Seasonal Abundance of Mango Fruit Flies (Diptera: Tephritidae) and Ecological Implications for Their Management in Mango and Cashew Orchards in Benin (Centre & North)

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ABSTRACT We report the results of a large-scale (six orchards) and long-term (5-yr) study on seasonal population fluctuations of fruit flies (Diptera Tephritidae) in mango (2005–2009) and cashew (2007–2009) orchards in the Borgou Department, Benin.

During the five consecutive years of mango fruit fly monitoring, 25 tephritid species were captured including three species of *Bactrocera*, 11 of *Ceratitis*, and 11 of *Dacus*, which is represented by 2,138,150 specimens in mango orchards. We observed significant differences in *Bactrocera dorsalis* (Hendel) counts between "high" and "low" mango production years from 2005 to 2008 but not in *Ceratitis cosyra* (Walker) counts. The native species, *C. cosyra*, the most abundant species during the dry season, peaked beginning of May, while the exotic species, *B. dorsalis*, the most abundant species during the rainy season, peaked in June. Preliminary results underlined the role of nine species of wild hosts and seven species of cultivated ones around mango orchards that played an important role in maintaining *B. dorsalis* in this Sudan zone all year round. The presence of *C. cosyra* stretched over 9 mo.

During the first 14 wk of tephritid monitoring on cashew orchards situated near mango orchards, most flies (62%) were captured in traps positioned in cashew orchards, showing the strong interest of an early fly control on cashew before the mango season. According to these results, in the Sudan zone, effective and compatible control methods as proposed by the IPM package validated by the West African Fruit Fly Initiative project against mango fruit flies are proposed for a large regional tephritid control program in same zones of West Africa.

KEY WORDS *Bactrocera dorsalis*, *Ceratitis* spp., seasonal distribution pattern, host range, Sudan zone, West Africa.

Mango (*Mangifera indica* L.) is an important tropical fruit for sub-Saharan Africa as an significant source of nutrition for rural populations and for reducing poverty by providing local income through national and international markets (Vayssières et al. 2008). Unfortunately, mango producers in Benin are confronted with three closely connected problems: 1) deterioration of fruit quality mainly because of tephritid fruit flies (Diptera, Tephritidae), 2) inadequacy of postharvest methods, and 3) over-production for the national market leading to wastage and lower prices.

The genus *Ceratitis* McLeay belongs to the tribe Ceratitidini, which is predominantly an Afrotropical group (De Meyer 2005). This genus, attacking mangoes and other fruit species, comprises several important pest species such as *Ceratitis cosyra* (Walker), *Ceratitis capitata* (Wiedemann), *Ceratitis quinaria* (Bezzi), *Ceratitis silvestrii* Bezzi, *Ceratitis fasciventris* (Bezzi), *Ceratitis anonae* Graham, and *Ceratitis rosa* Karsch (White and Elson-Harris 1992). Before the year 2003, mango-infesting fruit flies in West Africa were restricted to the genus *Ceratitis* (Vayssières et al. 2004).

Since 2003, a new invasive fruit fly species belonging to the genus *Bactrocera* Macquart was recorded in orchards in East Africa (Lux et al. 2003, Ekesi et al. 2006, Mwatawala et al. 2006), West Africa (Vayssières 2004, N'Dépo et al. 2009, Rey and Dia 2010), and Central Africa (Ndzana Abanda et al. 2008, Virgilio et al. 2011). It was described in 2005 as *Bactrocera invadens* Drew Tsuruta & White (Drew et al. 2005). This new invasive *Bactrocera* species belongs to the *dorsalis*-complex, as defined by Drew and Hancock (1994). It is noteworthy that the taxonomic status of *B. invadens* was under revision recently (San José et al. 2013, Schutze et al. 2013, Krosch et al. 2013). But two

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other references (Schutze et al. 2014a, b) put *B. invadens* definitively into the same species as *Bactrocera dorsalis* (Hendel). The oriental fruit fly is responsible for extensive economic losses to horticultural crops throughout West Africa and especially on mango value chain (Vayssières et al. 2009a), increasing the already considerable damage caused by native fruit flies. With its high reproductive rates (Salum et al. 2013), a large host spectrum (De Meyer et al. 2007), and high mobility (Vayssières et al. 2009b), this species is a major pest of economic significance.

The presence of large fruit fly populations has considerably dampened the potential economic benefits of mango cultivation. Fruit flies cause significant direct damage owing to the development of the larvae inside the fruits as well as secondary damage resulting from the development of pathogens around punctures caused by the females. This results in fruit decay but also in loss of quality (aesthetic and nutritional), thereby limiting marketing possibilities. Losses to fruit fly vary according to agro-ecological zones (Vayssières and Sangaré 1995), between grafted or nongrafted mangoes, between mango cultivars (Vayssières et al. 2009a), type of orchards (Ndiaye et al. 2012), fruit phenology (Diatta et al. 2013), and cropping systems (Gretchi et al. 2013).

Seasonal changes in mango fruit fly populations have been studied in Hawaï (Haramoto and Bess 1970, Vargas et al. 1990), Costa Rica (Jiron and Hedstrom 1991), Mexico (Aluja et al. 1996), India (Sarada et al. 2001), South East Asia (Clarke et al. 2001), Tanzania (Mwatawala et al. 2006), Burkina Faso (Ouedraogo 2011), Côte d'Ivoire (N'Dépo et al. 2009, 2013), and at regional scale (Vayssières et al. 2014). Globally, adult populations show periodic fluctuations throughout the year but the reasons of this variability are not always fully understood. In West Africa, despite the dominance of two species [*Ceratitis cosyra* (Walker) and *B. dorsalis*], food traps generally capture many other fruit fly species during the mango season. Many authors showed that tephritid species dominance is mainly affected by abundance–diversity of host species (cultivated and local), season, temperature, rains, and altitude (Ekesi et al. 2006, Rwomushana et al. 2008, Mwatawala et al. 2009a, Geurts et al. 2014).

The present study shows results of seasonal monitoring of *C. cosyra* and *B. dorsalis* adult populations in mango orchards in the Borgou Department, which is the most important area of mango production (75% of total area) in Benin (Vayssières et al. 2008). This study is different from precedent studies in Benin and other countries. We provide data obtained through long-term monitoring (5-yr) carried out simultaneously in six mango orchards. A long-term study on the variability of seasonal *C. cosyra* and *B. dorsalis* population fluctuations is useful for developing a control strategy against these species. Results can also be extrapolated to a regional level for similar agro-ecological zones in West Africa and adjacent ecosystems.

As a tool to specify the agro-ecological screening, we used recent botanic and floristic studies. Adjanohoun et al. (1989) distinguished 10 major vegetation types grouped into four floristic zones: Coastal zone, Guineo-Congolian zone, Sudan-Guinean transition zone, and Sudan zone. Here, we used the phytogeographical division for Benin, according to Adomou et al. (2006), based on extensive phytosociological surveys with a numerical-chronological approach (Adomou et al. 2007). The Borgou Department is included in the Sudan-Guinean and the southern Sudan zones, sometimes summarized as the Sudan zone.

One of the main characteristics of Borgou is the proximity of cashew orchards adjacent to mango orchards (Vayssières et al. 2008) in each locality. The main objectives of this study were to 1) define the fruit fly diversity in and around mango orchards by trapping, 2) estimate the fruiting season of cultivated and wild hosts around mango orchards, 3) document annual fluctuation patterns for the two dominant species *C. cosyra* and *B. dorsalis*, 4) monitor the abundance of *C. cosyra* and *B. dorsalis* in mango orchards and adjacent cashew orchards in relation to phenological stages of the trees, and 5) discuss ecological implications for mango fruit fly management.

Material and Methods

Study Area. Experiments were conducted during five consecutive years in the Borgou Department, located between latitude 09.094–09.948° N and longitude 002.561–002.713° E in the Sudan zone of Benin (Fig. 1). Six mango orchards were selected according to methodology described by Vayssières et al. (2009a) in the six best production localities of the Borgou Department: Tchatchou (AD), Korobourou (WZ), Korobourou (LA), Komiguea (Monastery), Kakara (AOB), and Ina (OG). The selected orchards had 1) an area of at least 6 ha of grafted fruit-bearing mango trees, 2) more than five commercially important cultivars per orchard, 3) regular spacing between the mango trees (~10 m), 4) availability of technical supervision to ensure no pesticide application and 5) absence of any nearby crops (cotton) requiring use of pesticides. Locations, districts, Global Positioning System (GPS) coordinates, surfaces, composition, and main characteristics of the six mango orchards are described (Table 1). All mango orchards were adjoining cashew plantations.

