Chapter 5
Fruit Fly Species Composition, Distribution and Host Plants with Emphasis on Mango-Infesting Species

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Abstract Mango is the most widely cultivated fruit tree in tropical and sub-tropical Africa. However, the sustainability of this lucrative business is threatened by infestations of fruit flies (Diptera: Tephritidae) that annually inflict heavy economic losses on the industry. The nutritional quality of different fruit species can influence the survival and fecundity of adult fruit flies. This host-insect interaction determines the species composition, distribution and abundance of the major frugivorous tephritids. The economic impact of fruit fly pest species includes direct yield losses and the loss of export markets due to quarantine restrictions implemented to prevent the entry and establishment of exotic fruit fly species in importing countries. The economically important tephritid fruit flies attacking mango in Africa can be divided into two major categories based primarily on their origin, i.e., invasive (*Bactrocera dorsalis*, *Bactrocera zonata* and *Zeugodacus cucurbitae*) and indigenous species (*Ceratitis anonae*, *Ceratitis capitata*, *Ceratitis catoirii*, *Ceratitis cosyra*, *Ceratitis ditissima*, *Ceratitis fasciventris*, *Ceratitis quinaria, Ceratitis rosa* [recent taxonomic advances have separated *C. rosa* into two species; *C. rosa* and *C. quilicii*], *Ceratitis silvestrii, Dacus ciliatus* and some unverified records of *Ceratitis punctata* and *Dacus bivittatus*). These species are known to have a wide host range and distribution across Africa. Their distribution is also influenced by competitive interactions between native and indigenous species. The host plant status and distribution of fruit fly species is an evolving phenomenon largely due to new invasions, misidentification and identification of hitherto unknown species. For this reason this review provides the current situation but should be updated on a regular basis.

Keywords Fruit flies • Mango • Invasive species • Indigenous species • Host plant relationships • Competitive interactions

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S. Ekesi et al. (eds.), *Fruit Fly Research and Development in Africa - Towards a Sustainable Management Strategy to Improve Horticulture*,
DOI 10.1007/978-3-319-43226-7_5

1 Introduction

Mango (*Mangifera indica* L.) is the most widely cultivated fruit tree in the Sahel and one of the most important tree crops in tropical and sub-tropical Africa. West Africa alone produces 1.4 million tonnes of mangoes per year – the 7th largest producer in the world. Although widely grown on the continent, mango is not indigenous to Africa, but native to South-East Asia, from where it was introduced to all other tropical regions. According to the FAO-Intergovernmental Sub-Group on Tropical Fruits, mango is one of the four major high-value commodities and ranks amongst the most internationally traded tropical fruit. FAO estimated mango production in 2013 to be around 42.7 million tons, which accounts for nearly 35 % of the world's tropical fruit production (http://www.fao.org/). Mango world imports were forecast to increase by 1.4 % annually until 2014, 9 % of which would be obtained from Africa (accounting for 2.6 million tons). In Africa over 80 % of the produce comes from smallholders who produce for both local and export markets (Jayne et al. 2001). This provides the much-needed cash income to improve the households' food and nutritional security as well as their overall livelihoods. Mango is a highly prized exotic fruit on the European market and one of the most important fruit crops grown in tropical and sub-tropical regions (Nakasone and Paull 1998).

However, several constraints hinder the sector from realizing its full potential, key amongst them being fruit flies (Ekesi et al. 2016). The key insect pests that prevent increased and sustainable production are tephritid fruit flies (Diptera: Tephritidae) (Norrbom et al. 1999). Tephritid fruit flies have been recognized as one of the most economically important groups of insects that pose a serious threat to fruit production in Africa (White and Elson-Harris 1992; Ekesi and Billah 2006; De Meyer et al. 2012). Fruit fly infestation leads to heavy losses in yield and quality of fresh fruits. In Africa, between 30 and 40 % of the mangoes produced annually are lost to fruit flies (Ekesi et al. 2006; Goergen et al. 2011). Economically important tephritid fruit flies in Africa are distributed within three genera: *Bactrocera* Macquart, *Ceratitis* MacLeay and *Dacus* Fabricius (White and Elson-Harris 1992). Historically yield losses in mango were due to native fruit flies and estimated to range between 30 and 70 % depending on the locality, season and variety (Lux et al. 2003). However, in 2003, a new species, *Bactrocera dorsalis* (Hendel) invaded Africa from the Indian subcontinent (Lux et al. 2003; Mwatawala et al. 2004; Drew et al. 2005). Within only a few years the species had spread across Africa and was detected in more than 30 countries (West, Central, Eastern and Southern Africa) (Drew et al. 2005; Vayssières et al. 2005, 2014; Ekesi et al. 2006; Mwatawala et al. 2004; De Meyer et al. 2007; Correia et al. 2008; Rwomushana et al. 2008; Goergen et al. 2011; Hussain et al. 2015; Isabirye et al. 2015). Mango is considered a primary host of *B. dorsalis* (Drew et al. 2005; Ekesi and Billah 2006) and direct damage has been reported to range between 30 and 80 % depending on the cultivar, locality and season (Ekesi et al. 2006; Rwomushana et al. 2008; Vayssières et al. 2009). In addition to *B. dorsalis*, other *Bactrocera* species of Asian origin such as *Zeugodacus cucurbitate* (Coquillett), *Bactrocera zonata* Saunders and *Bactrocera latifrons*

(Hendel) have also been introduced in to mainland Africa, and the islands of the Indian Ocean, thereby aggravating the economic significance of tephritid fruit flies in African horticulture systems (De Meyer et al. 2007; Mwatawala et al. 2004, 2010; Shehata et al. 2008; Elnagar et al. 2010).

In addition to direct losses, indirect losses attributed to quarantine restriction on fruit fly-infested fruits have been enormous and limit export to large lucrative export markets in Europe, the Middle East, Japan and USA, where the insects are quarantine pests. For example, the importation of fruit species that are hosts of *B. dorsalis*, such as mango, from Kenya, Tanzania and Uganda is currently banned in the Seychelles, Mauritius and South Africa. Trade of horticultural produce between Africa and the USA has been severely restricted by a federal order from the USA banning importation of several cultivated fruit species from African countries where *B. dorsalis* has been reported (USDA-APHIS 2008; Ekesi et al. 2016). Interceptions and rejection of African mangoes in the European Union (EU) due to fruit flies have been on the increase since the arrival of *B. dorsalis* (Guichard 2009) with 21 rejections in 2008 increasing to 38 by August 2009. Interceptions have been reported from countries such as Burkina Faso, Côte d'Ivoire, Gambia, Ghana, Guinea, Mali, Senegal, Cameroon, Central Africa Republic, Kenya and Egypt. The direct and indirect damage caused by *B. dorsalis* and other tephritid pests continues to have wide reaching socio-economic implications for millions of rural and urban populations involved in the mango value chain across Africa. This has been further compounded by the introduction of uniform and strict quarantine regulations and maximum residue level (MRL) by the EU which now jeopardizes export of mangoes from Africa estimated at 35,000–40,000 tons annually and worth over US$ 42 million (Lux et al. 2003). This value has gradually been eroded as a result of import bans by several countries due to fruit flies (Ekesi 2010).

2 Relationships Between Host Fruits and Fruit Flies

The relationship between host fruits and fruit flies can strongly influence their species composition and distribution. Usually tephritid fruit flies attack the mature fruit of their host plants that are still on the tree, although in some cases immature fruit are know to be attacked as well. Female fruit flies drill into the fruit using their ovipositor and lay their eggs under the skin. This behaviour causes blemishes on the fruit; the presence of such blemishes means that these fruit do not meet the stringent requirements of the export market. The larvae develop inside the fruit, feed on the tissue and then exit from the fruit completing their developmental cycle in the soil. Fruit fly damage may cause immature ripening and abortion in a wide variety of fruiting species (Stephenson 1981; Sallabanks and Courtney 1992). In many cases mature fruit that are harvested contain developing larvae. Fruits have many important ecological attributes that affect the insects that live, feed, mate, oviposit, grow, rest, and hide on them; these attributes determine whether they are suitable hosts for particular fruit fly species (Fletcher 1987; Robinson and Hooper 1989). Larvae cannot change host plant and therefore depend on both the efficiency of female host-choice and the nutritional quality of the fruit for survival. Fruits have a strong influence on fruit flies at this stage in their life cycle when the quality of nutrition they provide can affect the longevity and fecundity of subsequent adults (Bateman 1972). It is therefore important for any fruit fly species to be able to locate suitable hosts to ensure successful development of their progeny. Most fruit fly species in Africa are highly polyphagous and it is not surprising that mango is one of the fruits most commonly attacked by these pests. Although mango appears to be a preferred host for several fruit fly species on the continent, several other host fruit also act as refugia, often becoming important sources of inoculum at the onset of the mango season.

3 Species Composition of Major Mango-Infesting Fruit Flies in Africa

Globally, at least 5000 tephritid species in 500 genera have been recorded to date (Norrbom et al. 1999). The global species database lists 4710 tephritid fruit fly species (www.globalspecies.org), of which 1400 species are known to develop in fruits. Out of these, about 250 species are pests, inflicting severe damage to fruits of economic importance (White and Elson-Harris 1992; Thompson 1998). The number of recognized tephritid species is constantly evolving as a result of new descriptions, recategorization and genetic analysis. White and Elson-Harris (1992) described 915 fruit fly species in Africa comprising 148 genera, out of which 299 species developed in either wild or cultivated fruit. They belong, mainly, to four genera: *Bactrocera* (562 species), *Ceratitis* (92), *Dacus* (300) and *Trirhithrum* Bezzi (49), although the latter is not economically important. In recent years, the number of species known on the continent has increased largely due to new invasions and identification of hitherto unknown species, although they largely still fall within these four genera.

Most of the fruit fly species in Africa are highly polyphagous with their host ranges overlapping to a varying extent. Mango is one of the most commonly infested fruits that is attacked by a complex of fruit fly species. Several authors have clearly documented that mango is an important host. Economically important tephritid fruit flies attacking mango in Africa can be divided into two categories: invasive species such as the oriental fruit fly, *Bactrocera dorsalis* (Hendel); the melon fruit fly, *Zeugodacus cucurbitae* (Coquillett); and the peach fruit fly, *Bactrocera zonata* (Saunders); and indigenous species such as *Ceratitis anonae* (Graham); the Mediterranean fruit fly (medfly,) *C. capitata* (Wiedemann); the Mascarenes fruit fly, *Ceratitis catoirii* (Guérin-Méneville); the mango fruit fly, *Ceratitis cosyra* (Walker); *Ceratitis ditissima* (Munro); *Ceratitis fasciventris* (Bezzi); the Natal fruit fly, *Ceratitis rosa* (Karsch); *Ceratitis silvestrii* (Bezzi); the five-spotted fruit fly, *Ceratitis quinaria* (Bezzi); the cacao fruit fly, *Ceratitis punctata* (Wiedemann);

Ceratitis flexuosa (Walker); *Dacus bivittatus* (Bigot) and the lesser pumpkin fly, *Dacus* (*Didacus*) *ciliatus* Loew (White and Elson-Harris 1992; Mwatawala et al. 2004, 2009a; Vayssières et al. 2005, 2007; Rwomushana et al. 2008; Isabirye et al. 2016; Goergen et al. 2011; Nboyine et al. 2012; De Meyer et al. 2015). Of these, *B. dorsalis*, wherever it occurs on the continent is ranked as the most important pest of mango followed by *C. cosyra*. Other species of fruit flies are ranked as moderate, and are localized in their distribution with varying degree of infestation on mango depending on the agroecology.

