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Tephritid Fruit Fly (Diptera: Tephritidae) Invasions in and out of Africa*

by

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Keywords. — Afrotropical; Tephritidae; Invasions.
Summary. — This paper briefly presents the impact of tephritid fruit flies on the horticultural activities in Africa. It reviews the major pest species of exotic invasive fruit flies that have been introduced accidentally into Africa from their native ranges, as well as tephritid species of African origin that became established in other parts of the world. Both the oriental fruit fly, *Bactrocera dorsalis* (Hendel), and the melon fly, *Zeugodacus cucurbitae* (Coquillett), belong to the first category, while the olive fruit fly, *Bactrocera oleae* (Rossi), and the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), belong to the second one. In addition, the current technical limitations with regard to detection and monitoring programmes are shortly discussed.

Trefwoorden. — Afrotropisch; Tephritidae; Invasies.
Samenvatting. — *Invasies van en naar Afrika van Tephritidae fruitvliegen (Diptera: Tephritidae).* — Dit artikel presenteert in het kort de impact van Tephritidae fruitvliegen (ook boorvliegen genoemd) op de tuinbouwactiviteiten in Afrika. Het geeft een overzicht van de belangrijkste pestsoorten van exotische invasieve fruitvliegen die accidenteel vanuit hun oorspronkelijk areaal zijn geïntroduceerd in Afrika, alsook Tephritidae van Afrikaanse origine die zich in andere delen van de wereld hebben gevestigd. Zowel de oosterse fruitvlieg, *Bactrocera dorsalis* (Hendel), en de meloenfruitvlieg, *Zeugodacus cucurbitae* (Coquillett), behoren tot de eerste categorie, terwijl de olijven fruitvlieg, *Bactrocera oleae* (Rossi), en de mediterrane fruitvlieg, *Ceratitis capitata* (Wiedemann), tot de tweede behoren. Daarnaast worden de huidige technische beperkingen met betrekking tot detectie en monitoring programma's kort besproken.

Mots-clés. — Afrotropical; Tephritidae; Invasions.
Résumé. — *Invasions des mouches des fruits téphritides (Diptera:Tephritidae) vers et venant de l'Afrique.* — Cet article présente brièvement l'impact des mouches des fruits téphritides sur les activités horticoles en Afrique. Il passe en revue les principales espèces nuisibles de mouches des fruits exotiques envahissantes qui ont été introduites accidentellement en Afrique à partir de leur aire de répartition indigène, ainsi que les mouches des fruits d'origine africaine qui se sont établies dans d'autres parties du monde. La mouche

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orientale, *Bactrocera dorsalis* (Hendel), et la mouche du melon, *Zeugodacus cucurbitae* (Coquillett), appartiennent à la première catégorie, tandis que la mouche de l'olivier, *Bactrocera oleae* (Rossi), et la mouche méditerranéenne des fruits, *Ceratitis capitata* (Wiedemann), appartiennent à la seconde. En outre, les limitations techniques actuelles concernant les programmes de détection et de surveillance sont exposées succinctement.

Introduction

Horticulture, and in particular the production of fruits and vegetables, is one of the most important industries in Africa, generating substantial income for a large majority of rural families. In Kenya for example, it generates one billion USD/year in foreign exchange through export, and more than six hundred and fifty million USD/year on the domestic market (Ekesi 2010, Irungu 2011). The South-African export industry of citrus, deciduous and subtropical fruits was considered worth 1.6 billion USD in revenues in 2014/2015 (DAFF 2016). In addition to providing a livelihood and generating income in the rural economy, the horticultural production also adds to nutrition balance and improvement (Ekesi *et al.* 2016).

