balt2/zen-env-ent/zen-env-ent/zen00411/zen7448d11z	xppws	S=1	6/8/11	8:15	Art: EN-11-017	1st disk, 2nd kmb

Bactrocera invadens (Diptera: Tephritidae), a New Invasive Fruit Fly Pest for the Afrotropical Region: Host Plant Range and Distribution in West and Central Africa

GEORG GOERGEN,[1,2] JEAN-FRANÇOIS VAYSSIÈRES,[1,3] DÉSIRÉ GNANVOSSOU,[1] AND MAURICE TINDO[4]

Environ. Entomol. 40(4): 000–000 (2011); DOI: 10.1603/EN11017

AQ:1–2

ABSTRACT In 2003, the invasive fruit fly *Bactrocera invadens* Drew, Tsuruta & White (Diptera: Tephritidae) (Drew et al. 2005), of possible Sri Lankan origin, has been detected in the East and about 1 yr later in West Africa. In regular surveys in Benin and Cameroon covering 4 yr, samples from 117 plant species across 43 families have been obtained. Incubation of field-collected fruits demonstrate that in West and Central Africa (WCA) *B. invadens* is highly polyphagous, infesting wild and cultivated fruits of at least 46 species from 23 plant families with guava (*Psidium* spp.), mango (*Mangifera* spp.), and citrus (spp.), and the wild hosts tropical almond (*Terminalia catappa* L.), African wild mango (*Irvingia gabonensis* (Aubry-Lecomte) Baill.), and sheanut (*Vitellaria paradoxa* C.F.Gaertn.) showing the highest infestation index. *B. invadens* occurs in 22 countries of WCA with new records for Angola, Central African Republic, the Congo, DR Congo, Equatorial Guinea, Gabon, Gambia, Guinea Bissau, Mali, Mauritania, Niger, and Sierra Leone. Overall, the pest has spread across a North-South distance of ≈5,000 km representing a contiguous area of >8.3 million km^2 within WCA. *B. invadens* has adapted to a wide range of ecological and climatic conditions extending from low land rainforest to dry savanna. Because of its highly destructive and invasive potential, *B. invadens* poses a serious threat to horticulture in Africa if left uncontrolled. Moreover, the presence of this quarantine pest causes considerable restrictions on international trade of affected crops.

KEY WORDS Tephritidae, invasive fruit fly, polyphagous, quarantine pest, *Bactrocera dorsalis* complex

Worldwide, introduced invasive species constitute a serious threat to economies, the environment, and human health (Pimentel et al. 2005). To date, nonnative insects, weeds and disease organisms, together with climate change, are considered to be the main drivers for biodiversity loss at global scale (Mooney and Hobbs 2000) with growing world trade and increased travel accelerating the rate of new introductions (Josling et al. 2003). The proportion of insect pests in reported introductions is substantial, but lower than the one of weeds and pathogenic organisms (Pimentel et al. 2005, Waage et al. 2009). Because of complex intertrophic and ecosystem-interactions, the ecological impact of invasive insects is far-reaching and generally complex to assess (Kenis et al. 2009).

Fruit flies (Diptera: Tephritidae) belong to the most important pests of horticultural and vegetable crops worldwide, and a number of species, in particular frugivorous Dacinae, are considered high-risk quarantine organisms (Clarke et al. 2005, Follett and Neven 2006). The recent introduction of a new invasive tephritid into tropical Africa comes in addition to four earlier fruit fly invasions in Africa (White 2006) and the 66 records of insects and mites of economic importance known to have invaded this continent over the last century (Waage et al. 2009).

In February 2003, samples of a hitherto unknown fruit fly species belonging to the genus *Bactrocera* Macquart were collected along the Kenyan coast (Lux et al. 2003). The same species, later described as *Bactrocera invadens* Drew, Tsuruta & White (Drew et al. 2005), was detected for the first time in West Africa during faunistic surveys in central Benin in June 2004 (Drew et al. 2005). The detection of *B. invadens* nearly simultaneously on the west and east coast of the African continent supports the hypothesis of at least two separate introductions. When this pest arrived in West Africa is not known, but studies on mango fruit flies in Mali during 2000–2001 by using methyl eugenol and torula yeast traps (Vayssières et al. 2007a) point out that *B. invadens* must have been absent from Mali at that time.

[1] International Institute of Tropical Agriculture, 08 BP 0932, Cotonou, Republic of Benin.
[2] Corresponding author, e-mail: g.goergen@cgiar.org.
[3] Centre International de Coopération en Recherche Agronomique pour le Développement, Persyst, UPR HortSys-TA B-103/PS4-Bd de la Lironde-34398-Montpellier Cx 5-France.
[4] International Institute of Tropical Agriculture, BP 2008 (Messa) Yaoundé, Cameroon.

Subsequent to its discovery in Africa, examination of collection material obtained from methyl eugenol baited traps in Sri Lanka (Tsuruta and White 2001), India (Sithanantham et al. 2006), and Bhutan (Drew et al. 2007) suggests that *B. invadens* has invaded Africa from its putative original area in southern Asia (Drew et al. 2005, Khamis et al. 2009). The rapid expansion of this quarantine pest in the Afrotropics is well documented for east and southern African countries like Kenya, Mozambique, Sudan, Tanzania, Uganda, and the Comoros Islands where *B. invadens* has become a serious threat to horticulture (Drew et al. 2005; Ekesi et al. 2006; Mwatawala et al. 2006a, 2009; Correia et al. 2008; Rwomushana et al. 2008). By contrast, information about its occurrence and ecological requirements in the 15 West and Central African (WCA) countries, where the new pest has already been recorded (Drew et al. 2005, Vayssières et al. 2007b, Rwomushana et al. 2008) is far less accurate. The explosive spread suggests the actual distribution of *B. invadens* to be far larger than presently known.

Similarly, the actual knowledge about the host plant range of *B. invadens* in WCA is still scanty. Except for ten species recorded in Benin (Vayssières et al. 2005) and for guava in Cameroon in 2005 (Ndzana Abanda et al. 2008), published data with detailed fruit infestation levels and pest incidence on the presently recorded 30 hosts in 13 families are only available from East Africa (Ekesi et al. 2006; Mwatawala et al. 2006a, 2009; Rwomushana et al. 2008). Complementary information for WCA is particularly important because host acceptance, which is the result of a complex and dynamic process involving many ecological factors, is known to change in new environments (Aluja and Mangan 2008).

The impact caused by the accidental introduction and spread of *B. invadens* on cultivated and native fruits in tropical Africa cannot be underestimated. Within *Bactrocera*, the most diverse fruit fly genus with 520 described and mostly nonpestiferous species (Norrbom 2004), *B. invadens* belongs to the vastly destructive *B. dorsalis* species complex with 75 species, some of which are highly polyphagous and pestiferous (Drew and Hancock 1994, Clarke et al. 2005). By accepting a large range of unrelated hosts, *B. invadens* is likely to occupy niches not fully exploited by native fruit fly species thereby increasing the risk on horticultural crops. In addition, as shown from other *Bactrocera* species introduced into Africa (Duyck et al. 2004, 2008; Vayssières et al. 2007b), mixed fruit infestations can result in interspecific competition with native fruit fly species leading to shifts to other fruits or niche partitioning. Competitive displacement by *B. invadens* has already been observed in the faunal composition of mango fruit flies in Benin and Tanzania (Vayssières et al. 2005, Ekesi et al. 2009, Mwatawala et al. 2009), but its impact on flies on other fruits including wild hosts remains largely unknown. In addition, the presence of this new fruit fly with high-risk quarantine status is causing considerable restrictions on international trade of affected crops. For example, in 2009 the U.S. government has published a Federal Import Quarantine Order for host material of *B. invadens* regulating fruit trade from invaded African countries (APHIS 2009). The European Commission is presently preparing a similar order.