Among the six orchards, two were mixed mango orchards and four were homogeneous (comprising 100% mango trees; Table 1). The mixed orchards predominantly contained *M. indica* (mango), *Anacardium occidentale* L. (cashew), *Spondias mombin* L. (tropical plum) (Anacardiaceae), *Carica papaya* L. (papaya) (Caricaceae), *Irvingia gabonensis* (Aubry-lec) Baillon (African wild mango) (Irvingiaceae), *Psidium guajava* L. (common guava) (Myrtaceae), *Annona muricata* L. (soursop) (Annonaceae), *Citrus sinensis* (L.) Osbeck (sweet orange), *Citrus paradisi* Macfad (grapefruit), and *Citrus reticulata* Blanco (mandarin) (Rutaceae). The surrounding area includes local fruit species such as *Sclerocarya birrea* (A. Richt) Hoschst. (marula plum) (Anacardiaceae), *Annona senegalensis* Pers. (wild custard apple), *Hexalobus monopetalus* (A. Richt) E.D. (baboons' breakfast) (Annonaceae), *Saba senegalensis*

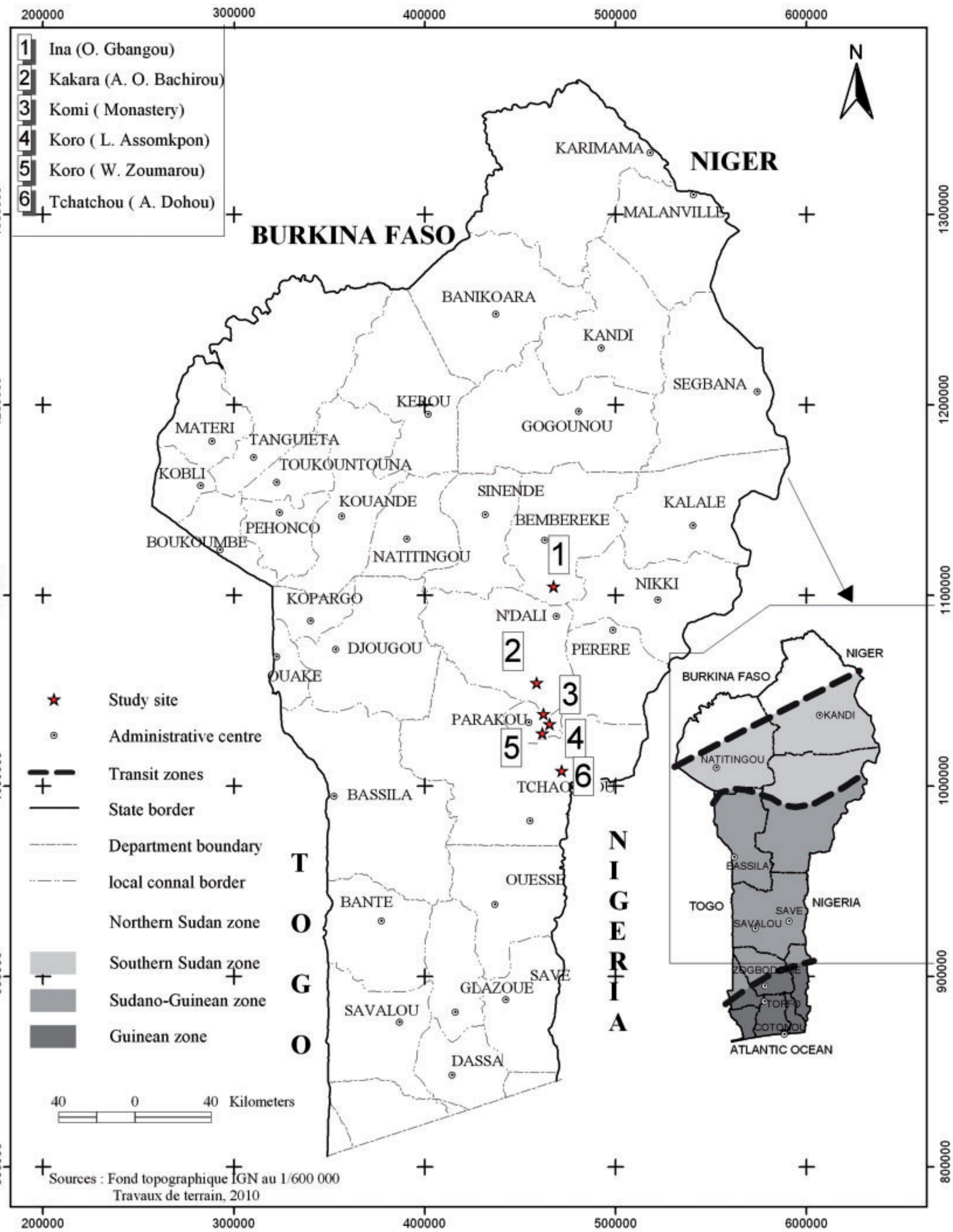


Fig. 1. Map of the Northern-Central area of Benin and mango orchards monitored (adapted from Adomou et al., 2006).

(A. DC) Pichon (Senegal saba) (Apocynaceae), *Cordyla pinnata* (A. Richt) Milne-Redhead (Caesalpinioideae) (cayor pear tree), *Strychnos spinosa* Lam. (monkey ball tree) (Loganiaceae), *Syzygium guineense* (Willd.) DC (waterberry) (Myrtaceae), *Sarcocephalus latifolius* (Smith) Bruce (African peach) (Rubiaceae), and *Vitellaria paradoxa* C.F. Gaertn (shea butter tree) (Sapotaceae). The 15 mango cultivars recorded in these six orchards matured at different times, (a) 'Gouverneur' is an early season cultivar like 'Amélie' and 'Ifac III,' (b) 'Zill,' 'Eldon,' 'Ruby,' 'Améliorée du Cameroun,' 'Dabchar,' 'Springfels,' 'Haden,' and 'Kent' are mid-season cultivars, (c) whereas 'Alphonse de Goa,' 'Smith,' 'Keitt,' and 'Brooks' are late season cultivars.

Table 1. Characteristics of the 6 mango orchards in Borgou Department

	Main characteristics of the different mango orchards in Borgou Department (4 districts)							
Nb	Location	GPS coordinates	Districts	Orchard type	Main mango cultivars	Surface	Cultivated fruits	Neighbouring crops
1	Ina (O.G.)	09° 37′01″ N 02° 57′08″ E	Bembèrèkè	Homogeneous mango orchard	Gouverneur, Ifac 3, Eldon, Améliorée du Cameroun, Dabshar, Ruby, Springfels, Kent, Smith, Palmer, Brooks	8 ha	*Mangifera indica*	Yam
2	Kakara (A.O.B.)	09° 56′ 20″ N 02° 57′23″ E	N'Dali	Homogeneous mango orchard	Gouverneur, Eldon, Haden, Kent, Miami late, Springfels, Kent, Brooks	8 ha	*Mangifera indica*	*Anacardium occidentale*
3	Komiguea (Monastery)	09° 43′59″ N 02° 52′38″ E	Parakou	Mixed mango orchard	Gouverneur, Ifac 3, Eldon, Améliorée du Cameroun, Dabshar, Springfels, Smith, Kent, Alphonse de Goa, Brooks	6 ha	*Mangifera indica, Anacardium occidentale, Annona muricata, Psidium guajava, Citrus sinensis, Citrus reticulata, Citrus x paradisi*	*Anacardium occidentale, Carica papaya* and vegetable crops
4	Korobourou (L.A.)	09° 38′ 55″ N 02° 51′ 33″ E	Parakou	Homogeneous mango orchard	Gouverneur, Ifac 3, Eldon, Améliorée du C., Dabshar, Springfels, Smith, Kent, Alphonse de Goa, Brooks	9 ha	*Mangifera indica*	*Anacardium occidentale*
5	Korobourou (W.Z.)	09° 37′ 01″ N 02° 57′ 10″ E	Parakou	Homogeneous mango orchard	Gouverneur, Ifac 3, Zill, Eldon, Améliorée du C., Atakora, Dabshar, Haden, Irwin, Springfels, Sabre, Ruby, Smith, Kent, Keitt, Brooks	~ 40 ha	*Mangifera indica*	*Anacardium occidentale*
6	Tchatchou (A.D.)	09° 09′ 45″ N 02° 56′ 18″ E	Tchaourou	Mixed mango orchard	Gouverneur, Eldon, Ruby, Smith, Kent, Alphonse de Goa, Keitt, Brooks	6 ha	*Mangifera indica, Anacardium occidentale, Psidium guajava, Citrus sinensis, Citrus lemon*	*Anacardium occidentale*

Placement and Service of Traps. During five consecutive years (2005–2009), we had traps set up inside mango orchards. Fluctuations of fruit fly populations were monitored by using 1) parapheromones-baited traps which efficiently captured the males of four species of economic significance and 2) food attractant traps that mostly captured females and also a few sexually immature males. The same type of device was used for each orchard—16 Tephri traps (from Sorygar SL – Madrid, Spain), 4 with terpinyl acetate, 4 with methyl eugenol, 4 with trimedlure, and four with cuelure, substances which were diffused from solid cylindrical substrates or plugs (from IPS Ltd., Ellesmere Port, Cheshire, United Kingdom), ensuring the release of homogeneous doses of the parapheromones. Insecticide-baited terpinyl acetate traps were used to mainly monitor population densities and periods of peak activity of *C. cosyra* [and also for *Ceratitis quinaria* (Bezzi) and *Ceratitis silvestrii* Bezzi, baited methyl eugenol traps for *B. dorsalis* (and also for *Ceratitis bremii* Guérin-Méneville), baited trimedlure traps for *Ceratitis fasciventris* (Bezzi) [and also for *C. capitata* and *Ceratitis anonae* Graham], baited cuelure traps for *Bactrocera cucurbitae* (Coquillett) (and also for some *Dacus* spp.). The capacity of the Tephri trap was 450 cc. Its dimensions were 1) total height, 142 mm; 2) yellow base diameter, 110 mm; 3) height of top, 40 mm; 4) holes diameter, 22 mm; and 5) invaginated hole diameter, 26 mm. The attractant was set up on a support in the upper part of the trap and the insecticide (DDVP) in the lower part. The capacity of the McPhail trap was 500 cc. Its dimensions were 1) total height, 198 mm; 2) yellow base diameter, 130 mm; 3) height of transparent top, 150 mm, and 4) invaginated hole, 54 mm. Each trap also contained a DDVP killing strip. Both parapheromone plug and DDVP strip were replaced monthly. For food attractants, three McPhail (from Chemtica Int, Costa Rica) traps baited with Torula yeast (three tablets dissolved in 300 ml of water per trap) were placed in each orchard. The Torula solution was replaced weekly, after washing of the traps. Traps were suspended on mango branches in the lower third of the foliage within human reach. The central coil of wire holding up the trap was coated with thick grease to prevent any predatory activity by weaver ants (*Oecophylla longinoda* Latreille (Hymenoptera: Formicidae)) on dead adult flies in the bottom of the trap. All traps used were rotated on a weekly basis in all the mango orchards. The trap density was four traps per hectare, irrespective of the attractant. They were set up at 10 m, at least, far in from the orchard edge. Traps were rotated clockwise at each weekly inspection day and provided data on fluctuations of fly populations.

