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Research

Efficiency of Food-Based Attractants for Monitoring Tephritid Fruit Flies Diversity and Abundance in Mango Systems Across Three West African Agro-Ecological Zones

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Abstract

Food baits are effective and widely used tools for monitoring diversity and abundance of tephritid fruit flies. Four food-baits—Nulure, BioLure, Mazoferm at 3 and 6%, and Torula yeast—were used in multi-lure traps over a 4-yr period in mango orchards in three Benin agro-ecological zones (AEZ) representing a large swath of environments in western Africa. Twelve tephritid fruit fly species were captured during the trials, with the highest richness in the Forest Savannah Mosaic (FSM), followed by the Southern Guinea Savannah (SGS), and the Northern Guinea Savannah (NGS) AEZ. Despite previous reports of displacement, the native species *Ceratitis cosyra* remained the dominant tephritid species in mango orchards in the NGS, with the invasive and exotic species *Bactrocera dorsalis* dominating the tephritid fauna in the SGS and FSM. Torula yeast captured the greatest number of fruit flies in each AEZ. Mazoferm-3% captures were similar to Torula yeast, except for lower captures in the NGS where it tended to harden. The rank order of relative efficiency indices (REI) of the food baits (relative to Torula yeast) is Mazoferm-3% > Nulure > Mazoferm-6% and BioLure. The latter captured more *Ceratitis* spp. than all the other baits, particularly at very low *Ceratitis* spp. abundance. To our knowledge, the study is the first to report relative efficiency indices for the selection of food baits in monitoring diversity and abundance of fruit flies. Ecological and practical implications for the use of food baits in comparison with male lures are discussed.

Key words: *Bactrocera dorsalis*, *Ceratitis cosyra*, Torula yeast, Mazoferm, BioLure

Tephritid fruit flies, with at least 200 pest species—largely in the five genera *Anastrepha* Schiner, *Bactrocera* Macquart, *Ceratitis* Macleay, *Dacus* Fabricius and *Zeugodacus* Hendel (Diptera: Tephritidae), are among the world's most economically important crop pests due to their potential to cause extensive damage to vegetable and tree fruits (White and Elson-Harris 1992, Hanna et al. 2005, De Meyer et al. 2010). Fruit fly pests occur on nearly all continents, but, except for a few temperate species, fruit flies are most damaging in sub-tropical and tropical regions of the world (Roessler 1989, White and Elson-Harris 1992). Historically, nearly 30% of known *Dacus* species and nearly all *Ceratitis* species have been restricted to Africa (Virgilio et al. 2014, Doorenweerd et al. 2018), except for a few high-profile African species like *Ceratitis capitata* (Wiedemann) and *Dacus ciliatus* Loew that have invaded other continents. The other two principal genera *Bactrocera* and *Anastrepha*, are generally restricted to Asia and the Americas respectively (White and Elson-Harris 1992), with at least 10 *Bactrocera* spp. considered indigenous to Africa (White 2006). Several Oriental *Bactrocera* species have invaded other continents where they have caused substantial damage to tree and fruit vegetables (Vargas et al. 2015). *Bactrocera dorsalis* (Hendel) is the most notorious of those invaders. The species was detected in Kenya in 2003 (Lux et al. 2003a) and was initially identified as *Bactrocera invadens* Drew, Tsuruta & White (Drew et al. 2005). By 2018, *B. dorsalis* has spread to nearly 35 countries in sub-Saharan Africa (CABI 2018) where it has caused substantial damage to tree fruit production, in addition to existing losses caused by native *Ceratitis* species. (Hanna et al. 2004, Ekesi et al. 2006, Mwatawala et al. 2006, Vayssières et al. 2008, Goergen et al. 2011, reviewed by Ekesi et al. 2016). The threat and impact of *B. dorsalis* to fruit production in Africa has spurred numerous national,

international research programs that have substantially advanced knowledge of the taxonomy, biology, ecology, and options for the management of fruit flies in Africa (reviewed by Ekesi et al. 2016). While research has targeted numerous crops, mango infestations by fruit flies and their management have received considerable attention in the last 15 yr.

Prior to the invasion of *B. dorsalis*, several *Ceratitis* species, with *C. cosyra* (Walker) being most widespread, have long been recognized as the primary pest of mango with losses in mango production of about 40% (Lux et al. 2003b). These losses increased to an average ranging from 40 to 75% depending on production region, fruit fly species composition and cultivar (Hanna et al. 2004, Ekesi et al. 2006, Vayssières et al. 2009a, Goergen et al. 2011, Vayssieres et al. 2015).

Because of the threat inflicted by fruit flies to fruit production, much emphasis has been placed on their early detection and eradication (Hall et al. 2005, Navarro-Llopis et al. 2008). Trap captures, using various baits and lures, are used to monitor, detect, delimit and verify the presence and abundance of fruit flies (reviewed by Epsky et al. 2014, Manrakhan 2016). Because of the need of adult fruit flies for proteins for ovarial maturation during their pre-reproductive phase (Hagen and Finney 1950, Christenson and Foote 1960, Mazor et al. 2002), various protein bait formulations have been widely used in detection and monitoring and particularly in fruit fly suppression when mixed with toxicants and used in spot sprays (e.g., GF-120 NF Naturalyte (DowElanco)) (Heath et al. 1997, Lux et al. 2003b, Manrakhan 2016, Vayssières et al. 2009b, Ekesi et al. 2014). Furthermore, with the availability of effective traps that capture both female and male pest insects, trapping systems may be used in behavioral control and, thus, could be added to the growing list of biologically-based technologies for insect control (Duyck et al. 2004b, Huxham 2004, Rousse et al. 2004, McQuate et al. 2005, Yee and Chapman 2005, Barry et al. 2006, Ekesi et al. 2006, Manrakhan 2016, McQuate 2009, Vayssières et al. 2009b, Ekesi et al. 2014).

Various food-based attractants have been available either as liquid protein hydrolysates (e.g., Nulure, Mazoferm), yeast products (e.g., Torula yeast and hydrolyzed waste yeast from breweries) and GF-120 (formulated with spinosad as toxicant), or dry bait (BioLure consisting of Putrescine, Trimethylamine, and Ammonium Acetate). While studies have compared the attractiveness and effectiveness of various commercially available baits (such as Torula yeast, BioLure, and Mazoferm) for monitoring (and more recently for suppression of fruit flies (Ekesi et al. 2014), there is little information on their performance under different environments with contrasting biophysical characteristics, including species composition, vegetation, temperature and relative humidity (RH), and rainfall, all factors that may affect fruit fly populations (e.g., Rwomushana et al. 2008, Vayssières et al. 2009a, Gnanvossou et al. 2017) and the trapping efficiency of food baits (Fabre et al. 2003, Ekesi et al. 2014, Epsky et al. 2014, Manrakhan et al. 2017). There is also insufficient information on the relative attractiveness of these baits to various fruit fly species, particularly from sub-Saharan Africa. Such comparisons are needed to select the most effective bait for specific environments (i.e., agro-ecological zone) for fruit flies detection, monitoring, and suppression. There are also questions around the use of food-baits compared with male lures to monitor diversity and abundance of fruit flies as there are indications that the differential attractiveness of male lures to specific species (and differences in seasonality of males and female flies) could bias information about the seasonality and relative abundance of specific species (Manrakhan et al. 2017).

In the present study, we report on the use of four commercially available food-based attractants—Torula yeast, Nulure, BioLure, and Mazoferm—to monitor diversity and abundance of fruit fly species in mango orchards across contrasting agro-ecological zones that represent a large swath of different agro-ecological zones (AEZ) in western Africa (see below for description). The study had three specific objectives. 1) Determine the diversity of fruit flies in mango orchards across the three AEZ and contrast them with those obtained in previous studies with the use of male lures. 2) Determine the best food-based attractant under each of the AEZ and develop a capture efficiency index of the other attractants relative to the best attractant for each species and AEZ. 3) Evaluate the relative attractiveness of the baits to the various species using the relative frequency of non-zero trap counts for each of the baits, because baits might not sample populations equally.