Although control strategies against *B. invadens* are being developed in collaboration with partners across Africa, the availability of basic field data concerning its natural host range and the ecological requirements in WCA are a crucial complement to information from East Africa. The current study therefore has the following two objectives to determine: 1) the host plant range of *B. invadens* in Benin (West Africa) and Cameroon (Central Africa), and 2) the spread and hence the colonizing potential of *B. invadens* using trapping data obtained from various geographic and ecological regions of WCA, to formulate better strategies to contain the global impact of such invasions.

Materials and Methods

Host Plant Range. *Study sites.* The host plant range of *B. invadens* was determined through regular monthly fruit collection surveys from December 2004 to March 2008 throughout all agro-ecological zones of Benin and mainly the southern and coastal areas of Cameroon. In addition to agroecological considerations, locations for collecting fruits were selected so as to ensure extensive coverage. In Benin (Table 1), T1 the following major sampling sites were regularly visited: 1) Pobé, Sakété, Ouidah, Glo-Djigbé, Niaouli, and the Lama forest, in the coastal zone with a mosaic of savanna and remains of humid forests in the southern third of the country; 2) Dassa-Zoumé, Akofodioulé, OKéméré, Tchatchou, Koro (near Parakou), Komiguea, Sirarou, Kakara, Ina, Djougou, in the moist savanna zone situated in central Benin; and 3) six sites from Tanguieta up to the extreme north at Malanville on the border to the Republic of Niger, in the dry savanna zone. In Cameroon, sampling activities were primarily conducted in the following areas: 1) the lowland coastal zone within 100 km of Douala; 2) the humid forest and moist savanna transition in central, southern, and eastern Cameroon; and 3) the northern-western and northern mid-altitude moist savannas (Table 1). In both countries, rainfall patterns are of the bimodal type in the southern regions with the first rainy cycle occurring between March and July and the second from September through mid-November. By contrast, a unimodal rainfall pattern is prevailing in the northern regions of the investigated countries with the main precipitation period from July to October. Generally, rainfall regimes decrease gradually northwards with annual mean rainfall for Benin ranging from 1200 to 1300 mm in coastal zones to 800–900 mm in dry savanna zones and for Cameroon from 2,000 to 3,000 mm in coastal zones to 1,500–2,000 mm in the rest of the sampling zones. Mean annual temperatures (in parenthesis: mean maxima and mean minima temperatures) in Benin vary from 26.6°C (27.8–31.1°C) in the south (Cotonou), 28°C (22.4–33.4°C) in the central region (Parakou), and 25.3°C (22.5–35.4°C) in the north (Kandi), whereas the values for Cameroon are

| balt2/zen-env-ent/zen-env-ent/zen00411/zen7448d11z | xppws | S=1 | 6/8/11 | 8:15 | Art: EN-11-017 | 1st disk, 2nd kmb |

Table 1. Major fruit sampling sites with their geographic coordinates

Country	Ecozone	Locality	Longitude	Latitude	Altitude (masl)
Benin	Coastal low land	Comé	06° 20′50″ N	01°53′52″ E	1
		Lama forest	06° 57′02″ N	02° 08′01″ E	60
		Niaouli	06° 43′59″ N	02° 08′00″ E	90
		Glo-Djigbé	06° 56′63″ N	02° 24′64″ E	30
		Ouidah (Ahozon)	06° 22′37″ N	02° 08′56″ E	15
		Sakété	06° 81′57″ N	02° 61′06″ E	50
		Pobé	06° 58′20″ N	02° 41′06″ E	115
	Moist savanna	Dassa-Zoumé	07° 46′53″ N	02° 10′57″ E	150
		Akofodioulé	07° 75′63″ N	02° 37′44″ E	196
		Okéméré	07° 87′02″ N	02° 17′30″ E	193
		Tchatchou	09° 16′00″ N	02° 54′80″ E	365
		Koro (Parakou)	09° 37′01″ N	02° 67′08″ E	362
		Komiguea	09° 43′19″ N	02° 62′53″ E	370
		Sirarou	09° 53′34″ N	02° 63′60″ E	353
		Kakara	09° 66′20″ N	02° 67′23″ E	404
		Ina	09° 96′35″ N	02° 72′58″ E	387
		Pénéssoulou	09° 14′47″ N	01° 33′05″ E	400
		Djougou	09° 40′01″ N	01° 41′56″ E	440
	Dry savanna	Malanville	11° 52′00″ N	03° 23′00″ E	180
		Papatia	10° 04′62″ N	01° 48′40″ E	362
		Natitingou	10° 18′47″ N	01° 23′19″ E	420
		Bongou	10° 37′04″ N	01° 36′04″ E	450
		Toucountouna	10° 49′26″ N	01° 38′44″ E	396
		Tanguieta	10° 36′53″ N	01° 16′20″ E	245
Cameroon	Coastal lowland	Douala (Ngoddi)	03° 59′44″ N	09° 49′59″ E	10
		Ekona	04° 12′46″ N	09° 19′53″ E	415
	Midaltitude	Foumbot	05° 30′52″ N	10° 39′01″ E	1070
	Forest-savanna transition	Ndikimeniki	04° 50′05″ N	11° 03′52″ E	580
		Bafia	04° 32′44″ N	11° 15′30″ E	560
	Humid forest	Nkometou	04° 02′24″ N	11° 38′47″ E	785
		Yaoundé (Nkolbisson)	03° 51′50″ N	11° 27′46″ E	755
		Mbalmayo	03° 28′16″ N	11° 29′08″ E	680
		Mengomo	02° 34′36″ N	11° 02′01″ E	575

25.5°C (21.4–29.9°C) in the lowland coastal region (Douala) and 24.4°C (18.8–27.9°C) in the plateau region (Yaoundé).

Plant Material. At any given sampling period, available fruits of various cultivated and wild plant species were collected from native or imported shrubs and trees in urban areas, fields, orchards, open woodland, and natural wild vegetation. Samples were taken at various maturity levels–depending on plant species (e.g., young fruits for cucurbits and mature fruits for trees and shrubs) and harvested directly from the plant or gathered from the ground. The number and size of samples from different plant species was primarily determined by the availability of fruits. Efforts were made to ensure a minimum collection of 20 fruits per sample from the same crop and location. Fruits from individual samples were kept together in paper bags, labeled with their concomitant data and brought back for rearing in the laboratories at the IITA stations in Cotonou, Benin or Yaoundé, Cameroon, respectively.

In the laboratory, fruits of each sample were counted and weighed. Fruits larger than 8–10 cm in diameter were incubated in groups of 3–4 in 15-liter cylindrical plastic containers (38 cm in diameter by 21 cm in height), whereas smaller size fruits were held in 1.5-liter plastic pots (12 cm in diameter by 13 cm in height). Fruits were placed on wire grids in bowl shape that were attached to the rim of the large containers or placed 5 cm above the bottom of the small containers. The bottom of each incubation unit was covered with a 1.5-cm layer of moist sand as pupating medium for fruit fly larvae. The incubating units were covered with fine-mesh gauze fixed with an elastic band. The samples were incubated for up to 4 wk until all fruit fly larvae had emerged from the fruits and pupated. The incubation units were maintained either in screened batten houses or well-aerated rooms under ambient climatic conditions i.e., at 28 ± 1°C and 70–90% RH at Cotonou and 25 ± 1°C and 70–80% RH at Yaoundé, respectively. AQ: 3

The sand layer in the incubation units was inspected at ≈3-d intervals to remove fruit fly pupae, which were transferred to petri dishes (9 cm in diameter by 1.5 cm in height) containing a wet cotton ball and a 1:3 mixture of hydrolyzed yeast and sugar to serve as food for emerging adult flies as in Rwomushana et al. (2008). Emerged adults were kept alive for ≈5 d until they reached full maturation and final coloration and then preserved in 70% ethyl alcohol. All fruit fly specimens were crosschecked, reference samples stage-mounted, and retained at the biosystematics unit at IITA Cotonou, Benin, where type material of *B. invadens* is deposited (Drew et al. 2005). Leaves, fruits, and if possible inflorescences from all collected plant species were photographed and hard-pressed dry voucher specimens conserved at IITA Cotonou, Benin. Samples from plants commonly encountered in the study area were determined using the keys by Akoègninou et al. (2006). For difficult identifications assistance was provided in Benin by Dr. P. O. Agbani, National Herbarium, Faculté des Sciences Techniques, Université d'Abomey-Calavi, Cotonou, Benin and in Cameroon by Dr. L. Zapfack, Cameroon National Herbarium of Cameroon, Yaoundé, Cameroon. All botanical names and authors follow the nomenclature and classification of the International Plant Names Index database (IPNI 2008).

