

Year-Round Production of Pest *Ceratitis* Species (Diptera: Tephritidae) in Fruit of the Invasive Species *Solanum mauritianum* in Kenya

ROBERT S. COPELAND^{1, 2} AND ROBERT A. WHARTON¹

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ABSTRACT To evaluate its importance as a possible reservoir host of tephritid pests (Diptera) of cultivated fruit, we sampled fruit of the exotic invasive *Solanum mauritianum* Scop. in various sites throughout its range in central and western Kenya. Tephritids were reared from *S. mauritianum* wherever the plant was found, except at the highest altitudes (2,200–2,500 m). *Ceratitis anonae* Graham and *Ceratitis fasciventris* (Bezzi) were reared from fruit sampled in western Kenya, whereas the latter and *Ceratitis rosa* Karsch were reared from fruit found in central Kenya. In Kakamega Forest in western Kenya, *C. anonae* was reared from *S. mauritianum* year-round, whereas *C. fasciventris* was present in only 52.6% of the collections at this locality. A host shift by *C. fasciventris* onto *S. mauritianum* during the drier months from November to January is suggested as an explanation for the observed change in relative rates of infestation of *S. mauritianum* by the two *Ceratitis* species in western Kenya. In Nairobi (central Kenya), *C. fasciventris* was reared from fruit collected year-round. *C. rosa* was not recovered until the last of 17 Nairobi collections. In Kenya, *S. mauritianum* maintains year-round populations of tephritid pests available to attack cultivated fruit. *S. mauritianum* should be considered a noxious invasive pest in Kenya, and efforts to eradicate or control it should be made wherever it occurs.

KEY WORDS Solanaceae, *Ceratitis anonae*, *Ceratitis fasciventris*, *Ceratitis rosa*

The tephritid genus *Ceratitis* MacLeay (Diptera) is endemic to sub-Saharan Africa and several Indian Ocean Islands. The genus presently contains 94 recognized species (De Meyer 1996, 1998, 2000; De Meyer and Copeland 2001, 2005; De Meyer and Freidberg 2006). Although the majority of these species are of no economic significance, the genus contains several important pests of cultivated fruit, including the widespread invasive species *Ceratitis capitata* (Wiedemann), the Mediterranean fruit fly. Within its home range in Kenya, the Mediterranean fruit fly is known to infest the fruit of at least 51 species of wild plants (Copeland et al. 2002). However, apart from *Coffea arabica* L., which it may attack heavily but in which it usually does no damage to the seed, the Mediterranean fruit fly is seldom found in commercial fruit in Kenya (Mukiama and Muraya 1994). In contrast, *Ceratitis rosa* Karsch, *Ceratitis fasciventris* (Bezzi) [originally described as a variety of *C. rosa* and recently elevated to specific status by De Meyer (2001)], *Ceratitis anonae* Graham, and *Ceratitis cosyra* (Walker) infest several important cultivated fruit (Mukiama and Muraya 1994, De Meyer et al. 2002). Orchards are routinely managed for *C. cosyra* in equatorial Africa and for *C. rosa* in South Africa, although

surprisingly little has been published on these species (Hancock 1989, Duyck and Quilici 2002).

In South Africa, *C. rosa* is a pest of plums, peaches, and many other cultivated fruit (Munro 1925, 1929; Annecke and Moran 1982). In coastal orchards, this species breeds throughout the year. In upland orchards, however, where freezing temperatures and winter frost are common, fruit production is seasonal and confined to the southern summer and early fall (Ripley and Hepburn 1930). High levels of infestation of early summer fruit suggest that *C. rosa* is successfully overwintering in the adult stage, and field observations by Ripley and Hepburn (1930) showed that the critical association was with stands of “bugweed” or “wild tobacco,” *Solanum mauritianum* Scop. (= *Solanum auriculatum* Aiton) (Fig. 1). This plant provides adult flies with winter food and leafy shelter, and ever-present berries as hosts of the first generation of flies in the spring (Ripley and Hepburn 1930). In addition to serving as a reservoir host of *C. rosa*, *S. mauritianum* is classified as a Category One alien invasive in South Africa (Wildy 2004), and there is an active biological control program directed against bugweed there (Olckers 1999, 2000). Although this has contributed greatly to our knowledge of some *S. mauritianum* herbivores (Olckers and Hulley 1989, 1991), little mention is made of *C. rosa* in these articles, undoubtedly because it would never be seriously considered as a weed biocontrol agent.