Materials and Methods

The bait experiments were conducted in mango orchards *Mangifera indica* L. in a south to north gradient crossing three agro-ecological zones (AEZ)—Forest Savannah Mosaic (FSM), Southern Guinea Savannah (SGS) and Northern Guinea Savannah—that are common from Nigeria west through much of western Africa (Fig. 1). There is, however, a general lack of consensus on the demarcation of AEZ because the choice often depends on the matrix of variables used in the classification (Sebastian 2009, Webber et al. 2012, van Wart et al. 2013). The classification that we used in this study were based on Jagtap (1995) and modified by the International Institute of Tropical Agriculture (T. Alabi, Head Geospatial Laboratory, pers. comm.) based on information on global agro-ecological zones (FAO 2012). The vegetational and climate characteristics of the three AEZ, where our experiments were conducted, were described in Gnanvossou et al. (2017) based on information from Bohlinger (1998), and Akoègninou et al. (2006). Briefly, the three AEZ represent a South to North gradient in vegetational composition from forest-savannah transition ecotone in the south, through secondary grasslands or savannahs in the Center and moist woodlands and savannahs in the North. Climate in all three AEZ is tropical and warm with two rainy seasons in the South transitioning to one rainy season in the North, along with an increase in average temperature and a decrease in RH, all modulated by the Harmattan phenomenon which brings cooler temperatures and lower RH during the long dry season.

The number of mango orchards used in this study varied between 8 and 12, with 8 orchards used in 2007 and 2008, and 12 and 10 orchards in 2009 and 2010 respectively. The number of sites used in any particular year was based on various practical criteria, including site availability and compliance with orchard size, mango variety composition, agronomic practices, and farmer acceptance of our trapping and harvesting approach. The number of sampling sites per AEZ was distributed as follows: two sites (FSM 2007–2010, SGS 2007–2008, and NGS 2010); four sites (NGS 2007–2009); and six sites (SGS 2009–2010). The size of the orchards varied between 2 and 4 ha, except for Lalo (0.5 ha), Papatia (75 ha), and Natitingou (100 ha). The orchards contained a range of mango cultivars representing those that are common in each targeted AEZ. In addition, potential fruit fly hosts within 500 m radius around the orchards were censused. The mango cultivars Gouverneur, Camerounaise, Eldon, Kent, and Keitt, were common to all three AEZ, while the cultivars Brooks, Dabschard, Ruby, and Smith were restricted to the SGS and NGS. The cultivar Alphonse was only encoutered in the NGS. The following host fruit species—for one more of the fruit flies in the mango system in Benin—were found in all three AEZ: *Spondias mombin* L., *Citrullus colocynthis* (L.) Schrad., *Lagenaria siceraria* (Molina) Standl., *Irvingia*

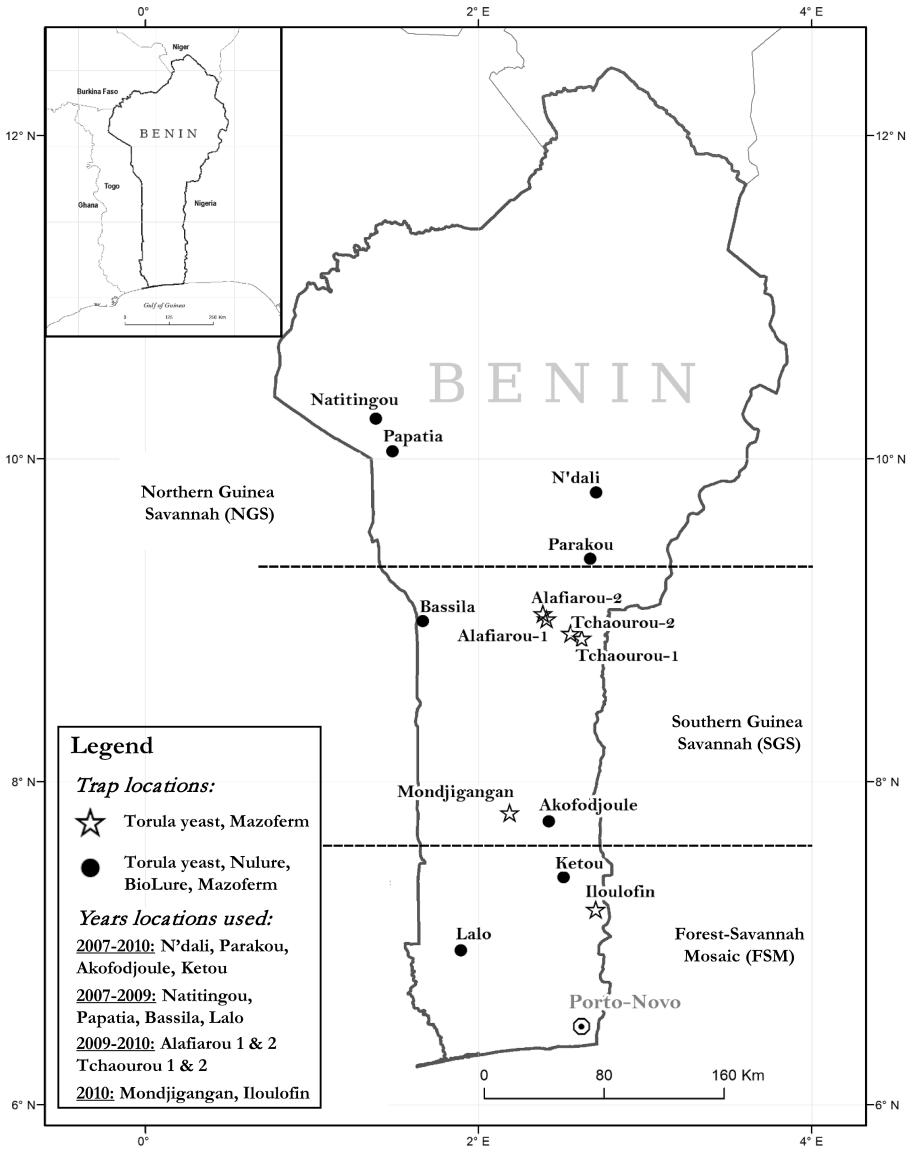

Fig. 1. Mango orchard locations in the Republic of Benin where food-bait attractants were used during four successive mango seasons between the years 2007 and 2010. Empty stars represent trap locations where Mazoferm-3% (2009) and Mazoferm-6% (2010) were compared to Torula yeast. Black-filled circles represent trap locations where Nulure (2007), BioLure (2008), Mazoferm-3% (2009), or Mazoferm-6% (2010) were compared to Torula yeast. Dotted lines are included to indicate approximate delineation of the borders of the agro-ecological zone where the experiments were conducted.

gabonensis (Aubry-Lecomte) Baill., *Psidium guajava* L., *Citrus* spp., *Blighia sapida* K.D. Koenig, and *Lycopersicum esculenta* Mill. *Annona senegalensis* Pers., *Annona muricata* L., *Momordica charantia* L., *Persea americana* Mill., *Manilkara zapota* (L.) P.Royen and *Chrysophyllum albidum* G.Don. were encountered only in the FSM and SGS. *Anacardium occidentale* L., *Sarcocephalus latifolius* (J.E. Smith) and *Vitellaria paradoxa* C.F.Gaertn. were encountered only in the SGS and NGS, while *Spondias cytherea* Sonner and *Capsicum frutescens* L. were encountered only in the FSM and SGS, respectively.