The fruit industry, however, is threatened by a number of pathogens and pests, among which tephritid fruit flies (Diptera: Tephritidae) feature as one of the more important groups. Tephritid fruit flies is one of the most diverse dipteran families, including close to four thousand seven hundred species worldwide and about one thousand in sub-Saharan Africa (Pape *et al.* 2009). Their life history is largely phytophagous with about four hundred species being frugivorous, infesting a large variety of fruits (and vegetables that are biologically fruits such as tomatoes, pumpkins, eggplants, etc.). After copulation, fertilized eggs are laid by female flies inside fresh and undamaged fruits using a piercer-like ovipositor that can penetrate the outside peel or skin of the fruit. After hatching, the larvae develop inside the fruit passing through three larval instars, after which the mature larva leaves the fruit and pupates in the soil. The adult fly will emerge from the puparium and the cycle is repeated (White & Elson-Harris 1994).

Infestation can be considerable and average losses vary between 40-53 % on some crops (Ekesi *et al.* 2016). As such, fruit flies can have a devastating impact, and anticipated losses in Africa are estimated at two billion annually (Ekesi *et al.* 2016). Losses are not only due to direct crop reduction but also to embargoes by importing countries. After all, trade and shipment, as well as movement of people, can result in accidental spread and introduction of infested fruits. As such, exotic fruit flies can be introduced and, if conditions are suitable, become established in foreign regions. Over time Africa has experienced several introductions of alien fruit fly pests, which has aggravated the existing problems caused by indigenous pests. Moreover, African fruit flies have spread outside the continent through trade and movement.

This paper gives an overview of the major fruit fly pests that spread in and out of Africa, and what their respective impact entails. Some of these invasions are lost in time, while for others we have reliable historical data. We will also briefly discuss the mechanisms that form the basis of the increased tendency of fruit fly incursions, and see what measures can be taken to monitor these and how this can lead to prevent introductions.

Invasions Lost in Time

Some of the invasions in and out of Africa have taken place from time immemorial. Olives have been grown in the Mediterranean region for a very long time. The first traces of domestication of the olive tree date back to around 4000 BC, occurring in the East Mediterranean (BOARDMAN 1976, LUMARET *et al.* 2004). Cyprus is considered one of the first places where the tree was introduced after domestication in the Levant (probably on the border between Syria and Turkey), followed by intensive trade and cultivation in Hellenistic times. The Iberian Peninsula, on the other hand, is seen as the most recent region in southern Europe Mediterranean where olive trees were introduced. The olive tree as such is thought to originate from the African continent and wild forms are still found in several parts of eastern and southern Africa (PALGRAVE 1983, BEENTJE 1994).

One of the major pests of both wild and domesticated olives is the olive fruit fly, *Bactrocera oleae* (Rossi) (fig. 1). This species belongs to the subgenus *Daculus* Speiser within the genus *Bactrocera*. *Daculus* is an afrotropical subgenus, and comprises nine species, four of which including *B. oleae* are closely associated with Oleaceae (COPELAND *et al.* 2004) and are found on the African continent. In Kenya *B. oleae* is exclusively infesting wild olive *Olea europaea* ssp. *cuspidata* (Wall. ex G. Don) Cif. (COPELAND *et al.* 2004).

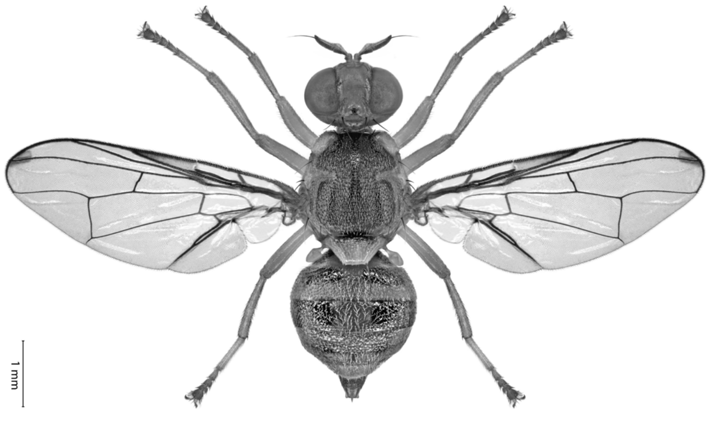

Fig. 1. — *Bactrocera oleae*, habitus image, dorsal view (© G. Goergen, IITA, reproduced with permission).