¹ Department of Entomology, Texas A&M University, College Station, TX 77843

² International Centre of Insect Physiology and Ecology, Box 30772, Nairobi, Kenya.



Fig. 1. Fruit of *S. mauritianum*. Barrel of pen is ≈ 1 cm in width.

Indigenous to South America (Roe 1972), *S. mauritianum* is a widespread invasive that has been introduced into Australia, Africa, and other parts of the world (Invasive Species Specialist Group 2004). It is an aggressive colonizer of disturbed areas with moderate-to-high rainfall, occurring in forest clearings and margins and along roadsides, sometimes forming impressive, nearly homogeneous stands. In Australia, it is the only known major host of the indigenous tephritid *Bactrocera cacuminatus* (Hering) and is rarely attacked by other tephritids (Fitt 1986, Hancock et al. 2000). *S. mauritianum* was probably introduced into South Africa around 1881 (Olckers and Hulley 1989). The earliest herbarium record for *S. mauritianum* in Kenya is from a specimen collected in Nairobi in 1931, accompanied by a note suggesting that it was possibly an escape from the local arboretum. Presently, *S. mauritianum* is substantially naturalized and well established in several Kenyan sites. In many areas, it makes up the dominant woody vegetation in partially shaded forest edge and ecotonal habitats. In contrast with its distribution in South Africa, *S. mauritianum* in Kenya is absent, to date, from coastal habitats, having been recorded only from central and western highland sites between $\approx 1,500$ and $2,500$ m above sea level. During an extensive survey of tephritids reared from wild fruit in Kenya (Copeland et al. 2002, 2004), fruit flies were consistently reared from *S. mauritianum*. The purpose of this study was to examine the importance of *S. mauritianum* as a reservoir host for pest tephritids and its potential to provide a year-round source of pest fruit fly populations in East Africa.

Materials and Methods

Details of the collection, transport, and laboratory handling of fruit samples are provided in Copeland et al. (2002). *S. mauritianum* was sampled intensively in Kakamega Forest, western Kenya (altitude 1,518–1,630 m) and in Nairobi in the central highlands (altitude 1,670–1,774 m); seven additional collections were made elsewhere (Table 1). In Kakamega Forest,

plants were sampled at the confluence of primary growth rain forest and open grassy glade, within disturbed primary and secondary forest, and along a roadway bordering secondary growth forest. In Nairobi, plants were sampled in suburban and semi-urban settings, making up roadway edges running in small valleys alongside gallery forest remnants, and in nonvalley settings where *S. mauritianum* may have been planted as an ornamental. In both areas, *S. mauritianum* fruit were sampled approximately monthly. Following Cowley et al. (1992), we present the quantitative results of our fruit rearings as an “infestation index,” expressed as adult tephritids per 1,000 fruit. A paired *t*-test was used to compare the number of adults of different tephritid species reared from the same fruit samples. Data were transformed ($\log_{10}(n + 1)$) before analysis to account for values of zero.

An indirect estimate of the number of flies infesting fruit at any one time in each of the two major sampling sites in western and central Kenya was calculated by multiplying estimated numbers of fruit by the mean annual infestation rate of each tephritid species. To estimate fruit productivity in Kakamega, *S. mauritianum* was sampled in June and July 2001 along a 4.55-km length of roadway bordering secondary growth forest. Every 10th tree above 2 m was examined along the right-hand side of the road (plants below 2 m had few or no fruit bunches, and there was no apparent difference in distribution of *S. mauritianum* plants between sides of the road). For each tree, the total number of fruit bunches was counted, and the mean \pm SD per plant was determined. Additionally, for each tree, the number of fruit in the largest bunch was counted. To save time and to avoid excessive destructive sampling, a crude mean \pm SD number of berries per bunch was determined by dividing the number of fruit in the largest bunch of each tree by 2. In Nairobi, trees were counted along a suburban roadway, ≈ 1.3 km of which bordered a disturbed gallery forest remnant where most of the *S. mauritianum* were concentrated. Mean numbers of bunches and berries per bunch from the Kakamega samples also were used to estimate tephritid productivity in Nairobi. The estimated number of total fruit at each site was then multiplied by the mean infestation rate at each site for *C. fasciventris* and *C. anonae*. For comparison of the two sites, results are expressed as tephritids per 500 trees and per 1.0-km stretch of roadside. Voucher specimens for all fly species have been deposited in the Royal Museum for Central Africa, Tervuren, Belgium.