4 Relative Abundance and Seasonal Phenology of Mango-Infesting Fruit Flies in Africa

There have been several studies in Africa examining the relative abundance and seasonal phenology of mango-infesting fruit fly species (Copeland et al. 2006; Mwatawala et al. 2006, 2009b; Virgilio et al. 2011; Ndiaye et al. 2012; N'depo et al. 2013; Rubabura et al. 2015; Vayssières et al. 2014). In general, there is a strong correlation between the availability of fruiting host plants and fruit fly populations. The relative abundance and seasonal phenology of fruit flies is highly dependent on the availability of host plants, prevailing weather conditions and the presence or absence of natural enemies that limit pest population growth (Mohamed et al. 2010). There is a distinct pattern in fruit fly population dynamics with numbers reaching a peak at fruit maturity and ripening stage and declining with fruit harvest. Temperature, relative humidity and rainfall are the major climatic factors influencing fruit fly populations.

In West Africa, fruit flies start appearing in orchards during the dry season (between September and January) reaching a peak in February or March and then a second peak in April or sometimes in June before decreasing in July (Vayssières et al. 2014). Furthermore, as precipitation increases from 50 mm in April to a peak of approximately 240 mm in September, there is a consistent increase in relative humidity (45.5–59 %) and a decrease in air temperature (34.9–29.8 °C). These conditions are very conducive to fruit fly population growth. In Ghana, populations of *C. cosyra* predominate during the period between January and April (Badii et al. 2015). The dominance of this fruit fly species at that time coincides with the fruiting of both early- and late-maturing mango varieties. Populations of *C. anonae* begin to build up in the middle of May and reach a peak in June before declining in August. In contrast, *C. fasciventris* and *C. ditissima* appear from late May to early June. It is also noteworthy that mango flowers can be attractive to *Ceratitis* adults, as already recorded for other fly species (Aluja and Mangan 2008) which influences pest abundance during the flowering period.

In West Africa, populations of *B. dorsalis* fluctuate in a similar fashion to native fruit fly species. In the dry season between November and January their populations decline considerably but at the beginning of the rainy season (March-April), populations rapidly build up to reach a peak in April and then a second peak in May or June. In the Guinea Savanna zone of Ghana the period between May and June when *B. dorsalis* populations are peaking coincides with maturation and harvesting of late-maturing mango cultivars such as Keitt and Kent (Badii et al. 2015). Thereafter the populations drop steadily to their lowest levels between October and December. The same trends have been reported in several West African countries (Vayssières et al. 2005, 2011, 2014; Hala et al. 2006; Ndiaye et al 2012; Nboyine et al. 2013; N'depo et al. 2013).

In Eastern Africa, as exemplified in a study in Lake Victoria Crescent, Uganda, *B. dorsalis* was present year-round and all stages of mango fruit development were susceptible to attack (Mayamba et al. 2014). Each year infestations peaked between June and July and again between January and February. Trap catches were larger during the major fruiting season than the minor fruiting season. The highest numbers of *B. dorsalis* were collected when mango was at the physiologically mature or ripening stage (Mayamba et al. 2014).

In Kenya, studies on the seasonal and annual population dynamics of *B. dorsalis* also showed that peak populations coincided with mango fruiting and maturity in the field (Rwomushana 2008). The availability of mango fruits was the most important factor governing population increase in this species. More *B. dorsalis* were captured during the season and throughout the year than any other fruit fly species; abumdance of *B. dorsalis* always significantly exceeded the abundance of the native fruit fly, *C. cosyra*, from all trap collections (Ekesi et al. 2006).

In Tanzania, the general trend of the population dynamics of fruit flies showed that *B. dorsalis* peaks at the end of January and mid February while the lowest abundance was observed between September and October (Mwatawala et al. 2006). This trend was influenced by weather as well as the phenological stage of the fruit (Mwatawala et al. 2006). *Ceratitis rosa* populations peaked between January and March while *C. cosyra* populations had the inverse pattern with a peak in abundance in November, corresponding with the early-mango season, and a second peak between August and September (Mwatawala et al. 2006, 2009b).

In Sudan, which experiences a winter period, fruit fly populations build up gradually from May with two peaks during the humid months of August and November. Thereafter, the populations decline from December until March (Fadlelmula and Ali 2014). The highest populations of *B. dorsalis* occur between July and August, which is associated with late-maturing varieties of mango, and the lowest populations occur in March. The highest population of *C. cosyra* were recorded in August while populations of *C. capitata* increased with the onset of rainfall during autumn, peaking in November. In the Blue Nile State, the seasonal phenology of *B. dorsalis* on mango at Damazine and Rosaries orchards were almost the same. The number of adult males captured was very low during the dry period (March – May) when no rainfall was recorded and temperatures were high (40–43 °C), but increased steadily from the start of the rains in May. Population peaks were observed between June and July and again between December and January, depending on temperature, rainfall and availability of the mango fruits (Fadlelmula and Ali 2014).

In Northern Africa, e.g. Egypt, populations of *C. capitata* occur throughout the year with population peaks reported between September and November and then again between May and June which coincides with ripening of mango, apple and peaches (Hashem et al. 2001). The lowest abundance of *C. capitata* was recorded in winter (between April and July) probably due to low temperatures. In Upper Egypt, Hashem et al. (1986) reported high *C. capitata* populations between August and December that had gradually been building up between January and July. In navel orange orchards, three peaks of *B. zonata* were recorded each year; the highest peak corresponded with the ripening of fruits in November while the other peaks were in April and May. *Bactrocera zonata* populations were completely absent in December and January.

In South Africa, the relative abundance and seasonal phenology of the three main species, *C. capitata*, *C. cosyra* and *C. rosa* were similar, with populations of all three species increasing during late spring (September and October), reaching a peak in the hot summer months (January to March) and declining into the winter (June to August) (De Villiers et al. 2013). Both *C. capitata* and *C. rosa*, population fluctuations varied significantly depending on whether samples were taken in home gardens or commercial orchards (De Villiers et al. 2013). Population peaks occurred earlier in the year in the home gardens (between January and March) compared with commercial orchards where populations peaked between March and May. The peak population levels were also higher for both *C. capitata* and *C. rosa* in home gardens than commercial orchards. Fruit fly populations, in particular *C. rosa,* were sustained in home gardens throughout the year, although during the winter months (June -August) population levels of both species was low.

5 Distribution of Mango-Infesting Fruit Flies in Africa

Regional integration between many African countries allows for trade and free movement of fruits; coupled with the many porous borders between countries, the continent is highly vulnerable to introduction of alien fruit fly species that attack mango. Both invasive and native fruit fly species have been reported to occur all year round, largely due to their ability to infest a wide range of wild host plants and overcome the challenges of geographical barriers (De Meyer et al. 2007; Lux et al. 2003; De Villiers et al. 2013). Here we describe the key fruit fly species that have been reared from mango and their geographic distribution on the continent.

5.1 Bactrocera dorsalis

Bactrocera invadens Drew, Tsuruta & White or the 'African Invader Fly', was the name given to the tephritid fruit fly that was introduced to East Africa from Sri Lanka and subsequently invaded the whole of Sub-Saharan Africa. With recent integrative taxonomic studies *B. invadens* was found to exhibit the same biological characteristics as *B. dorsalis* which is a complex of species known to cause extensive damage to fruits globally (Drew 1994). Consequently, *B. invadens* was synonymized with *B. dorsalis* in 2015 (Schutze et al. 2015). The pest arguably ranks first amongst all fruit fly species on the African continent, both native and exotic, and is responsible for causing the most extensive economic losses to horticultural crops. Losses sometimes exceed 80 % resulting in widespread trade restrictions and significant negative economic and social impacts to farming communities. Since its first report in Kenya in 2003 (Lux et al. 2003), *B. dorsalis* has spread rapidly and is now present in more than 30 countries beyond its native range.

In Africa it has been recorded from Angola, Benin, Bostwana, Burkina Faso, Burundi, Cameroon, Central African Republic, Cape Verde, Chad, Comoros Archipelago, Côte d'Ivoire, Mayotte, Republic of the Congo, Democratic Republic of Congo, Ethiopia, Eritrea, Equatorial Guinea, Gabon, Gambia, Ghana, Guinea, Guinea Bissau, Kenya, Liberia, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Senegal, Sierra Leone, South Africa, Sudan, Swaziland,Tanzania, Togo, Uganda, Zimbabwe and Zambia (Drew et al. 2005; Vayssières et al. 2005; Mwatawala et al. 2006; Correia et al. 2008; Rwomushana et al. 2008; Goergen et al. 2011; Manrakhan et al. 2011; Virgilio et al. 2011; De Meyer et al. 2008, 2012; Ibrahim Ali et al. 2013; Aidoo et al. 2014; Fekadu and Zenebe 2015; Hussain et al. 2015; Isabirye et al. 2015; http://www.africamuseum.be/fruitfly/AfroAsia.htm). It was discovered in Sri Lanka soon after it was reported from Africa (Drew et al. 2005). For global distribution and predictions see De Meyer et al. (2010).

5.2 Bactrocera zonata

Bactrocera zonata is native to South and Southeast Asia. In Africa, it occurs in northern Africa (Egypt and Libya). Recently it has been reported from several regions in Sudan, suggesting a southward spread and potential risk of invasion for the Sub-Saharan region (De Meyer et al. 2007; Shehata et al. 2008; Elnagar et al. 2010; El-Samea and Fetoh 2006). It is also become established on the Indian Ocean islands of Mauritius and La Réunion (Quilici et al. 2005).

5.3 Ceratitis anonae

Ceratitis anonae is found in Cameroon, Central African Republic, Côte d'Ivoire, Democratic Republic of Congo (Brazzaville), Gabon, Ghana, Equatorial Guinea, Kenya, São Tomé and Principé, Guinea (Conakry), Mali, Nigeria, Togo, Tanzania and Uganda (White and Elson-Harris 1992; Copeland et al. 2006).

5.4 Ceratitis capitata

Ceratitis capitata is the most widely distributed indigenous fruit fly species. In Africa, it is recorded from Algeria, Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Congo, Côte d'Ivoire, Democratic Republic of Congo, Egypt, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Libya, Malawi, Morocco, Mozambique, Niger, Nigeria, Senegal, South Africa, Sudan, Tanzania, Togo, Tunisia, Uganda, São Tomé and Principé, Mauritius, Sierra Leone, Seychelles, South Africa, La Réunion, and Zimbabwe (White and Elson-Harris 1992; De Villiers et al. 2013). For global distribution and predictions see De Meyer et al. (2008).

5.5 Ceratitis catoirii

This species has been reported in Mauritius, La Réunion and Seychelles (Duyck et al. 2004).

5.6 Ceratitis cosyra

This species is widespread in Africa and has been reported from Benin, Botswana, Central African Republic, Côte d'Ivoire, Democratic Republic of Congo, Guinea, Ghana, Kenya, Madagascar, Malawi, Mali, Mozambique, Namibia, Nigeria, Sierra Leone, South Africa, Sudan, Tanzania, Togo, Uganda, Zambia, and Zimbabwe (Javaid 1986; White and Elson-Harris 1992; De Meyer 1998; Copeland et al. 2006; De Villiers et al. 2013).

