Original article

Seasonal population fluctuations of *Bactrocera invadens* (Diptera: Tephritidae) in relation to mango phenology in the Lake Victoria Crescent, Uganda

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Seasonal population fluctuations of *Bactrocera invadens* (Diptera: Tephritidae) in relation to mango phenology in the Lake Victoria Crescent, Uganda.

Abstract – Introduction. Timing of management practices requires an understanding of pest population dynamics in given cropping systems. Our study was designed to establish the population trends of *B. invadens* in mango orchards and to determine if population fluctuations were reflected in fruit infestation levels during changes in mango phenology. **Materials and methods**. *Bactrocera invadens* flies were trapped weekly from February 2011 to November 2012, using methyl eugenol and DDVP (dichlorvos) insecticidal strips. Trapping was done in three mango orchards in the Luweero district of Uganda's Lake Victoria Crescent. Mango fruit samples were incubated for the retrieval of puparia to calculate positivity (proportion of fruits infested) and fruit infestation indices (number of puparia per kg of fruit) for each stage of fruit maturity. **Results**. Mean trap catches of adult *B. invadens* varied significantly over the months (range : ~11 flies per trap per day (FTD) to over 590 FTD; $P \leq 0.0001$). During each year, infestations peaked during June-July and January-February. Trap catches were higher in the major fruiting season compared with the minor fruiting season and were the highest when mango was at the physiological maturity and ripe stages. Fruit infestation and positivity were highest for fruit at the physiological maturity and ripe stages and lowest at the fruit set stage. **Discussion**. Our findings show that *B. invadens* is present year-round and all stages of mango fruit development are susceptible to attack. Thus, control measures should be implemented throughout the year and preferably started at fruit set to lessen fruit fly population build-up and damage to fruits.

Uganda / *Mangifera indica* / fruits / phenology / integrated pest management / Tephritidae / *Bactrocera invadens* / population dynamics

Fluctuations saisonnières des populations de *Bactrocera invadens* (Diptera : Tephritidae) en liaison avec la phénologie du manguier dans le Croissant du Lac Victoria en Ouganda.

Résumé – Introduction. La synchronisation des pratiques de gestion exige de comprendre la dynamique des populations des parasites dans un système de culture donné. Notre étude a été entreprise pour établir l'évolution des populations de *B. invadens* en vergers de manguiers et pour déterminer si les fluctuations de ces populations étaient liées aux niveaux d'infestation des fruits selon la phénologie de l'arbre. **Matériel et méthodes**. Des mouches de *B. invadens* ont été capturées chaque semaine de février 2011 à novembre 2012, en utilisant des bandes insecticides d'eugénol méthylique et de DDVP (dichlorvos). Le piégeage a été fait dans trois vergers de manguiers dans le district de Luweero du Croissant du Lac Victoria en Ouganda. Pour chaque étape de maturité de fruit, des échantillons de mangues ont été incubés pour la recherche des puparia afin de calculer la positivité (proportion de fruits infestés) et les taux d'infestation des fruits (nombre de puparia par kg de fruits). **Résultats**. Le nombre moyen de captures d'adultes de *B. invadens* dans les pièges a varié significativement au cours des mois [d'environ 11 mouches par piège et par jour (MPJ) à plus de 590 MPJ ; $P \leq 0{,}0001$]. Chaque année, les infestations ont culminé en juin-juillet et janvier-février. Les captures dans les pièges ont été plus importantes pendant la principale saison de production comparée à la saison mineure et elles ont été les plus hautes quand la mangue était au stade de maturité physiologique et au stade mur. L'infestation et la positivité des fruits ont été les plus hautes pour les fruits au stade de maturité physiologique et au stade mur et moindre pour le stade de nouaison. **Discussion**. Nos résultats montrent que les mouches de *B. invadens* sont présentes toute l'année et que tous les stades du développement des mangues sont susceptibles d'être attaqués. Par suite des mesures de contrôle devraient être maintenues tout au long de l'année et débuter de préférence dès la nouaison du fruit afin de limiter le développement des populations de mouches des fruits et leurs dommages aux mangues.