Results

S. mauritianum was found at altitudes between 1,518 and 2,500 m above sea level (Table 1). Ripe berries were present throughout the year in both regions (for logistical reasons, fruit were not sampled in Kakamega Forest during June 2000, but ripe fruit were collected in late May, and tephritids were reared from these fruit). In western Kenya, two species, *C. anonae* and *C. fasciventris*, were reared and one or both were

Table 1. Tephritidae reared from fruit of *S. mauritanium*

Region	Location	Altitude (m)	Collection yr	Collection mo	No. fruit	<i>C. anonae</i> /1,000 fruit	<i>C. fasciventris</i> /1,000 fruit	<i>C. rosa</i> /1,000 fruit
Central highlands	Gatamayu Forest	2,315	2001	2	29	0.0	0.0	0.0
		2,315	2002	4	127	0.0	0.0	0.0
		2,315	2003	1	48	0.0	0.0	0.0
		2,284	2004	7	87	0.0	0.0	0.0
		2,500	2003	12	116	0.0	0.0	0.0
	Kereita Forest Nairobi	1,670	1999	11	252	0.0	15.9	0.0
		1,670	1999	12	172	0.0	145.3	0.0
		1,670	2000	1	260	0.0	130.8	0.0
		1,670	2000	2	200	0.0	115.0	0.0
		1,774	2000	3	432	0.0	64.8	0.0
		1,670	2000	3	226	0.0	137.2	0.0
		1,670	2000	4	341	0.0	20.5	0.0
		1,670	2000	5	147	0.0	54.4	0.0
		1,700	2000	6	188	0.0	58.5	0.0
		1,670	2000	7	283	0.0	88.3	0.0
		1,700	2000	7	255	0.0	0.0	0.0
		1,700	2000	7	300	0.0	0.0	0.0
		1,670	2000	8	456	0.0	85.5	0.0
		1,670	2000	9	277	0.0	28.9	0.0
		1,670	2000	10	364	0.0	153.8	0.0
	1,670	2002	8	562	0.0	1.8	0.0	
	1,670	2004	8	1167	0.0	104.5	5.1	
	Western highlands	Tigoni	2,220	2001	10	305	0.0	6.6
1,612			1999	5	48	0.0	0.0	0.0
Kakamega Forest		1,630	1999	8	270	55.6	3.7	0.0
		1,590	1999	8	332	6.0	6.0	0.0
		1,630	1999	11	216	37.0	101.9	0.0
		1,570	1999	12	190	47.4	68.4	0.0
		1,612	2000	1	258	58.1	73.6	0.0
		1,612	2000	1	274	94.9	142.3	0.0
		1,518	2000	2	188	21.3	10.6	0.0
		1,530	2000	3	221	171.9	9.0	0.0
		1,612	2000	4	258	23.3	0.0	0.0
		1,612	2000	5	467	10.7	0.0	0.0
		1,530	2000	7	95	73.7	0.0	0.0
		1,630	2000	8	183	0.0	5.5	0.0
		1,612	2000	8	109	27.5	0.0	0.0
		1,630	2000	8	147	81.6	0.0	0.0
		1,580	2000	9	252	123.0	19.8	0.0
		1,530	2000	9	438	9.1	0.0	0.0
		1,612	2000	10	324	6.2	0.0	0.0
		1,630	2001	10	164	12.2	0.0	0.0
Kericho	1,940	2000	1	328	0.0	3.0	0.0	

