BIODIVERSITY AND BIONOMICS FOR FRUIT FLIES (*DIPTERA: TEPHRITIDAE*) IN MOROGORO, TANZANIA

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ABSTRACT

Studies on biodiversity and bionomics of fruit flies (Diptera: Tephritidae) were conducted in Morogoro Region, Central Tanzania from 2004 to 2006. Specifically studies aimed at determining the biodiversity of fruit flies, their host range, infestation rate, incidence and seasonality. These are among the pre-requisites for formulating an ecologically based Integrated Pest Management (IPM). Flies were collected using McPhail traps baited with parapheromones (methyl eugenol, Trimedlure and cue lure) and synthetic food baits (hydrolyzed yeast and 3 Component lure). Flies were also collected from infested fruits after incubation in the laboratory. A total of four sites and neighboring areas representing the three agro-ecological zones of Morogoro Region were used. Two key fruit fly pests were determined based on abundance, host range and infestation rate. The invasive fruit fly, *Bactrocera invadens* Drew, Tsuruta and White is the key pest in the low and medium altitude areas. On the other hand, the Natal fruit fly, *Ceratitis rosa* Karsch is the key frugivorous pest in the high altitude areas. Other native species like *C. capitata* (Wiedemann) and *Ceratitis cosyra* (Walker) were less abundant, had narrower host ranges and lower infestation rates. An IPM program based on the ecology of the key pests *B. invadens* and *C. rosa* is hereby proposed. Components of such a program include male annihilation technique (MAT), use of baits, farm hygiene and sanitation, quarantine, surveillance and post harvest treatment.

Key words: IPM, fruit flies, Tanzania

INTRODUCTION

The management of fruit fly pests has been a major problem throughout the world (Jackson *et al.*, 1998; White and Elson-Harris, 1992; Aluja and Liedo, 1993). Various methods for managing the flies have been reported by White and Elson-Harris (1992). According to Jackson *et al.* (1998) fruit fly eradication in the past relied upon insecticides. However, broad-spectrum insecticides in cover sprays are known to create ecological, toxicological and environmental problems (Cohen and Yuval, 2000). Evolving insect resistance to insecticides, public concern and increasingly restrictive environmental regulations have nearly precluded the use of aerial broadcasts (Jackson *et al.*, 1998). Insecticides are also expensive and cannot be affordable to smallholder farmers. An appropriate approach for the latter group is, therefore, Integrated Pest Management (IPM). IPM is emphasizes minimal use of pesticides (Kiss and Meerman, 1991; Daxl *et al.*, 1994; Allen and Rajotte, 1990). Knowledge of pest ecology and natural enemies as well as knowledge of socio-economic factors is essential in formulating an IPM program (Daxl *et al.*, 1994; Van Huis and Meerman, 1997). Studies on bionomics may include phylogeny, taxonomy, distribution, host plant resistance, demography, population genetics and behaviour ecology (Aluja, 1994). Bionomics also include studies on biodiversity, chemical ecology, vector relationship and natural enemy complexes. These are among pre-requisites for formulating an IPM program.

METHODOLOGY

Studies were conducted for two years starting October 2004 in Morogoro Region, Central Tanzania. Four sites, located within the three agro-ecological zones of then Region, were selected. They include Mkindo (River basin and valleys zone), SUA horticulture unit and Mikese (Plateau zone) and Nyandira (Mountain zone). The sites were chosen to represent the unimproved (traditional) and improved orchards. Descriptions of the study sites and details of fruits grown were given by Mwatawala *et al*. (2006).

Establishing fruit fly fauna, biodiversity host range

The study of the fruit fly fauna was undertaken in a period of two years and involved trapping and sampling of fruits from all four sites and surrounding areas. Modified McPhail traps (AgriSense, UK) were used. They were baited with five types of attractants; Trimedlure (TM) was used to attract members of the genus *Ceratitis*, sub-genera *Ceratitis* and *Pterandus*. Methyl eugenol (ME) was used to attract members of the genus *Ceratitis* sub-genus *Pardalaspis* and an invasive *B. invadens*. Cue Lure (CL) was used to attract members of *Dacus* spp. and *Bactrocera cucurbitae*. A three component lure (3C) was used to attract a wide variety of *Ceratitis* spp with emphasis on *Ceratitis cosyra*. An insecticide, dichlorovos (vapona) was placed in each trap to kill the adult flies. A protein bait (PB) was used to attract both sexes of different fruit fly species.