Four commercially available attractants including BioLure—a dry bait—and three liquid food-based baits Nulure, Mazoferm (two concentrations) and Torula yeast (dissolved tablets) were used in this study. BioLure and Torula yeast were sourced from Better World Manufacturing, Inc., Fresno, CA, while Nulure and Mazoferm E802 were sourced, respectively from Miller Chemical & Fertilizer Co., Hanover, PA, and Corn Products International, Nairobi, Kenya. The composition and use of all four attractants are well described in Ekesi et al. (2014). Torula yeast was selected as the standard attractant during all 4 yr based on preliminary data comparing all four food attractants (Hanna and Gnanvossou, unpubl. data) and the widely recognized attractiveness of Torula yeast to a broad spectrum of fruit flies (see Epsky et al. 2014, Manrakhan 2016). Each of the four other attractants was paired with Torula yeast in one of the 4 yr of the trials (Nulure in 2007, BioLure in 2008, and Mazoferm-3% and -6% in 2009 and 2010 respectively). An estimate of relative efficiency of each of the four non-Torula yeast attractants was obtained by comparing its catches with those of Torula yeast (see data analysis section).

Figure 1 shows the location of baits used for each of the 4 yr of the experiments. The attractants were placed inside a Multilure trap (MLT) (Better World Manufacturing, Inc., Fresno, CA) during all 4 yr. The all-plastic MLT is a modified version of the well-known McPhail trap; it has transparent and yellow top and bottom half

respectively to enhance fruit fly (particularly female) catches. The trap is versatile; it can be used for liquid baits—with a maximum capacity of 750 ml, or with dry baits or male lures with a killing agent. A 10-cm strip of DDVP—Dimethyl 2,2-dichlorovinyl phosphate (Hercon Environmental Corporation, Emigsville, PA) was added at the bottom of the MLT as killing agent with BioLure. The other three lures were used in 350 ml diluted solutions of commercial products—Nulure-9%, Mazoferm-3 and -6%, and Torula yeast at two 5 g pellets. Borax was added at 3% concentration to each liquid food-based attractant for fruit fly specimen's preservation, except for Torula yeast, which contains ~3% Borax. Three traps of each attractant were used in each orchard. All traps were randomly installed with a distance of ~20 m between traps. Traps were suspended with a wire in the mango tree canopy at a height of 1.5–2 m above the ground. Tanglefoot (The Tanglefoot Company, Grand Rapids, MI) was applied to the suspension wire to prevent predators and especially the ant *Oecophylla longinoda* (Latreille) from invading the traps. To avoid potential bias of particular trap placement, all traps in an orchard were permutated every 4 wk. Except for the Lalo orchard (which was 0.5 ha), the traps were placed in a centrally located 1-ha section of each of the orchards.

Traps were exposed from mid-March to early-to-late August (depending on completion of fruit harvest); however, all orchards within a particular year were monitored for the same period. Traps were serviced in the morning hours in all orchards at weekly and biweekly intervals for liquid and dry baits, respectively. Weekly counts of the dry bait (BioLure in 2008) were obtained by interpolation between two successive 2-wk counts to standardize the count intervals with those of the liquid attractants. Liquid and dry baits were renewed at 1- and 2-wk intervals, respectively. DDVP strips in the dry bait were replaced every 4 wk. All fruit fly specimens were preserved in 70% alcohol-filled plastic containers (70 ml and/or 600 ml of volume, depending on the quantity of catches) for later sorting and identification to species and sex in the laboratory. Fruit fly specimens were identified using the multi-character entry-key by Virgilio et al. (2014). Voucher specimens were deposited at the IITA Biodiversity Center, Abomey-Calavi, Benin, where a large tephritid reference collection is housed with numerous publicly available species records for West and Central Africa (http://projects.bebif.be/fruitfly/index.html).

Species abundance data were summarized by bait and AEZ. For brevity, fruit fly male and female counts were pooled for every week of sampling, but all baits had female biased counts. Relative abundance of each species was calculated for each of the three AEZ using total individuals captured for all species combined and for total captured for each of the two genera, *Bactrocera* and *Ceratitis*. Species richness—using total number of species present—was estimated using nonparametric extrapolation estimates; Chao (Chao 1987, Chiu et al. 2014), first-order jackknife and Bootstrap (Smith and van Belle 1984). Extrapolations estimate species richness assuming a greater effort is invested in collecting fruit flies in the system. Species diversity was estimated with the widely used Shannon and Simpson indices using R vegan package (Oksanen et al. 2017). The Shannon index incorporates both species richness and evenness, whereas the Simpson index measures evenness or species dominance (Magurran 2004). The Shannon index increases as both evenness and richness increase, while an increase in Simpson index indicates a decrease in species diversity (or an increase in species dominance). Due to non-normal distribution of the indices, the nonparametric Wilcoxon/Kruskall-Wallis was used to test for differences in diversity indices between AEZ, using JMP Pro 14.2 (SAS 2018).

A mixed model analysis of variance was used for fruit flies counts in Torula yeast traps only during all 4 yr of the experiments. AEZ and year were the fixed factors and location was the random factor. Tukey HSD ($\alpha = 0.05$) was used to compare counts of *B. dorsalis*, *C. cosyra* and all fruit flies in the three AEZ in all 4 yr, using JMP Pro 14.2 (SAS 2018). These analyses provided the basis for evaluating the fluctuations in fruit fly populations across all 3 AEZ and all 4 yr of the experiments.

The efficiency of food-based attractants relative to Torula yeast was evaluated in three analyses. First, a matched pairs analysis identified differences in trap catches (average per location per week of sampling) between each of the four baits (Nulure, BioLure, Mazoferm-3%, and Mazoferm-6%) paired with Torula yeast. Comparisons were stratified by AEZ for the two dominant species, *B. dorsalis* and *C. cosyra*, and for all fruit fly species combined. Second, linear regression analyses—with intercepts forced through zero—were used between Torula yeast and the bait with which it was paired in each of the 4 yr. This approach provided a relative efficiency index (REI) (slope of the regression forced through zero) for each of the 4 baits. The slope's standard error and a Bonferroni-corrected t-ratio were used to calculate confidence limits for determining the efficiency of Nulure, BioLure, Mazoferm-3%, and Mazoferm-6% relative to Torula yeast (slope $\neq 1$) and conduct post hoc simultaneous comparisons of relative efficiency of the four attractants within and between AEZ. Third, REI of each attractant was estimated from pooled trap catches of all three AEZ which allowed for simultaneous comparisons relative to Torula yeast (slope $\neq 1$) and among attractants using confidence limits with appropriate Bonferroni corrections. All matched pairs and regressions were conducted on log-transformed response variables to correct for unequal error variances inherent in count data, using JMP Pro 14.2 (SAS 2018).

Lastly, a matched-pair analysis (each of the attractant against Torula yeast) was conducted on the percentage of traps with one or more fruit flies of each species for each attractant and year for all AEZ combined. Percentage of traps with non-zero counts has been recommended for the evaluation of and comparison of intrinsic attraction of attractants to fruit flies, in the absence of controlled non-choice studies with known background fruit flies densities to determine the percentage of the population sampled by an attractant (Mangan and Thomas 2014). A similar analysis was conducted on counts of fruit flies in the traps. The data of the six most abundant species were used in these analyses (*B. dorsalis, C. cosyra, Ceratitis penicillata, Ceratitis silvestrii, Ceratitis fasciventris, and C. capitata*). Percentages and counts were log-transformed, and JMP pro 14.2 was used for these analyses.

Monthly climate data for temperature, RH and rainfall were obtained from either the nearest ASECNA (the Agency for Air Navigation Safety in Africa and Madagascar) or INRAB (National Institute of Agronomic Research in Benin) sources which corresponded to Bohicon, Dogbo, and Ketou for the FSM; Beterou, Dassa, Parakou, Save, and Tchaourou for the SGS; and Bembereke, Birni, Natitingou and Parakou for the NGS.