During the first 26 weeks (corresponding to the cashew and mango seasons) of three consecutive years (2007–2009) and for three orchards (Koro [LA], Koro [WZ], and Kakara [AOB]) parapheromone traps, following the same methodology as explained above were set up and operational inside cashew orchards adjacent to mango orchards. During these 3 yr, for each mango and cashew tree, fruit phenology was recorded weekly distinguishing four different reproductive and vegetative developments 1) flowering stage, 2) fruit-growing stages, 3) fruit maturity, and 4) vegetative stage (without fruit). We did not differentiate the different fruit-growing stages.

Abiotic Factors Recorded. Temperature (minimum–maximum), relative humidity, and rainfall were recorded every 3 mo. Data on temperature and relative humidity were provided by Tinytags Plus 2 (TGP-4500, Gemini Data Loggers Ltd.). Rainfall data were recorded from individual rain gauges installed in the six orchards.

Fly Identification. All fly specimens were identified and sexed in Cotonou by the WAFFI-IITA team. Specimens of doubtful identity were sent for confirmation to Marc De Meyer (Royal Museum for Central Africa, Tervuren, Belgium), for Ceratitinae and to Ian White (The Natural History Museum, London, United Kingdom) for Dacinae.

Biodiversity Indices. We used the Margalef index to characterize alpha diversity. It provides a better discriminating ability than Shannon and Simpson indices (Magurran 1991). The numerical species richness is the number of species per specified number of individuals or biomass (Kempton 1979). The Margalef index, which is a good species richness index, provides an instantly comprehensible expression of diversity. The Margalef index was calculated according to the formulae detailed by Magurran (1991).

Beta diversity measures how different (or similar) a range of habitats or samples are in terms of species composition (and sometimes relative abundances). The easiest way to measure the β diversity between pairs of sites is by use of similarity coefficients such as Jaccard and Sorenson indices (Magurran 1991). The Jaccard index takes only notice of presence of different species of the targeted community. The Sorenson index, which measures beta diversity between 0 (absence of similarity) and 1 (complete similarity), is used to compare biodiversity of Tephritidae from different sites of this study. The captures of different traps were pooled. Only the presence or absence data were used, as the difference in attractiveness of the different lures we used does not allow utilization of quantitative data.

Rearing. Regular monthly fruit collections were carried out from January 2005 to December 2009 to assess the host range of main fruit fly species. The following major sampling sites were regularly visited 1) Ina, Guessou-sud, Gamaré in the district of Bembéréké; 2) Kakara, N'Dali, and Ouénou in the district of N'Dali; 3) Komiguea, Koroborou, Gouniako, Dabou, Bakpérou in the district of Parakou; 4) Tchatchou-nord, Tchatchou-sud in the district of Tchaourou. At any given period, fruits of cultivated and wild plant species were collected from native or imported shrubs and trees in field, orchards, open woodland, and natural wild vegetation. Fruits were taken at various maturity levels depending on plant species (e.g., young fruits for cucurbits and mature fruits for trees and shrubs) harvested directly from the plants or gathered from the ground. The number and size of samples from different plant species were primarily determined by the availability of fruits. Efforts were made to ensure a minimum collection of 20 fruits per sample from the same crop and location. Fruits from individual samples were kept together in paper bags, labeled with their concomitant data, and brought back for rearing in the laboratory of the IITA-CIRAD guest house at Parakou.

In this laboratory, fruits of each sample were counted and weighed. Fruits >8–10 cm in diameter were incubated in groups of three to four in 15-liter cylindrical plastic containers (38 cm in diameter by 21 cm in height), whereas smaller size fruits were held in1.5-liter plastic pots (12 cm in diameter by 13 cm in height). Fruits were placed on wire grids in bowl shape that were attached to the rim of the large containers or placed 5 cm above the bottom of the small containers. The bottom of each incubation unit was covered with a 1.5-cm layer of moist sand (sterilized for each sample) as pupating medium for fruit fly larvae. The incubation units were covered with fine-mesh gauze fixed with an elastic band. The samples were incubated for up to 4 wk until all fruit fly larvae had emerged from the fruits and pupated. The incubation units were maintained in well-aerated rooms under ambient climatic conditions, i.e., at 28 ± 3°C and 60–80% relative humidity (RH) at Parakou. The sand layer in the incubation units was inspected at ~3-d intervals to remove fruit fly pupae, which were transferred to little boxes and Petri dishes (9 cm in diameter by 1.5 cm in height) containing a wet cotton ball and a 1:3 mixture of hydrolyzed yeast and sugar to serve as food for emerging adult flies. Emerged adults were kept alive for 5 d until they reached full maturation and final coloration and either mounted with micropins, or preserved in 70% ethyl alcohol. Samples from plants commonly encountered in the study area were determined using keys (Akoegninou et al. 2006). For difficult identifications, some assistance was provided in Benin by Dr. P. O. Agbani and Dr. Adomou, National Herbarium, Faculté des Sciences Techniques, Université d'Abomey-Calavi, Cotonou, Benin.

Data Analysis. $Log_{10}(x + 1)$ transformation of insect counts (x) was applied before analysis to stabilize the variance and normalize the data. Analysis of variance (ANOVA) was performed using the general linear model procedure, and means separation was done by pair-wise comparison test at $P = 0.05$ (SAS 2007, SAS Institute, Cary, NC). Correlation and lag correlation analyses were done to determine if there were any correlations between insect counts on both fruit trees (mango and cashew) with respect to time and phenological stages. The correlation analyses were done both on the raw monthly data for each year and the monthly data averaged over the 3 yr under study. The following aspects were also analyzed: 1) where were insects concentrated more—cashew or mango orchard? 2) Where were insects concentrated more—in relation with the phenological stages (fruit stages) of each fruit tree (mango and cashew)?

Results

Means of Main Climate Data. We averaged rainfall and temperatures of the six mango orchards during the period 2005–2009 (Fig. 2). This climadiagram shows a unimodal peak (in September) during the rainy season typical for this department in the Sudan zone. Although some aberrations (disruption of rain) during the rainy season can be observed, we had the same general trend every year. During these five years, the mean yearly rainfall recorded was 1,130 mm for these six mango orchards.

Fly Species Diversity in Mango Orchards. *Alpha Diversity.* Over the five years, 2,138,150 specimens were collected (Table 2) in traps set up in mango orchards. The specimens belonged to 25 tephritid species including 3 *Bactrocera* species, 11 *Ceratitis* species, and 11 *Dacus* species (Table 2). Of these, 53.03% belonged to *B. dorsalis*, while the second, third, and fourth most common species (*C. cosyra*, *C. quinaria*, and *C. silvestrii*) represented 35.98, 5.61, and 2.77%, respectively. The 21 remaining tephritid species contributed only 2.61% to the total. Table 2 shows the Margalef index calculated for each site. The Komi and Tchatchou sites showed the highest alpha diversity with 24 and 21 species, respectively. Koro-WZ and Kakara sites had a much lower alpha diversity with 14 species found at each site. Both *Ceratitis* (11 species) and *Dacus* presented the largest specific richness (11 species), while the genus *Bactrocera* included two invasive species (*B. dorsalis* and *B. cucurbitae*) of the three. There were significant differences ($P < 0.001$) in insect counts observed for combined year ANOVA in each mixed mango orchards versus each homogeneous mango orchard.

Beta diversity. In our study (Table 3) the highest similarity was observed between the two Koro orchards and between Kakara and Koro-LA based on the Jaccard and Sorenson indices. The lowest β diversity index concerned the northern site (Ina_OGB), which already had the lowest α diversity index compared with Komi, which had the highest α diversity and β diversity indices (Table 3).

Fruiting Phenology of Cultivated Local Fruit Species and Tephritid Population. The fruiting phenology for 15 exotic fruit species from mango orchards and 20 local (wild) species found in adjacent fields is shown in Figure 3. *B. dorsalis* can find mature fruits almost all year round in the Borgou Department of this Sudan area. Often intercropped in or around mango orchards, the most important cultivated fruit species were cashew, citrus, guava, soursop, and papaya, while the most important wild fruit species recorded were marula plum, wild custard apple, cayor pear tree, monkey ball tree, shea butter tree, and African peach.

From January to March, cashew provided lots of apples, which were mainly exploited by *C. cosyra*, and, to a lesser extent by *C. quinaria*, *C. silvestrii*, *B. dorsalis*, and *B. cucurbitae* (Fig. 3). From mid-May until mid-July, mangoes were largely infested by *B. dorsalis*, and, to a lesser extent, by *C. cosyra*, *C. fasciventris*, *C. anonae*, *C. capitata*, and *Dacus vertebratus* Bezzi. From May to September, guavas were largely infested by *B. dorsalis*, *C. fasciventris* (Fig. 3) and, less by *C. cosyra*. From May to December, citrus were infested by *B. dorsalis*, *C. fasciventris* (Fig. 3), and, to a lesser extent, by *C. capitata*, *Ceratitis ditissima* (Munro), and *B. cucurbitae*.

From March to mid-May, marula plums were largely infested by *C. cosyra* but also by *B. dorsalis* (Fig. 3). From April to September, wild custard apples were largely infested by *C. cosyra* but also to a lesser extent by other *Ceratitis* species (Fig. 3). From May to end--June, cayor pears were largely infested by *C. cosyra*

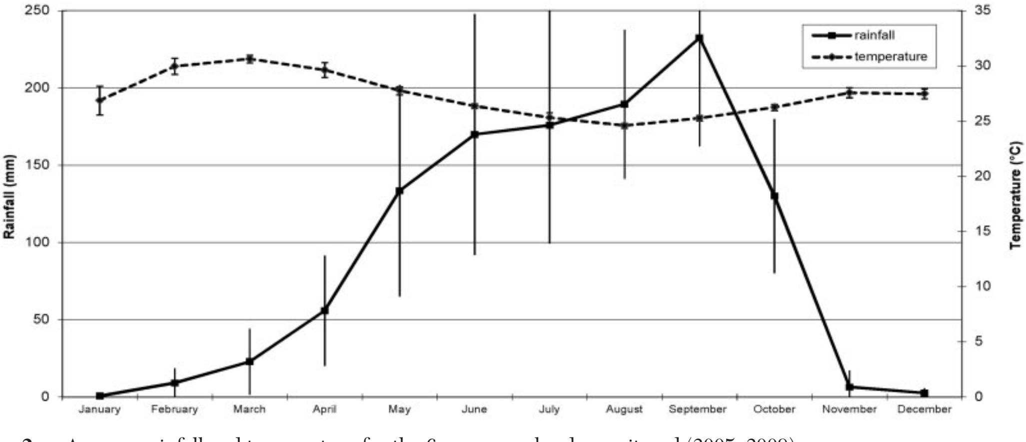


Fig. 2. Average rainfall and temperature for the 6 mango orchards monitored (2005–2009).