Distribution Data. *Trapping surveys.* Information on the distribution of *B. invadens* from host plant records was complemented with adult fly trapping data obtained through three approaches. First, various surveys were successively carried out between December 2004 and November 2007 in Benin, Burkina Faso, Cameroon, Côte d'Ivoire, Ghana, Guinea, Mali, Niger, Senegal, and Togo, by using either fixed sites for continuous trapping–to determine the seasonal dynamics of *B. invadens*– or temporary sites for short duration trap exposure (at most 48 h) for determining the presence or absence of the fly. Second, trapping was carried out by several collaborators from various countries in WCA by using the same trapping methods as described below with trap exposures varying from 2 to 60 d. Third, additional information about the occurrence of *B. invadens* was obtained through numerous identification requests invoiced to the IITA biosystematics unit mostly by horticultural producers in WCA. Because of the different methodologies adopted, exposure time, season, and sampling size, records were only evaluated qualitatively and reported as presence of *B. invadens* in WCA or absence for the assessed areas. Positive records were made available to CABI (United Kingdom) to update related Distribution Maps of Plant Pests (www.cabi.org/dmpp).

Trapping was done by using locally made bucket traps similar to those widely put in operation in Hawaii for fruit fly trapping (R. M., personal communication). AQ: 4
Traps consisted of a 1.8-liter clear plastic container (13 cm diameter by 14 cm height) with four 3-cm holes bored in the upper third for fruit fly entry. The bottom was perforated by several 1-mm holes to drain rainwater entering the trap. Traps contained a dental cotton wick (3.8 cm by 1 cm; L × D) soaked with 2 ml of the parapheromone methyl eugenol (International Pheromone System, Ltd., United Kingdom) and suspended by a cotton thread from the trap lid. A DDVP rubber strip (Hercon Vaportape II Aberdeen Road Company, Emigsville, PA)–suspended adjacent to the cotton wick–was used as killing agent. The traps were placed in shaded areas and suspended typically from tree branches at 1.8 m above ground. The wire was coated in the middle by a 5-cm band of Tanglefoot (The Tanglefoot Company, Grand Rapids, MI) to prevent ants from raiding the traps. In fixed trapping locations, trapped flies and other insects were collected at 15-d intervals and preserved in 75% alcohol for later identification and counting. Two ml of methyl eugenol were added to the cotton wick at monthly intervals and DDVP strips and wicks were replaced at two-month intervals. Old traps were replaced with new traps at four-month intervals. GPS coordinates including elevation data were referenced for every site.

Data Mapping. For the interpretation of distribution data, vegetation maps covering WCA were derived from ArcGIS. Prevailing vegetation types were expressed in LGP zones (Length of Growing Period). The following categories were presently used to differentiate between these zones: desert, <30 d of rain; semiarid, 30–90 d; dry savanna, 90–150 d; moist savanna, 150–210 d; subhumid, 210–270 d; and humid forest, >270 d. Because rainfall is the principal climatic factor determining the vegetation type in the Afrotropics, boundaries of the vegetation zones are more or less congruent with precipitation isohyets. Within the area under consideration, the trapping sites ranged from sea level up to 1,600 masl. Yet, because of the qualitative character of the sampling procedure, elevation could not be analyzed and was thus disregarded as a distribution factor.

Results

Host Plant Range. Regular field surveys in Benin and Cameroon carried out from October 2004 to March 2008 led to the collection 61,134 fruits (3,779 kg) and 766 samples representing 117 plant species distributed in 43 families, in total (Tables 2 and 3). Of T2–3
these, 72 plant species belonging to 32 families obtained from 206 samples and 15,114 fruits (209 kg) showed no *B. invadens* infestation (Table 3). The remaining 560 samples and 46,020 fruits (3,571 kg) revealed that *B. invadens* is able to develop naturally in fruits of 46 plant species belonging to 23 plant families (Table 2). Overall, 49,628 individuals of *B. invadens* emerged out of 100,264 tephritid puparia that were obtained from fruit incubation in the laboratory. The other puparia were either dead or produced other fruit fly species, such as of the genera *Bactrocera, Ceratitis, Dacus, Perilampsis,* and *Trirhithrum.* No pupal parasitoids were recorded. Of the *B. invadens* host plants recorded in this study, 31 species (67.4%) are exotic to tropical Africa, with approximately equal proportions of commercially grown fruit and noncultivated host species. Of all positively tested host plants, 17 species (36.9%) were recovered both in Benin and Cameroon, whereas 26 species (56.5%) were recorded only from Benin and three species (6.5%) only from Cameroon. Among cultivated fruits with at least 10 samples, the pest infestation index (the number of reared adult of *B. invadens* over the pooled weight of all sampled fruits for any given host plant) was highest for guava, mango, and citrus fruits scoring 16.2–13.7 and 3.2 flies/kg, respectively. As for noncultivated hosts collected on >10 occasions, *B. invadens* showed a marked affinity for tropical almond, African wild mango, and sheanut with pest densities reaching 72.0, 60.4, and 10.1 flies/kg, respectively. With nine out of the first 10 plants ranking highest in pest infestation index, wild plants showed substantially higher reproductive potential for *B. invadens* than commercially grown fruits. The most susceptible families in terms of

Table 2. Host plant range of *B. invadens* and infestation indices from fruits collected in Benin and Cameroon during 2004–2008