found in 18/20 fruit collections. The 19 *S. mauritanium* collections made in Kakamega Forest yielded a total of 4,434 fruit (5.97 kg). *C. anonae* was reared from significantly more samples (17) than was *C. fasciventris* (10) ($P = 0.029$; Fisher exact test, two-tailed). The two occurred together in 9/19 samples. *C. anonae* occurred in samples from every month, whereas *C. fasciventris* was absent from collections made in April, May, July, and October (Fig. 2). Over all collections, the mean number of *C. anonae* per 1,000 fruit (49.8) was approximately twice that of *C. fasciventris* (25.7) ($t = 3.54$, $df = 18$, $P < 0.01$).

In the central highlands, tephritids were reared from a significantly higher proportion of collections (16/18) made at or below 2,220 m than they were from collections (0/5) made above this altitude ($P < 0.001$; Fisher exact test). In Nairobi, *C. fasciventris* was reared from consecutive monthly collections made between November 1999 and October 2000 at the edge of remnant gallery forest (Table 1). It was absent from the only two collections made in suburban gardens

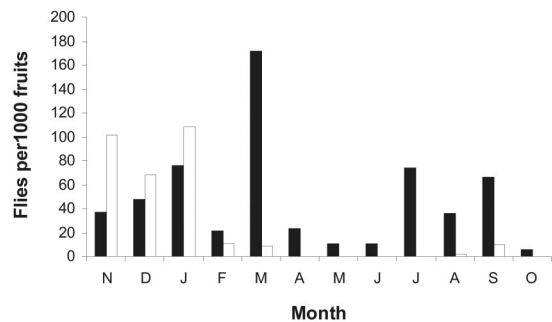


Fig. 2. Monthly infestation of *S. mauritanium* by *C. anonae* (dark columns) and *C. fasciventris* (white columns) in Kakamega Forest. Collections were made in consecutive months between November 1999 and October 2000. In months when more than one sample was collected (January, August, and September), the mean is presented. No collection was made in June, and the value for May (collection of 28 May 2000) is presented for both months.

during this period (Table 1). Including two collections made later (one collection in 2002 and one collection in 2004), 5,882 *S. mauritianum* fruit (9.82 kg) in total were sampled in Nairobi. *C. fasciventris* was reared from 15/17 collections. *C. anonae* was absent from all collections made in central Kenya, whereas *C. rosa* was reared from a single collection of fruit (Table 1). The annual mean number of *C. fasciventris* per 1,000 fruit and per kilogram was 73.3 and 45.9, respectively. Excluding collections made at altitudes above 2,220 m, the proportion of *S. mauritianum* plants that were infested by *C. fasciventris* was significantly higher in central Kenya (16/18), where it was the predominant tephritid, than in western Kenya (11/20) ($P = 0.033$; Fisher exact test, two-tailed).

Along 4.55 km of roadway, we counted 710 plants at least 2 m in height. Approximately 89% of these plants had fruit bunches. There were 12.2 ± 12.3 bunches per plant and 46.1 ± 27.5 berries per largest bunch. From these figures, we estimated that each plant produced an average of 281.2 fruit, yielding $\approx 140,605$ fruit per 500 plants. Using the annual mean number of adults per 1,000 fruit of *C. anonae* (45.2) and *C. fasciventris* (23.2) from *S. mauritianum* in Kakamega forest (Table 1), we estimated that, at any one point in time, 500 trees along this strip of forest road were infested by $\approx 6,355$ *C. anonae* and 3,262 *C. fasciventris* (9,617 total flies). A 1.0-km stretch of this road (one side only) would produce $\approx 3,001$ flies (1,983 *C. anonae* and 1,018 *C. fasciventris*). A similar census of a semiurban stand of *S. mauritianum* at the edge of a small gallery forest in Nairobi yielded a total of 528 plants over 1.3 km of road. Multiplying the annual mean number of *C. fasciventris* per 1,000 fruit in Nairobi (70.9) by the estimated number of fruit on the 528 trees yields 10,527 flies, or 9,969 flies per 500 trees (all *C. fasciventris*). Using similar calculations, the Nairobi site would yield $\approx 8,098$ flies per km.