Table 2. Number of fruit fly species captured in the 6 mango orchards in Borgou

Serial no.	Species	Tchatchou	Koro_WZ	Koro_LA	Komi	Kakara_AOB	Ina_OGB	Total	Proportion (%)
1	*B. cucurbitae* (Coquillett)	545	561	235	3497	184	112	5134	0.240
2	*B. dorsalis* (Hendel)	248,470	182,307	186,281	278,815	140,663	97,308	1,133,844	53.030
3	*B. mesomelas* (Bezzi)	7	0	0	28	0	0	35	0.002
4	*C. anonae* Graham	12	3	12	111	9	6	153	0.007
5	*C. bremii* Guérin-Méneville	120	118	180	305	98	76	897	0.042
6	*C. capitata* (Wiedemann)	2,250	1,413	1527	26,902	2,417	948	35,457	1.658
7	*C. cosyra* (Walker)	89,345	134,081	171,357	63,857	210,312	100,394	769,346	35.981
8	*C. ditissima* (Munro)	3	0	0	51	0	0	54	0.003
9	*C. fasciventris* (Bezzi)	202	142	657	510	335	198	2044	0.096
10	*C. lentigera* Munro	0	0	0	5	0	0	5	0.000
11	*C. pedestris* (Bezzi)	0	0	0	4	0	0	4	0.000
12	*C. punctata* (Wiedemann)	12	1	7	18	1	3	42	0.002
13	*C. quinaria* (Bezzi)	11,568	16,564	29,032	9,807	27,222	25,872	120,065	5.615
14	*C. silvestrii* Bezzi	4,552	13,942	13,062	5,111	14,070	8,675	59,412	2.779
15	*D. albiseta* White & Goodger	0	0	1	0	0	1	2	0.000
16	*D. bakingiliensis* Hancock	3	0	0	4	0	0	7	0.000
17	*D. bivittatus* Bigot	2,612	955	769	2,644	557	225	7,762	0.363
18	*D. ciliatus* Loew	1	0	0	231	1	3	236	0.011
19	*D. congoensis* White	0	0	0	5	0	0	5	0.000
20	*D. diastatus* Munro	1	0	0	2	0	0	3	0.000
21	*D. humeralis* Bezzi	3	0	0	3	0	0	6	0.000
22	*D. langi* Curran	5	3	1	7	1	0	17	0.001
23	*D. pleuralis* Collart	1	0	0	4	0	0	5	0.000
24	*D. punctatifrons* Karsch	1,301	390	349	1,000	241	64	3,345	0.156
25	*D. vertebratus* Bezzi	40	45	25	78	40	42	270	0.013
	Total	361,053	350,525	403,495	392,999	396,151	233,927	2,138,150	100.000
	Proportion (%)	16.9	16.4	18.9	18.4	18.5	10.9	100	
	Margalef index	1.563	1.018	1.084	1.785	1.086	1.132		
	Adjusted Margalef index	0.833	0.542	0.583	0.958	0.583	0.583		

Table 3. Fruit fly species diversity in the 6 mango orchards using Jaccard and Sorenson indices

Locations	Koro_WZ	Koro_LA	Komi	Kakara_AOB	Ina_OGB
Jaccard index 2005–2009 (%)					
Tchatchou	66.7	63.6	87.5	71.4	63.6
Koro_WZ		93.3	58.3	93.3	81.3
Koro_LA			56.0	87.5	87.5
Komi				62.5	56.0
Kakara_AOB					87.5
Sorenson Index 2005–2009 (%)					
Tchatchou	80.0	77.8	93.3	83.3	77.8
Koro_WZ		96.6	73.7	96.6	89.7
Koro_LA			71.8	93.3	93.3
Komi				76.9	71.8
Kakara_AOB					93.3

but also to a lesser extent by other *Ceratitis* species (Fig. 3). From June to August, monkey balls were infested by *C. fasciventris* but also to a lesser extent by other *Ceratitis* species (Fig. 3). From May to July, the shea butters were largely infested by *B. dorsalis*, *C. quinaria*, and *C. silvestrii*, but also to a lesser extent by *C. cosyra* (Fig. 3). From August to December, African peaches were heavily infested by *C. cosyra* but also to a lesser extent by other *Ceratitis* species and a few *B. dorsalis* adults (Fig. 3).

Figure 3 shows that *B. dorsalis* attacked 35 fruit species all year round, the main hosts being *M. indica*, *S. mombin*, *P. guajava*, *I. gabonensis*, *H. monopetalus*, and *V. paradoxa*. The main families of *B. dorsalis* hosts were Anacardiaceae, Myrtaceae, Irvingiaceae, Annonaceae, and Sapotaceae. In the same way, *C. cosyra* can attack 15 fruit species (Fig. 3) most of the year with main hosts *M. indica*, *S. birrea*, *A. senegalensis*, *C. pinnata*, and *S. latifolius*. The main families of *C. cosyra* hosts were Anacardiaceae, Annonaceae, Caesalpinioideae, and Rubiaceae.

Tephritid Population Fluctuations in Mango Orchards. Seasonal *C. cosyra* and *B. dorsalis* population fluctuations in the six orchards during five years are described in Figures 4 and 5. All six orchards showed that *C. cosyra* peaked at the beginning of May, while *B. dorsalis* at the beginning of June. The five-year average across all six orchards clearly showed that *C. cosyra* peaked earlier than *B. dorsalis* populations (Fig. 4). However, this pattern varied if population fluctuations were computed per orchard (Fig. 5) or on a yearly basis (Fig. 6a and b). The more southern orchard Tchatchou hosted higher *B. dorsalis* populations (Fig. 5) than the more northern and drier orchard in Ina. Furthermore, in the two mixed orchards (Komi and Tchatchou), with many other fruit trees, *B. dorsalis* populations were three times higher than *C. cosyra* populations (Fig. 5) compared with homogenous mango orchards.

Fly populations fluctuated from year to year (Fig. 6a and b). First, there is a yearly decrease of both *C. cosyra* and *B. dorsalis* populations between 2005 and 2009. Second, the bi-annual pattern with alternative high and low number of flies, linked to high- and low-yield years of mangoes every 2 yr (Fig. 6a and b) was confirmed. We observed significant differences in *B. dorsalis* counts ($P < 0.001$) for all orchards between

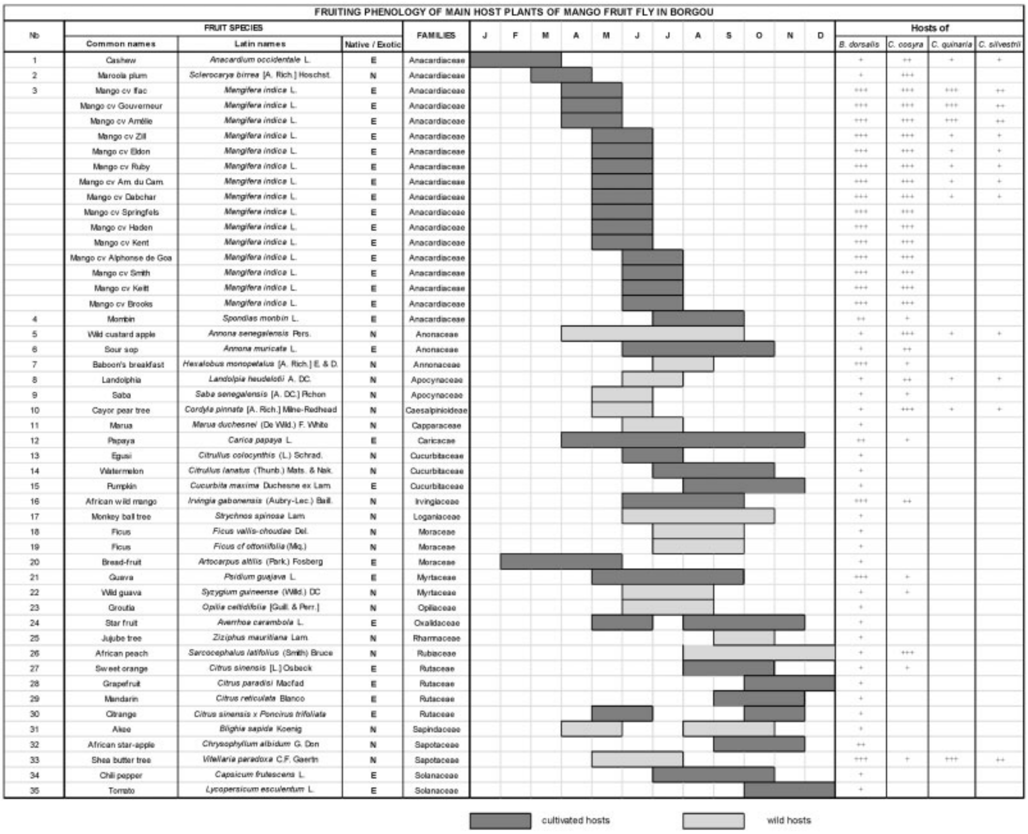


Fig. 3. Fruiting phenology of main hosts of mango fruit flies with estimation of their infestation (number of pupae per kg of fresh fruits: +: 0–25 / ++: 25–50 / +++: > 50).