Plant family and species	Common name	Origin	Country sampled[a]	No. of samples	No. of fruits	Sample wt (kg)	No. of Pupae	No. of adult *B. invadens*	*B. invadens*/kg fruits
Anacardiaceae									
Anacardium occidentale L.	Cashew nut	Exotic	BE	5	2,532	76.83	39	27	0.4
Mangifera indica L.	Mango	Exotic	BE, CA	73	8,087	1509.79	27,659	20.632	13.7
Sclerocarya birrea (A. Rich.) Hochst.	Marula plum	Indigenous	BE	8	1,877	20.23	2,952	356	17.6
Spondias cytherea Sonner.	Hog plum	Exotic	BE	3	67	7.90	1	1	0.1
Spondias mombin L.	Tropical plum	Exotic	BE	10	2,132	34.87	23	18	0.5
Annonaceae									
Annona muricata L.	Sour sop	Exotic	BE, CA	14	196	49.54	2942	17	0.3
Annona senegalensis Pers.	Wild custard apple	Indigenous	BE, CA	38	4,299	107.63	9,203	167	1.6
Apocynaceae									
Saba senegalensis (A. DC.) Pichon	Saba nut	Indigenous	CA	4	61	4.09	119	12	2.9
Capparaceae									
Maerua duchesnei (De Wild.) F. White	-	Indigenous	BE	1	42	0.35	16	2	5.7
Caesalpinioideae									
Cordyla pinnata (Lepr. ex A. Rich.) Milne-Redhead	Cayor pear tree	Indigenous	BE	6	203	9.91	1,427	41	4,1
Caricaceae									
Carica papaya L.	Papaya	Exotic	BE, CA	23	95	65.78	198	9	0.1
Clusiaceae									
Garcinia mannii Oliver	Chewing stick	Indigenous	CA	1	145	1.23	207	108	88.2
Combretaceae									
Terminalia catappa L.	Tropical almond	Exotic	BE	17	2,878	82.54	6,637	5.942	72.0
Cucurbitaceae									
Citrullus colocynthis (L.) Schrad.	Egusi	Indigenous	BE	5	103	2.06	31	4	1.9
Citrullus lanatus (Thunb.) Matsum. & Nakai	Watermelon	Indigenous	BE, CA	14	224	20.52	2,081	23	1.1
Cucumis sativus L.	Cucumber	Exotic	BE, CA	16	143	23.78	1,489	6	0.3
Cucurbita maxima Duchesne ex Lam.	Pumpkin, squash	Exotic	BE, CA	11	61	8.37	913	9	1.1
Cucurbita pepo L.	Gourd, squash	Exotic	BE, CA	24	297	60.04	2951	16	0.3
Lagenaria siceraria (Molina) Standl.	Bottle gourd	Indigenous	BE	8	573	39.13	2	1	0.01
Momordica charantia L.	Bitter melon	Exotic	BE, CA	5	115	1.38	20	1	0.7
Ebenaceae									
Diospyros montana Rox.	Mountain persimmon	Exotic	BE	7	122	16.94	380	148	8.7
Irvingiaceae									
Irvingia gabonensis (Aubry-Lecomte) Baill.	African wild mango	Indigenous	BE, CA	19	2,613	253.89	18,078	15,323	60.4
Lauraceae									
Persea americana Mill.	Avocado	Exotic	BE, CA	15	116	19.14	49	11	0.6
Moraceae									
Ficus cf. *ottoniifolia* (Miq.)	-	Indigenous	BE	2	78	0.73	16	11	15.0
Musaceae									
Musa x *paradisiaca*	Plantain	Exotic	BE, CA	3	41	9.41	2	2	0.2
~~*Musa acuminata*, &lquote; Dwarf Cavendish;~~	Cavendish banana	Exotic	BE	10	145	18.27	13	9	0.5
Myrtaceae									
Eugenia uniflora L.	Pitanga cherry	Exotic	BE	1	142	0.30	19	18	59.4
Psidium guajava L.	Common guava	Exotic	BE, CA	24	4,739	226.69	4,749	3,679	16.2
Syzygium jambos (L.) Alston	Rose apple	Exotic	BE	2	58	1.06	205	169	169.4
Syzygium malaccense (L.) Merr. & L. M. Perry	Malay apple	Exotic	BE	8	95	3.12	48	16	5.1
Oxalidaceae									
Averrhoa carambola L.	Carambola, starfruit	Exotic	BE	21	488	27.13	54	13	0.5
Rhamnaceae									
Ziziphus mauritiana Lamk.	Jujube	Indigenous	BE	1	67	0.74	89	52	70.3
Rosaceae									
Eriobotrya japonica (Thunb.) Lindl.	Loquat	Exotic	CA	2	194	4.51	203	101	22.4
Rubiaceae									
Sarcocephalus latifolius (Smith) Bruce	Guinea peach	Indigenous	BE	17	4,167	270.02	13,352	38	0.1
Rutaceae									
Citrus limon (L.) Burm. f.	Lemon large variety	Exotic	BE	6	135	21.53	90	69	3.2
Citrus reticulata Blanco	Mandarin orange	Exotic	BE, CA	9	200	13.82	100	9	0.7
Citrus sinensis Osbeck	Sweet orange	Exotic	BE, CA	20	3,082	311.99	1,226	983	3.2
Citrus paradisi Macfad.	Grapefruit	Exotic	BE	14	146	37.45	215	114	3.0
Citrus reticulata Blanco × *Citrus paradisi* Macfad.	Tangelo cv Orlando	Exotic	BE	5	150	16.18	223	209	12,91

Continued on following page

balt2/zen-env-ent/zen-env-ent/zen00411/zen7448d11z | xppws | S=1 | 6/8/11 | 8:15 | Art: EN-11-017 | 1st disk, 2nd kmb

Table 2. Continued

Plant family and species	Common name	Origin	Country sampled[a]	No. of samples	No. of fruits	Sample wt (kg)	No. of Pupae	No. of adult *B. invadens*	*B. invadens*/kg fruits
Citrus sinensis Osbeck × *Citrus reticulata* Blanco	Tangor cv Ortanique	Exotic	BE	3	90	12.59	25	20	1.58
Sapindaceae									
Blighia sapida K.D. Koenig	Ackee	Indigenous	BE	11	273	13.15	19	7	0.5
Sapotaceae									
Chrysophyllum albidum G. Don	African star-apple	Indigenous	BE	10	202	9.62	160	37	3.8
Manilkara zapota (L.) van Royen	Bully tree	Exotic	BE	12	425	14.13	88	31	2.4
Vitellaria paradoxa C.F.Gaertn.	Sheanut	Indigenous	BE	12	2,696	110.65	1,195	1,123	10.1
Solanaceae									
Capsicum frutescens L.	Chili	Exotic	BE, CA	14	751	7.33	229	8	1.1
Lycopersicon esculentum Miller	Tomato	Exotic	BE, CA	26	675	24.22	527	36	1.5

[a] BE = Benin; CA = Cameroon.

host plant diversity (number of species) were *Anacardiaceae, Rutaceae, Myrtaceae,* and surprisingly *Cucurbitaceae,* which were credited with three or more species records. However, this was not reflected by a particularly high suitability as exemplified by Cucurbitaceous plants, which belonged to the hosts producing the lowest fly densities per kg fruit. Among all recognized host plants, the highest number of *B. invadens* per kg fruit (159 flies/kg) was obtained from samples of rose apple (Syzygium jambos: Myrtaceae) collected in the coastal lowland of Benin.

Distribution. Data obtained from regular surveys, rearing, and incidental trapping showed that *B. invadens* occurred in 184 (96%) of the 192 monitored sites covering a wide range of agroecological conditions extending from Mauritania to Angola, a North-South distance of >5,000 km (Fig. 1). The presence of *B. invadens* has been confirmed for 22 WCA countries (see map). The farthest limits with verified presence of *B. invadens* were Kaedi, Mauritania, for the northeastern part of West Africa; Mutwanga, DR Congo as central delimitation; and Luanda, Angola for the southernmost trapping site within Central Africa. Within this range, *B. invadens* was recovered in male lure traps at all elevations from sea level to 1,600 masl, the highest trapping site being at Bangan, Cameroon. Overall, trapping data revealed that *B. invadens* has spread across most ecological and climatic zones of the Afrotropics with a contiguous distribution from the humid and subhumid forest to moist and dry savanna zones in all prospected countries, covering an estimated area of >8,3 million km^2 in WCA. Within this area, *B. invadens* occurred at least once in most surveyed localities (179 out of 186), all seven localities without *B. invadens* being at the northern limit of the fly's distribution (Fig. 1).

F1

Discussion

According to strict quarantine guidelines, one single infested fruit suffices for regulatory agencies to list a plant species as host fruit. This rigid approach, which strongly impacts the fruit and vegetable trade, led Aluja and Mangan (2008) to reappraise the criteria used for host status determination and propose new guidelines for future host plant reports stressing the need for increased accuracy when listing fruit fly associations. Thus, the circumstances of infestations, including collection location, geographical scope, number of emerging fruit fly pupae, frequency of infestation, etcetera, are proposed to be taken into account to ultimately determine whether a particular species is a natural host, a conditional or accidental host, or a nonhost. Our data comprising 117 plant species provide information about the broad ecological adaptations of *B. invadens* and lay the ground work for more focused monitoring to refine host suitability criteria.