Five replicates of each attractant were set at SUA (2 on mango, 2 on citrus and 1 on guava tress), four at Mikese (all on mango trees), and two each at Nyandira (1 on plum, one on peach) and Mkindo (both on citrus). At all the sites, the traps were hung on selected trees, placed 1.5 – 2 meters above the ground. All five traps were hung on the same tree. The distance between trees with traps was 50 - 100 meters away. Trapping followed guidelines given by the International Atomic Energy Agency and FAO (IAEA, 2003). The data were collected every week at the SUA site where all attractants were changed after four weeks except the protein bait, which was changed every week. Data were collected once every four weeks at the other sites. At these sites, all attractants were placed and left in the field for one week in every four weeks. The traps were rotated clockwise after collecting the flies to minimise location bias. The effect of location bias was also minimized by randomly positioning a trap with a particular lure on each replicate (tree) during setting up of the experiment. Infested fruits were collected and cultured in the laboratory in order to determine host specificity of the different fruit fly species and to establish the local fruit fly fauna. The fruits were collected each week following the procedure described by Copeland *et al*. (2002).The general methods of rearing the flies followed the protocols established by AFFI (Ekesi, 2006). The adults were then killed by placing vials in a freezer for 4 hours.

Flies were identified, counted and preserved in 70% alcohol. Specimens were preserved following methods described by White and Elson-Harris (1992). The identification of flies were done using keys and characters presented by White and Elson-Harris (1992), De Meyer (1996; 1998; 2000; 2001), Norrbom *et al*. (1998), CABI key (CABI, 2004), De Meyer and Freidberg (2006) and White (2006). The data collected include fruit fly species, fruits they attack, geographical location and their reservoir host. Fruit fly biodiversity of the different sites was determined using Jaccard, Sorensen and Morisita-Horn (quantitative) indices (Magurran, 1988).

Efficacy of lures

Efficacy of lures was compared in a split split plot design experiment at the SUA Horticulture Unit from January 2005 to January 2006. This one-year cycle was first divided into specific periods of observation of four weeks, coinciding with the time of changing the attractants. A total of thirteen periods of observation were scheduled. The weekly catches of each of the species in a respective lure during each period of observation were first pooled and the average number of flies per trap per week was calculated. There were three sources of variation; periods of observation (main-plot), lures (sub-plots) and orchards sub-sub-plots). Each treatment was replicated twice. Lures were set as sub-plots (instead of sub-sub-plots) in order to increase the chances of detecting effects of sub-orchards since the effect of lures was expected to be large and easier to detect. ME was tested against the synthetic food baits for efficacy to attract *B. invadens*. TM was tested against synthetic food baits for efficacy to attract *C. rosa*. 3C was tested against PB for efficacy in attracting all the three major fruit fly species (after pooling catches). In all three cases, CL was used as a control, since it does not attract any of the focused species.

The weekly catches of the three major species by each of the synthetic food baits (PB and 3C) were compared at SUA Horticulture Unit from January 2005 – January 2006. The sources of variation were times of observation (main-plots), fruit fly species (sub-plots), and orchards (sub-sub-plots). The rationale for assigning treatments to the main plots, sub plots and sub-sub-plots was the same as the one given above. The analysis of Variance (ANOVA) followed by means separation using the Least Significant Difference (LSD) were used to compare efficacy of lures and effect of lure aging in attracting fruit flies. The data were analysed using SAS version 9 (SAS institute Inc., USA).

Incidence of fruit flies

The incidence of each of the major fruit fly species was determined as the ratio of positive to the total number samples of a fruit species. Seasonal incidence curves were plotted using Microsoft Excel (Microsoft, USA). Chi-square goodness of fit test was used to determine the differences between the number of positive and negative samples in selected fruit species. The chi-square analyses were performed using GenStat (VSN International Ltd, UK) and fruit species with expected cell counts of less than five samples were removed.