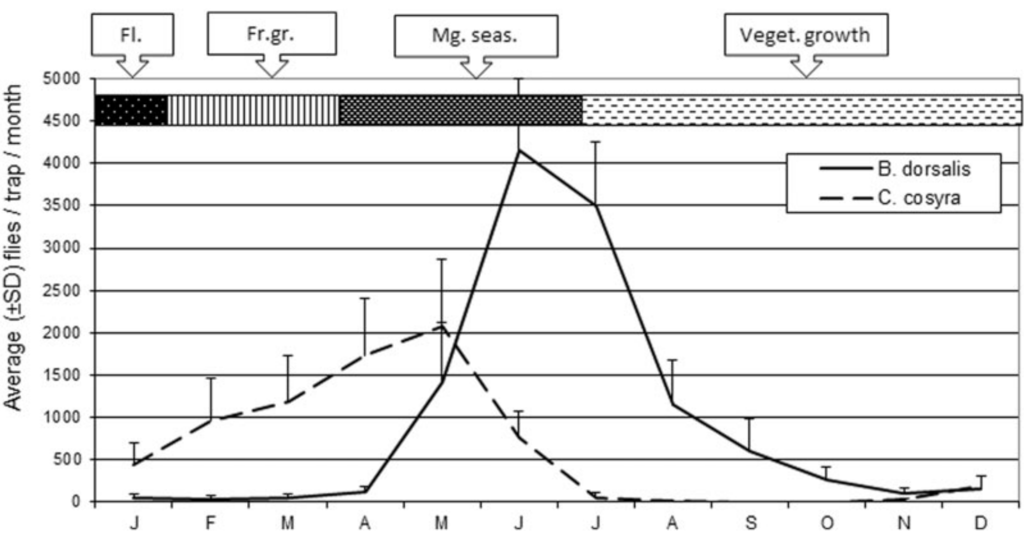


Fig. 4. Overall pattern of *C. cosyra* and *B. dorsalis* population fluctuations in all 6 mango orchards: mean of a 5-yr period (2005–2009).

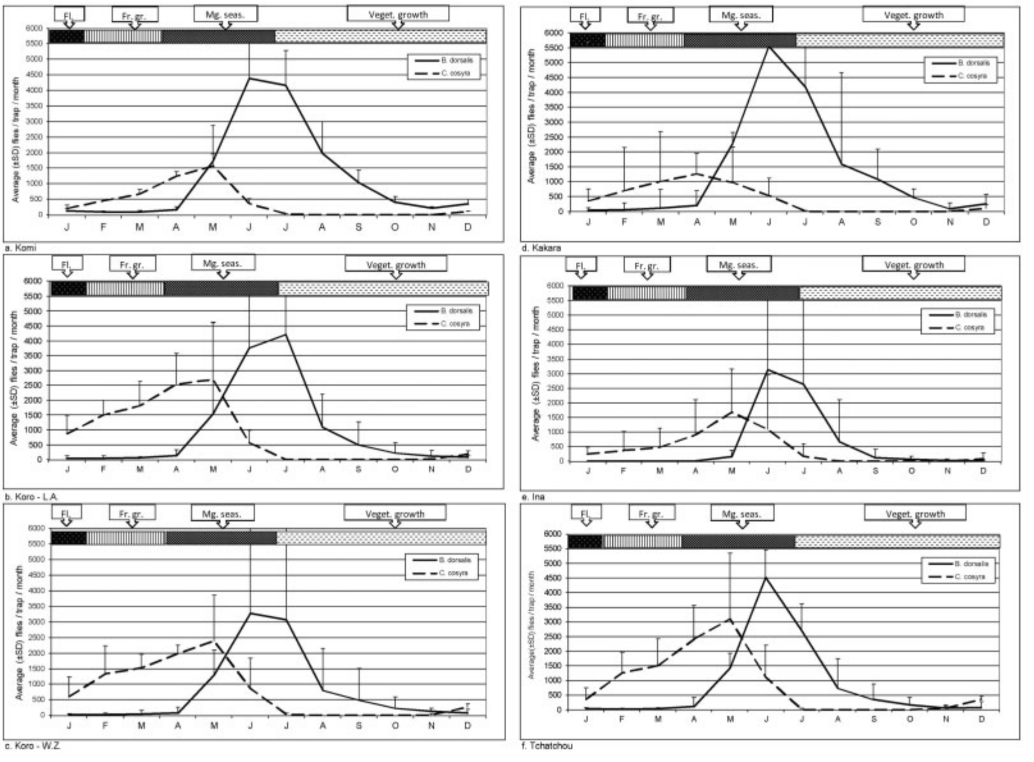


Fig. 5. Overall patterns of *C. cosyra and B. dorsalis* population fluctuations in every mango orchards: mean of a 5-yr period (2005–2009).
Fl.: flowering; Fr. gr.: fruit growing; Mg. seas.: mango season; Veget. growth: vegetative growth.

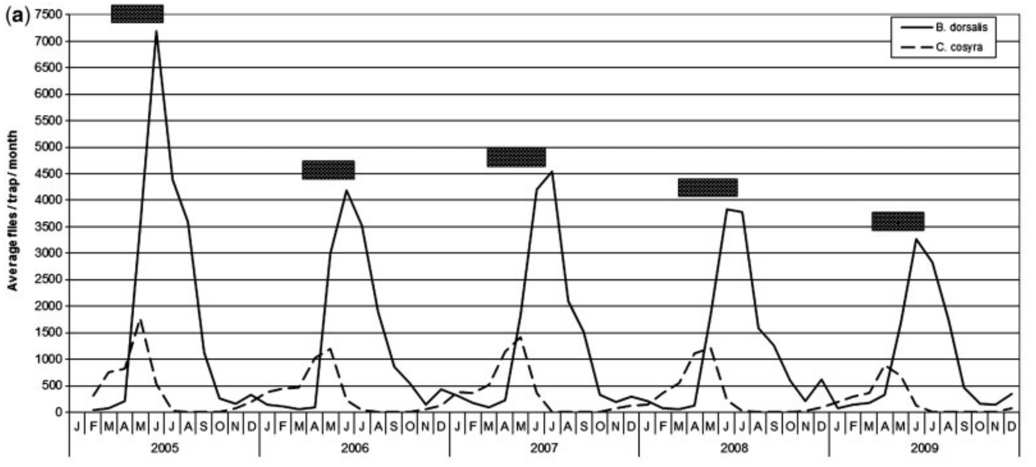
"high" and "low" mango years from 2005 to 2008. In contrast, no significant differences in *C. cosyra* counts between "high" and "low" mango years were recorded. The time interval between the two peaks (*C. cosyra* vs. *B. dorsalis*) was roughly the same for every year. As already stressed, the mixed mango orchard had higher *B. dorsalis* populations and lower *C. cosyra* populations than the homogeneous ones.

Tephritid Population Fluctuations in Cashew Orchards (nearby mango orchards). During the first 14 wk of the first 26, most fruit flies (62%) were captured in traps positioned in cashew orchards compared with traps in mango orchards. In cashew orchards, we captured two *Bactrocera* species (3% *B. dorsalis* and 2% *B. cucurbitae*), six *Ceratitis* species (75% *C. cosyra*, 8% *C. quinaria*, 4% *C. silvestrii*, and 2% *Ceratitis* spp.) and seven *Dacus* species (6%).

At the beginning of each year, the cashew apple was actually the first important fruit crop to be infested by tephritids, enabling the increase of fly populations. Because of significant interactions between factors as year, fruit tree, fruit stage and orchard (site), evaluations and interpretations were made on both main effects and interaction means. ANOVA results are presented in Tables 4 and 5, and correlation analysis results presented in Tables 6 and 7 for all tephritid species.

Figure 7 shows the trends in correlations and the lag correlations. Tables 4 and 5 demonstrate that fruit flies were concentrated more in cashew orchards than on mango orchards in all sites ($P < 0.001$) during the first 14 wk of every year of study. There were significant differences in insect counts observed at different fruit stages ($P < 0.001$) for combined year ANOVA in each site (Tables 4 and 5). Tephritid adults were more abundant during the maturity fruit stage, in both mango and cashew orchards and in all sites and years. Correlation and lag correlation analyses were done to determine if there were any correlations between insect counts on both fruit trees with respect to time or phenological stages. The result showed that there was 1–2 wk lag for the insects to crossover from cashew and mango (Tables 6 and 7; Fig. 7). Lag0 represents the original (cashew) data. Lag1 concerned cashew counts shifted down by 1 wk, Lag2 by 2 wk, etc. (in comparison to the position on mango counts). This is consistent with the maturity fruit stage of mango and cashew trees.

The maturity fruit stage (which overlapped the peak production period) occurred in the weeks between 7th and 22nd of the season in cashew orchards, and in the weeks between 13th and 25th in mango orchards; with the insect abundance peaking in the 14th and 15th weeks in cashew orchards in all sites, the 15th to 17th weeks in mango orchards in Kakara_AOB and Koro_WZ sites, and the 19th and 20th weeks in Koro_LA site (Table 8).