Ouganda / *Mangifera indica* / fruits / phénologie / gestion intégrée des ravageurs / Tephritidae / *Bactrocera invadens* / dynamique des populations

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1. Introduction

Bactrocera invadens Drew, Tsuruta & White, is a highly polyphagous pest of fruit and may cause over 90% fruit loss [1]. The species invaded East Africa in 2003 and has since spread to other countries of sub-Saharan Africa [2, 3], where it constitutes a major constraint to mango production and a barrier to trade[1] [4–6]. Control of *B. invadens* is difficult because it is multivoltine, polyphagous, and has the ability to thrive in a wide range of ecological conditions [4].

In Uganda, the majority of mango fruit is produced on small landholdings of less than a hectare each by resource-limited farmers[1]. Fruit flies are a key pest of mango, with on-farm losses estimated at between 40–80% of production volumes depending on the season and variety [unpublished NARL techn. rep., 2013]. The majority of growers have no access to established fruit fly control measures such as protein bait sprays or lures. However, commercial farmers of mango carry out routine sprays of synthetic pyrethroids, but with little success at containing fruit losses.

Nakasinga established that *Ceratitis* spp. and *Bactrocera* spp. were the main fruit fly species in Uganda [7]. *Bactrocera invadens* is present year-round in Uganda, but it is not established whether the pest is more prevalent at certain times of the year or has a more even temporal distribution. It is also not established if peak occurrence is related to mango phenology. Herms indicated that plant phenology can be used to time pest management as phenological events can act as indicators of insect prevalence [8]. The proper timing of management strategies using plant phenology greatly simplifies the logistics of planning, scheduling and monitoring pesticide application programs and other pest management activities for insect pests. One of the tenets of sustainable ecologically-based pest management is that application of pest control techniques should be synchronized with the (likely) availability/occurrence of the pest [9, 10]. Additionally, the study of Vayssières *et al.* on the effectiveness of spinosad showed a significant reduction in fruit fly-induced crop losses when management was applied earlier in the season compared with when it was applied later in the season [11].

Our study was designed to describe the seasonal population fluctuations of *B. invadens* on mango in the Lake Victoria Crescent, a key mango-producing area in Uganda. Mango was chosen because it is highly susceptible to *B. invadens* [12]; the tree is widely grown in the country and its production has high potential for commercialization in the fruit economic sub-sector[1]. Additionally, it was also important to determine if *B. invadens* populations in mango were synchronized with mango phenology. If so, this would facilitate the drafting of a more effective integrated fruit fly management program in mango orchards.

2. Materials and methods

2.1. Study area

Fruit fly sampling was conducted in three mango orchards located in the Luweero district, with GPS coordinates 0°41'18" N and 32°36'28" E and altitude of 1,157 m.a.s.l., in the Lake Victoria Crescent. The district is a key mango production area in Uganda, with two fruiting seasons in the year. It has a warm, humid to sub-humid climate, and a bimodal rainfall pattern with 1,200 mm of rain per year.

2.2. Monitoring adult *Bactrocera invadens* population

Adult flies were trapped using Lynfield traps baited with methyl eugenol [a synthetic parapheromone supplied by International Pheromone Systems (IPS), UK], for attracting males of *B. invadens*, and DVDP (2, 2 dichlorovinyl dimethyl-phosphate)

[1] Anon., Final report on market study for fruits sub-sector: pineapples, passion fruit, mango, FIT Uganda Ltd 2007, http://www.fituganda.com/manage/download/atm/marketreports/subsectorstudy-fruits.pdf, Access 28 October 2013.

insecticidal strips to immobilize trapped flies. The methyl eugenol used was formulated as solid cylindrical plugs. Trapping was conducted for a period of 22 months from February 2011 to November 2012. The trial was laid out as a randomized complete block design replicated three times; trap catches were the response variable. The placement of traps followed the procedure described in the fruit fly management manual [13]. In each orchard, three trees were selected and, on each, one trap was hung from a branch at a height of 2 m. The traps were rotated weekly using the same trees to compensate for possible errors due to specific trap location. The methyl eugenol lures were replaced after every eight weeks, as recommended by the manufacturer. Once a week for the 22-month period, each trap was inspected and trapped flies were collected into plastic containers and transported to the National Agricultural Research Laboratories (NARL) (Kawanda, Uganda) for identification and counting. Samples were kept in 70% ethanol as voucher specimens. Identification was achieved by using keys from the fruit fly management manual [13]. The number of flies trapped per week per orchard was recorded.