5.7 Ceratitis ditissima

This species is known to be localized mainly in West Africa, particularly Benin, Cameroon, Congo, Côte d'Ivoire, Ghana, Mali, Mozambique Nigeria, Uganda, and Zimbabwe (Vayssières et al. 2007; Foba et al. 2012; Aidoo et al. 2014)

5.8 Ceratitis fasciventris

Ceratitis fasciventris occurs in Côte d'Ivoire, Democratic Republic of Congo, Ethiopia, Ghana, Equatorial Guinea, Kenya, Mali, Nigeria, São Tomé and Principé, Tanzania and Uganda (White and Elson-Harris 1992; Copeland et al. 2006).

5.9 Ceratitis flexuosa

This species occurs in Angola, Cameroon, Congo (D.R), Côte d'Ivoire, Ghana, Guinea, Kenya, Niger, Nigeria, Tanzania, Togo, Uganda (URL: http://ZipcodeZoo.com/index.php/Ceratitis_flexuosa)

5.10 Ceratitis punctata

This species is found in Cameroon, Congo, Democratic Republic of Congo, Côte d'Ivoire, Guinea, Kenya, Rwanda, Senegal, South Africa Tanzania, Uganda, Zambia, and Zimbabwe (De Meyer 2000).

5.11 Ceratitis quinaria

Countries with established infestations of *C. quinaria* include Benin, Botswana, Burkina Faso,, Côte d'Ivoire, Guinea, Ghana, Namibia, Malawi, Mali, Senegal, South Africa, Sudan, Togo, Yemen and Zimbabwe (Hancock et al. 2001; White and Elson-Harris 1992; De Meyer 1998; De Meyer et al. 2002; Vayssières et al. 2005).

5.12 Ceratitis rosa

Ceratitis rosa is not highly invasive showing only limited expansion of its distribution beyond its historical native range, which includes Angola, Ethiopia, Democratic Republic of Congo, Kenya, Malawi, Mali, Mauritius, Mozambique, Nigeria, Islands of Mauritius and La Réunion, Rwanda, Seychelles, Republic of South Africa (KwaZulu Natal), Swaziland, Tanzania, Uganda, Zambia and Zimbabwe (White and Elson-Harris 1992; Copeland et al. 2006; De Villiers et al. 2013). No reliable records from West Africa have been found (De Meyer et al. 2015), although some authors have reported the pest in Côte d'Ivoire (N'depo et al. 2013).

However, recent integrative taxonomy approaches using larval and adult morphology, wing morphometrics, cuticular hydrocarbons, pheromones, microsatellites, developmental physiology, geographical distribution, behavioural and chemoecological data of *Ceratitis rosa* have revealed that this species is made up of two entities: 'R1', 'lowland' or 'hot rosa', and 'R2', 'highland' or 'cold rosa' (De Meyer et al. 2015) with varying distribution patterns. The new data led to the conclusion that these two types should be considered as two different species. Taxonomically, the type material of *C. rosa* belongs to the R1 type (De Meyer et al. 2015), and the R2 type is considered as a new species, which hereinafter is referred to as *Ceratitis quilicii* (De Meyer et al. in press). We should stress here that many publications in the last decades refer only to *C. rosa* and were largely unable to differentiate between the two types as different species although they could have likely been referring to *C. rosa*, *C. quilicii*, or a mixure of the two. Therefore, *C. quilicii* is only used in this chapter where there is a clear distinction between R1 and R2 types of *C. rosa* from published works.

The two species can occur sympatrically in some regions (Malawi, South Africa and Tanzania), but also show a disjunct distribution that appears to be correlated with temperature (Tanga et al. 2015). Only in the Cape and central parts of South Africa is *C. quilicii* alone present, as well as in the adventive populations on the Indian Ocean islands (Virgilio et al. 2013). Therefore, it is likely that the high altitude types were *C. quilicii* and low altitude types probably a mix of the two species. The current distribution of the R2 type or *C. quilicii* includes Botswana, Kenya, La Réunion, Malawi, Mauritius South Africa, Tanzania and Zimbabwe. However, the distribution range of *C. rosa* and *C. quilicii* remains non-exhaustive given that samples from many localities in the above listed countries have not been assigned (De Meyer et al. 2015).

5.13 Ceratitis silvestrii

This species has been reported attacking mango in Nigeria, Senegal, Mali, Burkina Faso and Niger (Vayssières et al. 2005)

5.14 Dacus bivittatus

Dacus bivittatus is known from Angola, Benin, Cameron, Congo, Côte d'Ivoire, Democratic Republic of Congo, Ethiopia, Gabon, Ghana, Guinea, Kenya, Madagascar, Malawi, Mozambique, Nigeria, Senegal, Sierra Leone, South Africa, Tanzania, Togo, Uganda, Zambia, and Zimbabwe (White and Elson-Harris 1992)

5.15 Dacus ciliatus

Dacus ciliatus is widely distributed in Africa occurring in Angola, Benin, Botswana, Burkina Faso, Cameroon, Chad, Democratic Republic of Congo, Côte d'Ivoire, Egypt, Ethiopia, Gabon, Ghana, Guinea, Kenya, Lesotho, Madagascar, Malawi, Mozambique, Namibia, Niger, Nigeria, Senegal, Sierra Leone, Somalia, South Africa, Sudan, Tanzania, Togo, Uganda, Zambia and Zimbabwe (White and Elson-Harris 1992).

5.16 Zeugodacus cucurbitae

Zeugodacus cucurbitae is an invasive pest species in Africa and has been recorded from Benin, Burkina Faso, Burundi, Cameroon, Côte d'Ivoire, Democratic Republic of Congo, Ethiopia, Gambia, Ghana, Kenya, Malawi, Mali, Mozambique Niger, Nigeria, Sierra Leone, Senegal, Sudan, Tanzania, Togo, and Uganda (White and Elson-Harris 1992; Vayssières and Carel 1999; De Meyer et al. 2007, 2015).

6 Relative Abundance of Mango-Infesting Fruit Flies in Africa

Generally, the diversity and species richness of a number of fruit fly species have been shown to increase with altitude while it is the reverse for other species. In addition to climate change, ecological gradients in host plants, parasitoids and predators, as well as physical gradients in temperature, rainfall, and humidity that are encountered along an altitudinal transect can have an impact on the density, diversity and life history of insects including fruit flies; this demands phenotypic flexibility and genotypic adaptability in many species (Bale et al. 2002; Hodkinson 2005; Vayssières et al. 2008). Below we describe the relative density of the major mango infesting-fruit flies in Africa.

6.1 Bactrocera dorsalis

Wherever it is commonly found, *B. dorsalis* is the most abundant pest on mango and in mango orchards generally. In Uganda, 98.9 % of trap collections were of *B. dorsalis* (Isabirye et al. 2016) and 97 % in Tanzania (Mwatawala et al. 2009b). In Kenya, 15.3 flies/kg and 87.9 flies/kg were recovered from mango fruits in the lowland and the highland respectively (Rwomushana et al. 2008). In Benin, 53.03 % of adult fruit flies reared from mango were *B. dorsalis* (Vayssières et al. 2008) and 97.5 % of trap catches in Guinea Bissau were of *B. dorsalis* (Ousmane et al. 2014). In West and Central Africa (WCA), the pest infestation index for mango was 13.7 flies/kg (Goergen et al. 2011). Across Africa, *B. dorsalis* has a particuliar affinity for tropical almond and 72 flies/kg have been reported in WCA (Goergen et al. 2011), 264.5 flies/kg in Kenya (Rwomushana et al. 2008) and, in Tanzania, 95.1 % of fruit flies recovered from tropical almond were *B. dorsalis* (Mwatawala et al. 2009a).

Currently, *B. dorsalis* is continuing to spread, not only in latitude but also in altitude (Ekesi et al. 2006; Mwatawala et al. 2009a; Geurts et al. 2012). However, the continuous spread and colonization of higher altitudes seems to be limited by climatic conditions, host availability and suitability (Mwatawala et al. 2006; Geurts et al. 2012), and inter-specific competition with cold-tolerant species such as *C. rosa* (Mwatawala et al. 2006). *Bactrocera dorsalis* prefers areas at low altitudes with a warm and humid climate where its preferred cultivated host, mango, is present and where it achieves highest abundances (Rwomushana et al. 2008; De Meyer et al. 2010; Geurts et al. 2012; Vayssières et al. 2014).

6.2 Bactrocera zonata

Bactrocera zonata mainly attacks peach, guava and mango (White and Elson-Harris 1992; Allwood et al. 1999; Shehata et al. 2008). It is reported from some of the islands in the Indian Ocean (Mauritius and La Réunion) and is now widespread in northern Africa (Egypt and Libya). There is a potential risk of invasion for Sub-Saharan region (De Meyer et al. 2007). Ni et al. (2012) have predicted that, under current climatic conditions, *B. zonata* would be able to establish itself throughout much of the tropics and subtropics.

In Egypt *B. zonata* reaches significantly higher abundances than any of the other native fruit fly species (Elnagar et al. 2010). It appears to prefer warmer conditions and seems well adapted to hot climates. Since its introduction in Egypt, *B. zonata* has gradually become so widespread that it has surpassed *C. capitata* as the major fruit pest in Egypt. The abundance of *B. zonata* is significantly correlated with temperature and relative humidity and its population growth rate is higher than that of native species. The availability of suitable host plant species plays a role in the abundance of *B. zonata*. (El-Gendy and Nassar Atef 2014). In Mauritius, it mainly feeds on mango, guava, peach and jujube (Sookar et al. 2014). In Egypt, sour orange was the most susceptible host, followed by sweet orange and guava (Amro and Abdel-Galil 2008). At Fayoum governorate (Egypt), *B. zonata* infested 15.5 % of Navel orange, 10 % of grapefruit, 7 % of mandarin, 5.7 % of sour orange, 0.3 % of lemon and 0.6 % of Valencia orange (Saafan et al. 2005). Potato tubers collected from Giza governorate, Egypt, during 2004 were also found to be infested by *B. zonata* (El-Samea and Fetoh 2006).

6.3 Ceratitis anonae

Ceratitis anonae is widely distributed throughout western and central Africa and regularly occurs as far east as western Kenya (De Meyer 2001). Its absence from the central highlands of Kenya, an area containing several native and cultivated fruit species that it successfully exploits in western Kenya, suggests that *C. anonae* has become isolated from the common ancestor of all members of the FAR group sometime after the creation of the Gregory Rift. In Kenya, *C. anonae* was only successfully reared from fruit collected in the western highlands at altitudes between 1518 and 1630 m above sea level (a.s.l.), where it was sympatric with *C. fasciventris*

(Copeland et al. 2006). *Ceratitis anonae* was the principal pest of mango in West Africa prior to the arrival of *B. dorsalis* (Badii et al. 2015). In Benin, 0.21 % of fruit flies successfully reared from mango were *C. anonae* (Vayssières et al. 2007) and in Uganda *C. anonae* has been successfully reared from mango, albeit only in low numbers (Isabirye et al. 2016). In Uganda, 0.3 % of trap collections from mango orchards were of *C. anonae* (Isabirye et al. 2016) and as low as 0.07 % in the Democratic Republic of Congo (Virgilio et al. 2011).