Results

Fruit Fly Species Diversity and Richness

A total of 73,850 fruit fly specimens from two genera—*Bactrocera* and *Ceratitis*—and 12 species were collected during the entire study period across the three AEZ, with 12, 10, 10 species, respectively in the FSM, SGS, and NGS (Table 1). Extrapolations with Chao, Jackknife (1st order) and Bootstrap produced species richness estimates of 15.5, 14.1, and 12.3, respectively in the FSM, and 10.7 to

Table 1. Fruit flies species abundance in traps of all five attractants across all 4 yr of trapping in each the three agro-ecological zones

Fruit fly species	AEZ		
	Forest-Savannah Mosaic[a]	Southern Guinea Savannah	Northern Guinea Savannah
Bactrocera dorsalis	5,816 (96.9, 100)	21,474 (64.3, 100)	6,911 (21.1, 100)
Ceratitis cosyra	61 (1.01, 33.0)	11,105 (33.3, 93.3)	26,210 (76, 95.1)
Ceratitis quinaria	4 (0.07, 2.12)	178 (0.53, 1.49)	738 (2.1, 2.68)
Ceratitis fasciventris	32 (0.53, 17.3)	347 (1.0, 2.91)	228 (0.66, 0.82)
Ceratitis silvestrii	0 (0, 0)	99 (0.3, 0.83)	311 (0.9, 1.13)
Ceratitis ditissima	58 (0.97, 31.4)	57 (0.17, 0.48)	45 (0.13, 0.16)
Ceratitis bremii	1 (0.02, 0.54)	47 (0.14, 0.39)	15 (0.04, 0.05)
Ceratitis capitata	9 (0.15, 4.86)	47 (0.14, 0.39)	8 (0.02, 0.03)
Ceratitis anonae	2 (0.03, 1.08)	26 (0.08, 0.22)	1 (0.003, 0.003)
Ceratitis neostictica	16 (0.27, 8.65)	1 (0.003, 0.008)	1 (0.003, 0.003)
Ceratitis acicularis	1 (0.02, 0.54)	0 (0, 0)	0 (0, 0)
Ceratitis penicillata	1 (0.02, 0.54)	0 (0, 0)	0 (0, 0)
Total captures[b]	6,001 (185)	33,381 (12,817)	34,468 (27,557)

[a]Values outside the brackets are total counts of trapped fruit flies, while values inside the brackets are respectively % of total of all species captures and % of total captures within a genus (i.e., *Bactrocera* spp. or *Ceratitis* spp.).

[b]Total captures of all species within an AEZ and total captures for *Ceratitis* spp. in parentheses. Total captures of *Bactrocera* spp. are the same as *B. dorsalis*.

12.0 in the SGS and NGS, indicating that more species could have been found with extended efforts with greater numbers in the FSM than in the SGS and NGS. Estimates of Shannon and Simpson diversity indices are presented in Fig. 1. The Shannon index—which includes both evenness and richness, was highest at the SGS, lowest at the FSM and intermediate at the NGS, while the Simpson index was significantly higher in the FSM and SGS—where *B. dorsalis* dominates—compared with the NGS (Fig. 2).

Table 1 presents a summary of the captures and relative abundance of each of the trapped species in each AEZ. *Bactrocera dorsalis* and *C. cosyra* were nearly equally represented in food-bait traps with 62.8 and 70.1% of all trapped specimens in the SGS and NGS respectively. *Bactrocera dorsalis* was most dominant in the FSM and SGS—at 96.9 and 64.3% respectively; while *C. cosyra* continued to be the dominant fruit fly species in mango orchards in the NGS—at 76% of all trapped fruit flies (Table 1). When *Ceratitis* spp. were considered separately from *B. dorsalis*, *C. cosyra* remained the most abundant species trapped—at 33, 93.3, and 95.1% in the FSM, SGS, and NGS, respectively. In the FSM, *Ceratitis ditissima* (Munro), *C. fasciventris* (Bezzi), *C. neostictica* (De Meyer), *C. capitata* (Wiedemann), and *C. quinaria* (Bezzi) represented respectively 31.4, 17.3, 8.65, 4.86, and 2.12% of all *Ceratitis* spp. trapped. *Ceratitis fasciventris*, *C. quinaria*, and *C. silvestrii* (Bezzi) represented 2.91, 1.49, and 0.83%, respectively of the species trapped in the SGS, and 0.82, 2.68 and 1.13%, respectively in the NGS. The remaining species—*Ceratitis bremii* (Guerin-Méneville), *Ceratitis anonae* (Graham), *Ceratitis acicularis* (Munro), and *C. penicillata* (Bigot)—were all represented at less than 1% of total species, or only of *Ceratitis* spp. (Table 1). The latter two species occurred only in the FMS, each with a capture of one individual (Table 1).

Abundance of Fruit Flies in Torula Yeast Traps

Counts of *B. dorsalis* were only affected by AEZ, with statistically non-significant numerical differences between years. Overall, *B. dorsalis* densities (flies/trap/week) were highest in the SGS (15.7 ± 1.38; mean ± SE) and FSM (10.2 ± 1.89) and least abundant at the NGS (6.12 ± 0.786) ($F = 5.60$; df = 2,9; $P = 0.024$) independent of year. Opposite trends were observed for *C. cosyra*, with highest abundance in the NGS (25.4 ± 1.01) followed by the SGS (9.49 ± 4.61) and lowest abundance at the FSM, where *C. cosyra* was nearly

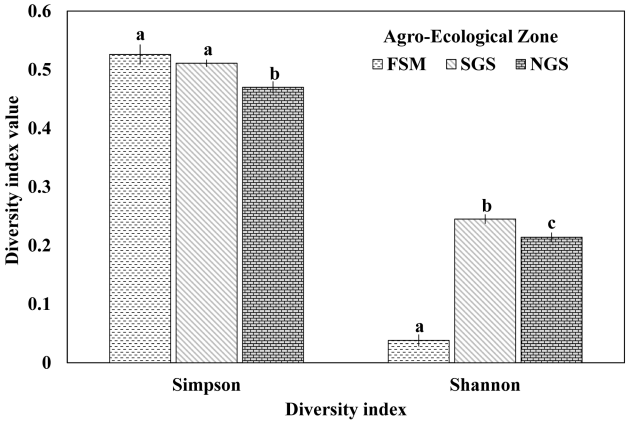

Fig. 2. Simpson and Shannon indices (means ± SE) of fruit fly diversity in the three AEZ—Forest Savannah Mosaic (FSM), Southern Guinea Savannah (SGS), and Northern Guinea Savannah (NGS). Means (vertical bars) followed by the same letter for each index are not significantly different (Wilcoxon / Kruskal Wallis nonparametric multiple comparisons; Simpson $\chi^2 = 8.74$, df = 2, $P = 0.013$, $Z = -0.284$–3.21; Shannon $\chi^2 = 329.7$, df = 2, $P < 0.001$, $Z = 2.33$–17.7. Counts for both indices were as follows: FSM = 814, SGS = 1697, and NGS = 1510.

absent (0.03 ± 0.012) ($F = 10.9$; df = 2,9; $P = 0.015$). Similar trends were observed for pooled means of all fruit fly species (10.4 ± 1.89, 25.7 ± 2.13 32.6 ± 4.78 for the FSM, SGS, and NGS, respectively). Trap catches of *B. dorsalis*, *C. cosyra* and all fruit flies combined were not affected by year of sampling, except for a non-significant decrease in *B. dorsalis* in the fourth year of the experiments (year effect for *B. dorsalis*—$F = 2.76$; df = 3,17; $P = 0.074$; *C. cosyra*—$F = 2.21$; df = 3,16; $P = 0.129$; all fruit flies—$F = 1.88$; df = 3,16; $P = 0.171$).