The host range data of *B. invadens* as presently assessed show full congruence with the range of plant families known to be key hosts of the *Bactrocera dorsalis* species complex (including *B. carambolae, B. correcta, B. dorsalis, B. kandiensis, B. papayae, B. zonata*); i.e., *Anacardiaceae, Annonaceae, Clusiaceae, Lauraceae, Moraceae, Myrtaceae, Rutaceae, Sapotaceae,* and *Solanaceae* (Clarke et al. 2005). All these fruit species are, however, not exploited equally because eventual damage by fruit flies depends on prior host finding and host acceptance, which are themselves influenced by the physiological state of the fly and the availability and quality of the host (Seo et al. 1983, Aluja and Mangan 2008). These factors translate into a preference hierarchy that governs local host utilization patterns by polyphagous species such as *B. invadens.* Large variations in host acceptance and fruit infestation data are therefore expected both within and between host plant species (Aluja and Mangan 2008). The varying number of hosts for *B. invadens* and the wide spectrum of infestation indices observed from disparate localities in Kenya for the same host, especially among species of the family *Rutaceae* (Ekesi et al. 2006, Rwomushana et al. 2008) underpin this view.

The present work complements first host plant range surveys in East Africa (Ekesi et al. 2006; Mwatawala et al. 2006a, 2009; Rwomushana et al. 2008) and in Benin (Vayssières et al. 2005) and adds to records

Table 3. Incubated fruits with no observed emergence of *B. invadens* from samples collected in Benin and Cameroon during 2004–2008

Plant family/species	Common name	Origin	Country sampled[a]	No. of samples	No. of fruits	Sample wt (kg)
Anacardiaceae						
Sorindeia grandifolia Engl.	-	Indigenous	BE	3	462	0.28
Annonaceae						
Annona squamosa L.	Custard apple	Exotic	BE	1	18	1.21
Uvaria chamae P. Beauv.	–	Indigenous	BE	1	102	0.20
Apocynaceae						
Thevetia peruviana (Pers.) K. Schum.	Yellow oleander	Exotic	BE	1	52	0.96
Arecaceae						
Elaeis guineensis Jacq.	Oil palm	Indigenous	BE	1	1,800	10.47
Asclepiadaceae						
Calotropis procera Dryander	Sodom apple	Indigenous	BE	2	24	0.34
Capparaceae						
Ritchiea capparoides Britten	–	Indigenous	BE	2	28	0.23
Cecropiaceae						
Myrianthus arboreus Beauv.	–	Indigenous	CA	4	20	6.03
Chrysobalanaceae						
Chrysobalanus icaco L.	Coco plum	Exotic	BE	2	84	0.82
Maranthes polyandra (Benth.) Prance	–	Indigenous	BE	3	165	0.57
Neocarya macrophylla (Sabine) Prance	–	Indigenous	BE	4	223	1.93
Parinari curatellifolia Planch. Ex Benth.	–	Indigenous	BE	4	191	2.42
Cochlospermaceae						
Cochlospermum planchonii Hook. f.	–	Indigenous	BE	3	60	0.05
Convolvulaceae						
Ipomoea eriocarpa R. Br.	–	Indigenous	BE	1	10	0.01
Combretaceae						
Combretum nigricans Leprieur ex Guill. & Perr.	–	Indigenous	BE	2	50	0.06
Terminalia mantaly H. Perrier	–	Indigenous	BE	2	120	0.13
Cucurbitaceae						
Coccinia grandis (L.) Voigt	–	Indigenous	BE	3	240	0.03
Cucumeropsis sp.	–	Indigenous	CA	1	9	1.45
Cucumis melo L.	Honeydew melon	Indigenous	BE, CA	3	35	8.29
Cucumis metuliferus E. Mey.	Horned melon	Indigenous	BE	3	50	6.25
Cucumis terrestris L.	–	Uncertain	BE	1	70	0.35
Cucurbita moschata Duchesne	Musk pumpkin	Exotic	BE	1	26	0.75
Luffa cylindrica (L.) M. Roem.	Loofah	Indigenous	BE, CA	7	98	4.78
Momordica balsamina L.	Balsam apple	Indigenous	BE	1	10	0.13
Momordica foetida Schum.	–	Indigenous	BE	1	26	1.03
Zehneria scabra (L. f.) Sond	–	Indigenous	BE	3	871	0.35
Dichapetalaceae						
Dichapetalum madagascariense Poir.	–	Indigenous	BE	3	140	0.36
Euphorbiaceae						
Flueggea virosa (Roxb.ex Willd) Voigt	–	Indigenous	BE	4	1,690	0.10
Flacourtiaceae						
Flacourtia indica (Burm.f.) Merr.	–	Indigenous	BE	2	19	0.19
Lamiaceae						
Hoslundia opposita Vahl	–	Indigenous	BE	2	101	0.23
Leguminosae						
Detarium microcarpum Guill. & Perr.	Tallow tree	Indigenous	BE	9	821	13.20
Loganiaceae						
Strychnos spinosa Lam.	–	Indigenous	BE	9	72	9.16
Malvaceae						
Hibiscus acetosella Welw. ex Fic.	African rosemallow	Indigenous	BE	1	40	0.48
Moraceae						
Artocarpus heterophyllus Lam.	Jackfruit	Exotic	BE	1	5	24.86
Ficus asperifolia Miq.	–	Indigenous	BE	4	48	1.37
Ficus exasperata Hort. Kew.	–	Indigenous	BE	5	214	0.52
Ficus glumosa DeliIe	–	Indigenous	BE	1	10	0.01
Ficus ingens Miq.	–	Indigenous	BE	4	132	1.12
Ficus platyphylla Delile	–	Indigenous	BE	1	10	0.01
Ficus sur Forssk.	–	Indigenous	BE	1	40	0.29
Ficus sycomorus L.	–	Indigenous	BE	1	10	0.20
Myrtaceae						
Eugenia aqueum Alston	Bell fruit	Exotic	BE	1	20	0.29
Syzygium guineense (Willd.) D.C.	–	Indigenous	BE	1	65	0.08
Oleaceae						
Jasminum dichotomum Vahl	Gold Coast jasmine	Indigenous	BE	1	10	0.01
Olacaceae						
Ximenia americana L.	Monkey plum	Exotic	BE	3	132	1.98

Continued on following page

Table 3 Continued

Plant family/species	Common name	Origin	Country sampled[a]	No. of samples	No. of fruits	Sample wt (kg)
Passifloraceae						
Adenia lobata (Jacq.) Engl.	–	Indigenous	BE	2	16	0.15
Passiflora edulis Sims	Passion fruit	Exotic	BE	3	68	3.67
Passiflora foetida L.	–	Exotic	BE, CA	9	977	2.92
Polygalaceae						
Carpolobia lutea G. Don		Indigenous	BE	1	300	0.52
Coccoloba uvifera (L.) L.	Sea grape	Exotic	BE	1	200	0.95
Rhamnaceae						
Ziziphus abyssinica Hochst ex A. Rich	Catch thorn	Indigenous	BE	5	295	1.85
Rubiaceae						
Coffea canephora Pierre ex. A. Froehner	Coffee	Indigenous	BE	1	186	0.24
Gardenia erubescens Stapf & Hutchinson	–	Indigenous	BE	1	20	0.40
Rutaceae						
Citrus aurantifoliae (L.) Burm. f.	Lime	Exotic	BE	7	1,921	70.02
Solanaceae						
Capsicum annuum L.	Bell pepper	Exotic	BE, CA	9	143	4.65
Physalis angulata L.	Cutleaf ground cherry	Exotic	BE, CA	6	374	0.45
Physalis minima L.	Sunberry	Exotic	BE	5	277	0.02
Physalis pubescens L.	Downy ground cherry	Exotic	BE	2	233	0.28
Nicotiana tabacum L.	Tobacco	Exotic	BE	1	60	0.08
Solanum aethiopicum L.	Egg-plant	Indigenous	BE, CA	17	164	10.79
Solanum macrocarpon L.	Gboma	Indigenous	BE	2	40	1.20
Solanum scabrum Mill.	Huckleberry	Uncertain	CA	4	760	0.39
Solanum torvum Sw.	Turkey berry	Exotic	BE	2	60	0.10
Sterculiaceae						
Cola acuminata (P. Beauv.) Schott & EndI.	Cola nut	Indigenous	CA	1	44	2.84
Cola chlamydantha (K. Schum)	–	Indigenous	CA	1	23	0.38
Cola millenii K. Schum.	–	Indigenous	BE	1	20	0.32
Sterculia setigera Delile	–	Indigenous	BE	1	10	1.00
Ulmaceae						
Trema orientalis (L.) Blume	Gunpowder tree	Indigenous	BE	1	10	0.01
Verbenaceae						
Lantana ukambensis (Vatke) Verdc.	Tickberry	Exotic	BE	3	250	0.12
Vitex doniana Sweet	African oak	Indigenous	BE	4	230	1.35
Zingiberaceae						
Aframomum sceptrum K. Schum	Guinea grains	Indigenous	BE	1	10	1.01