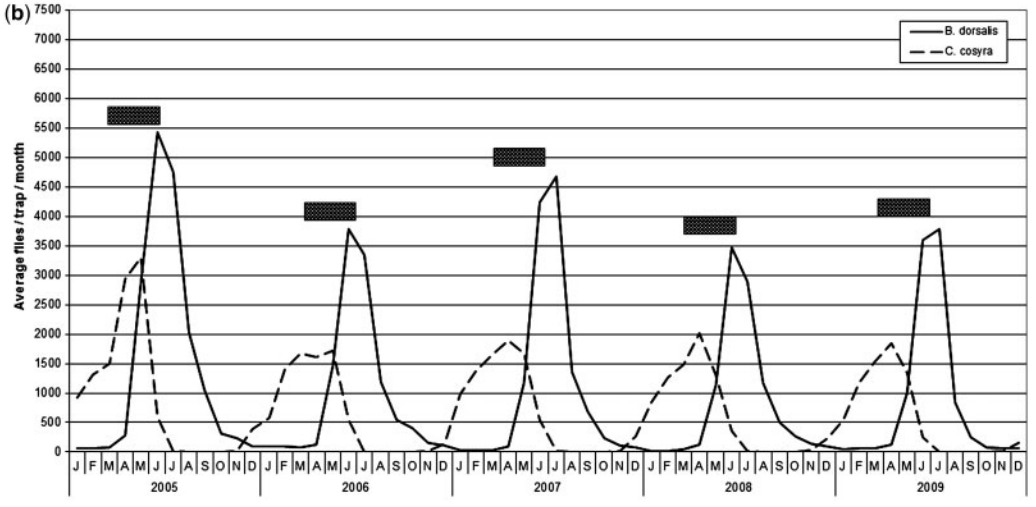


Fig. 6. **a.** Yearly pattern of *C. cosyra* and *B. dorsalis* population fluctuations in a mixed mango orchard (Komi - Monastery) during 5-yr period (2005–2009). - Horizontal bars: mango season. **b.** Yearly pattern of *C. cosyra* and *B. dorsalis* population fluctuations in a homogeneous mango orchard (Koro - WZ) during 5-yr period (2005–2009). - Horizontal bars: mango season.

So, in an initial stage *C. cosyra* (but also to a lesser extent *B. dorsalis*, *C. quinaria*, and *C. silvestrii*) were capable to develop large population sizes in cashew orchard in the first weeks before transferring to the mango orchards and infesting mangoes.

Discussion

The Margalef index pointed out differences in species diversity between four homogeneous mango orchards and two mixed ones harboring more diverse fruit hosts. This significant difference in fruit fly diversity was already stressed in Benin for tephritids of economic significance between a single mixed mango orchard versus a homogenous one (Vayssières et al. 2009a). The tephritid diversity associated with fruit diversity was confirmed in this important mango production area. The actual diversity sampled (25 tephritid species) in these Beninese orchards through adult trapping was not particularly high for such a long-term (5-yr) study. All species were previously reported in Benin except *Dacus albiseta* White and Goodger described in 2009 (White and Goodger 2009). The specific richness of tephritid associated with mangoes in Burkina was similar for homogeneous mango orchards in the same agro-ecological zone around Bobo-Dioulasso (Ouedraogo et al. 2011). The observed biodiversity of fruit flies collected in and around orchards also underlines the crucial necessity of properly identifying all trapped fruit flies. This could be effective with multientry identification keys (Virgilio et al. 2014) through different taxonomic trainings for staff of NARS in sub-Saharan Africa. For instance, the knowledge of the differentiation of two very closely related species, *B. dorsalis* and *Bactrocera zonata* (Saunders), could

Table 4. Mean and standard error (S.E.) of Tephritid counts per mango by fruit-stage, orchard and year of survey

	Kakara_AOB							
	2008		2009		2010		All 3 Years	
Mango Fruit_Stage	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.
Flowering	6	7.0 ± 2.1 *c*	6	32.8 ± 11.7 *c*	8	22.3 ± 10.2 *d*	20	20.9 ± 5.6 *C*
Fruit Growing	36	146.6 ± 19.4 *b*	33	185.8 ± 21.9 *b*	31	130.8 ± 14.7 *b*	100	154.6 ± 11.2 *B*
Maturity	19	475.8 ± 54.1 *a*	24	390.7 ± 51.7 *a*	25	372.9 ± 47.6 *a*	68	408.0 ± 29.5 *A*
Without Fruit	17	116.7 ± 12.5 *b*	15	133.2 ± 11.5 *b*	17	89.4 ± 14.1 *c*	49	112.3 ± 7.7 *B*
F-value		*23.14*		*22.56*		*41.09*		*77.74*
d.f.		*3;74*		*3;74*		*3;77*		*3;225*
P-value		*< 0.001*		*< 0.001*		*< 0.001*		*< 0.001*

	Koro_LA							
	2008		2009		2010		All 3 Years	
Mango Fruit_Stage	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.
Flowering	8	35.5 ± 17.1 *c*	9	61.6 ± 9.4 *c*	9	33.9 ± 11.4 *c*	26	44.0 ± 7.5 *D*
Fruit Growing	31	162.0 ± 19.2 *b*	30	264.2 ± 38.8 *b*	30	170.8 ± 23.5 *b*	91	198.6 ± 16.8 *B*
Maturity	28	306.4 ± 33.4 *a*	30	377.0 ± 34.9 *a*	34	380.6 ± 24.7 *a*	92	356.9 ± 17.9 *A*
Without Fruit	11	83.9 ± 10.4 *b*	9	77.3 ± 16.1 *c*	8	33.6 ± 5.0 *c*	28	67.4 ± 7.7 *C*
F-value		*28.33*		*18.85*		*44.19*		*87.17*
d.f.		*3;74*		*3;74*		*3;77*		*3;225*
P-value		*< 0.001*		*< 0.001*		*< 0.001*		*< 0.001*

	Koro_WZ							
	2008		2009		2010		All 3 Years	
Mango Fruit_Stage	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.
Flowering	8	58.8 ± 25.1 *c*	8	44.8 ± 10.2 *c*	8	8.8 ± 2.7 *c*	24	37.4 ± 9.7 *D*
Fruit Growing	33	218.1 ± 28.2 *b*	28	250.2 ± 52.4 *b*	28	192.2 ± 41.2 *b*	89	220.0 ± 23.3 *B*
Maturity	30	552.7 ± 53.5 *a*	29	608.0 ± 80.0 *a*	30	528.7 ± 50.3 *a*	89	562.6 ± 35.7 *A*
Without Fruit	7	127.4 ± 18.9 *b*	13	115.1 ± 18.2 *b*	15	138.3 ± 24.9 *b*	35	127.5 ± 13.0 *C*
F-value		*42.83*		*20.96*		*42.63*		*97.56*
d.f.		*3;74*		*3;74*		*3;77*		*3;225*
P-value		*< 0.001*		*< 0.001*		*< 0.001*		*< 0.001*

Comparison of Fruit Stages (Down): Means with the same letter(s) are not significantly different at 0.05 level.
Analysis and comparison (pair-wise tests) were done on log10 transformed insects counts.

become necessary for African countries after the recent record of *B. zonata* in Sudan (Salah et al. 2012), though the two species have different climatic preferences (De Meyer et al. 2007).

The dominant fly species found at all sites studied in this department remain *C. cosyra* and *B. dorsalis*, representing 89.01% of all individuals trapped in all sites. This is confirmed through fruit sampling in the field: mango infestation by these two species accounted for >80% of all infestations. These findings are consistent with similar experiments in Costa Rica (Jiron and Hedstrom 1991) and Mexico (Celedanio-Hurtado et al. 1995, Aluja et al. 1996) about the *Anastrepha* species, in Hawaii (Vargas et al. 1990) about *B. dorsalis*, and more recently in Tanzania (Mwatawala et al. 2006), Burkina Faso (Ouedraogo 2011), and Côte d'Ivoire (N'Dépo et al. 2009, 2013) about *B. dorsalis* and *C. cosyra*. In this study, as in all studies cited above, the two most common species captured in an orchard were invariably associated with the fruit type being grown in the same orchard.

From 2005 until now, we recorded the same general outbreak trends for *B. dorsalis* every year (from end of March to mid-May) in relation with increasing rain–RH. As the first important rain events (end of March–end of April) overlapped first mango prematurity in the field, *B. dorsalis* still needed both abiotic primary factors and biotic secondary factors to boost its populations in mango orchards (Vayssières et al. 2009a). When *B. dorsalis* populations were "installed" in the mango orchards (and in the savannah around them), they were present from the beginning of May to September, i.e., from mid-fruiting season to the vegetative stage of mango tree. Although the high reproductive rate and population increase of *B. dorsalis* indicate r-selection (Ekesi et al. 2006, Geurts et al. 2012), competition with the present fruit fly entomofauna indicate K-selection (Vayssières et al. 2005, Mwatawala et al. 2009b). With its high invasive potential, the oriental fruit fly can unfortunately not only colonize many more new areas (Duyck et al. 2007) in tropical but also in subtropical regions (De Meyer et al. 2010).

In a preliminary study, *C. cosyra* populations in sub-Saharan Africa seem to be restricted by biotic factors (availability of hosts and inter-competition with *B. dorsalis*) but also by abiotic ones (altitude, relative humidity, and temperature; Geurts et al. 2014). In this Beninese study, some species were not well represented such as *C. fasciventris* and *C. anonae* in comparison to some similar monitoring of mango fruit flies in the same Sudan zone in 2000 before the arrival of *B. dorsalis* (Vayssières et al. 2004). Some tephritid

Table 5. Mean and standard error (S.E.) of Tephritid counts per cashew by fruit stage, orchard and year of survey

	Kakara_AOB							
	2008		2009		2010		All 3 Years	
Cashew Fruit_Stage	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.
Flowering	6	77.3 ± 16.4 *d*	3	45.7 ± 6.7 *c*	3	45.7 ± 6.7 *c*	12	61.5 ± 9.4 *D*
Fruit Growing	15	209.7 ± 14.8 *b*	18	197.6 ± 14.7 *b*	15	179.1 ± 13.1 *b*	48	195.6 ± 8.3 *B*
Maturity	27	368.7 ± 35.5 *a*	27	399.0 ± 36.7 *a*	27	349.4 ± 39.6 *a*	81	372.4 ± 21.4 *A*
Without Fruit	30	154.7 ± 15.1 *c*	30	169.6 ± 17.9 *b*	36	180.4 ± 27.4 *b*	96	169.0 ± 12.6 *C*
F-value		*26.01*		*28.64*		*8.13*		*39.74*
d.f.		*3;74*		*3;74*		*3;77*		*3;225*
P-value		*< 0.001*		*< 0.001*		*< 0.001*		*< 0.001*