RESULTS

Fruit fly fauna of Morogoro (including new host records)

Table 1 and 2 presents the list of fruit flies collected from the three agro-ecological zones of Morogoro Region. A total of 25 fruit fly species belonging to 5 genera emerged from one or more of the 37 fruit species that were collected. The highest number of emerged flies belongs to *B. invadens* followed by *C. cosyra*, *B. cucurbitae* and *C. rosa*. All the species that emerged from fruits were also recorded by trapping, except *Capparimyia melanaspis*, which was only recorded from *Maerua* sp., but was never caught in any trap. *B. invadens* was the dominant species, with more than 82% flies collected from sampled fruits (Table 1) while more than 97% of flies recorded from traps (Table 2). In trapping, the next highest catches were of *B. cucurbitae* and *C. rosa*. Two invasive *Bactrocera* species have been recorded during the study, first, *B. invadens* (Mwatawala *et al.*, 2004) and second *B. latifrons* (Mwatawala *et al.*, 2007). Diversity of fruit flies between the sites is presented in Table 3. A high similarity was observed between sites located in the low to medium altitude (SUA, Mikese and Mkindo) where tropical fruits are grown. These sites were highly dissimilar to the high altitude site of Nyandira site where mostly temperate fruits are grown. A highest similarity was observed between SUA and Mikese (both in located in the medium altitude) followed by Mikese and Mkindo, the latter being a low altitude site.

Table 1 : List of fruit flies recorded from various fruits collected from the four study sites and elsewhere in Morogoro.

Genus	Species	Total	Percentage
Bactrocera	*cucurbitae*	1350	3.16
	invadens	35326	82.76
	latifrons	209	0.49
Capparimyia	*melanaspis*	494	1.16
Ceratitis	*rosa*	1059	2.48
	cosyra	2828	6.63
	capitata	235	0.55
Dacus	*bivittatus*	34	0.08
	punctatifrons	5	0.01
	ciliatus	1126	2.64
Tririthrum	*Coffeae*	20	0.05
Total		**42686**	**100**

Table 2 : List of fruit flies recorded from four study sites by trapping.

Genus	Species	Mikese	Mkindo	Nyandira	SUA	Total	%
Bactrocera	*amplexa*	0	0	0	1	1	0.0003
	cucurbitae	3 528	83	148	5 875	9 634	2.4699
	invadens	27 072	36 812	30	307 860	37 1774	95.3147
	latifrons	0	0	0	2	2	0.0005
Ceratitis	*aliena*	0	0	31	0	31	0.0079
	capitata	95	0	1	148	244	0.0626
	cosyra	72	2	0	125	199	0.0510
	dumeti	0	0	0	1	1	0.0003
	fasciventris	0	0	1	11	12	0.0031
	flexuosa	1	0	0	0	1	0.0003
	rosa	200	3	1 487	3 290	4 980	1.2768
	rubivora	0	0	59	1	60	0.0154
Carpophthoromyia	*dimidiata*	1	0	0	0	1	0.0003
Dacus	*bivittatus*	185	116	41	486	828	0.2123
	chiwira	14	1	0	12	27	0.0069
	ciliatus	32	0	1	13	46	0.0118
	durbanensis	1	3	0	12	16	0.0041
	humeralis	228	61	9	508	806	0.2066
	hyalobasis	0	0	15	0	15	0.0038
	katonae	2	1	1	3	7	0.0018
	punctatifrons	415	119	52	754	1 340	0.3435
	vertebratus	8	0	0	11	19	0.0049
Perilampsis	*curta*	1	0	0	0	1	0.0003
Tririthrum	*coffeae*	0	0	4	0	4	0.0010
	Total	**31 855**	**37 201**	**1 880**	**319 113**	**39 0049**	
Total number of species		**16**	**10**	**14**	**18**	24	

Table 3 Diversity of fruit flies at four study sites.

	Mkindo	SUA	Nyandira
Jaccard index (%)			
	Mkindo	**SUA**	**Nyandira**
Mikese	62.5	61.90	42.86
Mkindo		50	41.2
SUA			52.4
Sorensen index (%)			
	Mkindo	**SUA**	**Nyandira**
Mikese	76.92	76.47	60
Mkindo		71.43	58.33
SUA			68.75
Morisita-Horn index (ratio)			
	Mkindo	**SUA**	**Nyandira**
Mikese	0.913	0.955	0.029
Mkindo		0.780	0.004
SUA			0.150

Abundance of the major fruit fly pests

Table 4 shows the abundance of fruit flies determined by trapping using two different food baits, 3C and PB and reported as mean weekly catches of fruit flies per trap. The baits were chosen because their non-specificity to species and sex. When using PB, the catches were significantly different, with highest mean weekly catch being that of *B. invadens* with the lowest catch being that of *C. cosyra*. The mean weekly catches of *B. invadens* by PB, were almost twice that of *C. rosa*, and almost twenty times that of *C. cosyra*. Similarly, when using 3C, the mean weekly catches of the three species were also significantly different. However, in this case, high catch was that of *C. rosa* followed by *B. invadens*. As pointed out earlier, 3C was used while still an experimental lure, and main inference can be made based on PB catches.