6.4 Ceratitis capitata

Ceratitis capitata, is native pest to sub-Saharan Africa. Because of its its ability to tolerate cooler climates better than most other species of tropical fruit flies, and its wide range of hosts, it is often ranked first amongst the economically important fruit fly species in more cooler climates on the continent. *Ceratitis capitata* has a widespread distribution in South Africa (De Villiers et al. 2013) and De Meyer (2001) has described its geographic distribution in Africa extensively, including modelling its potential geographic niches on the continent (De Meyer et al. 2008). In Kenya, the host plant relationships and the geographic distribution of the pest have also been described in detail (Copeland et al. 2002).

6.5 Ceratitis catoirii

Ceratitis catoirii is reported to be an endemic species to Mauritius and La Réunion, found mostly in moist regions at low altitude (Duyck et al. 2006a, b). There are few studies on the distribution of this species although it is believed that its limited host range probably plays a role in determining its distribution and abundance. In La Réunion, *C. catoirii* is very rare and did not seem to have a specific niche, either in terms of climate or in terms of host fruit species. Indeed, there is evidence to suggest that *C. catoirii* is approaching extinction in La Réunion (Duyck et al. 2008). In recent years, there have also been no records of *C. catoirii* from Mauritius either from fruit or from area-wide trapping, suggesting that it might have become extinct there already (Sookar et al. 2008).

6.6 Ceratitis cosyra

Ceratitis cosyra is a native African species mainly found on mango. The economic importance of *C. cosyra* has been growing since the more widespread commercialization of mango and the introduction of exotic mango varieties. Late-maturing varieties of mango reportedly suffer the most due to *C. cosyra* infestation. *Ceratitis cosyra* is widespread in sub-Saharan Africa, occurring in at least 27 countries. It is highly adaptable being recorded from near sea level to 2100 m a.s.l. This makes *C. cosyra* the most widely distributed fruit fly species, particularly on mango (Ekesi et al. 2006). However, studies done in Tanzania by Mwatawala et al. (2006) have shown that *C. cosyra* was the most abundant species at 781 m and 1105 m a.s.l, and has also been reported from mango and marula at Nguruman, Kenya which is 700 m a.s.l (Rwomushana et al. 2008). The abundance of *C. cosyra* is correlated with high temperature, low relative humidity and the presence of mango (Geurts et al. 2012). Despite its wide geographical distribution compared to other *Ceratitis* species, *C. cosyra* has a restricted host range (Copeland et al. 2006). In South Africa and Swaziland, *C. cosyra* distribution generally follows a similar pattern to the distribution of marula, an important wild host (Magagula and Ntonifor 2014; De Villiers et al. 2013).

The abundance of *C. cosyra* is influenced by: the bimodal nature of rainfall in sub-tropical Africa; mixed cultivation of early- and late-maturing mango varieties that ensures mangoes are present in the field for a long time; the fact that mango fruits twice a year in some areas; and the proximity of wild hosts to mango orchards. In eastern Africa, *C. cosyra* is the most abundant fruit fly species on mango after *B. dorsalis*. Vayssières et al (2015) reported that *C. cosyra* was the most abundant species during the dry season in Benin and recovered > 50 pupae per kg of fruit from 15 different mango varieties. Displacement of *C. cosyra* by other mango-infesting species, especially *B. dorsalis* has been reported from Uganda (Isabirye et al. 2015), Tanzania (Mwatawala et al. 2009b) and Kenya (Ekesi et al. 2009). In Mali, *C. cosyra* represented 85.58 % of fruit flies recovered from mango (Vayssières et al. 2007) and 52.25 % in Benin (Vayssières et al. 2005). In Kenya, Copeland et al. (2006) recorded 1723 *C. cosyra* per 1000 fruits. Significant numbers of *C. cosyra* larvae have also been recovered from mango in Tanzania (Geurts et al. 2012).

6.7 Ceratitis fasciventris

In 2006, Copeland et al (2006) demonstrated that *C. fasciventris* was distributed widely throughout the Central Kenyan Highlands, at elevations of up to 2220 m a.s.l., but that it was absent from coastal areas. Populations of *C. fasciventris* on coffee, *Coffea arabica* Linnaeus, have also been reported from the Central Highlands of Kenya at Ruiru (1609 m a.s.l) and Rurima (1228 m a.s.l). *Ceratitis fasciventris* has been reared from fruit collected year-round and is known to be sympatric with *C. anonae*, both species often occuring together in the same sample of wild fruit (Copeland and Wharton 2006). In the Democratic Republic of Congo the largest numbers of fruit flies captured using lures were of *C. fasciventris* in the mid altitudinal areas of South Kivu (Rubabura et al. 2015).

6.8 Ceratitis quinaria

Ceratitis quinaria is widely distributed in West Africa and abundant in mango orchards (Vayssières et al. 2005; 2007; 2009; 2011). Trapping and rearing data indicate that *C. quinaria* is most abundant during the dry season, causing damage only to early-maturing cultivars of mango (Vayssières et al. 2005). There is a positive relationship between high temperature, relative humidity and rainfall with *C. quinaria* populations (Vayssières et al. 2005). In Mali 4.89 % of fruit flies reared from mango were *C. quinaria* (Vayssières et al. 2007) and 5.61 % in Benin (Vayssières et al. 2015).

6.9 Ceratitis rosa

Ceratitis rosa, which is also an indigenous African fruit fly has been reported in coast areas and the Central Highlands of Kenya (Copeland et al. 2006), in the Cape region of South Africa (De Villiers et al 2013) and on the islands of Mauritius and La Réunion (White et al. 2001). This species has also been reported as the dominant fruit fly species in temperate fruit species such as peach, apple and pear (Mwatawala et al. 2009b), which are only grown at high altitudes in Africa. High abundances of *C. rosa* occured during the wet months (February and March) in higher altitude areas in Tanzania (Mwatawala et al. 2009a). For example, at 1305 m there were seven fruit fly species with relatively similar abundances, whereas at 1650 m there were 11 species present but *C. rosa* was the most abundant. Several studies have also confirmed that *C. rosa* is a species that can withstand colder temperatures (Duyck et al. 2004, 2006a, b; Grout and Stoltz 2007; De Meyer et al. 2008, 2010; Duyck and Quilici 2002).

Interestingly, *C. rosa* is considered as potentially invasive as *C. capitata* and feared to be a global threat due to its cold tolerance and its presence at higher altitudes than *C. capitata* in Kenya and La Réunion (Copeland et al. 2006). Some studies have shown greater tolerance of *C. rosa* to lower temperatures than *C. capitata* and *C. catoirii* (Duyck and Quilici 2002). This could explain why *C. rosa* is regularly reared, in small numbers, from fruit of two indigenous plants, two naturalized invasive plants, and an exotic garden ornamental collected in four sites in the Central Highlands of Kenya at altitudes of 1533–1771 m a.s.l. (Copeland et al. 2006). Initially, *C. rosa* was limited mainly to coastal lowland habitats (5–436 m), where it often co-existed with *C. fasciventris* (Copeland et al. 2006). Using genetic algorithms for rule-set prediction (GARP), De Meyer et al. (2008) predicted that much of sub-Saharan Africa and Madagascar were highly suitable for *C. rosa*. In Swaziland, *C. rosa* was the dominant fruit fly species in guava orchards comprising 68.8 % of all fruit flies collected, and regularly co-exists in guava with *C. capitata* and *C. cosyra* (Magagula and Ntonifor 2014). In South Africa *C. rosa* is mostly found in the cooler regions of the country and positively correlated with precipitation (De Villiers et al. 2013). In Côte d'Ivoire, 0.02 % of fruit flies recovered from infested mango were *C. rosa* (N'depo et al. 2013).

As described earlier in this chapter (Sect. 5.12), the recently described species *C. quilicii* occurs sympatrically with *C. rosa* in some regions and does not show clear geographic isolation (De Meyer et al. 2015). It is therefore highly likely that some of the records of abundance of *C. rosa* particularly in the highland areas might indeed be of *C. quilicii*. In Tanzania, a gradual shift was observed with *C. rosa* and *C. quilicii* occurring at lower altitudes (with predominance of *C. rosa*) while only *C. quilicii* was observed at the highest elevations (Mwatawala et al. 2015). For instance, *C. quilicii* was more abundant at higher altitudes, reaching a peak at Langali (1268 m asl) while being absent at the lower elevation at Sokoine (550 m asl). However, when examined across an altitudinal transect, *C. rosa* was more abundant (61.2 %) than *C. quilicii* (38.8 %) (Mwatawala et al. 2015). It can be inferred that the impact of *C. quilicii* might be more pronounced on temperate fruits like peach, avocado and apple and earlier host plants records for *C. rosa* at higher elevations could possibly be C. *quilicii*.

6.10 Ceratitis silvestrii

Ceratitis silvestrii is an important pest of mango in several parts of West Africa, mainly found co-existing with *C. quinaria* (Ouedraogo et al. 2010; Sawadogo et al. 2013). *Ceratitis silvestrii* is most abundant during the dry season causing damage to early-maturing mango cultivars (Vayssières et al. 2005; Vayssières et al. 2009). In Mali, 7.28 % of fruit flies reared from mango were *C. silvestrii* (Vayssières et al. 2007) and in Benin 2.77 % of fruit flies were *C. silvestrii* (Vayssières et al. 2015).

6.11 Ceratitis punctata

There have only been records of *C. punctata* from mango in Cote d'Ivoire. Hala et al. (2006) reported 0.15 % of fruit flies reared from mango were *C. punctata* and N'depo et al. (2013) reported 0.18 % of of fruit flies were *C. punctata*.

6.12 Dacus *and* Zeugodacus *species*

On La Réunion (1996–1999), *Z. cucurbitae* (Coquillet) and *D. ciliatus* are reported to mainly infest a range of 16 cucurbit species (Vayssières and Carel 1999). However, there have been recent records of *Z. cucurbitae* also infesting mango (Vayssières et al. 2008; Mwatawala et al. 2010; De Meyer et al. 2015). The altitudinal limits of *Z. cucurbitae* and *D. ciliatus* are 1200 m and 1400 m, respectively during the dry season. These two species overlap on all cucurbit crops up to 600 m during the wet season and up to 1200 m during the dry season. At least one abiotic factor (altitude) and two biotic factors (host availability, interspecific competition) are responsible for the dominance of these species in La Réunion. Studies in Tanzania showed that *Z. cucurbitae* was either absent or less abundant at higher elevations along a transect from approx. 600 m a.s.l to 1650 m a.s.l (Mwatawala et al. 2010). However, the exact relationship between these biotic and abiotic factors and populations of *Z. cucurbitae* and *D. ciliatus* are currently poorly understood and require further investigation. *Dacus bivittatus* has also been reported from mango in Côte d'Ivoire. Approximately 0.42 % and 0.07 % of fruit flies reared from mango in Côte d'Ivoire were *D. bivittatus*, as reported by Hala et al. (2006) and N'depo et al. (2013) respectively.