Parasitoids also were reared from these samples but only infrequently. One sample from Nairobi, collected in November 1999, produced 18 *Tetrastichus giffardii* Silvestri (Eulophidae) from puparia of *C. fasciventris*. Three of the other samples, one sample from Kakamega and two samples from Nairobi, produced an undetermined species of *Trichopria* (Diptera: Trichopriidae), which is more likely to be a drosophilid parasitoid based on the small body size and small numbers per fruit sample (suggesting that they are not gregarious parasitoids of tephritids as with *T. giffardii*). Thus, we were unable to confirm parasitism of tephritids on *S. mauritianum* in Kakamega; in Nairobi, parasitism was <1%.

Discussion

Tephritids were reared from *S. mauritianum* at altitudes up to 2,220 m, but they were absent from samples collected at or above 2,284 m. Berries of *S. mauritianum* were present year-round in both upland sites, a situation similar to the continuous fruit production noted for this species in Mauritius and Reunion (Quilici et al. 2001). We consistently reared

adults of both *C. fasciventris* (in Nairobi and Kakamega Forest) and *C. anonae* (in Kakamega Forest) from year-long, monthly field collections of berries, suggesting that *S. mauritianum* in Kenya provides a permanent reservoir of adults of those species, available to attack cultivated fruit. Although *S. mauritianum* fruit are fed on by birds in central and western Kenya (R.S.C., unpublished data) and by monkeys in Kakamega Forest (Cords 1987), the impact of fruit predators on host availability is probably minimal due to the high fruit densities of *S. mauritianum*. It is not known whether vertebrate predators preferentially select (or avoid) tephritid-infested fruit, which would increase larval mortality. In Australia, where vertebrate predation on *S. mauritianum* berries is high, there is some evidence that predators feed preferentially on tephritid-infested berries (Drew 1987).

In western Kenya *C. fasciventris* and *C. anonae* are sympatric and often occur together in the same samples of wild fruit (Table 2; R.S.C., unpublished data). The patterns of infestation differed substantially between the *Ceratitidis* spp. in Kakamega Forest. During the entire period from February through October, *C. anonae* occurred in a higher percentage of monthly collections of *S. mauritianum*, and in greater numbers, than *C. fasciventris* (Fig. 2). From November through January, this pattern was reversed, and *C. fasciventris* outnumbered *C. anonae*. In Kakamega, infestation rates by *C. anonae* did not differ substantially on a seasonal basis (although variation from one sample to the next is high; Table 1), but *C. fasciventris* only attacked *S. mauritianum* sporadically from April to October. This, together with the high, year-round infestation of fruit in Nairobi by *C. fasciventris*, strongly suggests a seasonal shift to an alternate host in Kakamega. Host preferences (for certain wild fruit that do not occur in the more disturbed forests in Nairobi) may be responsible. It is unlikely that this shift is driven by competition, because availability of *S. mauritianum* fruit did not seem to be a limiting resource.

We did not rear *C. anonae* from *S. mauritianum* collected in central Kenya. *C. anonae* was also absent from all collections of indigenous ($n = 1074$) and exotic ($n = 23$) fruit collected in this region between 1999 and 2004 (R.S.C., unpublished data). The single previous record of a female of this species from Nairobi in 1938 was probably either a result of laboratory contamination, a recording error, or the chance result of a single immigration event.

During extensive sampling of wild fruit in Kakamega Forest from 1999 to 2003, we recorded several indigenous hosts of these two tephritid species (Table 2). During the drier months of November through January (Copeland et al. 1996), the wild fruit *Leptactina platyphylla* (Hiern) Wernh (Rubiaceae) and *Antiaris toxicaria* Lesch. (Moraceae) were available, and these species were heavily infested by *C. anonae* but not by *C. fasciventris* (Table 2). Although we make no claim to having sampled all fruiting plants during this period, we were unable to find wild hosts infested by *C. fasciventris* during those months.