Table 4: Comparison of mean weekly catches of fruit flies by synthetic food baits

Species	Mean number of flies per trap per week	
	PB	3C
B. Invadens	7.1394a	0.3317b
C. Rosa	3.6442b	1.9038a
C. Cosyra	0.3702c	0.0192b
LSD (0.05)	1.166	0.407
CV	98.39	170.04
R - square	0.789	0.85

Means in a column followed by the same letter are not significantly different (ANOVA and LSD).

The efficacy of lures in attracting the respective fruit fly species was determined and the results are summarized in Table 5. Catches of *B. invadens* by different lures were significantly different, whereby highest catches were recorded in ME followed by the synthetic food baits. The catches by synthetic food baits were not statistically different. Similarly, the catches of *C. rosa* by the different lures were significantly different, with Trimedlure recording the highest catch compared to the to the synthetic food baits. However the catches by synthetic food baits were statistically different with PB recording higher catch than 3C. The experimental lure three 3C was also compared to PB in attractiveness to the three species (with their catches pooled together). In this case, the catches of PB were high and significantly different form those of 3C. In most cases the parapheromones recorded highest catches of respective species compared to the non-specific food baits.

Table 5: Efficacy of lures

Lure	Mean number of insects per trap per week		
	B. invadens	*C. rosa*	*B. invadens*, *C. rosa* and *C. cosyra*
ME	430.86a	N/A	N/A
PB	7.14b	3.6442b	0.37019a
3C	0.33b	1.9038c	0.01923b
CL (control)	0.02b	0.0000d	0.0000b
TM	N/A	6.7136a	N/A
LSD (0.05)	49.423	1.527	0.1028
CV	115.967	128.06	202.815
R - square	0.908	0.883	0.692

Means in a column followed by the same letter are not significantly different (ANOVA and LSD). N/A denotes not applicable

Host range and incidence of the major fruit fly species

In total, 1145 fruit samples, totalling about 980kg, were collected between October 2004 and October 2006. They were from 48 fruit species belonging to 20 different plant families (Table 1). Of these, 645 samples (56.3%) were positive for emerging fruit flies. Only positive samples for the main five fruit fly species (*B. invadens, C. rosa, C. cosyra, C. capitata* and *B. cucurbitae*) are presented in Table 6. Another five species (*Bactrocera latifrons* (Hendel), *Capparimyia melanaspis* (Bezzi), *Dacus bivittatus* (Bigot), *D. ciliatus* Loew, *Trirhithrum coffeae* Bezzi) emerged from a minimal number of samples but are not included in the analysis or discussion of this paper. *Bactrocera invadens* was recorded in the largest subset of samples (527 or 46% of all samples and 81.7% of all positive samples). Other main fruit fly species recorded were *Bactrocera cucurbitae*, *Ceratitis capitata*, *C. cosyra*, and *C. rosa* with positive samples varying between 23 and 87 of all collected fruit samples. Of all fruit types sampled frequently (more than 50 samples), tropical almond had the highest incidence (95.1%), which was largely by *B. invadens*. The positive samples belonged to 35 different plants. Again, *B. invadens* was found in the largest subset of collected fruit species (27) and seems to have the largest host range. Host range of the other main fruit fly species ranged between 6 and 19. The host range of the major fruit fly species was diverse with respect to plant families except *B. cucurbitae* which was recorded mainly from Cucurbitaceae while *C. cosyra* showed a predominance for Annonaceae and Anacardiaceae species.

