Global Invasion and Phenotypic Plasticity of The Asian Tiger Mosquito *Aedes* (*Stegomyia*) *Albopictus* (Skuse) (Diptera: Culicidae), An Invasive Vector of Human Diseases: Review of The Problem and The Evidence

Ahmed Tabbabi

Department of Hygiene and Environmental Protection, Ministry of Public Health, Tunis, Tunisia
tabbabiahmed@gmail.com

Abstract: The Asian tiger mosquito *Aedes* (Stegomyia) *albopictus* (Skuse) (Diptera: Culicidae) is an important vector of viral and parasitic pathogens including dengue and chikungunya viruses. It is actually known as the most threatening invasive species in the world. In recent years these mosquitoes have invaded and adapted to both tropical and temperate climes where have been responsible for large outbreaks of diseases. The success keys of their invasion and establishment are mainly their phenotypic plasticity and adaptation to different environments. Its ecological plasticity and its superior competitive ability were reviewed and discussed based on the available published and unpublished reports. The consequences of their invasion on public health are also highlighted. Further, control measure plans related to the management and diseases transmitted by this invasive vector species are also discussed.

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1. Introduction:

Aedes (Ae) albopictus mosquito is native to Asia and considered invasive since the 1980s due to the increase of its range in over 28 countries (Benedict et al., 2007). In addition to the ecological problems related to its global dispersion, the public health problems inherent in this vector are increasingly important. Indeed, *Ae. Albopictus* has the ability to transmit many arboviruses, including dengue fever and especially chikungunya. The ability of the tiger mosquito to transmit chikungunya and dengue to a lesser extent is well established. The epidemics of chikungunya and dengue in Reunion Island (2006), in the Indian Ocean (2006), in India (2007) in Italy (2007) are proof of these findings (Angelini et al., 2008; Halstead, 2007; Trop2008, 2008; Parola et al., 2006; Pialoux et al., 2007). In addition, its vector competence (experimental laboratory infections) has been demonstrated or suspected in relation to other viruses including yellow fever, Japanese encephalitis, West Nile, St. Louis encephalitis, Ross River, Mayaro, Rift Valley fever (Gubler, 2003).

Aedes albopictus is a mosquito with a great ecological plasticity characterized by a good adaptation to many environments, both adult and larval. Thus, it develops in the larval state in many types of containers, both artificial and natural (Hawley, 1998). Here we reviewed the problem and the evidence of the global invasion and the phenotypic plasticity of *Ae. Albopictus*, the invasive vector of human diseases. The available published and unpublished reports on the Asian tiger mosquito were collected and reviewed.

2. Global distribution of *Aedes Albopictus*:

Originally from Southeast Asia and the Indian Ocean, the tiger mosquito has spread worldwide since the late 1970s. International tire trade is at the root of its dispersion. An unsheltered tire receives rainwater that persists inside, creating an ideal developmental breeding. Eggs of *Ae. albopictus*, resistant and laid on the inner side of a tire can be disseminated all over the world and hatch thousands of kilometers from their original site (Simon et al., 2008). In Europe, where it was first detected in 1979 in Albania and then in 1990 in Italy, it is now well established in the northern part of the Mediterranean, from south-east Spain to Greece. Its presence has been proven since 1985 on the American continent where its introduction in Brazil and the United States were almost simultaneous (Sprenger, 1986; Forattini, 1986). During the 2000s, the tiger mosquito spread to North and sub-Saharan Africa, particularly in Nigeria, Cameroon, Equatorial Guinea and Gabon (Paupy et al., 2009; Bonizzoni et al., 2013; Tabbabi & Bekhti, 2017).

3. Public health implications:

Long considered a secondary vector in relation to *Aedes (Ae) aegypti*, the tiger mosquito has recently been identified as the main or only vector of Dengue epidemics in Hawaii, Asia and Africa (Bonizzoni et al., 2013; Tsuda et al., 2015). The tiger mosquito was also revealed to the general public as the main vector of chikungunya during the major epidemics that affected the islands of Reunion Island, Mauritius, Mayotte and Madagascar between 2005 and 2007, as well as in Central Africa (de Lamballerie et al., 2008; Paupy et al., 2009; Bonizzoni et al., 2013).