Temporal changes in fruit infestation levels were determined by incubating ten mango fruits picked randomly from each of the three mango orchards. The picking of mango fruit samples started one month after fruit set. The samples were collected at two-week intervals for three fruiting seasons: (i) the major fruiting season, which occurred from February-July 2011, (ii) the minor fruiting season from September 2011 to January 2012, and the subsequent major fruiting season from February-July 2012. The fruit maturity stages were indicated for each variety at every collection as follows: immature small green (1 month after fruit set), immature medium green fruit (about 2 months after fruit set), physiologically mature fruits and ripening (3 or 4 months after fruit set). At the laboratory, each fruit was weighed and placed in well-aerated circular plastic containers (~15 cm diameter) with sterile sand to a depth of 2–3 cm, according to the procedures of Mwatawala *et al.* [14]. The containers were placed on open shelves in ambient laboratory conditions (20–30 ºC, 60%-80% relative humidity) and held for 4–6 weeks to recover all puparia from them. Incubation containers were checked every day and puparia collected from the sand with a pair of soft forceps for counting. The rotting fruits were dissected to completely recover all remaining puparia before discarding. Puparia were held in small ventilated transparent cylindrical plastic tubes until eclosion to determine species identity. Infestation level indices were calculated as number of puparia recovered per kilogram of fresh fruit [15, 16]. Samples of the emerged flies were preserved in 70% ethanol and representative specimens were sent to the Royal Museum for Central Africa (in Tervuren, Belgium) for confirmation of the identification. *Bactrocera invadens* infestation of mango was also analyzed as %positivity, that is, the percentage of fruits sampled that were infested.

Data on mango tree phenology were collected on a monthly basis by recording the most frequent phenological stage observed at a given orchard. The stages were: dormancy (when there was no active growth by the mango trees), leaf flush (when there was active growth of mango trees with new apical leaves), flowering (when the trees had flower buds and opened flowers), fruit set (when fruits were 2 weeks – 1 month after fruit formation), fruit development (when fruits were 2 months after fruit formation), physiological maturity (when fruits were 3–4 months after formation but not ripe) and the ripe fruit stage.

2.3. Data analysis

The number of catches of flies per trap per day (FTD) was computed using the formula FTD = (total number of flies / number of serviced traps) × (average number of days while traps were exposed in the field) [16]. The FTD data was subjected to repeated measures ANOVA at the 5% significance level. Means were separated using Tukey's HSD (Honest Significant Difference) test. Data for fruit fly infestation levels in mango fruits for the three sampled seasons of the study period were subjected to one-way ANOVA after

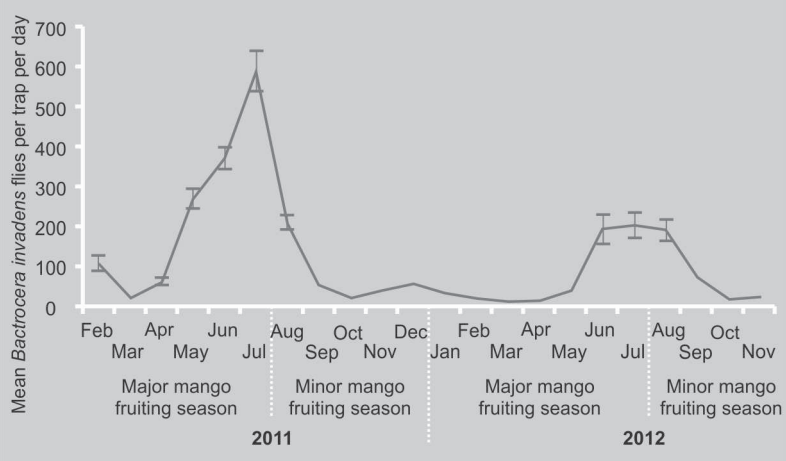

Figure 1.
Seasonal population fluctuations (mean ± standard error) of *Bactrocera invadens* in mango orchards in the Lake Victoria Crescent (Luweero district), Uganda, during 2011 and 2012.