Relative Efficiency of Food-Based Attractants

Matched pairs data for each of the 4 yr are presented in Table 2 for *B. dorsalis*, *C. cosyra* and all fruit flies species found in Nulure, BioLure, Mazoferm, and Torula yeast traps. Nulure, BioLure, and Mazoferm-6% trap catches were consistently lower than Torula yeast trap catches in all three AEZ for all three groups of fruit flies.

Table 2. Matched pair analysis of each of four attractants against Torula yeast

AEZ	Attractant	Fruit fly species[a]		
		Bactrocera dorsalis	*Ceratitis cosyra*	All fruit flies
FSM	Nulure	5.45 ± 1.84	0.026 ± 0.02	5.49 ± 1.84
	Torula yeast	12.5 ± 3.51	0.03 ± 0.02	12.6 ± 3.51
	t-ratio, df, P-value	*2.39, 38, <0.001*	*NS*	*2.46, 38, 0.019*
SGS	Nulure	11.8 ± 2.49	6.91 ± 1.68	18.8 ± 3.34
	Torula yeast	27.7 ± 5.52	21.7 ± 5.87	49.9 ± 10.6
	t-ratio, df, P-value	*3.85, 38, <0.001*	*3.07, 38, 0.004*	*3.74, 38, <0.001*
NGS	Nulure	2.91 ± 0.55	10.7 ± 1.94	14.5 ± 2.21
	Torula yeast	8.57 ± 1.82	23.6 ± 5.62	33.6 ± 6.71
	t-ratio, df, P-value	*4.37, 75, <0.001*	*2.24, 75, 0.028*	*4.03, 75, <0.001*
FSM	BioLure	1.57 ± 0.45	0.5 ± 0.21	2.71 ± 0.73
	Torula yeast	8.45 ± 2.23	0.109 ± 0.04	8.74 ± 2.3
	t-ratio, df, P-value	*5.92, 45, <0.001*	*2.32, 45, 0.025*	*3.51, 45, 0.001*
SGS	BioLure	1.03 ± 0.23	3.61 ± 0.89	5.03 ± 0.99
	Torula yeast	12.1 ± 2.45	13.9 ± 2.38	26.7 ± 4.4
	t-ratio, df, P-value	*7.7, 45, <0.001*	*2.32, 45, <0.001*	*9.23, 45, <0.001*
NGS	BioLure	0.059 ± 0.02	5.34 ± 0.95	5.58 ± 0.98
	Torula yeast	2.71 ± 0.71	45.0 ± 13.5	48.5 ± 13.6
	t-ratio, df, P-value	*5.89, 92, <0.001*	*7.42, 92, <0.001*	*8.1, 92, <0.001*
FSM	Mazoferm-3%	**4.60 ± 1.5**	0.011 ± 0.01	**4.69 ± 1.50**
	Torula yeast	**5.97 ± 1.65**	0	**6.16 ± 1.68**
	t-ratio, df, P-value	***0.818, 43, 0.418***	*NS*	***0.637, 43, 0.527***
SGS	Mazoferm-3%	**17.6 ± 2.64**	**5.42 ± 0.85**	**23.6 ± 3.07**
	Torula yeast	**19.3 ± 2.92**	**6.20 ± 0.97**	**26.4 ± 3.52**
	t-ratio, df, P-value	***1.31, 101, 0.131***	***1.76, 101, 0.201***	***1.53, 101, 0.128***
NGS	Mazoferm-3%	6.35 ± 1.54	**11.2 ± 1.61**	18.5 ± 2.66
	Torula yeast	9.3 ± 1.94	**13.4 ± 1.74**	24.5 ± 3.19
	t-ratio, df, P-value	*2.78, 84, 0.007*	***1.88, 88, 0.063***	*2.7, 84, 0.008*
FSM	Mazoferm-6%	6.31 ± 3.48	0	6.34 ± 3.49
	Torula yeast	14.2 ± 6.19	0	14.3 ± 6.20
	t-ratio, df, P-value	*4.82, 42, <0.001*	*NS*	*4.83, 42, <0.001*
SGS	Mazoferm-6%	4.86 ± 0.89	2.89 ± 0.49	7.95 ± 1.18
	Torula yeast	10.0 ± 1.34	6.67 ± 1.06	17.1 ± 2.17
	t-ratio, df, P-value	*6.81, 122, 0.001*	*4.62, 122, <0.001*	*6.82, 122, <0.001*
NGS	Mazoferm-6%	0.537 ± 0.18	2.11 ± 0.70	2.72 ± 0.74
	Torula yeast	2.84 ± 0.79	8.41 ± 2.18	11.4 ± 2.49
	t-ratio, df, P-value	*3.46, 40, <0.001*	*4.62, 40, <0.001*	*4.8, 40, <0.001*

Means for each attractant were estimated using pooled means for all locations and sampling dates within each agro-ecological zone.

[a]Values in boldface indicate the nonsignificant difference ($P > 0.05$) between Torula yeast and Mazoferm-3% trap catches. All other differences were significantly different ($P < 0.05$) according to the indicated probablity values corresponding with the t-ratio and degrees of freedom. NS indicates available data not sufficient for a meaninful test.

Mazoferm-3% was the most effective attractant compared with Torula yeast, except at the NGS where Mazoform-3% catches were lower than those of Torula yeast (Table 3), probably due to the tendency of Mazoferm to harden at the high temperatures of the NGS.

Relative efficiency indices (REI) for Nulure, BioLure, and the two concentrations of Mazoferm are presented in Table 3. While the matched pairs analysis restricted the comparisons of each pair of attractants within an AEZ, the REIs provided a quantitative response that can be compared between AEZ using confidence limits of the estimates. Relative efficiency of Nulure was consistently less than 1 (0.5–0.804) and was statistically similar in all three AEZ except for its lower REI for *B. dorsalis* in the NGS. REI of BioLure was considerably lower than that of Nulure (0.035–0.518) but was least effective in trapping *B. dorsalis* in the NGS where it had an REI of 0.035, and in the SGS where BioLure REI was 0.299. The REI of BioLure for *C. cosyra* and all species combined was similar across AEZ. Mazoferm-3% was the most effective—compared with Torula yeast—in trapping all fruit fly species in all three AEZ with REI values 0.724–0.914 nearing equality with Torula yeast trap catches. At 6% concentration, Mazoferm-6% was less efficient than Mazoferm-3% (0.26–0.678) but performed similarly for all groups of fruit flies, except at the NGS were its REI for *B. dorsalis* was less than that of the other two AEZ.

Pooling trap catches over the three AEZ for each of the three fruit fly groups facilitated direct comparisons of the REIs of all baits. The upper limit of the confidence intervals of the relative efficiency of all attractants was less than 1—i.e., none of the attractants was as efficient as Torula yeast (Table 4). For *B. dorsalis* and all species combined, the rank order of the baits' REI (in increasing order) was: Mazoferm-3% > Nulure > Mazoferm-6% > BioLure. The rank order of the REIs for *C. cosyra* trap catches was similar to that of the other two groups except that Mazoferm-6% REI was similar to that of BioLure (Table 4).