The important part taken by *Ae. albopictus* as a vector of chikungunya seems to be particularly due to a very worrying case of parallel evolution of the virus to a form particularly adapted to the species. Indeed, three independent events of substitution of an Alanine residue by a Valine took place at position 226 (A226V) of the E1 viral gene, ensuring the virus better replication and transmission by the tiger mosquito (de Lamballerie et al., 2008). Recently, this viral genotype has been recognized as responsible for a chikungunya outbreak in Thailand (Wanlapakorn et al., 2014); the spread of this new viral form in this country demonstrates that the global invasion of *Ae. Albopictus* can also have adverse consequences in territories where it is considered endemic.

4. Ecological Characteristics of *Aedes albopictus*:

It is known that the tiger mosquito originates from the forests of Southeast Asia (Hawley, 1988). Within its native range, however, the species is present in many tropical and temperate areas. *Aedes albopictus* is now often found in peri-urban and rural areas (Hawley, 1988; Paupy et al., 2009). Its presence in man-made environments is explained by the use of a wide variety of nesting sites both natural and especially artificial. This type of nesting site makes the tiger mosquito often found in areas of industrial activity or less active areas such as cemeteries (Paupy et al., 2009; Bonizzoni et al., 2013). However, unlike other anthropophilic species such as *Ae. aegypti*, the tiger mosquito is mainly found outside homes. Females favor dark (potentially rich in organic matter) and near-ground laying sites (Hawley, 1988; Williges et al., 2014).

When present, the human is today the main host on which the female *Ae. albopictus* performed its blood meal, which has been demonstrated by choice experiments or the analysis of the blood meal content of natural populations (Paupy et al., 2009; Bonizzoni et al., 2013). Human can, however, be easily replaced in the least anthropised areas (Sivan et al., 2015) and these analyzes also show that the host spectrum, which extends mainly to mammals, can also concern birds, amphibians and reptiles (Hawley, 1988; Paupy et al., 2009; Bonizzoni et al., 2013).

Several studies based on field recapture tagging experiments have estimated that the dispersion ability of *Ae. albopictus* are in the order of a few hundred meters (Hawley, 1988; Niebylski & Craig, 1994; Bellini et al., 2014; Liew and Curtis, 2004; Marini et al., 2010). The flight, practically close to the ground in this species, could in particular limit its dispersal capacities by the wind (Hawley, 1988). Thus, if the maximum measured distances reach 600 to 800 meters, most of the available data yield averages less than 400 meters.

In mosquitoes, competition is mainly in the larval stage. Numerous studies have clearly shown a benefit of *Ae. albopictus* compared to *Ae. aegypti*, the competition may have asymmetrical consequences (i.e. more severe for Ae. aegypti) on the survival of the adult and lead to the exclusion of this species from certain peri-urban and rural areas (Paupy et al., 2009; Bonizzoni et al., 2013; Alto et al., 2015). Other studies have also indicated a benefit of *Ae. albopictus* against *Aedes sierrensis* (Kesavaraju et al., 2014), *Culex quinquefasciatus* (Allgood and Yee, 2014) and *Culex coronator* (Yee and Skiff, 2014). However, the majority of this work concerns laboratory experiments; the complexity of the natural environment sometimes makes it possible to observe the co-existence of *Ae. albopictus* with other species including *Ae. aegypti* through the use of different micro-habitats, which can then vary the intensity and consequences of competition (Bonizzoni et al., 2013).

5. The general biological invasion process:

The successive stages of a biological invasion are therefore the introduction, establishment, expansion, and impact on the invaded ecosystem. We will examine these stages in order to better understand the process.

The transport of species can be ensured by natural phenomena such as the active flight of individuals, anemochoria (winds), zoochoria (animals), hydrochory (marine currents). However, cases of biological invasions where transport and introduction are human-made have proven to be faster, more dynamic and generally covering even larger geographical extents (Lockwood et al., 2013). Human has thus often introduced species voluntarily for food purposes (livestock or draft animals, fruits, vegetables ...etc.) (Reichard & White, 2001) or for recreation (hunting, fishing, ornamental plants) (Lockwood, 1999). But many introductions are accidental and are an indirect consequence of human activities such as the permanent transport around the world of thousands of marine species via cargo ballast whose content is released on arrival (Cariton & Geller, 1993). There are therefore many ways for a species to be transported far from its native range in a new ecosystem.