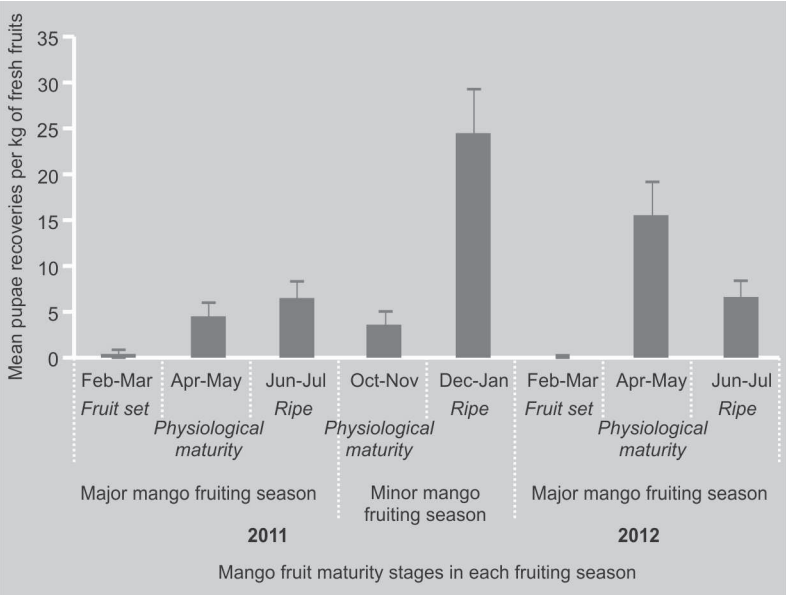

Figure 2.
Infestation index (mean ± standard error) of mango fruit at different stages of fruit maturity during 2011–2012 in the Lake Victoria Crescent (Luweero district), Uganda.

log transformation [$\log_{10}$ (x+1)]. Comparison of mean puparia differences was also carried out on the transformed values using Tukey's HSD Test. The chi-square test was used to test for any association between positivity and fruit maturity stages.

3. Results

3.1. Population dynamics of adult *Bactrocera invadens*

Bactrocera invadens was present throughout the 22 months of trapping. Trap catches for *B. invadens* significantly varied over the 22 months of trapping ($F_{21,\ 8.420} = 50.275$, $P \leq 0.0001$) and were high to very high in any one month (range: ~11 flies per trap per day to over 590 flies per trap per day). Two peaks were observed during the trapping period; the first was recorded in the period of June to July 2011, and another in the period of June to August 2012 (*figure 1*). The *post-hoc* comparison of mean fly catches per trap per day showed the months of July and June of 2011 with the highest trap catches [(590.05 ± 51.2 and 371.60 ± 29.1) flies per trap per day, respectively]. In any one year, there was a major peak of infestation (June-July/August) followed by a decline and then a slight population rise starting in the month of November, culminating in a smaller peak around January/February. Thereafter, catches declined again and began to rise around April before the annual major infestation peak occurred. The lowest *B. invadens* trap catches were recorded in the months of March 2012 (11.47 ± 1.8 flies per trap per day) and April 2012 (16.29 ± 3.4 flies per trap per day). The peak periods of fruit fly trap catches corresponded to harvesting periods when mango fruits were at physiological maturity to ripeness, while the lowest trap catches corresponded to periods of fruit set when fruits were very small and immature.

3.2. *Bactrocera invadens* infestation levels on mango fruits

There was a significant difference in the infestation levels of *B. invadens* at the three mango development stages recorded for the two years of the study ($F_{7,\ 4.798} = 20.575$, $P < 0.0001$) (*figure 2*). Comparison of treatment means showed that mango fruits at the ripe stage and physiological maturity stage recovered the highest numbers of puparia per kg (2011: 24.56 ± 4.8 puparia per kg

fruit at the ripe stage; 2012: 15.68 ± 3.57 puparia per kg fruit at the physiological maturity stage, respectively). On the other hand, the lowest infestation indices were recorded at the fruit set stage (2011: 0.59 ± 0.4 puparia per kg fruit; 2012: 0.17 ± 0.17 puparia per kg fruit) and differed from the infestation indices of the other fruit maturity stages.

