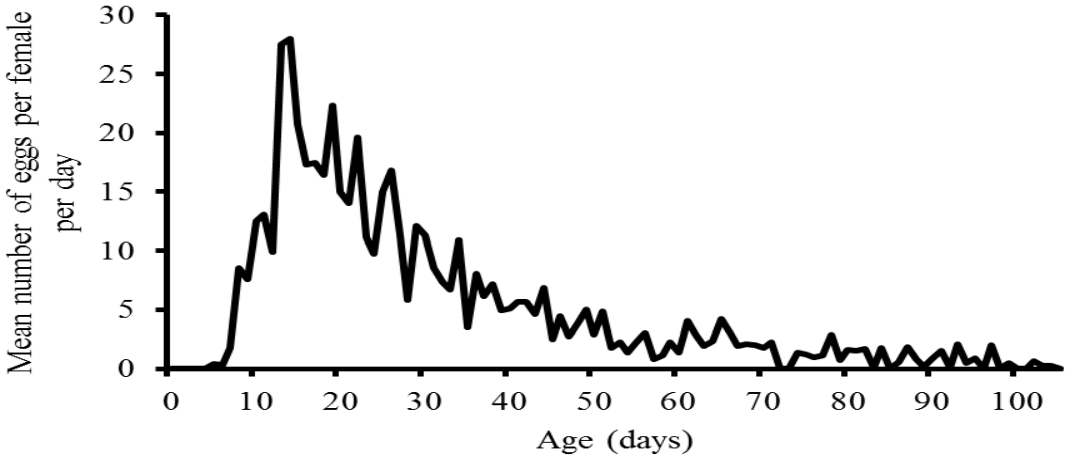

Fig-3. Number of eggs laid by *B. invadens* females per day reared on mango at 27.5 ± 1°C; 79.5 ± 3% RH ; 12:12 L:D (n= 34).

Table-1. Variation of ovariole number in the left and right ovaries and per ovary of females (n = 100) in *B. invadens* reared on mango at 27.5 ± 1°C; 79.5 ± 3% RH; 12:12 L: D.

Parameters recorded	Right ovary	Left ovary	Per ovary of one female
Maximum number of ovarioles	51	50	50.5
Minimum number of ovarioles	22	22	26
Mean number of ovarioles (ovarioles ± SD)	40.87 ± 5.22	41.06 ± 4.99	40.97 ± 4.72
Statistics	F = 0.360 ; df = 2 ; P = 0.964		

n = number of females dissected

Table-2. Mean fecundity and mean number of punctures recorded in females (n = 34) of *B. invadens* reared on mango at 27.5 ± 1°C; 79.5 ± 3% RH; 12:12 L:D.

Mean number of punctures (punctures ± SD)*			Mean fecundity (eggs ± SD)*		
Per female	With oviposition	With no oviposition	Per female	Per female per day	Per female per puncture
63,21 ± 28,04a	59,21 ± 26,78a	4 ± 3,95b	535,74 ± 235,70a	15,22 ± 5,59b	8,83 ± 2,24b
F = 73.520 ; df = 2 ; P < 0.001			F = 167.763 ; df = 2 ; P < 0.001		

* Means followed by different letters in the same line are significantly different (ANOVA followed by Student Newman-Keuls comparison tests, P < 0.05); n = total number of females reared.

Table-3. Mean development time and mean survival rates of immature stages of *B. invadens* reared on mango at 27.5 ± 1°C; 79.5 ± 3% RH ; 12:12 LD.

Development stages	Mean development time (days ± SD)*	Mean survival rate (% ± SD)*
Eggs	1.28 ± 0.02d	92.67 ± 4.68bc
L_1	1.14 ± 0.03d	89.86 ± 2.82c
L_2	1.10 ± 0.05d	95.18 ± 1.12ab
L_3 on natural diet (mango pulp)	6.44 ± 1.15c	92.33 ± 4.02bc
L_3 emerged fom natural diet (mango pulp)	1.90 ± 0.19 d	97.98 ± 1.01a
Puparia	9.37 ± 0.19b	95.56 ± 1.95ab
Egg to adult	21.71 ± 0.99a	68.50 ± 5.13d
Statistical tests	F = 1018 ; df = 6 ; P < 0.001	F = 53.204 ; df = 6 ; P < 0.001

* Means followed by different letters in the same column are significantly different (ANOVA followed by Student Newman-Keuls comparison tests, P < 0.05).

Table-4. Mean development time and mean pupal development time of males and females of *B. invadens* reared on mango at 27.5 ± 1°C; 79.5 ± 3% RH; 12:12 L:D.

Mean pupal development time (days ± SD)		Mean development time (days ± SD)	
Male	Female	Male	Female
9.37 ± 0.20	9.38 ± 0.19	21.71 ± 1.00	21.72 ± 0.98
F = 0.005 ; df = 1 ; P = 0.943		F = 0.000 ; df = 1 ; P = 0.989	

Table-5. Growth parameters of *B. invadens* reared on mango at 27.5 ± 1°C; 79.5 ± 3% RH ; 12:12 L:D.

Parameters	Formula	Calculated value
Net reproductive rate (R_0)	$R_0 = \sum_{x=0}^{w} l_x m_x$	98.499
Generation time (G)	$G = \frac{\sum_{x=0}^{w} l_x m_x . P}{R_0}$	45.635
Intrinsic rate of population increase (r_m)	$r_m = \frac{lnR_0}{G}$	0.101
Doubling time (DT)	$DT = \frac{ln2}{r_m}$	6.891

w = last age class; x = age base class