[a] BE = Benin; CA = Cameroon.

casually obtained with the discovery of the species (Drew et al. 2005). Although fruit collections in the study area were extensive and revealed 46 host plants from 23 families, a comparison with the results from East Africa suggests that the actual host range may be even larger. Overall, *B. invadens* infests predominantly fruits exotic to tropical Africa (67.4%), a behavior probably reflecting an adaptation to host accessibility in its putative home range. Available data on the occurrence of *B. invadens* outside the African continent, however, are still scarce and limited to records from methyl eugenol trapping (Tsuruta and White 2001, Sithanantham et al. 2006, Drew et al. 2007).

In Tanzania, Mwatawala et al. (2006b, 2007, 2009) recorded 27 host plants across 12 families, among them 11 species not found as hosts elsewhere, i.e., *Thevetia peruviana* (Apocynaceae), *Cucumis figarei* (Cucurbitaceae), *Flacourtia indica* (Flacourtiaceae), *Syzygium cumini*, *Psidium littorale* (Myrtaceae), *Malus domestica*, *Prunus persica* (Rosaceae), *Coffea canephora* (Rubiaceae), *Citrus grandis*, *Fortunella japonica* (Rutaceae), and *Solanum aethiopicum* (Solanaceae). Similarly, Rwomushana et al. (2008) monitored the infestation of *B. invadens* on 15 fruit species across eight plant families in nine different localities within Kenya and added four yet unlisted host plants namely *Annona cherimola* and *A. squamosa* (Annonaceae), *Cordia* sp. cf *myxa* (Boraginaceae), and *Sorindeia madagascariensis* (Anacardiaceae). Results from our study and from published data show that throughout tropical Africa the following five plants are invariably recognized as host (see Table 2): sour sop, *Annona* (*muricata* L.), mandarin orange (*Citrus reticulata* Blanco), and sweet orange (*Citrus sinensis* Osbeck), mango, and guava. With the exception of custard apple (*Annona squamosa* L.) and egg-plant (*Solanum melongena* L.) collected in Benin on one and 17 occasions respectively (Table 3), all hosts found suitable in East Africa (Ekesi et al. 2006; Mwatawala et al. 2006b, 2009; Rwomushana et al. 2008) are also hosts of *B. invadens* in West or Central Africa. Our study reveals new host species not yet observed in East Africa namely tangor (*Citrus sinensis* Osbeck × *Citrus reticulata* Blanco), tangelo (*Citrus reticulata* Blanco × *Citrus paradisi* Macfad.), African wild mango, sheanut, African star apple (*Chrysophyllum albidum* G. Don), bully tree (*Manilkara zapota* (L.) van Royen), gourd (*Cucurbita pepo* L.), and bitter melon (*Momordica charantia* L.).

Overall, this extension of the host plant range clearly demonstrates the great ability of *B. invadens* to adapt to a large range of unrelated wild and cultivated hosts. To date, its host range therefore comprises 72

balt2/zen-env-ent/zen-env-ent/zen00411/zen7448d11z | xppws | S=1 | 6/8/11 | 8:15 | Art: EN-11-017 | 1st disk, 2nd kmb

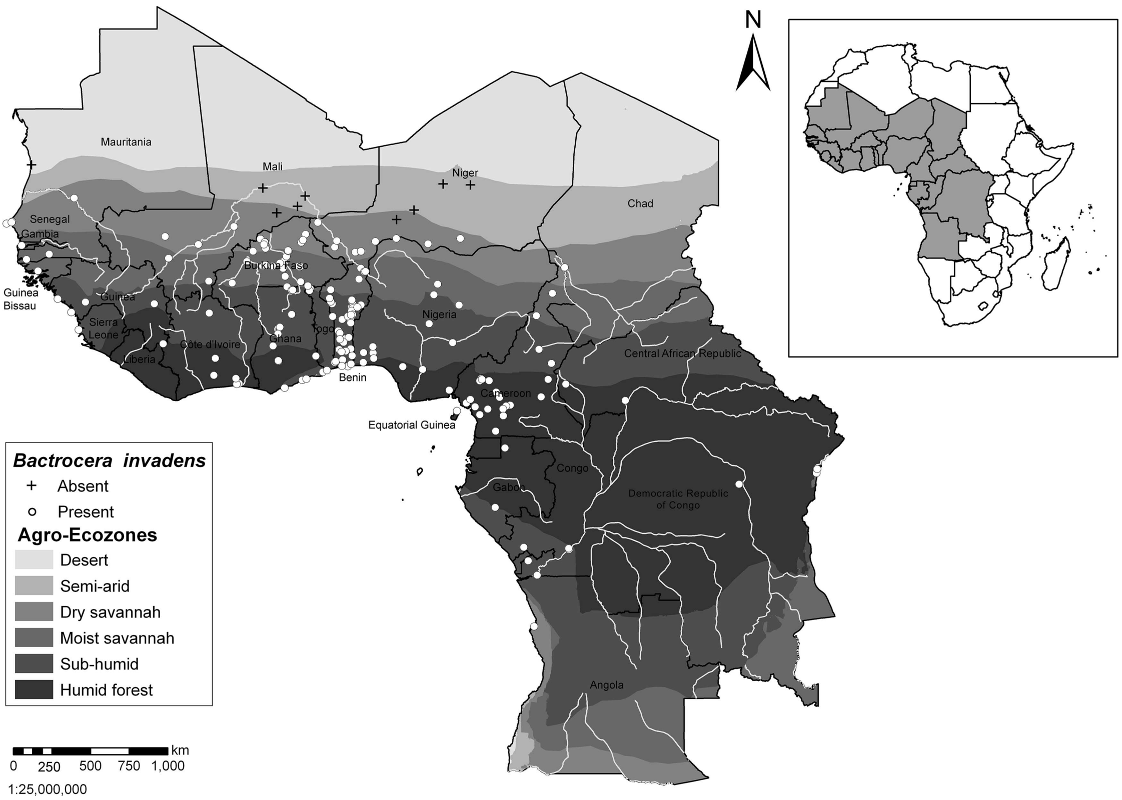

Fig. 1. Distribution of *B. invadens* in West and Central Africa from samples collected during 2004–2008.

plant species spread across 28 families (Vayssières et al. 2005; Ekesi et al. 2006; Mwatawala et al. 2006b, 2007; Ndiaye et al. 2008; Rwomushana et al. 2008). These records place *B. invadens* in the rank of the fourth most polyphagous fruit fly within the *Bactrocera dorsalis* species complex–after *B. papayae* (209 host species across 51 plant families), *B. dorsalis* (124 host species across 42 families), and *B. carambolae* (77 host species across 27 families) (Drew and Hancock 1994, Clarke et al. 2005). This is all the more astonishing considering that the species was described in 2005 (Drew et al. 2005) and has been known from Africa only since February 2002 (Lux et al. 2003). There is little doubt that records will increase as *B. invadens* spreads into new countries and encounters new potential host species. Among all these host species, *B. invadens* preferred tropical almond, African wild mango, sheanut, guava, mango, and tangelo in descending order (on the basis of the infestation index, i.e., adult flies per kg fruit). These fruits were collected in large quantities (Table 2) and therefore provide a robust basis for comparing their suitability for *B. invadens.* The fact that emergence rates from numerous noncultivated hosts were substantially higher than those generally observed on cultivated plants, has significant implications for prevalence and population dynamics of *B. invadens* particularly during 'off-seasons' of cultivated fruits. This is especially true for tropical almond, a fast growing native of Asia (Akoègninou et al. 2006) that produces fruits almost year-round in humid environments (Thomson and Evans 2006).