Positivity was associated with fruit maturity stages ($\chi_2 = 5.991$; $P = 0.001$; contingency coefficient = 0.34). Irrespective of the year of sampling, about 1% of fruit at fruit set was infested, and positivity rose to between 10% and 21% for fruit at the physiological maturity and ripe stages (*figure 3*). The highest positivity was recorded for the ripe stage of the minor fruiting season (December 2011 – January 2012).

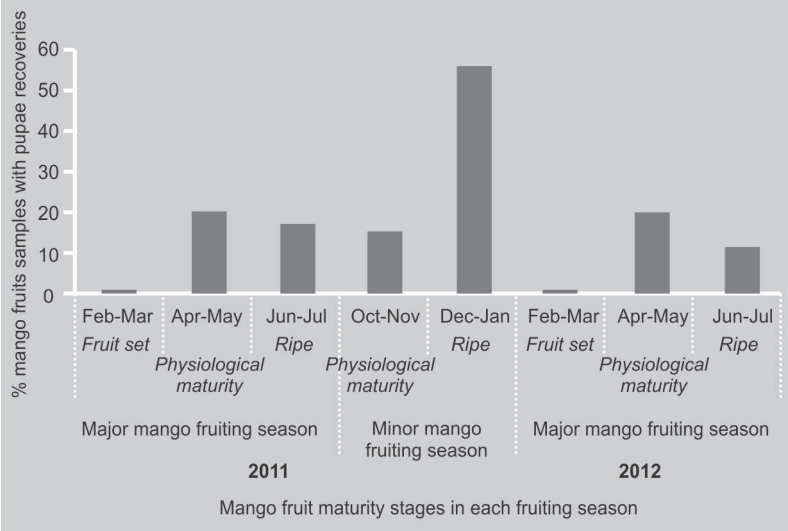

Figure 3.
Percentage of mango samples infested by fruit flies (positivity) at different stages of fruit maturity during 2011–2012 in the Lake Victoria Crescent (Luweero district), Uganda.

4. Discussion

As a livelihood pathway, the commercial production and trade of fruit holds promise for a large fraction of the population in eastern Africa[1] [17]. Production of tradable volumes is, however, hampered by a host of pest and disease problems. For mango, *Bactrocera invadens* infestation is a key production constraint across a range of agro-ecological habitats/zones, for which management interventions are desperately needed. Our study has established that *B. invadens* is available all year round within the Lake Victoria Crescent but with two distinct population peaks that are synchronized with the major mango fruiting seasons, especially when the majority of the fruits were either physiologically mature or ripe. First, fruits at these stages are large and have strong visual and olfactory cues [18] that attract fruit flies into the orchards and thus account for the higher trap catches, infestation indices and positivity at that time. Secondly, at these stages, the fruit pericarp is softer, thus making it easier for female flies to oviposit[2] [19, 20–22]. While methyl eugenol attracts only males [16], *Bactrocera invadens* has a 1:1 sex ratio [23] and males normally search for females prior to mating. The trap catches of males are thus an adequate indication of the number of female flies that would be in the orchards in search of oviposition sites (fruits). During the periods when there are no physiologically mature or ripe mango fruits (such as during leaf flush and flowering), *Bactrocera invadens* utilizes alternative fruit hosts within the surrounding landscape [13–16, 24]. Mango, however, is a strongly preferred host species for *B. invadens* [5, 12] and will be readily infested when available.

Our findings show that all stages of fruit development are susceptible to attack by *B. invadens*. The higher infestation index at the ripe stage, complemented by higher positivity for the same stage in December 2011 – January 2012, is perhaps explained by a lower availability of fruits during the minor fruiting season when there is lower fruit production. Mangoes are known for alternate bearing [25], and a relatively short

[2] Thomas M. C., Heppner J. B., Woodruff R.E., Weems H.V., Steck G.J., Fasulo T.R., Featured creatures: Mediterranean fruit fly, Fla. Dep. Agric. Consum. Serv., Div. Plant Ind. Univ. Fla., U.S.A., 2001, (http://creatures.ifas.ufl.edu/fruit/mediterranean_fruit_fly.htm).

flowering period normally occurs after heavy fruiting. Lower fruit availability typical of the minor fruiting season would create competition for oviposition sites for female flies and thus result in more oviposition punctures per fruit (more puparia per fruit) and more fruit attacks (higher positivity). It is also apparent that, in 2012, trap catches in real terms were lower than in 2011, although the differences were not statistically significant. This may be a consequence of the continuous trapping done during 2011 that started to deplete the fly population. Vayssières *et al.* have also reported that continuous trapping in orchards gradually reduced the relative abundance of fruit flies, and attributed it to the effect of successive trapping of the flies from one year to another [1].