As such, *B. oleae* is considered to be of African origin. This is supported by the fact that: its hosts, the cultivated olive and its wild relatives, also appear to be of African origin (Besnard *et al.* 2007, 2009); its closest relatives are restricted to the afrotropical region (White 2006); and by the significantly greater genetic diversity in African olive fruit fly populations compared with European ones (Nardi *et al.* 2005). In Africa, it is mainly found in southern and eastern Africa (White 2006) with sporadic records from the Indian Ocean (White *et al.* 2001). Furthermore, it is found in the Mediterranean region, Pakistan, Mexico, and California and Hawaii (USA).

When exactly the olive fruit fly spread to the Mediterranean region out of Africa, is unknown. Population genetics research by Augustinos *et al.* (2005) discovered three subgroups in the Mediterranean populations: Cyprus, Greece+Italy+Turkey, and the Iberian Peninsula. They also observed a gradual decrease in heterozygosity from the eastern toward the western Mediterranean. They suggested that this was the result of historical variations in the dates when olive trees were domesticated and introduced into different parts of the Mediterranean. As such, *B. oleae* would have followed the westward expansion of the olive industry. An alternative scenario was presented by Nardi *et al.* (2010) who stated that the presence of wild olive trees in the Mediterranean pre-dated domestication, with diversification occurring at the start of the Pliocene between African and Asian lineages of wild forms of the olive tree which were a suitable host for *B. oleae*. Their mitogenomic data provide evidence for post-glacial arrival of wild olive trees in the Mediterranean region, rather than historical spread as a result of introduction of domesticated olive trees. In this scenario, the infestation of domesticated olives is the result of a host shift from wild to cultivated olives.

The invasion of *B. oleae* in Mexico and California is a recent phenomenon with the first record dating back to 1998 from Pacific Northern Mexico and Los Angeles respectively (Rice 2000, Nardi *et al.* 2005). The new developments in the olive industry in California (canning but increasingly also for oil; see Yokoyama 2012) have led to further dispersal of the pest within the state of California. The origin of the introduction into California appears to be from the eastern Mediterranean (Zygouridis *et al.* 2009, Nardi *et al.* 2010). The occurrence in Hawaii is a very recent introduction with first records dating back to August 2019 (Matsunaga *et al.* 2019). Currently it is found on two of the Hawaiian islands (Hawai'i and Maui).

The impact of the olive fruit fly on the olive industry is predominantly in the Mediterranean region, where more than 90 % of olive production is located (Mostakim *et al.* 2012), and where losses can reach 80-100 % (Katsoyannos 1992, Broumas *et al.* 2002). *Bactrocera oleae* is a stenophagous fruit fly attacking only *Olea* species. Damage worldwide is estimated at around eight hundred million US dollars annually in countries around the world where olives are grown (Manousis & Moore 1987, Montiel-Bueno & Jones 2002, Tzanakakis 2003). However, in Africa the commercial olive industry is limited and restricted to South Africa, where *B. oleae* is not considered a serious pest, probably due to the presence of natural enemies that keep it at bay (Hancock 1989, Costa 1998, Mkize *et al.* 2008).

Another fruit fly species for which the actual date of invasion into Africa is unclear is the melon fly or *Zeugodacus cucurbitae* (Coquillett) (fig. 2). This is an oriental species, probably originating from Central Asia or the Indian subcontinent (although the first specimens were collected and described from Hawaii) and spreading from there to other parts of the world (Virgilio *et al.* 2010, Wu *et al.* 2012). *Zeugodacus cucurbitae* is the only species of this genus found in Africa and no other close relatives are found in the region. All other African representatives of the Dacina belong to either *Dacus* or *Bactrocera* (White 2006). The genus *Zeugodacus* as such comprises about two hundred species from the oriental, Australasian and eastern Palaearctic regions (Doorenweerd *et al.* 2018) and was formerly considered as a subgenus of *Bactrocera*. Recently, it was given generic status (Virgilio *et al.* 2015, De Meyer *et al.* 2015).