7 Competitive Displacement Amongst Tephritid Fruit Flies in Mango Agroecosystems

The introduction of species into a new area can alter successional patterns, mutualistic relationships, community dynamics, ecosystem function and resource distribution (Mooney and Cleland 2001). Several studies have shown that, where exotic tephritid species have been introduced into areas already occupied by a native tephritid species, interspecific competition occurs that results in a decrease in numbers and niche shifts of the indigenous species, albeit without leading to complete exclusion (Duyck et al. 2004, 2006a; Ekesi et al. 2009; Mwatawala et al. 2009b). Reitz and Trumble (2002) defined competitive displacement as "the removal of a formerly established species from a habitat through superior use, acquisition or defense of resources by another species". This can occur through many different mechanisms that are often broadly categorized as exploitation or interference. Factors such as superior competitive abilities, resource pre-emption, release from natural enemies and abiotic factors including temperature and anthropogenic disturbances, are amongst the reasons an invasive species could become dominant (Rwomushana et al. 2009). In many cases, larger body size, shorter developmental period and higher realized fecundity, coupled with superior behavioural traits and the absence of coevolved natural enemies, are major factors behind the competitive advantage of alien invasive species over native ones (Reitz and Trumble 2002). Another factor that influences competitive displacement is niche differentiation between tephritid fruit fly species. For example, the large populations of *C. rosa* found in the highlands of La Réunion and Kenya (although reported here and elsewhere as *C. rosa*, recent taxonomic advances suggest this species may be *C quilicii*), where no other species are found, are suggestive of a climate-dependent change in competitive hierarchy. Host fruit preference, although less well studied, might have similar effects.

The most notable examples of competitive displacement outside Africa include displacement of *C. capitata* by the Queensland fruit fly, *Bactrocera tryoni* (Froggatt) in the Sydney area in Australia (Debach 1966) and displacement of the same species by *B. dorsalis* from the coastal areas in Hawaii in 1945 (Duyck et al 2004). According to Vargas et al. (1995), in the latter case, the displacement was, to some extent, mediated by host fruit species in that *C. capitata* persists in the lowlands on coffee, their presumed ancestral host in Africa to which it is better adapted.

A well documented case of this phenomenon in Africa is from the Mascarene Islands where the indigenous species, *C. catoirii*, is reported to have been displaced by *C. capitata* and *C. rosa* in La Réunion occurring in small numbers on the east and south coast of the island, while in Mauritius it seems to have disappeared entirely (Duyck et al. 2004). In a series of fruit fly invasions of La Réunion, Duyck et al. (2006b) further reported that the invasive species *B. zonata,* tended to have a higher rank than the previously established invasive (*C. rosa* and *C. capitata* from mainland Africa) and native (*C. catoirii*) species in the hierarchy. Presumably, the invasion of *B. zonata* in Mauritius in 1987 and La Réunion in 1991 may have further compounded the displacement of the indigenous species. Duyck et al. (2006b) suggested that, because the endemic fruit fly species in La Réunion had no specific climatic niches, they had become very rare species, and could be at risk of extinction due to invasion (Duyck et al. 2008). Large body size and shorter developmental time of the exotic species, *B. zonata*, was associated with superior competitive ability, demonstrating the importance of these traits for its superior competitive response (scramble and interference) compared with all the *Ceratitis* species. (Duyck et al 2006a). Some data also suggest that *C. capitata* and *C. rosa* appear to leave detectable chemical signals that influence the laying behaviour of conspecifics. These two species commonly display the ‘dragging ovipositor’ behaviour that is classically associated with hostmarking in tephritids and leads to inhibition of oviposition by conspecifics subsequently visiting the same fruit (Nufio and Papaj 2004) in response to the host-marking pheromones that have been deposited (Roitberg and Prokopy 1983; Nufio and Papaj 2001). Interestingly, *B. zonata* is able to detect and avoid signals left by *C. capitata* and *C. rosa*, while the response of *Ceratitis* species to each other’s signals is not significant.

In Kenya, Ekesi et al. (2006) speculated that competitive displacement was ongoing because there was a shift in dominance between the native fruit fly *C. cosyra* and the invasive species *B. dorsalis* in mango orchards at Nguruman in the Rift Valley Province of Kenya. The results of their study clearly indicated rapid displacement of *C. cosyra* by *B. invadens* within 4 years of its detection in the country, and was corroborated by Rwomushana et al. (2008, 2009) who showed that *B. dorsalis* constituted up to 98 % of the total fruit flies reared from mango in Kenya. Ekesi et al. (2009) argued that displacement interference could be explained by the aggressive behaviour demonstrated between interacting females of these species at laying sites; this behaviour was highly asymmetrical and this gave *B. dorsalis* a competitive advantage over the resident fruit fly species. Aggressive behaviour has also been been observed by Shelly (1999) who demonstrated that females of *B. dorsalis* defended oviposition sites on mango against conspecific females by lunging at opponents and driving them off through threat displays; occasionally this escalated to head-butting and pushing. As such it is then perhaps not surprising that both sexes of *B. dorsalis* would launch several aggressive behaviours against *Ceratitis* species. In related laboratory experiments, *B. dorsalis* was observed to out compete *C. capitata* and inhibit its development by superior scramble competition (Keiser et al. 1974).

In Tanzania, the Relative Abundance Index (RAI) of *B. dorsalis* to *C. capitata*, *C. cosyra*, *C. rosa* in 19 evaluated hosts was higher (more than 0.5) and in favour of *B. dorsalis*; in some hosts (sweet orange, *Citrus sinensis* (L.) Osbeck; ambarella, *Spondias cytherea* L. and tropical almond, *Terminalia catappa* L.) it reached 1, implying that only *B. dorsalis* was present (Mwatawala et al. 2009a). Certainly, in fruit species such as tropical almond, only *B. dorsalis* emerged. This trend lends credence to the suggestion that the exotic species is slowly displacing other fruit fly species on the same hosts. Trapping data confirms the dominance of *B. dorsalis* (Mwatawala et al. 2004, 2006).

Despite these cases of displacement activity there are several reasons why *Ceratitis* species have not been completely displaced from the mango agroecosystem. *Ceratitis* species have some advantages that allow for some level of coexistence with *B. dorsalis. Ceratitis* species have a more specialized host-searching ability and have had close associations with several host plant species over a long period in Africa. Secondly, *Ceratitis* species have been recorded from several hundred plant species in Africa (Lux et al. 2003; Copeland et al. 2006) compared with the host range of *B. dorsalis* that currently stands at just over 40 known cultivated and wild host species, though this is growing (Vayssières et al. 2009). It is likely that *Bactrocera* species can switch to other suitable hosts when there is pressure on the carrying capacity, providing some niche on mango for *Ceratitis* species to survive. High infestations found on wild hosts like *T. catappa*, even when mango is present, attest to this. Generally, most *Bactrocera* species, including *B. dorsalis*, are believed to be lowland residents (Vargas et al. 1983; Wong et al. 1985; Harris et al. 1986; Ekesi et al. 2006), enabling *B. dorsalis* to successfully displace *Ceratitis* species in lowland ecologies. At higher elevations, such as Embu in the Eastern Province of Kenya, *C. cosyra* remains the dominant species, probably because of the poor tolerance of *B. dorsalis* to low temperatures (Ekesi et al. 2006). It is therefore probable that *B. dorsalis* may be restricting populations of *C. cosyra* to the highlands. Indeed, such phenomena have been reported from Hawaii, where *B. dorsalis* largely displaced *C. capitata* from the low-elevation coastal zones and restricted *C. capitata* populations to cooler climates at high altitudes where *B. dorsalis* does not occur (Vargas et al. 1995). Subsequently distribution and abundance of the major mango-infesting fruit flies in Africa will continue to be dependent of the competitive interactions between native and exotic species.

8 Host Plants of Mango-Infesting Fruit Flies in Africa

Despite the economic significance of tephritid fruit flies, the host spectrum throughout their distribution range remains limited or is continuously evolving to include hitherto unknown hosts. Several studies have documented the current fruit fly pests in Africa and their host plants (Liquido et al. 1991; White and Elson-Harris 1992; N'Guetta 1994; Copeland et al. 2002, 2004, 2006; Vayssières and Kalabane 2000; De Meyer et al. 2002; Ekesi et al. 2006; Vayssières et al. 2005; Ndzana Abanda et al. 2008; Rwomushana et al 2008; Vayssières et al. 2010). De Meyer et al. (2002) provided an annotated host check list for all *Ceratitis* species from Africa and Goergen et al. (2011) has provided a detailed listing of host plants for *B. dorsalis* in West and Central Africa. The host plants for each fruit fly species has been documented from published papers on host plants in Africa and insect records that are publicly available from the Royal Museum for Central Africa (http://projects.bebif.be/fruitfly/index.html Table 5.1). The authorities for each species follow the nomenclature of the International Plant Names Index (www.ipni.org) which was cross referenced with the Global Species Database (www.globalspecies.org), the Plant List (www.plantlist.org) and the Herbarium Catalogue www.kew.org/herbcat) (Global Species 2015; Herbarium Catalogue 2015; IPNI 2015; Plant List 2015).We present a summary of the host plant specialization of different fruit fly species, fruit fly species richness and abundance on particular hosts and the compartmentalization of the plant–fruit fly food web.

Table 5.1 Host plants of mango infesting fruit fly species in Africa

Plant family	Host plant species, common name and which species they support
Actinidiaceae	*Actinidia deliciosa* (A. Chev.) C.F. Liang & A.R. Ferguson (kiwifruit)☼
Amaryllidaceae	*Allium cepa* L. (dry onions)€
Amaranthaceae	*Sericostachys scandens* Gilg & Lopr.♣
Anacardiaceae	*Anacardium occidentale* L. (cashew nut)*☼Δ♥♠Ω, *Mangifera indica* L. (mango)*§ß☼‡Δ♣♥♠Ω€◊Ʉ◙∞, *Sclerocarya birrea* (A. Rich.) Hochst. (marula)*ΔΩ, *Sorindeia madagascariensis* Thouars ex DC.*, *Spondias dulcis* Parkinson (otaheite apple)*☼, *Spondias mombin* L. (tropical plum)*Δ♣, *Spondias cytherea* Sonner. (hog plum)*, *Harpephyllum caffrum* Bernh. ex C.Krauss☼♣♠, *Spondias purpurea* L. (red mombin)☼, *Spondias tuberosa* Arruda☼, *Spondias* sp (wild plum)Δ
Anisophylleaceae	*Anisophyllea laurina* R.Br. ex SabineΔ♣
Annonaceae	*Annona cherimola* Mill. (cherimoya)*☼Δ♠, *Annona muricata* L. (soursop)*ß☼Δ♣♠€, *Annona senegalensis* Pers.*ßΔ♣♠Ω, *Annona squamosa* L. (sugar apple)*§☼♠€, *Annona reticulata* L. (custard apple)§ß☼‡Δ♠€, *Annona macroprophyllata* Donn. S.M.ß, *Annona montana* Macfad.ß, *Anonidium mannii* (Oliv.) Engl. & Diels ß, *Artabotrys monteiroae* Oliv.ß♣, *Cananga odorata* (Lam.) Hook.f. & Thomson (perfume tree)*☼♠, *Lettowianthus stellatus* Diels♠, *Monanthotaxis parvifolia* (Oliv.) Verdc.♣, *Monanthotaxis fornicata* (Baill.) Verdc.♠, *Monodora grandidieri* Baill.♠, *Monodora* sp., Dunalß, *Rollinia mucosa* (Jacq.) Baill. (wild sweetsop, wild sugar apple)ßΔ, *Rollinia* A.St.-Hil. sp.ß, *Sphaerocoryne gracilis* (Engl. & Diels) Verdc.♠, *Thevetia peruviana* K. Schum. (exile tree, yellow oleander)♠, *Uvaria acuminata* Oliv.♠, *Uvaria catocarpa* Diels♠, *Uvaria lucida* Bojer ex Sweet♠