Of the three fruit maturity stages, infestation at fruit set was the lowest in both years but it was demonstrated that *B. invadens* can also attack very young fruit, although the degree of successful eclosion from such fruit is unknown. Our findings are in conformity with those of Vayssières *et al.,* who found that mangoes were infested as early as 4–10 weeks after fruit set [5]. When fruit has reached physiological maturity, several fruits in any 1-kg sample are normally infested (*figure 3*), and often with more than one puparium (*figure 2*). Within the context of mango trade, this means that many individual fruits would be infested, which further raises the risk of spread of fruit flies in a region. Fruit spoilage is furthermore a major concern for growers in areas already infested by *B. invadens*. The observed high fecundity may account partly for the high weekly trap catches. This pattern of infestation underscores the severity of the fruit fly problem in the Lake Victoria Crescent and justifies the need for urgent interventions to contain the problem.

5. Conclusion

Bactrocera invadens is present in mango orchards of the Lake Victoria Crescent all year round, and at levels that far exceed economic thresholds set in other parts of the world [26]. *Bactrocera invadens* population and infestation levels progressively rise as fruit matures and ripens, followed by a rapid decrease in population numbers after harvest. The population peaks match well with fruit availability (physiologically mature or ripe fruit stages). It is recommended that fruit fly control measures be carried out throughout the year, but with increased intensity soon after fruit set when populations start to build up, in order to minimize damage to later stages of fruit development.

Acknowledgments

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Fluctuaciones estacionales de las poblaciones de *Bactrocera invadens* (Diptera: Tephritiadae) en relación con la fenología del mango en la media luna del Lago Victoria en Uganda.

Resumen – Introducción. Para la sincronización de las prácticas de gestión se necesita entender la dinámica de las poblaciones de los parásitos en un sistema dado de cultivo. Nuestro estudio se realizó para establecer la evolución de las poblaciones de *B. invadens* en vergeles de mangos y para determinar si las fluctuaciones de estas poblaciones estaban ligadas a los niveles de infestación de los frutos en función de la fenología del árbol. **Material y métodos**. Se capturaron moscas de *B. invadens* cada semana de febrero 2011 a noviembre 2012, utilizando bandas insecticidas de eugenol metílico y de DDVP (diclorvos). El trampeo se realizó en tres vergeles de mangos en el distrito de Luwero en la media luna del Lago de Victoria en Uganda. Para cada etapa de madurez del fruto, se incubaron muestras de mangos para buscar los puparios con el fin de calcular la positividad (proporción de frutos infestados) y los índices de infestación de los frutos (número de puparios por kg de frutos). **Resultados**. El número medio de capturas de adultos de *B. invadens* en las trampas varió significativamente a lo largo de los meses [de aproximadamente 11 moscas por trampa y por día y (MPJ) a más de 590 MPJ; $P \leq 0{,}0001$]. Cada año, las infestaciones culminaron en junio-julio y enero-febrero. En comparación con la estación menor, las capturas en las trampas fueron más importantes durante la estación principal de producción y aún más altas cuando el mango estaba en el estado de madurez fisiológica y en el estado maduro. La infestación y la positividad de los frutos fueron más altas para los frutos en estado de madurez fisiológico y en estado maduro y menor para los frutos en estado de fructificación. **Discusión**. Nuestros resultados muestran que las moscas de *B. invadens* están presentes todo el año y que todas las fases del desarrollo de los mangos son susceptibles de ser atacadas. Por consiguiente, se deberían mantener las medidas de control todo el año y empezar, preferentemente, a partir de la fructificación del fruto con el fin de limitar el desarrollo de las poblaciones de moscas de los frutos y sus daños en los mangos.

Uganda / *Mangifera indica* / frutas / fenología / gestión de lucha integrada / Tephritidae / *Bactrocera invadens* / dinámica de poblaciones