The observed host preference hierarchy also may reflect a specific ecological context. For example, infestations of hosts such as Carambola and several cucurbit species (Table 2) were only observed under temporary scarce primary host availability in central Benin, but not in the more humid southern regions, where *B. invadens* never emerged from hundreds of tested fruits of these same species. The relatively large number of indigenous and exotic fruits species attacked by *B. invadens* within the family *Cucurbitaceae* is equally surprising. In tropical Africa, cucurbit fruits are generally hosts of various *Dacus* species among the native dacine tephritids and also of *B. cucurbitae* (White and Elson-Harris 1992, Vayssières et al. 2007b). Among the 16 cucurbit plant species or varieties that were sampled in the current study (in 107 collections amounting to 2,951 fruits and 178.7 kg), seven species in total were found infested by *B. invadens* namely bottle gourd (*Lagenaria siceraria* (Molina) Standl.), bitter melon, cucumber (*Cucumis sativus* L.), Egusi (*Citrullus colocynthis* (L.) Schrad.), gourd, pumpkin (*Cucurbita maxima* Duchesne ex Lam.), and watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai). For all these species *B. invadens* infestations were low (ranging from 0.01 to 1.9 flies per kg fruit), confirming the fact that the host status for members of the *Cucurbitaceae*, with the exception of *Cucumis* spp., is uncharacteristic of the *B. dorsalis* species complex (Clarke et al. 2005) to which *B. invadens* belongs.

Overall, *B. invadens* is cryptic among native *Bactrocera* species in its home range (Tsuruta and White 2001, Sithanantham et al. 2006, Drew et al. 2007). The same species is, however, a widespread pest in the 22 prospected countries in WCA. Adding to available data (Drew et al. 2005, Mwatawala et al. 2006b, Rwomushana et al. 2008) the present distribution of *B. invadens* seems to be contiguous from West to East Africa for latitudes below 15° N. Furthermore, data with positive response observed in 184 sites covering virtually the complete range of climatic and ecological conditions prevailing in WCA clearly show that *B. invadens* is adapted to most ecological and climatic zones of the Afrotropics ranging from lowland rainforest to moist and dry savanna zones. In West Africa, the observed ecological boundaries were found to fit the transition zone demarcating the dry savanna zone from semiarid conditions. These limits, where the plant growing season is short and occupation by *B. invadens* can be only temporary, constitute an ecological condition that has not been observed in earlier studies in East Africa (Ekesi et al. 2006, Mwatawala et al. 2006a, Rwomushana et al. 2008).

In addition to West, Central, and Eastern Africa, *B. invadens* poses a considerable threat to horticultural production in countries of southern Africa. Recent records of the new pest from Mozambique and Zambia and predictive ecological niche models (De Meyer et al. 2010) support the view that *B. invadens* will likely continue to spread into other countries of Southern Africa, especially Madagascar and the coastal areas in South Africa including Swaziland, but less likely into continental Namibia and Botswana. It is also likely that *B. invadens*, if left uncontrolled, will spread into other continents. The threat of continued invasions by *B. invadens* will likely translate into rigorous restrictions for African export markets, which will undoubtedly affect the emerging horticultural sector that is becoming increasingly prominent in numerous countries of tropical Africa.

In summary, *B. invadens* is revealed as an opportunistic, mutivoltine, and very mobile species. It exploits a broad-range of pulpy fruits, has no diapause, and can easily escape the need for synchronization with the fruiting phenology of a specific host. Our data demonstrate that cultivated and wild plants are infested in roughly equal proportions (Table 2), which calls for particular attention to the relative abundance of noncultivated hosts when control strategies against this new pest are to be developed for a particular fruit crop.

Acknowledgments

This work was supported financially by IITA core donors, special project funds provided to IITA on Biodiversity research by the Austrian Ministry of Foreign Affairs, on crop pest management by the International Fund for Agricultural Development (IFAD), the German Ministry for Economic Cooperation and Development (BMZ), the French Cooperation (SCAC), and the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD). We gratefully acknowledge R. Hanna (IITA) for the generous sharing of his field and fruit fly rearing data and P. Neuenschwander (IITA) together with two unnamed reviewers for their helpful suggestions to improve the manuscript. Similarly, we thank P. Agbani and E. Ewédjè, University of Abomey Calavi, and Benin and L. Zapfack, Cameroon National Herbarium of Cameroon, Yaoundé, Cameroon for assistance in the identification of numerous plant samples. In addition we are grateful to the following collaborators who provided valuable assistance in the collection of field data: A. Adandonon, I. Agnontcheme, A. Allowanou, D. Ayegnon, N. Famah, H. Houngue, I. Ouagoussounon, A. Sinzogan and P. Soglo (Benin), P. Menozzi and S. Ouedraogo (Burkina Faso), J.-P. Lyannaz (Cameroon), G. Bani (Republic of Congo), K. Tatahangy (DR Congo), F. Hala N'Klo (Côte d'Ivoire), K. Camara and L. Traoré (Guinea), M. Noussourou (Mali), V. Umeh (Nigeria), C. Farjeot (RCA), M. T. Gueye, and J.-Y. Rey (Senegal) and to our IITA colleague K. Sonder for his help in drafting the distribution map. Lastly, we thank Prof. R.A.I. Drew, Griffith University, Queensland, Australia for confirming the identity of the new *Bactrocera* species.

References Cited

Akoègninou, A., W. J. van der Burg, and L.J.G. van der Maesen. 2006. Flore analytique du Bénin. Wageningen Agricultural University papers 06.2. Leiden: Backhuys Publishers, The Netherlands.

Aluja, M., and R. L. Mangan. 2008. Fruit fly (Diptera: Tephritidae) host status determination: critical conceptual, methodological, and regulatory considerations. Annu. Rev. Entomol. 53: 473–502 + supplemental materials.

APHIS. 2009. Federal Import Quarantine Order for Host Materials of *Bactrocera invadens* (Diptera, Tephritidae), invasive fruit fly species. 1–4.

Clarke, A. R., K. F. Armstrong, A. E. Carmichael, J. R. Milne, S. Raghu, G. K. Roderick, and D. K. Yeates. 2005. Invasive phytophagous pests arising through a recent tropical evolutionary radiation: the *Bactrocera dorsalis* complex of fruit flies. Annu. Rev. Entomol. 50: 293–319.

Correia, A. R., J. M. Rego, and M. Olmi. 2008. A pest of significant economic importance detected for the first time in Mozambique: *Bactrocera invadens* Drew, Tsuruta & White (Diptera: Tephritidae: Dacinae). Boll. Zool. Agr. Bachic. Ser. II 40: 9–13.

De Meyer, M., M. P. Robertson, M. W. Mansell, S. Ekesi, K. Tsuruta, W. Mwaiko, J.-F. Vayssières, and A. T. Peterson. 2010. Ecological niche and potential geographic distribution of the invasive fruit fly *Bactrocera invadens* (Diptera, Tephritidae). Bull. Entomol. Res. 100: 35–48.

Drew, R.A.I., and D. L. Hancock. 1994. The *Bactrocera dorsalis* complex of fruit flies (Diptera: Tephritidae: Dacinae) in Asia. Bull. Entomol. Res. Suppl. 2: 1–68.