Incidence of the major fruit fly pests

Tables 7-9 present the incidence of three fruit fly species in selected fruit species that were sampled regularly during the two years. In most cases, the number of positive samples of *B. invadens* were highest than the number of negative samples except in soursop, avocado and mango. In this case, the highest difference was recorded in tropical almond, while the difference in sweet orange was minimal. For the fruits that recorded the more negative than positive samples, the highest difference was observed in soursop, while the difference in mango was minimal. Peach had less than five positive samples of *B. invadens* while feijoa was not attacked by this species.

For *C. cosyra*, the number of positive samples was less than those of negative samples for all the tested fruit species except in soursop. The highest difference between the number of positive and negative samples was recorded in mango followed by tropical almond, in both cases the number of negative samples exceeded the number of positive samples.

Table 6 : Host range and infestation rate of the major fruit fly species

Host	B. invadens (No. / kg)			C. rosa (No. / kg)			C. cosyra (No. / kg)			C. capitata (No. / kg)			B. cucurbitae (No./ kg)		
	Aver.	Min	Max.	Aver.	Min.	Max.	Aver.	Min.	Max.	Aver.	Min.	Max.	Aver.	Min.	Max.
Annona cherimola	29.60			67.40			17.70								
Annona muricata	34.30	1.40	453.80	21.90	3.40	125.30	79.00	1.00	474.50	14.18					
Annona reticulate							95.80						4.31		
Carica papaya													25.75	4.23	59.23
Citrullus lanatus	3.10	2.30	4.50												
Citrus limon	14.30	0.50	103.20												
Citrus grands	4.70														
Citrus reticulate	11.50	1.20	33.40	0.78											
Citrus sinensis	10.40	0.30	213.40	0.60		4.00	0.60	12.70	0.91						
Citrus paradis	23.00	1.70	43.00												
Coffea arabica				35.70											
Coffeea canephora	370.40			75.60	37.00	120.40									
Circuumis figarei	7.40														
Cutcumis satious	3.50	2.80	3.90										210.94	2.42	459.83
Cucurbila sp.	37.60												50.34	4.31	1038.46
Eriobotrya japonica	264.40	10.60	852.30	23.50	3.80	76.00									
Feijoa selloviana				65.20	4.00	153.60									
Ficus carica				17.60					1.63						
Flacortia indica	40.00	2.60	65.10	12.80					89.69	61.47	152.38				
Fortumella marganila	96.70	1.70	489.40	5.00								177.66	98.16	558.82	
Luffa acutangula															
Lycopersicon esculentum				43.50											
Malus domestica	24.70			35.50	3.58	91.80									
Mangifera indica	115.10	0.80	504.80	2.20	0.80	5.70	11.10	0.80	30.20			1.16	0.58	2.22	
Persea Americana	9.70	0.80	124.30	4.40	0.50	35.10	10.10	4.80	10.70						
Prunus persica	1.30	0.60	2.60	14.80	1.20	87.10									
Sidium guajava	121.60	1.90	591.10	11.60	1.10	53.90	4.40	2.10	6.10	8.47	1.38	29.59			
Psidum litorale	302.20	7.10	1063.70				45.10			46.15	14.60	91.95			
Pyrus commonis				33.70	2.90	62.90									
Sclerocarya birrea	112.20						32.42	9.71	78.05						
Salamun aetiopicum	41.90	11.50	70.30												
Pondias cytherea	51.70	1.50	358.50				9.40								
Syzigium cumini	28.70	4.00	110.70	7.90	3.40	18.60	5.60			4.50	1.79	6.76			
Terminalia catapapa	288.50	2.60	1274.00				14.50	1.10	78.70						
Theovetia peruviana	61.70	7.50	233.90				39.60			47.90	14.93	97.74			
Total	78.16			24.02			28.36			26.68					

This is in contrast to *B. invadens*, in which more samples of tropical almonds were positive, while more samples of soursop were negative. Jew plum, loquat, common guava, peach and feijoa were not attacked by *C. cosyra*. The highest difference was recorded in avocado, in which the number of negative samples greatly exceeded the number of positive samples. Less number of infested samples (compared to unifested samples) by *B. invadens* were also recorded in avocado. Tropical almond, common guava, loquat, sweet orange and mango had less than five positive samples infested by *C. rosa*, and the species was not recorded from jew plum. Where there were less than five positive samples, the fruit species was left out in the analyses. Because of this, the number of fruit species included for analysis with regard to a particular fruit fly species differs.