In the last analysis, we compared relative frequency of non-zero counts of the baits to their average captures to indirectly determine their attractiveness to the various species, as suggested by Mangan

Table 3. Comparison of the relative trapping efficiency of Nulure, BioLure, Mazoferm-3% and Mazoferm-6%—compared with Torula yeast—calculated separately for *Bactrocera dorsalis*, *Ceratitis cosyra* and all fruit fly species combined in each the three agro-ecological zones (AEZ)

		Bactrocera dorsalis		*Ceratitis cosyra*		All fruit fly species	
AEZ	df	Relative efficiency ± SE[a]	Confidence limits[a]	Relative efficiency ± SE	Confidence limits	Relative efficiency ± SE	Confidence limits
Nulure							
FSM	37	0.64 ± 0.064aA	0.480, 0.800	0.5 ± 0.141aA	0.147, 0.853	0.639 ± 0.064aA	0.479, 0.799
SGS	37	0.723 ± 0.045aA	0.610, 0.836	0.658 ± 0.048aA	0.538, 0.778	0.804 ± 0.025aA	0.741, 0.867
NGS	74	0.614 ± 0.037aA	0.523, 0.705	0.791 ± 0.033aB	0.710, 0.872	0.75 ± 0.041aA	0.650, 0.850
BioLure							
FSM	44	0.429 ± 0.042aA	0.324, 0.534	1.06 ± 0.33aA	0.239, 1.881	0.49 ± 0.063aA	0.333, 0.647
SGS	44	0.299 ± 0.03aA	0.224, 0.374	0.516 ± 0.04aB	0.416, 0.616	0.518 ± 0.033aB	0.436, 0.600
NGS	91	0.035 ± 0.013bA	0.003, 0.067	0.497 ± 0.028aB	0.429, 0.565	0.461 ± 0.03aB	0.388, 0.534
Mazoferm-3%							
FSM	42	0.764 ± 0.064aA	0.604, 0.924	0	0	0.767 ± 0.063aA	0.610, 0.924
SGS	100	0.9 ± 0.038aA	0.807, 0.993	0.837 ± 0.038aA	0.744, 0.930	0.914 ± 0.033aA	0.834, 0.994
NGS	83	0.724 ± 0.049aA	0.604, 0.844	0.784 ± 0.053aA	0.654, 0.914	0.777 ± 0.048aA	0.660, 0.894
Mazoferm-6%							
FSM	44	0.6 ± 0.06aA	0.451, 0.749	0	0	0.565 ± 0.06aA	0.416, 0.714
SGS	121	0.647 ± 0.032aA	0.569, 0.725	0.625 ± 0.034aA	0.542, 0.708	0.678 ± 0.035aA	0.593, 0.763
NGS	39	0.276 ± 0.055bA	0.138, 0.414	0.425 ± 0.059aA	0.277, 0.573	0.424 ± 0.058bA	0.279, 0.569

The higher the relative efficiency index of an attractant, the closer it is to the capture efficiency of the reference attractant Torula yeast.

[a]Relative efficiency values within columns and fruit fly species for each attractant that are followed by the same letter are not significantly different using Bonferroni-corrected confidence limits with an effective $\alpha = 0.0167$.

Table 4. Relative efficiency of four baits—compared with Torula yeast—for trapping *Bactrocera dorsalis*, *Ceratitis cosyra* and all fruit fly species in mango systems across three agro-ecological zones

Attractant	df	Relative efficiency ± SE[a]	Confidence limits[a]
Bactrocera dorsalis			
Nulure	154	0.667 ± 0.026a	0.601, 0.733
BioLure	185	0.277 ± 0.019b	0.228, 0.326
Mazoferm-3%	231	0.833 ± 0.027c	0.764, 0.902
Mazoferm-6%	237	0.595 ± 0.026d	0.529, 0.661
Ceratitis cosyra			
Nulure	154	0.745 ± 0.024a	0.684, 0.806
BioLure	185	0.504 ± 0.022b	0.450, 0.558
Mazoferm-3%	231	0.818 ± 0.03c	0.742, 0.894
Mazoferm-6%	237	0.570 ± 0.027b	0.503, 0.637
All fruit fly species			
Nulure	154	0.762 ± 0.021a	0.708, 0.816
BioLure	185	0.406 ± 0.022b	0.351, 0.461
Mazoferm-3%	231	0.845 ± 0.026c	0.780, 0.910
Mazoferm-6%	237	0.615 ± 0.025d	0.552, 0.678

[a]Relative efficiency indicies followed by the same letters are not significantly different using Bonferroni-corrected confidence limits with an effective $\alpha = 0.0125$.

and Thomas (2014). The results of this comparison are presented in Fig. 3. We present the comparisons for *B. dorsalis* and *C. cosyra* since the two species were the most abundant during our study. Mean percent of traps with one or more individual of a species are juxtaposed to the mean counts of a species in traps for each attractant and each year for visual appreciation. In the previous analysis based on trap counts, means densities of *B. dorsalis* and *C. cosyra* in Mazoferm-3% were comparable to those of Torula yeast, and counts of *C. cosyra* in BioLure were similar to counts of this species in Torula yeast (Tables 3 and 4), while both Nulure and Mazoferm-6% underestimated *B. dorsalis* and *C. cosyra* densities and BioLure underestimated *B. dorsalis* densities. Interesting relationships emerge, however, when the percent of traps of each of the attractant with a particular species are considered. First, percent of Nulure traps with *B, dorsalis* or *C. cosyra* were similar to those of Torula yeast ($P = 0.113$ and 0.948 for the two species, respectively). This is in contrast for more than twofold counts of the two species in Torula yeast compared with Nulure. Based on the non-zero counts only, Nulure seems to have the same attraction as Torula yeast for both species, and Nulure is slightly more attractive to *B. dorsalis* than to *C. cosyra*.

Second, percent of BioLure traps with *B. dorsalis* are considerably lower than those in Torula yeast ($P < 0.001$) which also corresponds to lower *B. dorsalis* counts in BioLure compared with Torula yeast. Percentage of BioLure traps with *C. cosyra*, however, were similar to those of Torula yeast ($P = 0.389$), whereas counts of *C. cosyra* in BioLure traps were considerably lower than in Torula yeast traps. Third, Mazoferm-3% is the only attractant for which percent of traps with either *B. dorsalis* or *C. cosyra* corresponded with those of Torula yeast ($P = 0.338$ and 0.392 for the two

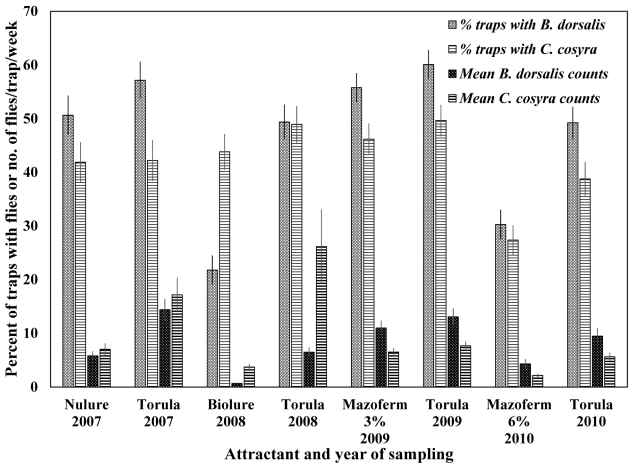

Fig. 3. Percentage of traps with one or more individual (non-zero count) of *Bactrocera dorsalis* and *Ceratitis cosyra* and average count of the species in the food bait traps in each of the years of the experiments. For each bait, the two bars on the left are for percentage of traps with one or more fruit fly individuals of *B. dorsalis* or *C. cosyra*, while the two bars on the right for each bait are average counts of flies per trap per week pooled across the three AEZ.

species, respectively), similar to a species counts in the two attractants. In the case of Mazoferm-3%, relative attraction corresponded with the relative counts in traps for both species. Fourth, Mazoferm-6% attraction of both species was lower than those of Torula yeast ($P < 0.001$, = 0.031 for the two species, respectively), which are comparable to the lower relative efficiency of Mazoferm-6% for the two species. These differences are caused by the lower attractiveness of Mazoferm-6% to *B. dorsalis* and *C. cosyra* compared with Torula yeast and Mazoferm-3%. We conducted similar analyses for the remaining species but did not include them in Fig. 3 to reduce crowding and conserve visual clarity. Briefly, similar patterns were observed for Nulure—attractiveness of Nulure was similar to Torula yeast ($P = 0.177–0.50$) while captures in Nulure were lower than in Torula yeast. The same patterns were observed for Mazoferm-6% except for *C. fasciventris* and *C. anonae* where Mazoferm was less attractive than Torula yeast ($P = 0.033$ and 0.025). Both Mazoferm-3% and BioLure were less attractive to *C. ditissima* than Torula yeast ($P < 0.001$ and $P = 0.012$, respectively). BioLure was also less attractive to *C. sylvestrii* and *C. ditissima* than Torula yeast ($P < 0.001$ and $P = 0.012$).