Fig. 2. — *Zeugodacus cucurbitae*, habitus image, dorsal view (© G. Goergen, IITA, reproduced with permission).

Zeugodacus cucurbitae is widespread throughout Central and East Asia (including Pakistan, India, Bangladesh, Nepal, China, Indonesia and the Philippines) and Oceania (including New Guinea and the Mariana Islands) and became established in some areas of the Pacific (Dhillon *et al.* 2005). The first specimens from Africa date back to 1936 (initially from Tanzania and shortly afterwards from Kenya; see De Meyer *et al.* 2015). However, historical links between eastern Africa and the Indian subcontinent and Asia, date back to the 12th century. At that time, an intensive trade route existed between the so-called "Swahili culture" along the coastline from East Africa (from Somalia to Mozambique) and parts of Asia, exchanging various commodities which were transported by local boats, called "dhows"

(GILBERT 2004). For decades, the species was only recorded in East Africa (in particular Kenya and Tanzania) and appeared not to have dispersed any further although it was also recorded in the Mascarenes (Mauritius since 1942, Réunion some time before 1972; see WHITE *et al.* 2001). By the end of the 20th and early 21st century the species was, however, also encountered in a number of central and western African countries (DE MEYER *et al.* 2015), as well as the Seychelles (WHITE *et al.* 2001). In eastern Africa, the species dispersed and was recorded in Ethiopia, Sudan, Malawi, Uganda, Burundi and Mozambique (DE MEYER *et al.* 2015). It is unclear whether these new occurrences were the result of more intensive surveillance or due to actual dispersal and/or introduction into new areas within Africa. Because of limited interpopulation variability, molecular data obtained so far are inconclusive. Microsatellite studies (DELATTE *et al.* 2019) demonstrate that both the western and eastern African samples date back to the 20th century, but that western African ones were more recent. This seems to confirm the idea that the western African records have been reflecting intracontinental movement from eastern Africa in recent times. The exact pathways are, however, unknown.

Losses worldwide incurred by *Z. cucurbitae* are considered substantial (30-100 %, according to DHILLON *et al.* 2005) and several countries are trying to curb the spread of this pest, including through the sterile insect technique (SIT) which appeared successful in southern Japan (KUBA *et al.* 1993). In Africa, there is an ongoing effort on Mauritius to implement this technology for this and other invasive species. *Zeugodacus cucurbitae* as such is mainly a pest of several Cucurbitaceae plants, but can also infest non-cucurbit hosts (WHITE & ELSON-HARRIS 1994, DHILLON *et al.* 2005). In Africa, it is a major pest of economic crops such as cucumber, melon, pumpkin and watermelon (DE MEYER *et al.* 2015) but studies in Tanzania have shown that non-cucurbit hosts mainly belong to the Solanaceae and can be found with infestation rates and incidence much lower (MWATAWALA *et al.* 2009, MZIRAY *et al.* 2010).

Historical Invasions

The major species for which we have historical evidence of its spread is the Mediterranean fruit fly: *Ceratitis capitata* (Wiedemann) (fig. 3). The Mediterranean fruit fly belongs to *Ceratitis*, an afrotropical genus with approximately a hundred different species, and in particular to the subgenus *Ceratitis* s.s. It is found throughout the afrotropical region except in the driest areas such as the Namib and Sahara deserts (DE MEYER *et al.* 2008). Other subgeneric relatives are found in eastern or southern Africa (DE MEYER *et al.* 2004, MALACRIDA *et al.* 2007). In the mid-19th century, the species was introduced in the Mediterranean region (FIMIANI 1989) and it spread from there to other parts of the world, *i.e.* the Americas and Australia. However, it was never established in the oriental region. An overview of the first encounters outside the African mainland was given by Gasperi *et al.* (2002), White *et al.* (2001) and Papadopoulos (2014). The initial spread could be linked to the age of the naval supremacy of European nations, which coincided with colonialism of non-European territories and medical evidence that citrus fruits could curb scurvy. Scurvy was considered the number one cause of death among transcontinental naval voyages (Bown 2003). The Scottish physician James Lind published a treatise providing information on clinical trials to curb scurvy, and proposed citrus fruits as a possible remedy (Lind 1753). The provision of taking citrus rations on board became standard procedure by the British navy, and later on by other maritime nations at the end of the 18th century (Bown 2003). Actually, the type specimen of *C. capitata* was most likely collected on one of these naval voyages from Europe to India, by a Danish explorer on an intermediate stopover in Africa or in the Indian Ocean (De Meyer *et al.* 2004). It is plausible that the transport of citrus fruits has aggravated the spread of this pest to other continents.