	Koro_LA							
	2008		2009		2010		All 3 Years	
Cashew Fruit_Stage	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.
Flowering	9	56.7 ± 10.6 *c*	6	119.8 ± 21.9 *b*	6	60.2 ± 16.5 *b*	21	75.7 ± 10.6 *B*
Fruit Growing	12	195.3 ± 15.8 *a*	15	290.9 ± 35.1 *a*	12	196.6 ± 16.1 *a*	39	232.5 ± 16.6 *A*
Maturity	33	261.5 ± 29.5 *a*	33	301.6 ± 27.5 *a*	33	364.6 ± 27.3 *a*	99	309.2 ± 16.6 *A*
Without Fruit	24	150.4 ± 20.0 *b*	24	71.8 ± 6.4 *c*	30	111.7 ± 19.4 *b*	78	111.3 ± 10.4 *B*
F-value		*13.82*		*45.96*		*19.10*		*52.66*
d.f.		*3;74*		*3;74*		*3;77*		*3;225*
P-value		*< 0.001*		*< 0.001*		*< 0.001*		*< 0.001*

	Koro_WZ							
	2008		2009		2010		All 3 Years	
Cashew Fruit_Stage	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.	N	Mean ± S.E.
Flowering	6	95.2 ± 21.2 *b*	6	103.2 ± 21.3 *c*	6	125.0 ± 25.3 *b*	18	107.8 ± 12.7 *C*
Fruit Growing	18	294.1 ± 29.2 *a*	18	234.4 ± 15.9 *b*	15	272.7 ± 13.4 *b*	51	266.7 ± 12.7 *B*
Maturity	33	504.7 ± 69.5 *a*	27	594.5 ± 58.3 *a*	36	626.3 ± 48.3 *a*	96	575.6 ± 34.2 *A*
Without Fruit	21	416.2 ± 57.7 *a*	27	331.8 ± 45.6 *b*	24	366.6 ± 76.4 *b*	72	368.0 ± 34.7 *B*
F-value		*6.54*		*7.81*		*10.56*		*20.55*
d.f.		*3;74*		*3;74*		*3;77*		*3;225*
P-value		*< 0.001*		*< 0.001*		*< 0.001*		*< 0.001*

Comparison of Fruit Stages (Down): Means with the same letter(s) are not significantly different at 0.05 level.
Analysis and comparison (pair-wise tests) were done on log10 transformed insects counts.

species such as *C. capitata* were also poorly represented in West Africa, probably displaced by *B. dorsalis*, in Citrus production areas of southern Benin and southern Ghana. *Bactrocera dorsalis* has changed the landscape of pest fruit flies in sub-Saharan Africa, but, according to Duyck et al. (2004), complete exclusion of dominated fly species usually did not occur, but shifts toward particular niches were observed.

The presence of noncommercial fruits as fruit fly reservoirs is a key factor for dissemination of invasive species (Haramoto and Bess 1970, Vargas et al. 1983, 1990, Mwatawala et al. 2009a, Ndiaye et al. 2012, Aluja et al. 2014). In Benin, *I. gabonensis*, *H. monopetalus*, and *V. paradoxa* are the wild primary hosts outside the crop area for *B. dorsalis*, as are *Sclerocarya birrea*, *A. senegalensis*, *C. pinnata*, and *S. latifolius* for *C. cosyra*. Both of them are commonly found in the savannah regions of Borgou and in most other Beninese departments (Vayssières et al. 2010). So, it is not surprising that these two species were widespread in the Sudan savannah all the year round, except during the second part of the rainy season for *C. cosyra*. In this study, we recorded 35 *B. dorsalis* hosts, cultivated and wild, in this Sudan zone. In other West African countries like Senegal, >30 fruit species were found to be infested (Ndiaye et al. 2012) by this exotic species and 20 fruit species were attacked in Côte d'Ivoire (N'Dépo et al. 2010). Among many hosts, three primary cultivated and three primary local hosts gave a strong comparative advantage to *B. dorsalis*, which also infested 29 secondary or accidental other hosts in this Sudan area. In Hawaii, the major *B. dorsalis* hosts outside the crop area were wild strawberry guava, *Psidium cattleianum* Sabine, and common guava, *Psidium guajava* L. (Vargas et al. 1990).

Tephritid populations fluctuate from year to year and a decrease can be attributed probably to the impact of the weekly trapping of both species. To understand tephritid population fluctuations, 1- or 2-yr studies are not appropriate, but a minimum of 4 yr is better adapted to overcome the large variation in trap capture data and also to take into account the direct result of alternation in fruit bearing (Litz 1997), as observed here. It is clear that these tephritid population fluctuations are the direct results of the fly infestations of mango and other fruit species in and around the six orchards studied. If the diversity of cultivated fruit trees in orchards is the key factor, the habitat surrounding them should also play an important role. According to some recent studies (De Meyer et al. 2007, Mwatawala et al. 2009a, Goergen et al. 2011), the principal factor driving large-scale tephritid populations in fruit

Table 6. Lagged correlation of weekly seasonality data - for individual years (Correlations of Insect counts on Mango with Lagged counts on Cashew)

	Cashew_lag0	Cashew_lag1	Cashew_lag2	Cashew_lag3	Cashew_lag4
Kakara_AOB 2007					
Mango	0.15033	0.71503	0.61269	0.24390	0.06326
P	0.4636	<0.0001	0.0015	0.2621	0.7797
N	26	25	24	23	22
Kakara_AOB 2008					
Mango	0.20248	0.12747	0.18148	0.52214	0.25904
P	0.3212	0.5437	0.3960	0.0106	0.2444
N	26	25	24	23	22
Kakara_AOB 2009					
Mango	0.14722	0.71174	0.67063	0.29352	0.03833
P	0.4637	<0.0001	0.0002	0.1639	0.8621
N	27	26	25	24	23
Koro_LA 2007					
Mango	0.79981	0.45244	0.19500	0.13769	0.01819
P	<0.0001	0.0232	0.3612	0.5310	0.9360
N	26	25	24	23	22
Koro_LA 2008					
Mango	0.03303	0.34079	0.04236	0.05678	0.05938
P	0.8727	0.0955	0.8442	0.7969	0.7929
N	26	25	24	23	22
Koro_LA 2009					
Mango	0.35334	0.38688	0.34638	0.40481	0.45549
P	0.0706	0.0509	0.0899	0.0497	0.0290
N	27	26	25	24	23
Koro_WZ 2007					
Mango	0.31046	0.05954	0.46420	0.20292	−0.29819
P	0.1227	0.7774	0.0223	0.3531	0.1777
N	26	25	24	23	22
Koro_WZ 2008					
Mango	−0.05877	−0.21091	0.20815	0.58481	0.03755
P	0.7755	0.3115	0.3290	0.0034	0.8683
N	26	25	24	23	22
Koro_WZ 2009					
Mango	0.49588	0.55583	0.64859	0.52568	0.15604
P	0.0085	0.0032	0.0005	0.0083	0.4771
N	27	26	25	24	23

orchards was availability of cultivated hosts inside orchards and wild hosts outside orchard boundaries same as for *B. dorsalis* in Hawaii (Vargas et al. 1989). The fallen fruits thereby enhance the dynamics of fruit fly populations and play an important role. The location of orchards and the position of trees inside them are also very important, as attested by the large differences between sampling sites. Thus, fruit trees planted near rivers or in some humid microhabitat were more often infested. It is suspected that these humid microclimate zones shelter some *B. dorsalis* adults, thereby acting as refuges during the dry season (J.F.V., unpublished data).

As already recorded in the Borgou Department, mango growers very often have a cashew nut tree plantation next to their mango orchard, which translates into fruit production in the same site from January (beginning of cashew nut production) to June end (end of mango production). Our results highlight that this influences the mango fruit fly populations. Cashew and mango are infested by the same flies but cashew ripens first; thus, fly populations can build up in cashew and then shift to mango orchards. This migration of tephritid pests from cashew orchards needs to be taken into account when an integrated pest control program, with a large biological control component (Van Mele et al. 2007, Vayssières et al. 2011) is being planned and implemented. Launching an integrated pest management (IPM) package, from sanitation to biological control activities, against fruit flies in Beninese cashew orchards at the beginning of the year should be strongly recommended before any control activity in mango orchards is undertaken. Furthermore, an effective IPM package should necessarily take into account nine species of wild hosts, which could be used to attract tephritids around the mango and cashew orchards before and after the seasons. Our results showed that the application of GF-120 NF Naturalyte Fruit Fly bait sprays on their hosts (Vayssières et al. 2009b) and the promotion of their natural enemies (Van Mele et al. 2007) had largely decreased the fruit fly populations in other mango plantations than these six control orchards. The same treatments have to be carried out in cashew orchards first, where it could be linked with sanitation activities (cashew apples set up in augmentarium, as already done with mangoes in Benin) to control more effectively mango and cashew fly pests.