Climate data for the FSM, SGS and NGS were respectively: 850–1473, 1076–1272, and 1290–1396 mm rainfall/month; while temperature means were 28.2–28.8°C, 28.3–28.4°C, and 27.8–28.0°C; and RH means were 68.9–73.8%, 63.5–65.0%, and 59.9–65.5%.

Discussion

The present study was part of a large program for the management of fruit flies in mango and other orchard fruit systems in sub-Saharan Africa. These program was largely developed following the invasion of Africa by *B. dorsalis* and the subsequent large losses in fruit production and exports (Lux et al. 2003a; Hanna et al. 2005; Vayssieres et al. 2005; Mwatawala et al. 2006; Ekesi et al. 2006b; Hanna et al. 2008; Goergen et al. 2011; Gnanvossou et al. 2016, 2017). In this 4-yr study, we quantified the diversity of fruit fly species and compared the efficiency of food-baits in estimating fruit flies abundance in mango orchards in a cross-section of AEZ that are characteristic of much of sub-Sahalian western Africa.

In our sampling efforts during four mango seasons, a total of 12 fruit fly species were captured in the three targeted AEZ. These differences in species richness among AEZ are likely caused by differences in host plant preferences among fruit fly species as well as perhaps climatic preferences and interactions with other species. Extrapolation techniques (see description above) showed that fruit fly species richness can be higher by 2–4 species if sampling efforts were increased. Assuming that all species have equal capture probabilities, which is unlikely to be true as in most ecological communities, the FSM would be considered to have higher species richness than the other two AEZ; but this difference is due to the capture of two additional species—*C. acicularis* and *C. penicillata—in* the FSM, each represented by one individual. Ten of the twelve captured species have been reared from mango and other fruits generally found in and around mango orchards (Ekesi et al. 2006b, Vayssieres 2008, Hanna and Gnanvossou, unpublished data). The two other species—*C. acicularis* and *C. penicillata—are* only known from hosts other than mango (De Meyer and Friedberg 2005).

Previous studies on the diversity and seasonality of fruit flies in mango systems in western Africa used the male lures methyl eugenol and terpinyl acetate (Gnanvossou et al. 2017) plus Trimedlure (Vayssieres et al. 2015). Our estimates of fruit fly species richness and relative abundance obtained from food-based attractants contrast with those obtained from male lure captures (Vayssieres et al. 2015, Gnanvossou et al. 2017). In the NGS, which was common to all three studies, the locations used from 2007 to 2010 by the present study were also used for the same periods by Gnanvossou et al. (2017), while those used by Vayssieres et al. (2015) were in the same general areas in the NGS in northern Benin and were sampled from 2005 to 2009. The three studies produced considerably different relative abundance patterns of *B. dorsalis* and *Ceratitis* spp. in the NGS, after exclusion of the species captured with Cue-lure, which was used by Gnanvossou et al. (2017) and Vayssieres et al. (2015) (but not in our study) for *Dacus* spp. and *Zeugodacus* spp. The three studies—Vayssierees et al. (2015), Gnanvossou et al. (2017), and the present study—obtained respectively the following relative abundance patterns in the NGS: 53, 72, and 21% for *B. dorsalis*; 36, 21, and 76% for *C. cosyra*; 5.7, 0.96, and 2.1% for *C. quinaria*; 2.58, 0.595 and 0.9 for *C. silvestrii*; 0.096, 0.151, and 0.66% for *C. fasciventris*, 0.003, 0 and 0.13% for *C. ditissima*; 0.007, 0, and 0.003% for *C. anonae*. Moreover, Vayssieres et al. (2015) captured the three *Ceratitis* spp. - *C. lentigera* Munro, *C. pedestris* (Bezzi) and *C. punctata* (Wiedemann) which were not captured by Gnanvossou et al. (2017) and the present study. The latter, however, captured the three species—*C. neostictica*, *C. acicularis*, and *C. pencillata* which were not captured by Vayssieres et al. (2015) and Gnanvossou et al. (2017). All six species occurred in very low frequency. Their absence or presence in male lure or food-based traps could be due to various site-specific conditions of host availability and climate, differences in attractions to male lures and food-based attractants, or for some other unknown reasons. Together, the three studies from Benin identified 17 fruit fly species from mango orchards across three AEZ.

De Meyer et al. (2013) provided a comprehensive review and analysis of the frugivorous fruit fly fauna in western Africa. The authors used an ecoregional classification based on Burgess et al. (2004) in which our FSM corresponds to their Guinean Forest Savannah Mosaic (GFSM) and our SGS and NGS are pooled in the West Sudanian Savannah (WSS). All the fruit fly species captured in the three AEZ in our study corresponded to their occurrence following the ecoregional classification used by De Meyer et al. (2013); except our records of *C. acicularis*, *C. quinaria*, and *C. neostictica* which were captured in the GFSM (or our FSM). These three species

were reported, however, from the East Guinan Forest (EGF) ecoregion (De Meyer et al. 2013). Interestingly, the single individual of *C. acicularis* captured in a BioLure trap in the FSM in our study is the only record of *C. acicularis* from Benin. The specimen was captured in Ketou, an area close to the EGF of De Meyer et al. (2013).

The differences in species richness notwithstanding, the comparisons of relative species abundance, particularly for *B. dorsalis* and *C. cosyra*, from male lure and food-bait trapping studies, call for caution when using relative species abundance to infer species dominance and more importantly such phenomenon as competitive exclusion and the practical outcome of suppression trials. In the two studies of Vayssieres et al. (2015) and Gnanvossou et al. (2017), relative abundance of *B. dorsalis* in the NGS was respectively 53 and 72%, but only at 21% in the present study. In contrast, *C. cosyra* relative abundance was 36, 21, and 76% for the three studies. These differences have led to two contrasting conclusions: 1) *B. dorsalis* is the dominant species in the NGS (Vayssieres et al. 2015, Gnanvossou et al. 2017), while 2) the present study, using food-based attractants, arrived at the opposite conclusion—that *C. cosyra* continues to be the dominant species in the NGS and has not been competitively displaced to the extent of the conclusions of the other two studies. Correcting for differences in trapping period during the year does not change the overall comparisons since densities of all fruit flies during the off-season are low compared with their abundance during the mango season. We argue that the differences in relative abundance between the studies using male lures and those using food-based attractants is caused by differences in the attractiveness of methyl eugenol to *B. dorsalis* and terpinyl acetate and trimedlure to *C. cosyra* and other *Ceratitis* spp. The differential strength in attraction of the lures to their respective species can cause cascading effects on the estimated relative abundance of all species since *B. dorsalis* total catches were likely inflated (due to its strong attraction to methyl eugenol). Our study suffers also from the same species-attraction bias, but likely to a lesser magnitude, because the relative attractiveness of Torula yeast and all the other food-based attractants used in this study to *B. dorsalis* and *Ceratitis* spp. under field conditions is not well known. We considered, however, a possible solution to this potential bias on which we expand below.