(continued)

Table 5.1 (continued)

Plant family	Host plant species, common name and which species they support
Apocynaceae	*Acokanthera oppositifolia* (Lam.) Codd☼♣, *Acokanthera schimperi* (A.D.C.) Schweinf. (round-leaved poison bush)☼♣, *Ancylobothrys* sp. Pierreß, *Carissa carandas* L. (caranda plum, mahakaranda)☼Δ♠, *Carissa edulis* (Forssk.) Vahl (Egyptian carissa)☼, *Carissa grandiflora* (E. Mey.) A. DC (natal plum) ♠, *Carissa macrocarpa* (Eckl.) A.D.C. (natal plum)☼ ♠, *Carpodinus hirsuta* Hua◊, *Dictyophleba lucida* (K.Schum.) Pierre♠, *Landolphia* P. Beauv.sp*◊, *Landolphia heudelotii* StapfΩ, *Landolphia kirkii*, Dyer Δ, *Saba comorensis* (Boj.) PichonΔ, *Saba senegalensis* (A.DC.) Pichon*ΔΩ, *Tabernaemontana longiflora* Rusby◊, *Tabernaemontana penduliflora* K. SchumΔ, *Thevetia peruviana* K.Schum. (exile tree, yellow oleander)☼, *Voacanga chalotiana* Pierre ex Stapf. ◙, *Voacanga dregei* E.Mey.◊
Araliaceae	*Irvingia* F. Muell. sp.ß
Arecaceae	*Butia eriospatha* (Mart. ex Drude) Becc.☼, *Cocos plumosa* Hook. f.ß, *Elaeis* Jacq. spß, *Phoenix dactylifera* L. (date-palm)§☼€
Asparagaceae	*Dracaena steudneri* Engl.*
Asteraceae	*Helianthus annuus* L. (sunflower)€
Boraginaceae	*Cordia sinensis* Lam.*, *Ehretia cymosa* Thonn.☼♠
Brassicaceae	*Brassica oleracea var. botrytis* (Caulifolower)€, *Brassica oleracea* var. *capitata* (Broccoli)€
Bromeliaceae	*Ananas comosus* (L.) Merr. (pineapple)*, *Ehretia cymosa* Thonn.
Cactaceae	*Cereus peruvianus* (L.) Mill.♠,*Hylocereus undatus* (Haw.) Britton & Rose (dragon fruit)☼♠, *Opuntia ficus-indica* (L.) Mill. (prickly pear)☼♠, *Pereskia aculeata* Mill. (lemon-vine)☼
Caesalpinioideae	*Cordyla pinnata* (Lepr. ex A. Rich.) Milne Redhead (cayor pear tree)*, *Cynometra* L. sp.ß
Canellaceae	*Warburgia salutaris* (Bertol. f.) Chiov. (pepper-bark tree)Δ♣, *Warburgia ugandensis* Sprague (pepperbark tree, greenheart)Δ
Capparaceae	*Capparis sepiaria* L. (indian caper)☼, *Crateva tapia* L.☼, *Maerua duchesnei* (De Wild.) F. White*☼,
Caricaceae	*Carica papaya* L. (papaya)*§☼‡♠ €Ʉ, *Vasconcellea cauliflora* (Jacq.) A. DC.♠
Cecropiaceae	*Myrianthus* P. Beauv. sp.ß, *Myrianthus arboreus* P.Beauv. ◙
Celastraceae	*Salacia elegans* Welw. ex Oliv.♠
Chrysobalanaceae	*Chrysobalanus icaco* L. (icaco plum)☼Δ Ω, *Parinari curatellifolia* Planch. ex BenthΔ
Clusiaceae	*Calophyllum tacamahaca* Willd.☼♠, *Calophyllum* sp. L. (beauty-leaf)☼, *Garcinia livingstonei* T. Anderson (african mangosteen)☼,*Garcinia mannii* Oliv.*, *Garcinia* × *mangostana* L (mangosteen)ß☼♠
Combretaceae	*Terminalia catappa* L. (tropical almond)*§ß☼‡Δ♠

(continued)

Table 5.1 (continued)

Plant family	Host plant species, common name and which species they support
Crassulaceae	*Cotyledon orbiculata* L.Ʉ
Cucurbitaceae	*Benincasa hispida* (Thunb.) Cogn. (Chinese melon)€, *Cephalendra indica* Naud. (Kundru)€, *Citrullus colocynthis* (L.) Schrad. (colocynth)*€Ʉϕ, *Citrullus lanatus* (Thunb.) Matsum. & Nakai (watermelon)*€Ʉϕ, *Citrullus vulgaris* Schrad (African melon)€, *Coccinia grandis* (L.) Voigt (Wild cucurbits)€Ʉϕ, *Coccinia indica* Wight & Arn. (Ivy gourd)€, *Coccinia dipsaceus* Ehrenb. ex Spach (Wild cucurbits)€, *Coccinia palmate* M.Roem.Ʉ, *Coccinia quinqueloba* (Thunb.) Cogn.Ʉ, *Coccinia trilobata* (Cogn.) C.JeffreyɄϕ, *Corallocarpus ellipticus* Chiov.Ʉϕ, *Cucumis aculeatus* Cogniauxϕ, *Cucumis metuliferus* Naudin (African horned cucumber)ϕ, *Corallocarpus schimperi* Hook.f.Ʉ, *Cucumeropsis edulis* Cogn. Ʉ, *Cucumis anguria* L. (Wild cucurbit)€Ʉ, *Cucumis ficifolius* A.Rich.*, *Cucumis melo* L. (melon)*☼, *Cucumis sativus* L. (cucumbers, gerkins)*☼€Ʉϕ, *Cucumis africanus* L.f.Ʉϕ, *Cucumis dipsaceus* Ehrenb. ex Spach (hedgehog gourd)☼Ʉϕ, *Cucumis melo* C. melo var. conomon (Muskmelon)€ϕ, *Cucumis melo* var. momordica (Snap melon)€Ʉ, *Cucumis pubescens* Willd. (Wild cucurbit)€, *Cucumis sativus* L. (cucumber)Ʉ, *Cucumis trigonus* Roxb. (Wild cucurbits)€, *Cucumis utilissimus* Roxb (Long melon)€, *Cucumis vulgaris* var *fistulosus* (Squash melon)€, *Cucurbita maxima* Duchesne (giant pumpkin)*♠€Ʉϕ, *Cucurbita moschata* Duchesne (butternuts)€, *Cucurbita pepo* L. (ornamental gourd, squash)*€Ʉϕ, *Diplocyclos palmatus* (L.) C.Jeffrey. (Balsam apple)€, *Kedrostis leloja* (Forsk. ex J.F.Gmel.) C. JeffreyɄϕ, *Kedrostis foetidissima* Cogn.Ʉϕ, *Lagenaria abyssinica* (Hook.f.) C.JeffreyɄ, *Lagenaria amebicana* (Wild cucurbits)€, *Lagenaria siceraria* (Molina) Standl. (calabash, water bottle)*€Ʉϕ, *Lagenaria sphaerica* E.Mey.Ʉ, *Lagenaria vulgaris* Ser. (Bottle gourd)€, *Luffa* sp Mill.§, *Luffa aegyptiaca* Mill.Ʉϕ, *Luffa acutangula* (L.) Roxb. (Ribbed gourd)€Ʉϕ, *Luffa cylindrica* M. Roem. (Sponge gourd)€Ʉ, *Momordica balsamina* L.Ʉϕ, *Momordica charantia* L. (bitter gourd)*§€Ʉϕ, *Momordica calantha* Gilg♣, *Momordica rostrata* Zimm.Ʉϕ, *Momordica trifoliolata* Hook.fɄ, *Mukia maderaspatana* (L.) M.Roem.Ʉ, *Telfairia pedata* Hook.Ʉ, *Trichosanthes anguina* L€, *Trichosanthes cucumeria* (Snake gourd)€Ʉ, *Peponium mackenii* Engl.Ʉϕ, *Peponium vogelii* Engl.Ʉ, *Sycos pachycarpus* (Wild cucurbit)€, *Sechium edule* (Jacq.) Sw.Ʉ, *Trichosanthes dioica* Roxb. (Pointed gourd)€, *Trichosanthes cucumerina* Linn. (Wild cucurbit)€Ʉϕ
Dichapetalaceae	*Dichapetalum bangii* (Didr.) Engl.ß
Ebenaceae	*Euclea divinorum* Hiern☼♣, *Diospyros abyssinica* (Hiern) F. White☼, *Diospyros kabuyeana* F.White♠ *Diospyros kaki* Thunb. (persimmon)*☼ ♠, *Diospyros malabarica* (Desr.) Kostel. (malabar ebony) ☼, *Diospyros mespiliformis* Hochst. ex A.DC. (ebony diospiros)☼Δ, *Diospyros montana* Roxb.*♣, *Diospyros pallens* (Thunb.) F.White☼, *Diospyros virginiana* L. (persimmon, common)☼

(continued)

Table 5.1 (continued)