Data collected during five years and over a large area in one of the largest mango production areas in Benin provide relevant information for a regional pest management approach. Large area generalizations in

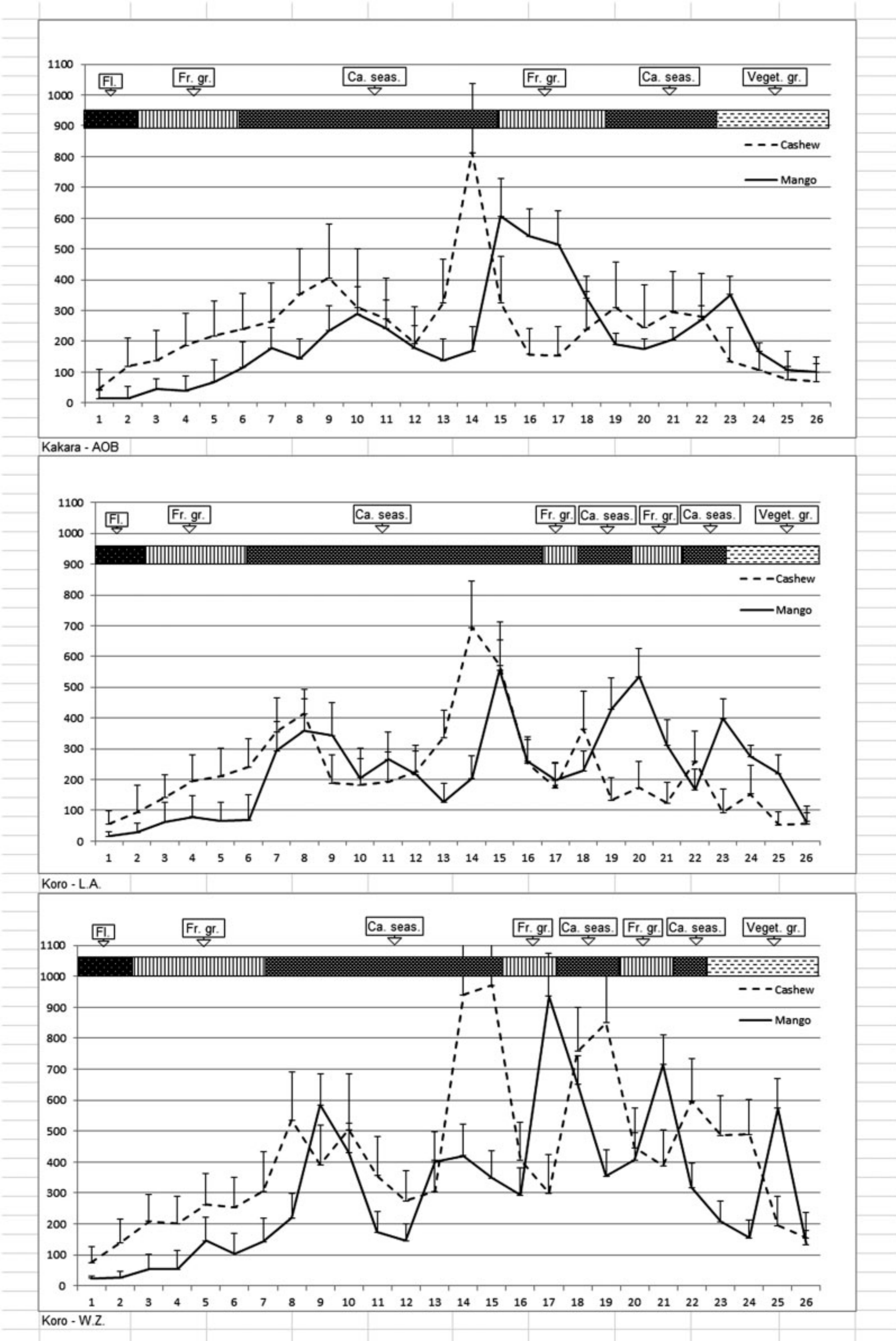


Fig. 7. Average (2007–2009) of weekly abundance of fruit fly species of economic significance in neighbouring cashew orchards vs mango orchards. Fruit stages are mentioned for cashew trees. Fl.: flowering; Fr. gr.: fruit growing; Ca. seas.: cashew season; Veget. gr.: vegetative growth.

Table 7. Lagged correlation of weekly seasonality data—averaged of 2007–2009 (correlations of insect counts on mango with lagged counts on cashew)

	Cashew_lag0	Cashew_lag1	Cashew_lag2	Cashew_lag3	Cashew_lag4
Kakara_AOB					
Mango	0.12364	0.65416	0.68054	0.52033	0.23335
P	0.5473	<0.0004	0.0003	0.0109	0.296
N	26	25	24	23	22
Koro_LA					
Mango	0.39294	0.50244	0.26705	0.20503	0.20125
P	<0.0471	0.0105	0.2071	0.3480	0.3691
N	26	25	24	23	22
Koro_WZ					
Mango	0.27041	0.24364	0.60074	0.67572	0.04068
P	0.1815	0.2406	0.0019	0.0004	0.8574
N	26	25	24	23	22

Table 8.Weekly Summary Statistics of Fruit Fly Counts (per tree) over 3 years (2007–2009)

Week	*N*	Kakara_AOB		Koro_LA		Koro_WZ	
		Cashew Mean ± SE	Mango Mean ± SE	Cashew Mean ± SE	Mango Mean ± SE	Cashew Mean ± SE	Mango Mean ± SE
1	9	44.2 ± 3.3	13.3 ± 6.6	55.2 ± 12.6	16.8 ± 4.3	74.8 ± 12.5	25.1 ± 8.4
2	9	117.9 ± 2.1	15.1 ± 6.7	94.6 ± 18.3	27.9 ± 8.8	140.8 ± 15.9	27.6 ± 9.7
3	9	138.9 ± 7.1	44.7 ± 12.1	143.3 ± 21.6	62.6 ± 11.9	209.4 ± 15.7	53.8 ± 18.0
4	9	186.1 ± 15.4	39.1 ± 9.2	194.8 ± 16.6	79.6 ± 17.2	202.7 ± 17.6	54.1 ± 19.2
5	9	219.1 ± 1.9	68.3 ± 11.9	211.3 ± 20.4	66.0 ± 10.9	262.8 ± 19.1	147.3 ± 14.4
6	9	238.2 ± 6.8	114.3 ± 25.1	240.6 ± 22.5	68.6 ± 12.4	253.9 ± 18.2	104.8 ± 15.5
7	9	264.3 ± 23.5	178.3 ± 25.7	356.7 ± 49.9	294.3 ± 44.0	305.9 ± 18.4	144.0 ± 24.8
8	9	353.0 ± 22.0	143.7 ± 34.8	414.8 ± 37.6	359.7 ± 34.2	536.6 ± 72.6	219.3 ± 39.2
9	9	406.9 ± 43.6	234.9 ± 40.3	188.8 ± 22.7	342.6 ± 86.4	391.4 ± 28.7	584.9 ± 110.9
10	9	310.8 ± 28.9	289.4 ± 47.2	183.6 ± 43.4	206.3 ± 36.8	505.3 ± 79.8	432.2 ± 92.7
11	9	274.3 ± 30.0	243.3 ± 18.6	193.8 ± 46.5	266.7 ± 58.3	356.2 ± 67.1	173.1 ± 38.2
12	9	193.7 ± 18.6	177.1 ± 23.4	226.0 ± 25.9	216.2 ± 27.6	276.0 ± 56.9	147.0 ± 23.3
13	9	325.3 ± 30.9	137.0 ± 29.1	235.9 ± 29.8	127.8 ± 10.2	306.3 ± 69.1	401.7 ± 24.9
14	9	813.2 ± 42.7	168.3 ± 17.5	395.1 ± 30.9	204.9 ± 33.2	941.9 ± 132.4	420.6 ± 91.0
15	9	324.9 ± 42.3	607.6 ± 120.6	572.1 ± 44.3	555.9 ± 48.0	971.1 ± 94.7	348.0 ± 79.4
16	9	157.6 ± 14.0	541.1 ± 60.0	254.0 ± 33.8	260.3 ± 40.3	405.9 ± 93.7	293.6 ± 57.4
17	9	154.2 ± 24.4	513.4 ± 110.5	173.7 ± 39.4	198.0 ± 58.9	299.3 ± 64.5	1236.0 ± 98.9
18	9	239.7 ± 51.4	340.0 ± 70.4	365.4 ± 71.0	228.9 ± 35.0	758.4 ± 52.0	653.0 ± 79.2
19	9	309.2 ± 27.7	191.0 ± 35.5	133.0 ± 34.1	430.1 ± 49.7	850.3 ± 88.0	355.3 ± 74.9
20	9	244.2 ± 37.8	176.4 ± 29.7	174.4 ± 45.4	534.0 ± 40.8	446.4 ± 79.3	407.8 ± 37.9
21	9	296.4 ± 60.1	205.8 ± 37.6	124.4 ± 28.3	312.6 ± 51.7	389.2 ± 75.4	715.0 ± 94.9
22	9	280.9 ± 48.7	271.3 ± 44.7	260.3 ± 56.1	168.2 ± 46.6	597.2 ± 128.3	318.1 ± 47.0
23	9	133.9 ± 28.8	352.1 ± 58.4	94.0 ± 16.1	399.0 ± 63.0	486.1 ± 107.2	207.9 ± 36.8
24	9	107.4 ± 12.6	166.8 ± 28.0	153.4 ± 41.8	275.3 ± 36.8	489.4 ± 83.5	155.1 ± 36.1
25	9	74.9 ± 12.9	107.4 ± 11.0	53.7 ± 10.8	218.7 ± 63.1	194.4 ± 26.1	574.4 ± 122.2
26	9	68.6 ± 21.0	101.6 ± 24.0	56.9 ± 18.1	64.0 ± 16.8	156.0 ± 39.9	133.8 ± 16.2

well-known agro-ecological area such as large mango production basin of Borgou are likely to be accurate at the resolution level needed to fine tune tephritid management. The IPM program of *B. dorsalis* in Hawaii (Mau et al. 2007, Vargas et al. 2008, Piñero et al. 2009) using sanitation activities about fallen fruits, GF-120 bait sprays on cultivated and wild hosts, natural enemies such as parasitoids (Vargas et al. 2013) had developed similar system approach. More globally, this IPM system is strongly recommended for *B. dorsalis*, *C. cosyra*, *C. capitata*, and *B. cucurbitae* management in sub-Saharan Africa. The management of weaver ants, compatible with other control methods in mango orchards, which also gave good results in cashew–citrus orchards (J.F.V., unpublished data) could be included in it. For control methods to be effective in this agro-ecological zone, the whole production basin has to be included (Jang et al. 2008, Vargas et al. 2010). As proposed by Diversity of cropping systems and ecologically based-pest management in West Africa (DIVECOSYS), and according to Mau et al. (2003), the implementation of a Geographic Information System with integrated control tactics is crucial for area-wide fruit fly management at large scale. This precious tool should be used in tephritid monitoring used for the quick implementation of control methods after the economic injury level (E.I.L.) has been overshot (Vayssières et al. 2009c). Moreover, the present study lends itself for being used in population modeling.

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