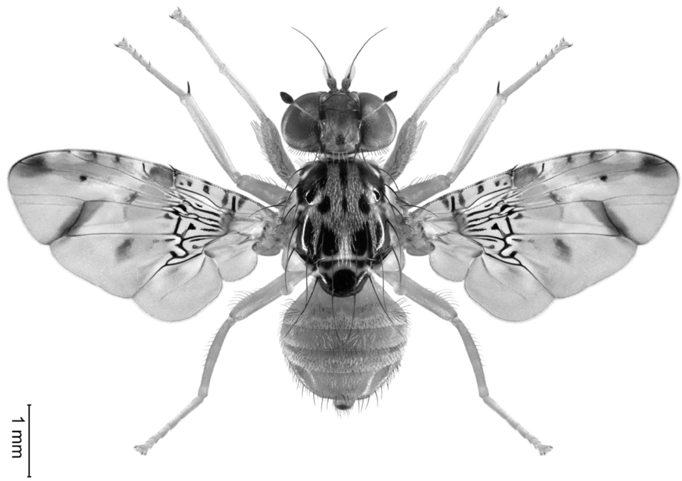

Fig. 3. — *Ceratitis capitata*, habitus image, dorsal view (© G. Goergen, IITA, reproduced with permission).

Ceratitis capitata is considered one of the most destructive fruit fly pests worldwide because of its extreme polyphagy (White & Elson-Harris 1994, Liquido *et al.* 2014) and its adaptability to different conditions (Yuval & Hendrichs 2000, Papadopoulos *et al.* 2001, Terblanche *et al.* 2010). In Africa it can cause tremendous losses in subtropical or temperate regions. In the Western Cape of South Africa alone, the estimated loss in value due to crop loss and control cost is about US 7.5 million each year (Barnes 2016), which has led to the establishment of an area-wide control programme in specific parts of the province, using the SIT (Enkerlin 2005, Barnes 2016). For most African countries, however, no exact figures on economic losses are available.

In 2003, an exotic *Bactrocera* species was discovered along the Kenyan coast (Lux *et al.* 2003). Initially it was considered a species new to science and described as *Bactrocera invadens* Drew, Tsuruta & White (fig. 4), based upon specimens from Africa and from the presumed area of origin, *i.e.* Sri Lanka (Drew *et al.* 2005). Recent research (Schutze *et al.* 2014a,b), however, concluded that *B. invadens* (as well as *B. papayae* Drew & Hancock) is synonymous with the oriental fruit fly, *B. dorsalis* (Hendel). The latter is of Asian origin, found throughout Central Asia and reaching Southeast Asia as well as southern China. It belongs to the subgenus *Bactrocera* s.s., and in particular to the *B. dorsalis* complex, a grouping of more than sixty species (Drew & Romig 2013).

Fig. 4. — *Bactrocera dorsalis*, habitus image, dorsal view (© G. Goergen, IITA, reproduced with permission).