DISCUSSION

Ecological implications of the observed results

The status of an insect as a pest is determined by, among other things, the value of commodity attacked and its population numbers. Tephritid distribution and abundance are markedly structured by various biotic and abiotic factors which include temperature, humidity, host fruit and natural enemies, and these have direct effect on species themselves as well as an indirect effect by modulating interspecific competition (Duyck *et al*., 2004; Duyck *et al*., 2006).The widespread abundance of preferred hosts, the availability of major hosts throughout the year as well as the presence of a large number of fruits could result into large numbers of fruit fly populations. On the other hand, introduction of a polyphagous tephritid into an area already occupied by another tephritid may result into a decrease of numbers of the native tephritid due to interspecific competition (Duyck *et al*., 2004).

Influence of abiotic factors

Rainfall seems to have greatly influenced the populations of *B. invadens* and *C. rosa*. The general trend of the populations of these two species seems to be associated with the rainfall pattern. For example, high populations of *B. invadens* and *C. rosa* were recorded during the short and long rainy seasons. The former corresponds to the main mango season, and the latter is the main season of many fruit species including guava and citrus. The population of *C. cosyra* was very low with no obvious peaks throughout the study period. Populations of *Bactrocera* species have been reported to increase during the rainy season and decrease during drought (Amice and Sales, 1997, Leweniquila *et al*., 1997). Another abiotic factor that had an influence on observed population trends is humidity. A study by Duck *et al*. (2006) has shown that atmospheric humidity strongly influences the survival of the fly pupae whereas high relative humidity is optimal for *C. rosa*, *C. catoirii*, *C. capitata* and *B. zonata*. The survival of these species has been reported to decrease in dry conditions. According to Vayssières *et al*. (2005) increased population of *B. invadens* is directly related to increase in relative humidity at the beginning of the rainy season. Temperature also might have influenced distribution of the three major fruit fly species, for example high numbers of *B. invadens* were recorded in the low and medium altitude areas. These areas are generally warm throughout the year. Similarly *Bactrocera* spp. are considered lowland pests (Wong *et al*., 1985; Harris *et al*. 1986) and there is inverse relationship between the infestation rate of *B. invadens* and the elevation at which fruits are found (Ekesi *et al*., 2006).).

Influence of host availability

Availability of the hosts had a marked effect on populations of B. *invadens*, *C. rosa* and *C. cosyra*. Among the three species, *B. invadens* attacked a wide range of fruits including cucurbits. Of the studied species, *C. rosa* had the widest host range of all *Ceratitis* species in the study area. The data show that *C. rosa* is a major pest of temperate fruits like peach and feijoa grown in the highlands, while *B. invadens* is the major pest of tropical fruits grown in low and medium altitude areas. The wide host range of *B. invadens* relates to its high numbers collected from infested fruits. The wide host range of *B. invadens* ensures its high population for longer periods of the year compared to the two *Ceratitis* species. Vayssières *et al.* (2005) reported that an increase in population of *B. invadens* appeared to be directly linked to the ripening of different mango cultivars. Host availability has been shown to have an impact on seasonal abundance of fruit flies in earlier studies (Tora Vueti *et al.*, 1997) although climatic variables such as temperature and rainfall can also play a role (Amice & Sales, 1997). Wide spread host availability and abundance are among the factors responsible for high population levels of *Bactrocera* species (Drew and Hooper, 1983; Vargas *et al.*, 1990; Leblanc and Allwood, 1997; Tora Vueti *et al.*, 1997) as well as other fruit fly species (Harris *et al.*, 1986; Segura *et al.*, 2006).

Effects of competition

The population of *B. invadens* in both rainy seasons was high compared to the population of *C. rosa* and *C. cosyra* in the low and medium altitude areas. The population of *C. cosyra* was lowest in all agro-ecological zones. As a native pest of mango, *C. cosyra* was expected to occur in large numbers at least during the short rainy season when ripe mango fruits were abundant. The low numbers of *C. cosyra* could either be due to the competition with *B. invadens* or due to less availability of its alternative hosts that are needed to increase its population. Interspecific competition could result into the elimination of one of the species or a stable equilibrium in which two species co-exist.