Based on the number of flies captured in food-based attractants, we showed that the most abundant fruit fly species were, in increasing order, *B. dorsalis* in the FSM and the SGS, and *C. cosyra* in the NGS. Temperature, RH, rainfall (Ndiaye et al. 2008, Rwomushana et al. 2008, Vayssières et al. 2009a, Winsou 2012, Nboyine et al. 2013, Gnanvossou et al. 2017) and host plant suitability and diversity (Raghu et al. 2004, Goergen et al. 2011), have been shown to be some of the major factors affecting the abundance and seasonality of *B. dorsalis*. Species-specific response to RH and temperature could also explain the persistence of *C. cosyra* in the NGS and to a lesser extent in the SGS, and the dominance of *B. dorsalis* in the FSM and SGS, especially during the second half of the mango season in the NGS. Winsou (2012) showed that the survival of *B. dorsalis* pupae decreases sharply with decreasing RH—independent of temperature, conditions that prevail during the dry season in western Africa, particularly in the NGS and SGS (Vayssieres et al. 2009a, 2015; Gnanvossou et al. 2017). This corroborates with our results in the SGS and NGS, where the numbers of *B. dorsalis* were low during the first half of the mango season when RH is low and temperatures are high. *Bactrocera dorsalis* increased in numbers during the second half of the season, i.e., at the onset of rains and mango maturation period when temperatures decreased and RH increased (Vayssieres et al. 2009a, Vayssieres et al. 2015, Gnanvossou et al. 2017). In the same study of Winsou (2012), *C. cosyra* pupae were considerably more tolerant to low RH than *B. dorsalis*, with survival of *C. cosyra* pupae decreasing moderately with increasing RH and opposite trends for *B. dorsalis*. The differential effects of RH on pupal survival, in addition to possibly other factors such as interspecific competition and differences in the prevalence of alternative hosts during the dry season (e.g., *S. latifolius*, and *A. senegalensis*) probably explain in part the higher prevalence of *C. cosyra* and possibly *C. fasciventris*, *C. quinaria*, and *C. silvertrii* in the NGS and SGS compared with the FSM (Table 1).

The low numbers of *C. cosyra* in the FSM compared with the NGS and SGS, could be the result of competitive displacement by the highly aggressive *B. dorsalis*. Competitive displacement is not uncommon among tephritid fruit fly species (Duyck et al. 2004a, 2008). The perceived displacement phenomenon observed in the FSM was also observed during the wet season and towards the end of the mango season in the SGS and to a lesser extent in the NGS. These interactions between *B. dorsalis* and *C. cosyra* have been demonstrated or suggested in Kenya (Ekesi et al. 2009), Tanzania (Mwatawala et al. 2009), and western Africa (Vayssieres et al. 2015, Gnanvossou et al. 2017).

When total number of fruit fly captures by each attractant was considered by AEZ, irrespective of species, Torula yeast was the most superior food-bait attractant because it captured the highest number of fruit flies overall in mango orchards. The same trends were observed when *B. dorsalis* and *C. cosyra* captures were compared. Torula yeast consistently captured more fruit flies than all the attractants except for two cases: 1) BioLure captured higher numbers of *C. cosyra* than Torula yeast in the FSM, indicating that BioLure is more effective in attracting *Ceratitis* species, especially when they occur at low densities, which is a case to be made for BioLure for the detection of species occurring at low densities (Manrakhan et al. 2017). BioLure also captured one individual of each of *C. acicularis* and *C. penicillata*, which were not captured by any of the other attractants used in other study, or with terpinyl acetate used in the same sites by Gnanvossou et al. (2017). 2) Mazoferm at 3% concentration was equivalent to Torula yeast in both the FSM and the SGS, but not in the NGS where it captured fewer fruit flies than Torula yeast. The reduction in Mazoferm-3% trapping efficiency in the NGS is probably due to its tendency to dry (or cake) in hot and dry conditions, a property common to liquid food bait (Epsky et al. 2014, Manrakhan 2016). Doubling Mazoferm concentration to 6% reduced its effectiveness compared with Torula yeast across all AEZ.

The comparative trapping efficiencies reported in our study are consistent with those reported in other studies: 1) Torula yeast versus BioLure and Nulure (Epsky et al. 1993, Ekesi et al. 2014), 2) Torula yeast and Mazoferm versus BioLure and Nulure (Ekesi 2010), and 3) Torula yeast versus Nulure (Leblanc et al. 2010). Our results, however, contrast with more recent studies that reported equal captures of fruit flies with Torula yeast and BioLure (Epsky et al. 2011) or higher captures of *Ceratitis* spp. and *B. dorsalis* in BioLure traps compared with other food-based attractants (Manrakhan et al. 2017). The discrepancy among the various studies could be attributed to various factors, including species (or biotypes), sex, age, feeding history, and physiological state; trap design, bait quality, and cropping systems (Jacome et al. 1995, Piñero et al. 2002, Díaz-Fleischer et al. 2009, Shelly et al. 2018). There are also factors related to the level of pH due to alkalization in case of liquid baits (Heath et al. 1994), as well as the ecological conditions (Aluja et al. 1996, Cornelius et al. 2000) that prevail in the environments where the experiments were conducted. Such differences call for continued efforts to test existing and new baits in specific environments to optimize their use in detection, monitoring, and suppression of fruit flies.

In addition to direct comparisons of trap counts, our study introduced the REI, a tool that has not been used in comparing the efficiency of food-based attractants. REI provides a quantitative index for comparing the efficiency of various attractants—relative to Torula yeast as the most efficient attractant used in our study. The REIs of Nulure and Mazoferm-3% were consistent across AEZ and species, whereas BioLure and Mazoferm-6%, were particularly poor attractants of *B. dorsalis* in the NGS, possibly due to lower BioLure longevity and increased hardening of Mazoferm-6%, and to lesser extent Mazoferm-3%, in the NGS. Cunningham et al. (1978) and Robacher (2006) showed that liquid baits are likely to be more effective in hot and dry environments due to increased water stress on the fruit flies. The flipside of that, however, is that liquid baits are prone to hardening under those environments (Manrakhan 2016) as we encountered with Mazoferm in the NGS.

Pooling the data of all three AEZ allowed us to compare the REI of the various attractants for *B. dorsalis*, *C. cosyra*, and all species combined. The general conclusions remain the same except that all REI values were less than one (using Bonferroni-adjusted CL) indicating that none is as efficient as Torula yeast. Should any of the attractants (Nulure, BioLure, or Mazoferm) be used in the place of Torula yeast, the REIs and their confidence limits provided here could be used as correction factors for the abundance of fruit flies in the mango system.

Epsky et al. (2014) and Manrakhan (2016) reviewed the approaches for evaluating the attractiveness of male lures and food baits to fruit flies. There is, however, lingering uncertainty about the relative attractiveness of food baits to two or more fruit fly species under field conditions. In addition to controlled experiments (where total populations of fruit flies are known), the relative frequency of non-zero trap counts might provide an additional approach to compare baits, particularly for detection and regulatory purposes (Mangan and Thomas 2014). While we demonstrated that the patterns of fruit fly counts in traps and relative frequency of non-zero count traps are similar—at least for *B. dorsalis* and *C. cosyra* in Nulure, Torula yeast and Mazoferm-3%, the risk of overestimation of relative species abundance using these baits is diminished and the difference in attraction to *B. dorsalis* and *C. cosyra* is probably much less than the difference caused by using methyl eugenol and terpinyl acetate. We call for the use of integrative diversity and abundance studies that simultaneously include male lures, food-based attractant, and fruit host infestations, in addition to controlled studies on the relative attraction of each of the male lures and food-based attractants to each of the species—similar to the approach of Leblanc et al. (2010).

The broad objective of our study was to develop a standard approach to the use of food-baits across AEZ in western Africa. From the practical side, we can recommend that Mazoferm-3% and Torula yeast could be used interchangeably for fruit flies monitoring as they are equally effective in attracting the principal fruit fly species in mango orchards, similar to the recommendations of Ekesi et al. (2014) for Kenya. Other studies that used Nulure and BioLure could rely on the REI developed for the baits used in our study. There is a continuing need, however, to improve our understanding of the relative attractiveness of the various baits to the principal fruit fly species through controlled experiments or validation of results through published data and/or new studies. Moreover, and in a next step, we would need to develop an estimate of the number of traps and distances among traps for both monitoring and suppression and to relate the information from traps to the timing and levels of fruit infestations and established economic thresholds of fruit flies.

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