Table 2. *C. anonae* and *C. fasciventris* reared from wild fruit in Kakamega Forest

Collection mo	Plant species	No. fruit	<i>C. anonae</i> /1,000 fruit	<i>C. fasciventris</i> /1,000 fruit
1	<i>Antiaris toxicaria</i> Lesch.	1,437	496.0	1.5
	<i>Prunus africana</i> (Hook. f) Kalkman	1,214	0.0	0.8
2	<i>Antiaris toxicaria</i>	599	123.2	0.0
	<i>Synsepalum brevipes</i> (Baker) T. D. Penn.	236	42.4	156.8
3	<i>Antiaris toxicaria</i>	127	63.0	0.0
4	<i>Morus mesozygia</i> Stapf.	156	6.4	0.0
	<i>Strombosia scheffleri</i> Engl.	249	93.4	108.4
5	<i>Englerophytum oblanceolatum</i> (S. Moore) T. D. Penn.	821	24.5	18.5
	<i>Pouteria altissima</i> (A. Chev.) Baehni	214	47.2	2.8
6	<i>Antiaris toxicaria</i>	34	147.1	0.0
	<i>Englerophytum oblanceolatum</i>	935	106.7	18.5
	<i>Pouteria altissima</i>	66	60.6	30.3
	<i>Rawsonia lucida</i> Harv. & Sond.	201	26.1	30.4
7	<i>Tiliacora funifera</i> (Miers.) Oliv.	1662	1.8	0.0
	<i>Manilkara butugi</i> Chiov.	191	0.0	5.2
8				
9				
10				
11	<i>Leptactina platyphylla</i> (Hiern) Wernham	228	333.3	0.0
12	<i>Leptactina platyphylla</i>	81	185.2	0.0

The sites on either side of the Rift Valley have apparently similar infestation rates by flies (regardless of species composition). Thus, the annual mean for *C. anonae* + *C. fasciventris* at Kakamega was equivalent to the rate for *C. fasciventris* alone at Nairobi. The infestation index that we used is also nearly identical (97.3 versus 96.6) for the November–January period for *C. fasciventris* at both the western and central Kenyan sites.

Presently, *S. mauritianum* is absent from lower elevation and coastal habitats in Kenya. Its distribution in South Africa and on the Indian Ocean islands of Mauritius and Reunion, where it also has been introduced, includes the coastal lowlands (Ripley and Hepburn 1930, Quilici et al. 2001) and suggests that it is also capable of establishing itself on the Kenyan coast, should the plant be introduced or transported there by migrating birds. In Reunion (Quilici et al. 2001), *S. mauritianum* is an important host of *C. rosa*, as it is in parts of South Africa (Ripley and Hepburn 1930, Olckers and Hulley 1991). In Kenya, *C. rosa* is well established in coastal habitats, where it is a pest of common guava, *Psidium guajava* L., and where *S. mauritianum* could become an important reservoir host. Of perhaps greater interest to farmers with fruit orchards is the apparently recent invasion of the central Kenyan highlands by *C. rosa*. *C. rosa* was absent from the 493 collections of various wild fruit made in the central highlands before 7 December 2001. Since that date, it has been reared from five indigenous and exotic species in 12/618 samples. It was reared from *S. mauritianum* for the first time from a collection made in August 2004, although collections with larger sample sizes might have revealed its presence earlier. Presumably, *S. mauritianum* will prove an important reservoir for *C. rosa* in the highlands of Kenya.

S. mauritianum is recognized as an important pest plant in South Africa. There, it and other alien invasives use far more water than the indigenous plants they have replaced (Wildy 2004). In highland areas, it

also contributes to the pest tephritid problem (Ripley and Hepburn 1930) as it does in Kenya. In Kenya, *S. mauritianum* rarely occurs in either completely shaded, undisturbed forest or areas open to continuous, direct sunlight. It is nearly always confined to discrete, manageable patches of riverine vegetation or forest margin (where plants are partially shaded) and is a good candidate for regional eradication. At the very least, clearing of all *S. mauritianum* in the vicinity of productive commercial fruit orchards should appreciably diminish tephritid infestation, given the large number of flies being produced from these trees and the almost complete absence of attack by parasitoids.

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