Invaders are generally assumed to be r-strategists, and this means that during the colonization phase invaders like *B. invadens* are at an advantage but they have to compete at a later stage in order to establish a large stable population. However, exotic invaders like *B. invadens* tend to be more competitive and they are able to quickly dominate the indigenous species. Where polyphagous tephritid species have been introduced into an area already occupied by other polyphagous tephritids, interspecific competition has resulted into a decrease in number and niche shift of pre-established species (Duyck *et al*., 2004). Most cases of tephritid invasions as reviewed by Duyck *et al*. (2004), species of genus *Bactrocera*, invaded in the presence of, and ultimately dominated numerically one or more species of the genus *Ceratitis* and the reverse was not observed. According to Duyck *et al.* (2004), invasive *B. dorsalis* has dominated the established *C. capitata* on at least two independent occasions while the reverse was not observed.

A theory by Tillman (1994) states that co-existence between species can be promoted by competition-colonisation trade-offs among different species, i.e., the bad competitors must be good colonizers because their maintenance depends on their being first to colonise empty spaces. It seems that *B. invadens* has been able to override the colonization – competition trade off. This invasive species has been able to display r- selected traits during the colonization phase, and then later it has successfully competed with and probably excluded the pre-established species from their original niches. In this case, the proposition that a poor competitor is a good colonizer (or vice versa) could not hold. Similarly, the larger body size of *B. invadens* (which is a K- selected trait) may be an advantage in exploitative as well as interference competition. The reason that

Vayssières *et al.* (2005) suggested *B. invadens* to be a K-strategist was mainly on the basis of its body size.

In Réunion islands, the invader *B. zonata,* was the best competitor and tended to occupy fruits and lay on them for more time than the *Ceratitis* species (Duyck *et al*., 2006). The large body size of *B. zonata* may be an advantage in exploitative as well as in interference competition. The fact that *B. invadens* has a larger body size, wing length ranging from 5.4 to 6.9mm (Drew *et al*., 2005) than *C. rosa* whose wing length ranges from 4.5 to 5.75mm) (De Meyer, 1998b) and *C. cosyra* whose wing length ranges from 3.4 to 5.2mm (De Meyer and Freidberg, 2006). This suggests that a relatively K-like strategy may underlie the apparent directionality of interactions between the genus *Bactrocera* and *Ceratitis*, although further confirmations are needed. *B. invadens* seem to out compete *Ceratitis* spp., especially *C. cosyra* from mango because mango has been known to be the major host of *C. cosyra*. A few samples collected in 2003 in Morogoro Region did exhibit significant differences in infestation rate of the two flies (Mwatawala *et al*., 2004). Additionally, climatic niche partitioning between *B. invadens* and *C. rosa* might have occurred but these assertions cannot be confirmed because of lack of data on rearing as well as abundance of these two species in this region prior to the introduction of *B. invadens*.

Effects of natural enemies

Other causes of the observed high populations of *B. invadens* against low populations of *C. cosyra* could be due to lack of natural enemies of the former in the new environment. Import fluxes and lack of natural enemies have traditionally been put forward as primary determinants of invasions, and less emphasis was given to the competitive ability of invaders themselves. In a few cases, natural enemies have been shown to play a key role in the population dynamics of some tephritid species. The impact of generalist predators would affect more or less equally the different tephritid species in a given biotope. Parasitoids, however, are more specific and could affect differentially the tephritid species coexisting in a biotope. However, the impact of natural enemies on tephritid population appears limited except in a few cases (Duyck *et al*., 2004). This study however, did not include the determination of effects of the natural enemies of fruit flies.

Practical significance of the results in formulating an IPM program for fruit flies

The first step in formulating an IPM program is establishing the pest complex in a cropping system, since IPM focuses on pest complexes and does not aim at solving a single pest problem. This study has been able to establish the biodiversity of fruit fly pests in orchards in different agro-ecological zones of Morogoro region. Based on the results of this study, control practices against fruit fly pest complexes in orchards should be aimed at *B. invadens* (key pest in orchards in low to medium altitudes) and *C. rosa* (key pest in high altitude areas). The timing of the implementation of control program is also important in IPM. Studies of seasonality of fruit flies have revealed that the populations of the fruit fly pests start to increase at the onset of the rainy seasons, and the populations are generally low during dry periods of the year. The infestation rates of fruit flies in many fruits as well as the incidences of fruit flies are high during the long rainy season when many fruits are available. This implies that control practices should be started when the trees have started to bear fruits.