Plant family	Host plant species, common name and which species they support
Ericaceae	*Arbutus unedo* L. (arbutus)☼, *Vaccinium corymbosum* L. (blueberry)☼
Euphorbiaceae	*Euphorbia heterophylla* L.Ʉ, *Croton* L. sp.ß, *Drypetes* Vahl sp.ß♣, *Drypetes gerrardii* var. *gerrardii* Hutch.♣♠, *Drypetes natalensis* (Harv.) Hutch.☼♠, *Drypetes gossweileri* S. Moore∆, *Phyllanthus acidus* (L.) Skeels (star gooseberry)♠, *Ricinus communis* L.Ʉ, *Uapaca kirkiana* (wild loquat) Müll. Arg.∆
Fabaceae	*Cordyla africana* Lour. (wild mango)∆, *Cordyla pinnata* (A. Rich.) Milne-Redh. (cayor pear tree)∆, *Gliricidia maculata* (Humb., Bonpl. & Kunth) Steud.∆, *Inga laurina* (Sw.) Willd. (ice cream bean)♠, *Pericopsis elata* (Harms) Meeuwen◙, *Vigna sesquipedalis* (L.) Fruw. (Cowpea)€, *Vigna sinensis* (L.) Savi (Cowpea)€, *Vigna unguiculata* (L.) Walp. (Long bean or Cowpea)€
Flacourtiaceae	*Dovyalis* E. Mey. ex Arn. sp.ß♣, *Dovyalis hebecarpa* (Gardner) Warb. (ceylon gooseberry, ketembilla)☼♠, *Flacourtia* Comm. ex L'Her. sp.ß∆, *Rawsonia lucida* Harv. & Sondß♣. *Dovyalis caffra* (Hook. f. & Harv.) Warb. (kei apple)☼∆♣♠, *Flacourtia indica* (Burm. f.) Merr. (governor's plum),☼‡♠, *Ludia mauritiana* J.F. Gmel.♠*Rawsonia lucida* Harv. & Sond.♣♠, *Rawsonia usambarensis* Engl. & Gilg.♣,
Flagellariaceae	*Flagellaria guineensis* Schumach☼
Goodeniaceae	*Scaevola plumieri* (L.) Vahl☼, *Scaevola sericea* Vahl☼, *Scaevola taccada* (Gaertn.) Roxb. (beach naupaka)☼
Guttiferae	*Calophyllum tacamahaca* Willd☼♠
Hippocrataceae	*Salacia elegans* Oliv.♠
Irvingiaceae	*Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill. (wild mango)*, *Irvingia smithii* Hook. F.ß
Juglandaceae	*Carya illinoinensis* (Wangenh.) K. Koch (pecan)☼, *Juglans regia* L. (walnut)☼
Lauraceae	*Cinnamomum verum* J.Presl (cinnamon)☼, *Persea americana* Mill. (avocado) *§ß ☼‡∆♣♠€
Lecythidaceae	*Careya arborea* Roxb. (tummy wood)§, *Napoleonaea gabonensis* Liben◊◙
Leguminosae	*Cajanus cajan* (L.) Millsp. (Pigeon pea)€, *Cordyla pinnata* (A.Rich.) Milne-Redh.*, *Dolichos lablab* L. (Hyacinth bean)€, *Faidherbia albida* (Delile) A.Chev.Ω, *Inga laurina* (Sw.) Willd. (Spanish oak)♠, *Pithecellobium dulce* (Roxb.) Benth.☼, *Angylocalyx braunii* Harms♠, *Phaseolus vulgaris* L. (French bean)€ϕ, *Phaseolus limensis* L. (Lime bean)€, *Phaseolus radiatus* L. (Green gram)€
Loganiaceae	*Strychnos decussata* (Pappe) Gilg☼, *Strychnos henningsii* Gilg☼♠, *Strychnos mellodora* S. Moore*, *Strychnos potatorum* L.f. ☼, *Strychnos pungens* Soler☼, *Strychnos spinosa* Lam.∆♣♠
Lythraceae	*Punica granatum* L. (pomegranate)§☼‡
Malpighiaceae	*Malpighia glabra* L. (acerola)☼
Malvaceae	*Abelmoschus esculentus* (L.) Moench (Okra)€Ʉϕ,*Cola natalensis* Oliv.☼♠, *Durio zibethinus* L. (durian)*☼, *Grewia asiatica* L. (phalsa)§,
Melastomataceae	*Bellucia* Neck. ex Raf. sp.ß
Meliaceae	*Ekebergia capensis* Sparrm. (dog plum, Cape ash)☼♣♠, *Sandoricum koetjape* (Burm.f.) Merr. (santol)☼

(continued)

Table 5.1 (continued)

Plant family	Host plant species, common name and which species they support
Menispermaceae	*Tiliacora funifera* (Miers) Oliv.ß♣
Mimosaceae	*Inga laurina* (Sw.) Willd. (Sackyca)♠, *Pithecellobium dulce* (Roxb.) Benth. (Manila tamarind, guamuchil)♠
Moraceae	*Antiaris toxicaria* Lesch. (antiaris, false iroko, false mvule)*ß♣∞, *Antiaris toxicaria* subsp. *africana* (Engl.) C.C.Berg (upas-tree)ß∞, *Artocarpus* J.R. Forst. & G. Forst. sp.ß, *Artocarpus altilis* (Parkinson ex F.A.Zorn) Fosberg (breadfruit)☼, *Ficus carica* L. (fig)§♠€ ☼♣♥, *Ficus ingens* var. ingens (Red-leaved fig)Ω *Ficus ottoniifolia* Miq.*, *Ficus sycomorus* L. (sycamore fig)*, *Dorstenia* L. sp.ß∞, *Ficus* L. sp. (fig)ß, *Morus mesozygia* Stapf.ß♣, *Morus nigra* L. (black mulberry)☼
Muntingiaceae	*Muntingia calabura* L. (Jamaica cherry)☼
Musaceae	*Musa acuminata* Colla (cavendish banana)*♠, *Musa* × *paradisiaca* L. (plantain)*☼, *Musa* sp L. (banana)*, *Musa nana* Lour (banana)♠, Musa sp. (Chinese banana)€, *Musa paradisiaca* sp. *sapientum* (Blue field banana)€
Myrtaceae	*Acca sellowiana* (O. Berg) Burret*☼♠, *Eugenia brasiliensis* Lam. (brazil cherry)☼, *Eugenia paniculata* Jacq.☼, *Eugenia uniflora* L. (surinam cherry, pitanga cherry)*ß☼‡Δ♠, *Eugenia* L sp.ß, *Feijoa sellowiana* (O.Berg) O. Berg (Horn of plenty)☼ ♠, *Psidium araca* Raddi.♠, *Psidium cattleianum* Afzel. ex Sabine (strawberry guava, cherry guava)§ß☼‡♠, *Psidium friedrichsthalianum* (O.Berg) Nied. (wild guava)☼♠, *Psidium guajava* L. (guava)*§ß☼‡Δ♣♥♠€Ʉ◊, *Psidium longipes* (O.Berg) McVaugh (strawberry guava)☼♠, *Syzygium aqueum* (Burm.f.) Alston (watery roseapple)‡♠, *Syzygium cumini* (L.) Skeels (black plum)☼♠, *Syzygium jambos* (L.) Alston (rose apple)*§☼‡♣♠, *Syzygium malaccense* (L.) Merr. & L.M.Perry (malay-apple)*☼♠, *Syzygium samarangense* (Blume) Merr. & L.M. Perry (water apple)*§☼♠
Oleaceae	*Olea europaea* subsp. *europaea* L. (olive)☼, *Olea woodiana* Knobl.☼
Opiliaceae	*Opilia amentacea* Roxb.☼♣♠
Oxalidaceae	*Averrhoa carambola* L. (carambola, starfruit)*☼‡Δ♠€Ʉ, *Averrhoa bilimbi* L. (blimbe)☼♠
Orchidaceae	*Bulbophyllum patens* King ex Hook.f. (Zingerone)€,
Olacaceae	*Strombosia scheffleri* Engl.ß♣♠, *Ximenia americana* L. var americana (Hog plum)☼♣ Ω
Passifloraceae	*Passiflora coerulea* Auct. (blue-crown passion flower)☼ Ʉ, *Passiflora edulis* Sims (passionfruit)☼‡ €, *Passiflora molissima* (Kunth) (banana passion)♠, *Passiflora foetida* L.ß, *Passiflora suberosa* L. (corkystem passion flower)☼, *Passiflora subpeltata* Ortega♣, *Passiflora seemannii* Griseb. (passion fruit)€, *Passiflora quadrangularis* L. (giant passion fruit) €Ʉ
Phyllanthaceae	*Adenia lobata* (Jacq.) Engl.Δ *Antidesma dallachyanum* Baill.☼, *Antidesma venosum* E. Mey. ex Tul.☼, *Flueggea virosa* (Roxb. ex Willd.) Royle☼
Poaceae	*Zea mays* L. (maize, corn)€

(continued)

Table 5.1 (continued)

Plant family	Host plant species, common name and which species they support
Podocarpaceae	*Podocarpus elongatus* (Aiton) L'Hér. ex Pers. (african yellow wood)[☼]
Polygalaceae	*Carpolobia lutea* G. Don[Δ]
Polygonaceae	*Coccoloba uvifera* (L.) L. (seaside grape)[☼♠]
Proteaceae	*Banksia prionotes* Lindl.[☼]
Rhamnaceae	*Ziziphus abyssinica* Hochst. ex A.Rich. (indian jujube)[§ß♣], *Ziziphus jujuba* Mill. (common jujube)[☼‡♠], *Ziziphus joazeiro* Mart.[☼], *Ziziphus mauritiana* Lam. (jujube)[*§☼♠], *Ziziphus spina-christi* (L.) Willd.[♥]
Rosaceae	*Cydonia oblonga* Mill.[*§☼♠], *Eriobotrya japonica* (Thunb.) Lindl. (loquat) [§*☼‡♣♠], *Fragaria chiloensis* (L.) Mill. (Strawberry)[€], *Malus communis* Poir. (apple tree)[§☼♠], *Malus domestica* Borkh. (apple)[*☼♠], *Malus floribunda* Siebold ex Van Houtte[☼], *Malus pumila* Mill. (apple)[§], *Mespilus germanica* L. (medlar)[☼], *Prunus africana* (Hook. f) Kalkman[ß♣], *Prunus armeniaca* L. (apricot)[§☼♥♠], *Prunus persica* (peach) (L.) Stokes[*☼‡Δ♣♥♠€], *Prunus* sp. L. (stone fruit)[☼♣], *Prunus avium* (L.) L. (sweet cherry)[☼], *Prunus capuli* Cav. ex Spreng.[♣], *Prunus domestica* L. (plum)[☼], *Prunus salicina* Lindl. (Japanese plum)[☼♠], *Pyrus communis* L. (European pear)[☼♠€], *Pyrus malus* L. (Apple)[€]*Pyrus pyrifolia* (Burm. f.) Nakai (Oriental pear tree)[☼], *Pyrus syriaca* Boiss.[☼], *Rubus idaeus* L. (raspberry)[☼], *Rubus loganobaccus* L.H. Bailey (loganberry)[☼]
Rubiaceae	*Sarcocephalus latifolius* (Sm.) E.A. Bruce (pin cushion tree, Guinea peach)[*ΔΩ], *Coffea arabica* L. (arabica coffee)[ß☼♣♠], *Coffea canephora* Pierre ex A. Froehner (robusta coffee)[ß☼♣], *Leptactina platyphylla* (Hiern) Wernh.[ß♣], *Coffea liberica* Hiern (Liberian coffee)[☼], *Guettarda speciosa* L.[☼], *Vangueria infausta* Burch.[☼], *Sarcocephalus esculentus* Sabine[Δ], *Calycosiphonia spathicalyx* (K.Schum.) Robbr.[♠], *Tricalysia pallens* Hiern[♠]
Rutaceae	*Aegle marmelos* (golden apple)[§], *Casimiroa edulis* La Llave (white sapote)[☼♣], *Citrus aurantiifolia* (Christm.) Swingle (lime)[☼], *Citrus aurantium* L. (sour orange)[*§ß☼Δ♠◊], *Citrus grandis* (Linn.) Osbeck (Shaddock/pummel)[€], *Citrus hystrix* DC.[◊], *Citrus japonica* Thunb. (round kumquat)*, *Citrus limetta* Risso (sweet lemon)[☼], *Citrus limon* (L.) Burm. f. (lemon)[*☼♣], *Citrus* × *limon* (L.) Osbeck (mandarin lime)[☼], *Citrus maxima* (Burm.) Osbeck (pummelo) [☼], *Citrus medica* L. (citron)[☼], *Citrus nobilis* Lour. (tangor)[☼♠], *Citrus x paradisi* Macfad. (grapefruit and Orlando)[*ß☼♠◙], *Citrus reticulata* Blanco (mandarin and Tangelo cv and Ortanique)[*§ ß☼‡♠€], *Citrus reticulata x paradisi* (tangelo)[☼], *Citrus sinensis* (L.) Osbeck (navel orange and Tangor cv)[*ß☼♣♥€◙], *Citrus* × *tangelo* J.W.Ingram & H.E.Moore (tangelo)[♣], *Murraya exotica* L. (Chinese box)[ß], *Murraya* J.Koenig sp.[ß], *Murraya paniculata* (L.) Jack (orange jessamine)[☼♠], *Clausena anisata* (Willd.) Hook.f. ex Benth. (horsewood)[☼], *Fortunella* sp. Swingle (kumquats)[☼], *Fortunella japonica* (Thunb.) Swingle (round kumquat)[☼], *Harrisonia abyssinica* Oliv.[♣], *Toddalia asiatica* (L.) Lam.[♠], *Vepris trichocarpa* (Engl.) Mziray[♣], *Vepris undulata* Verdoorn & C. A. Sm.[☼]
Salicaceae	*Flacourtia indica* (Burm. f.) Merr. (governor's plum)*
Salvadoraceae	*Azima tetracantha* Lam. (beehanger)[☼]
Santalaceae	*Santalum album* L. (Indian sandalwood)[☼]