After its initial discovery in Africa in 2003, *B. dorsalis* (under the junior synonym *B. invadens*) was rapidly reported from other parts of the African mainland, including areas far apart (Malavasi *et al.* 2013). Multiple introductions are a plausible explanation although the current information and pathway analysis are inconclusive (Khamis *et al.* 2009, Malavasi *et al.* 2013). In recent years, the southward spread has been well documented (Cugala *et al.* 2011, Manrakhan *et al.* 2015) and corresponds with the predictive models that were established (De Meyer *et al.* 2010, De Villiers *et al.* 2016).

Bactrocera dorsalis is currently considered the most important threat to fruit production in Africa. In addition, it has resulted in several export embargoes and quarantine restrictions that also have major implications for the fruit and vegetable industry and trade in Africa (Ekesi 2010, Cugala *et al.* 2013, Ekesi *et al.*

2016). Over the last few years, it also had a tremendous impact on several of the islands in the western Indian Ocean where it is now considered a major pest species and several actions are ongoing to aim at its eradication (SOOKAR *et al.* 2016). Its expansion into other areas outside sub-Saharan Africa is also seen as a major threat to the European fruit industry, especially as particular areas in the Mediterranean region are climatically suitable for the establishment of this pest (DE MEYER *et al.* 2010, DE VILLIERS *et al.* 2016).

Tendencies in Invasiveness

As mentioned earlier, the impact of invasive pests is dual: they cause direct losses through reduction in crop yields, but also indirectly by trade embargoes preventing export to other regions. International transport is actually the primary cause of unwanted introductions, especially as these introductions can become invasive pests when they become established, naturalize and spread (LIEBHOLD & TOBIN 2008). In recent decades the transcontinental movement of goods has increased tremendously because of higher demand in (sub)tropical and out-of-season fruits. In addition, fruits are introduced not only through commercial shipments but also in passenger luggage (LIEBHOLD *et al.* 2006). As a result, the number of alien fruit fly detections has increased for the past seventy years (PAPADOPOULOS 2014) increasing the risk of unwanted introductions. Additionally, climate change may accelerate the spread of these alien pests as certain parts can become more suitable for establishment, as shown through modelling (VERA *et al.* 2002, STEPHENS *et al.* 2007, NI *et al.* 2012).

Therefore, sound data on the current occurrence of fruit flies in Africa through monitoring programmes, as well as rapid detection and surveying programmes to quickly identify new intrusions, are required. The former will allow African growers to have those areas that are pest free recognized as such, according to internationally accepted rules and guidelines (ISPM 2015, 2017). This will facilitate international trade. Detection and monitoring actions will prevent a repetition of the disastrous introductions that the continent experienced in the recent past. Although these programmes are a costly undertaking, they are small in comparison with the economic loss that could be prevented. It is recommended that such programmes are not conducted solely at a national level, in order to be efficient, but that international collaboration and data exchange is stimulated. Fruit flies do not know any borders and measures taken by one country can be nullified by the lack of measures in a neighbouring country. Most activities in Africa, however, are largely conducted at a national level, although some regional initiatives (such as the West African Regional Programme) have been initiated.

A universal drawback is that all of these programmes rely on the attractiveness and sensitivity of specific or generic lures and traps. SHELLY (2014) reviewed the literature on this aspect and showed that for *C. capitata* and the use of trimedlure as an attractant, the minimum population size needs to attain a few thousand flies before there is a 99.9 % probability that it can be detected. As such there is the possibility that population size is at a sub-detectable level and this has consequences for eradication programmes (Papadopoulos *et al.* 2013). Currently, there is a heated debate whether invasive flies in areas like California maintain established populations despite eradication programmes, or whether these eradication programmes are successful and invasive species are reintroduced time and again (Carey *et al.* 2017, McInnis *et al.* 2017). Genetic tools could help in deciphering the origin of intercepted flies and tell whether the trapped individuals are direct descendants of individuals trapped at previous events or if they have a different origin.

Emphasis in the forthcoming years, therefore, should focus on stimulating international collaboration in surveillance activities, the development of more sensitive detection methodologies, and genetic tools to trace origin of intercepted fruit flies. As such, it is hoped that the African agriculture and horticulture can be supported in the control of one of the major pest groups found in the continent.

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