Quarantine, surveillance and post-harvest treatment

Quarantine, surveillance and post-harvest treatment should be the first lines of defense against fruit flies. An invasion by solanum fruit fly *B. latifrons* was recorded for the first time in Africa from this study. This is a second invasion by *Bactrocera* species in Tanzania in a span of three years. The losses due to *B. invadens* are undoubtedly very high whereas the presence of *B. latifrons* could have an impact on the trade of non-traditional export crops like chillies.

Male annihilation and perimeter trapping

Perimeter trapping and male annihilation can be incorporated into IPM programs, especially in low and medium altitude areas because of the high responsiveness of males of the key pest, *B. invadens,* to methyl eugenol and protein bait. A proper trapping design has to be established for integration of this method in an IPM program. The use of male annihilation is one of components of IPM of Bactrocera *dorsalis* in India (Varghese *et al*., 2006). Methyl eugenol is the most powerful male lure for oriental fruit flies (Peňa *et al*., 1998) and it has been used successfully to control *B. dorsalis* in Oahu (Steiner and Lee, 1955) and to reduce infestation to sub-economic levels in Pakistan (Mohyuddin and Mahmood, 1993). Similarly, trimedlure is considered as one of the most important parapheromone for use with *C. capitata* (Peňa *et al*., 1998).

Farm hygiene and sanitation

Hygiene and sanitation can be an effective method of reducing fruit flies populations if re-enforced by strong legislative measures. These techniques will only be effective if carried out simultaneously and in extensive areas including the wild habitats e.g. in a village, ward or division. For example, in many parts of coastal Tanzania, tropical almond is popular as a shade tree grown together with mango and orange in the homesteads. Another example is marula plum which is found around many semi-commercial farms e.g. Mikese in Morogoro. These non-commercial fruits in proximity of commercial fruits increase the availability of suitable hosts and ensure survival of fruit flies during the times when commercial hosts are unavailable.

Fruits bagging

Bagging fruits can be useful in small orchards with a few trees, like home gardens. Some fruit trees observed during this study e.g. unimproved mango varieties are too tall (Figure 2) for a person to reach the fruits borne at the top. This technique, which aims at preventing the female's ovipositor from reaching and puncturing the skin of the fruit, is too laborious and could be risky when dealing with tall trees. Nevertheless, it can be a control measure for a few short trees in the home garden.

Chemical control

According to Aluja (1996) any designed IPM program for managing fruit flies should be viewed as a transition from a chemical dependent control to an ecological model pest management. Natural products like neem should be researched on their ability to reduce populations of fruit flies. In this regard in the study by Verghese *et al*. (2006) included a neem-based product, Azadirachtin, in their IPM program for *B. dorsalis*. The botanical insecticides like neem are safer to use and are compatible with organic farming. Many new tools and approaches recently developed may be very effective at controlling the fruit fly problem, but whether these tools are compatible with the entire crop production scheme in respect to cost effectiveness is rarely considered (Aluja, 1996).

Sterile Insect Technique (SIT)

The widespread availability of many non-commercial and wild fruits attacked by different fruit flies within Tanzania and across the borders, makes SIT difficult to implement, unless it is done under area-wide control programs. Obviously, all the programs aimed at the eradication of fruit flies in the mainland Tanzania will not be feasible because of the great chances of re-infestation from the neighboring regions or countries.

Other methods

Augmentive parasitoid release and habitat manipulation could be incorporated into an IPM program for fruit flies if natural enemies can be found. This study did not involve searching for natural enemies of the fruit flies. Searching for natural enemies of *B. invadens* is underway in Sri Lanka. However, as pointed out earlier, natural enemies have limited impact on tephritid populations except in a few cases. Techniques like stimulo-diversion deterrents and insect growth regulators are more specialized and further research is required before any generalization can be made about them.

CONCLUSION

The invasive *B. invadens* seems to be the dominant fruit fly species in terms of host range, incidence and abundance. This makes this species a key pest in the low to medium altitude areas and any management program should focus around the species. The species is sporadically present in the high altitude areas, where *C. rosa* is dominant. The remaining native *Ceratitis* species like *C. cosyra* and *C. capitata* where recorded ion low numbers. Competitive displacement of the two species is speculated but not confirmed due to lack of previous data on their abudance.

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