Drew, R.A.I., K. Tsuruta, and I. M. White. 2005. A new species of pest fruit fly (Diptera: Tephritidae: Dacinae) from Sri Lanka and Africa. Afr. Entomol. 13: 149–154.

Drew, R.A.I., M. C. Romig, and C. Dorji. 2007. Records of Dacine fruit flies and new species of *Dacus* (Diptera: Tephritidae) in Bhutan. Raffles Bull. Zool. 55: 1–21.

Duyck, P. F., P. David, and S. Quilici. 2004. A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). Ecol. Entomol. 29: 511–529.

Duyck, P. F., P. David, S. Pavoine, and S. Quilici. 2008. Can host-range allow niche differentiation of invasive polyphagous fruit flies (Diptera: Tephritidae) in La Reunion. Ecol. Entomol. 33: 439–452.

Ekesi, S., P. W. Nderitu, and I. Rwomushana. 2006. Field infestation, life history and demographic parameters of *Bactrocera invadens* Drew, Tsuruta & White, a new invasive fruit fly species in Africa. Bull. Entomol. Res. 96: 379–386.

Ekesi, S., M. K. Billah, P. W. Nderitu, S. A. Lux, and I. Rwomushana. 2009. Evidence for competitive displacement of the mango fruit fly, *Ceratitis cosyra* by the invasive fruit fly, *Bactrocera invadens* (Diptera: Tephritidae) on mango and mechanisms contributing to the displacement. J. Econ. Entomol. 102: 981–991.

Follett, P. A., and L. G. Neven. 2006. Current trends in quarantine entomology. Annu. Rev. Entomol. 51: 359–385.

[IPNI] International Plant Names Index. 2008. Published on the Internet (http://www.ipni.org).

Josling, T., D. Roberts, and D. Orden. 2003. Food Regulation and Trade. Towards a Safe and Open Global System. Institute for International Economics, Washington, DC.

Kenis, M., M.-A. Auger-Rozenberg, A. Roques, L. Timms, C. Péré, M.J.W. Cock, J. Settele, S. Augustin, and C. Lopez-Vaamonde. 2009. Ecological effects of invasive alien insects. Biol. Invasions 11: 21–45.

Khamis, F. M., M. De Meyer, N. Karam, S. Ekesi, A. Bonomi, L. M. Gomulski, F. Scolari, P. Gabrieli, P. Siciliano, D. Masiga, et al. 2009. Uncovering the tracks of a recent and rapid invasion: the case of the fruit fly pest *Bactrocera invadens* (Diptera: Tephritidae) in Africa. Mol. Ecol. 18: 4798–4810.

Lux, S. A., R. S. Copeland, I. M. White, A. Manrakhan, and M. K. Billah. 2003. A new invasive fruit fly species from the *Bactrocera dorsalis* (Hendel) group detected in East Africa. Insect Sci. Appl. 23: 355–361.

Mooney, H. A., and R. J. Hobbs. 2000. Invasive Species in a Changing World. Island Press, Washington, DC.

Mwatawala, M. W., M. De Meyer, R. H. Makundi, and A. P. Maerere. 2006a. Biodiversity of fruit flies (Diptera, Tephritidae) at orchards in different agro-ecological zones of the Morogoro region, Tanzania. Fruits 61: 321–332.

Mwatawala, M. W., M. De Meyer, R. H. Makundi, and A. P. Maerere. 2006b. Seasonality and host utilization of the invasive fruit fly *Bactrocera invadens* (Dipt., Tephritidae) in central Tanzania. J. Appl. Entomol. 130: 530–537.

Mwatawala, M. W., M. De Meyer, I. M. White, A. Maerere, and R. H. Makundi. 2007. Detection of the Solanum fruit fly, *Bactrocera latifrons* (Hendel) in Tanzania (Dipt., Tephritidae). J. Appl. Entomol. 131: 501–503.

Mwatawala, M. W., M. De Meyer, R. H. Makuni, and A. P. Maerere. 2009. An overview of *Bactrocera* (Diptera: Tephritidae) invasions and their speculated dominancy over native fruit fly species in Tanzania. J. Entomol. 6: 18–27.

Ndiaye, M., E. O. Dieng, and G. Delhove. 2008. Population dynamics and on-farm fruit fly integrated pest management in mango orchards in the natural area of Niayes in Senegal. Pest Manage. Hortic. Ecosyst. 14: 1–8.

Ndzana Abanda, F.-X., S. Quilici, J.-F. Vayssières, L. Kouodiekong, and N. Woin. 2008. Inventory of fruit fly species on guava in the area of Yaoundé, Cameroon. Fruits 63: 19–26.

Norrbom, A. L. 2004. Updates to Biosystematic Database of World Diptera for Tephritidae through 1999. Diptera Data Dissemination Disk (CD-ROM) 2. Systematic Entomology Laboratory, United States Department of Agriculture, Washington DC.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. 52: 273–288.

Rwomushana, I., S. Ekesi, I. Gordon, and C.K.P.O. Ogol. 2008. Host plants and host plant preference studies for *Bactrocera invadens* (Diptera: Tephritidae) in Kenya, a new invasive fruit fly species in Africa. Ann. Entomol. Soc. Am. 101: 331–340.

Seo, S. T., C. Tang, S. Sanidad, and T. Taneka. 1983. Hawaiian fruit flies (Diptera: Tephritidae): variation of index of infestation with benzyl isothiocyanate concentration and color of maturing papaya. J. Econ. Entomol. 76: 535–538.

Sithanantham, S., P. Selvaraj, and T. Boopathi. 2006. The fruit fly *Bactrocera invadens* (Tephritidae: Diptera) new to India. Pestology 30: 36–37.

Thomson, L.A.J., and B. Evans. 2006. *Terminalia catappa* (tropical almond), version 2.2., pp. 1–20. *In* C. R. Elevitch (ed.), Species Profiles for Pacific Island Agroforestry. Permanent Agriculture Resources (PAR), Hōlualoa, Hawaii. (http://www.traditionaltree.org).

Tsuruta, K., and I. M. White. 2001. Eleven new species of the genus *Bactrocera* Macquart (Diptera: Tephritidae) from Sri Lanka. Entomol. Sci. 4: 69–87.

Vayssières, J.-F. 2004. Rapport de mission sur l'essai piégeage de Tephritidae du manguier au Sénégal, pp 1–21. Coleacp-PIP, Ceres-DPV, Dakar, Sénégal. AQ: 5

Vayssières, J.-F., G. Goergen, O. Lokossou, P. Dossa, and C. Akponon. 2005. A new *Bactrocera* species in Benin among mango fruit fly (Diptera: Tephritidae) species. Fruits 60: 371–377.

Vayssières, J.-F., F. Sanogo, and M. Noussourou. 2007a. Inventory of the fruit fly species (Diptera: Tephritidae) linked to the mango tree in Mali and tests of integrated control. Fruits 62: 329–341.

Vayssières, J.-F., J. Y. Rey, and L. Traoré. 2007b. Distribution and host plants of *Bactrocera cucurbitae* in West and Central Africa. Fruits 62: 391–396.

Waage, J. K., J. W. Woodhall, S. J. Bishop, J. J. Smith, D. R. Jones, and N. J. Spence. 2009. Patterns of plant pest introductions in Europe and Africa. Agric. Sys. 99: 1–5.

White, I. M. 2006. Taxonomy of the Dacina (Diptera: Tephritidae) of Africa and the Middle East. Afr. Entomol. Mem. 2: 1–156.

White, I. M., and M.-M. Elson-Harris. 1992. Fruit flies of economic significance: their identification and bionomics. C.A.B. International, London, and Australian Centre for International Agricultural Research, Canberra, Australia.

Received 20 January 2011; accepted 19 April 2011.