(continued)

Table 5.1 (continued)

Plant family	Host plant species, common name and which species they support
Sapindaceae	*Allophylus ferrugineus* Taub.♣, *Allophylus pervillei* Blume♠, *Blighia sapida* K.D. Koenig (Akee apple)*, *Dimocarpus longan* Lour. (longan tree)☼♠, *Euphoria longan* Lam. (Longan)€, *Filicium decipiens* (Wight & Arn.) Thwaites (fernleaf)♣, *Filicium decipiens* (Wight & Arn.) Thwaites☼, *Litchi chinensis* Sonn. (lichi)☼Δ♠€, *Nephelium lappaceum* L. (rambutan)☼ß, *Pancovia laurentii* (De Wild.) Gilg ex De Wildß, *Pancovia turbinata* Radlk♣
Sapotaceae	*Argania spinosa* (L.) Skeels (argan tree)☼, *Chrysophyllum albidum* G. Don (white star-apple)*ß♣◊◙, *Chrysophyllum beguei* Aubrév. & Pellegr.◙, *Chrysophyllum cainito* L. (common star apple)☼‡♠, *Chrysophyllum carpussum* L.☼♠, *Chrysophyllum imperiale* (Linden ex K.Koch & Fintelm.) Benth. & Hook.f.ß, *Chrysophyllum natalense* Sond.♠, *Chrysophyllum oliviforme* L.☼, *Chrysophyllum pruniforme* Engl ◙, *Chrysophyllum viridifolium* J.M.Wood & Franks☼, *Englerophytum magalismontanum* (Sond.) T.D.Penn.☼ ♠, *Englerophytum natalense* (Sond.) T.D.Penn.Δ♣, *Englerophytum oblanceolatum* (S. Moore) T.D. Penn.ß♣, ♠, *Manilkara butugi* Chiov. ☼ß♣, *Manilkara sansibarensis* (Engl.) Dubard☼, *Manilkara zapota* (L.) P. Royen (sapodilla, chicle)*☼‡♣, *Mimusops* L sp.ß, *Mimusops bagshawei* S. Moore☼, *Mimusops caffra* E.Mey. ex A.DC.☼, *Mimusops elengi* L. (Spanish cherry)§☼‡, *Mimusops fruticosa* Bojer☼, *Mimusops obtusifolia* Lam.☼, *Pachystela* sp. Pierre♠, *Pouteria altissima* (A.Chev.) Baehniß♣, *Pouteria caimito* (Ruiz & Pav.) Radlk.☼, *Pouteria sapota* (Jacq.) H.E. Moore & Stearn (mammey sapote)☼, *Pouteria adolfi-friedericii subsp. usambarensis* (J.H.Hemsl.) L.Gaut. ◊, *Pouteria viridis* (Pittier) Cronquist (green sapote)☼, *Richardella campechiana* (Kunth) Pierre☼♠◊, *Sideroxylon inerme* L.☼, *Synsepalum brevipes* (Baker) T.D. Penn.ß♣, *Synsepalum dulcificum* (Schumach. & Thonn.) Daniell (miraculous fruit)☼♠, *Pouteria campechiana* (Kunth) Baehni (canistel)♠, *Synsepalum subverticillatum* (E.A.Bruce) T.D.Penn.♠, *Vitellaria paradoxa* C.F. Gaertn. (shea butter)*ßΔ♣♥Ω◙
Simaroubaceae	*Brucea antidysenterica* J.F.Mill.☼
Solanaceae	*Capsicum annuum* L. cov. *longum* A. DC. (bell pepper)*☼‡ ϕ, *Capsicum frutescens* L. (chilli)*☼♠€, *Cyphomandra* sp. Mart. ex Sendtn.☼, *Cyphomandra betacea* (Cav.) Miers (tree tomato)☼, *Lycium* L.sp. (boxthorns)☼, *Lycium barbarum* L. (Matrimonyvine)☼, *Lycium europaeum* L. (european boxthorn)☼, *Physalis peruviana* L. (Cape gooseberry)☼, *Solanum giganteum* Jacq.♠, *Solanum incanum* L. (grey bitter-apple)☼, *Solanum lycopersicum* L. (tomato)*☼‡♠ €Ʉϕ, *Solanum* sect. *Lycopersicon* spp.ϕ, *Solanum macrocarpon* L. (local garden egg)☼, *Solanum mauritianum* Scop. (bugweed, bugtree)ß☼♣♠, *Solanum melongena* L. (eggplant)☼€Ʉ, *Solanum nigrum* L. (black nightshade)☼, *Solanum muricatum* Aiton (melon pear)☼, *Solanum pseudocapsicum* L. (Jerusalem-cherry)☼, *Solanum tuberosum* L. (potato)§, *Solanum seaforthianum* Andrews (Brazilian nightshade)☼
Sterculiaceae	*Cola bruneelii* De Wild.◊, *Cola natalensis* Oliv.Ʉ, *Sterculia* L. sp.ß, *Theobroma cacao* L. (cocoa)*ß☼♣♠◊◙
Vitaceae	*Vitis vinifera* L. (grapevine)*☼♠, *Vitis trifolia* Linn. (Galls grape vine)€
Urticaceae	*Myrianthus arboreus* P. Beauv.ß☼♣♠

**B. dorsalis;* §*B. zonata;* ß*C. anonae*; ☼*C. capitata;* ‡*C. catoirii;* Δ*C. cosyra;* ◙*C. ditissima;* ♣*C. fasciventris;* ∞*C. flexuosa;* ◊*C. punctata;* ♥*C. quinaria;* ♠*C. rosa* (probably includes *C. quilicii* in published records)*;* Ω*C. silvestrii*; Ʉ*D. bivittatus*; ϕ*D. ciliatus* and €*Zeugodacus cucurbitae*

9 Future Perspectives

In most African countries, production of fruits and vegetables is recognized as a major source of income generation for rural communities and has been accorded high priority in national development plans. The domestic demand for fruits and vegetables continues to grow, thereby providing ready market outlets for increased domestic production and exports from Africa thereby generating opportunities for smallholder growers. Trade within Africa in agricultural commodities such as fruits has opened up in recent years due to regional integration that has largely removed many tariff and non tariff barriers that had hitherto restricted regional trade. Despite these inherent advantages, many countries in Africa do harbour a wide diversity of plant species that can support exotic tephritid fruit fly pests, and lack the quarantine and phytosanitary capacity to detect and restrict the entry of invasive insect species into their countries. Therefore, trade has become the principal means for unwitting introduction of invasive pests to new areas and constrained the potential growth of the horticultural industry (Ekesi et al. 2016). Owing to their high reproductive capacity coupled with the lack of competitors and efficient natural enemies, and further compounded with the poor quarantine infrastructure in Africa, invasive pests have spread widely to new locations with far reaching social and economic consequences.

Subsequently, many African countries have taken their own measures to address the fruit fly problem utilizing several Integrated Pest Management (IPM) technologies and innovations that have been tested and proven to be effective in field suppression (Ekesi et al 2016). However, the resources required for fruit fly management remain enormous and elusive for the small-holder grower. Fruit fly management also requires an area-wide approach, particularly monitoring and surveillance to prevent new invasions (Manrakhan et al. 2011). Countries also need to continously scan the horizon for other emerging invasive fruit fly species already reported elsewhere to prevent their entry and establishment. Key among these is *B. zonata* which has been reported from some of the islands in the Indian Ocean (Mauritius and La Réunion), northern Africa (Egypt and Libya), several countries in the Arabian Peninsula (i.e. Oman, Saudi Arabia, United Arab Emirates and Yemen) and recently from the Gezira region in Sudan, suggesting a southward spread and potential risk of invasion into the sub-Saharan region (De Meyer et al. 2007). The way that *B. zonata* has shown its dominance over *B. dorsalis* in some parts of India is alarming, as such, urgent phytosanitary measures should be enforced to limit further spread. Similarly, *B. latifrons* is another exotic pest only recently established in Tanzania and Kenya (Mwatawala et al. 2007) which has the potential to increase the complex of pests on Solanaceae. *Zeugodacus cucurbitae* recently invaded the African continent and is causing havoc to a wide range of cucurbits (Mwatawala et al. 2010; De Meyer et al. 2015). Therefore, trans-regional invasions by these alien invasive pests would require an integrated and system-wide regional approach for their early detection and management.

The synomymization of *B. invadens*, *Bactrocera philippinensis* Drew and Hancock and *Bactrocera papayae* Drew and Hancock as part of the *B. dorsalis* species complex does suggest that all the ‘sub-species’ could inhabit similar environments and have the potential to establish if they were ever to invade the continent because they infest similar host plants. Additionally, resolution of the cryptic species within the FAR complex through integrative taxonomy approaches concluded that *C. rosa* belonged to the R1 type and that the R2 type was a new species, *C. quilicii*. This new information does require new research to understand the geographical limits of both species and resolve the host plant status that was, hirtherto, all attributed to *C. rosa*. The cases of *B. dorsalis* and *C. quilicii* will require a different approach to trade, quarantine and field control measures. Strategies and policies to deal with invasive pests need to be put in place to safeguard the entry of such species, but also to restrict the spread to new areas of those already established in Africa. It also calls for a need for regular surveillance and quarantine to restrict introduction. There should be a concerted effort in all African countries in addressing the fruit fly problem particularly with regards to fruit fly surveillance and management.

Significant gaps still exist in human capacity and technological application to the management of fruit flies that need to be addressed. There is also need for capacity building in taxonomy for both the fruit fly pests and their host plant species. Although, the fragmented structure of horticulture across Africa has greatly impeded the application of area-wide IPM, there still exists the potential for implementation in targeted agroecological zones. The use of Sterile Insect Techniques (SIT), for instance, in isolated ecologies is an approach that could be exploited more (Ekesi et al. 2016). The expansion of research activities on postharvest treatments and the need for standardized treatment regimes is crucial. Therefore, long-term protection of African horticulture against new invasive tephritids should be as important as the short-term suppression of invasive pests that are already present in Africa.

Acknowledgements The *icipe*-led African Fruit Fly Programme (AFFP) received funding from GIZ/BMZ, Biovision, EU, and DFID for its activities.

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