Once the species is introduced, it must be able to establish and spread. These stages are conditioned by the characteristics of the environment and those of the species (Lockwood et al., 2013). The species can only colonize an ecological niche favorable to its development; if the introduced zone has abiotic characteristics different from its zone of origin, it must show an ecological plasticity allowing it to adapt to its new environment. The colonized environment can be more or less receptive to the presence of the exotic species. It is recognized that disturbed environments facilitate invasions. Disturbances such as fires, agricultural abandonment, deforestation or urbanization (McKinney, 2006) can lead to changes in habitat and resource availability and thus create an opening ("window") that an invasive species endowed with certain characteristics may occupy (Johnstone, 1986). More generally, ecological disturbances in the environment are discrete events over time that disrupt the structure of ecosystems, communities or populations and modify resources, substrate availability or the physical environment (Lockwood et al., 2013). For example, deforestation can create colonization microsites that favor the establishment of pioneer species whose biological characteristics allow them to develop rapidly (Rejmánek & Richardson, 1996). Indeed, in these non-occupied habitats, the probability of a species being established is related to a high intrinsic rate of population growth that favors rapid colonization (Crawley, 1986). Some features of life history are thus linked to a high intrinsic rate of natural increase: rapid pre-imaginal development, early reproduction, or small size of individuals associated with low adult longevity (Pianka, 1970). Such a life strategy is advantageous in non-competitive environments, such as those created by ecological disturbances. These environments generally have a lower specific richness which decreases the biotic resistance of the habitat (Simberloff & Von Holle, 1999). Biotic resistance refers to the complex of predators, parasitoids, pathogens, and competitors present in the native community that can hinder the expansion of the newcomer and limit invasion (Crawley 1986; Levine et al., 2004). For example, in different islands, introduced populations of spiders never increase beyond their initial size due to the presence of predatory lizards that reduce their short-term survival and not because of the heterogeneity of the islands (Schoener & Spiller, 1995). However, the same mechanisms described above as likely to limit the expansion of the species can under other conditions facilitate it, when the effects on the local populations are more drastic than on the introduced populations (Bulleri et al., 2008).

The fourth stage of the biological invasion concerns the impact of this species on its ecosystem. This can be translated at different levels, ecological or economic as mentioned above, but also epidemiological if the species involved are of importance in public health (Reaser et al., 2007) as in our case study.

6. Importance of plasticity and adaptation in the success of the invasion of *Aedes albopictus*:

The invasive success of the tiger mosquito lies in the diversity of ecological traits of this species. The use of artificial spawning sites has contributed to its dispersal via the maritime trade of used tires, and mosquitoes have also been intercepted in the containers of "lucky bamboo", ornamental plants of the genus Dracaena, in the United States and the Netherlands from China (Madon et al., 2002; Schaffner et al., 2004). The success of this diffusion by artificial containers is also favored thanks to the possibility of its eggs to resist the unfavorable conditions during transport by quiescence or diapause. The diapause is certainly one of the major assets for the colonization of the temperate zones, allowing individuals to spend the winters in the form of a particularly resistant egg. The tiger mosquito could sometimes have a competitive advantage, allowing it to be maintained through replacement or cohabitation with local species.

This amplitude in the ecological niche of *Ae. albopictus* has sometimes been described as "ecological plasticity" (Delatte et al., 2008; Paupy et al., 2009; Porretta et al., 2012; Bonizzoni et al., 2013). However, this term fuzzes the biological processes responsible for the mosquito's suitability for the different environments in which it is present. Indeed, the features favorable to the invasion of the tiger mosquito correspond to the compilation of the observations made on a set of populations, and thus do not make it possible to distinguish which ones are really plastic of those which are the product of adaptation and therefore are a genetic polymorphism within the species.

Cases of phenotypic plasticity have been documented in *Ae. albopictus*. Vitek and Livdahl (2009) have shown that rainfall frequency (simulated by submersion) can modulate the time before hatching of eggs in a laboratory line. Thus, rare rainfall, which can be interpreted as an index of prolonged drought risk (probably exceeding the tolerance of the species), causes an early hatch in *Ae. albopictus*. Moreover, the photoperiodic regime can also induce a plastic response: in the United States, several populations showed an increase in development time with the duration of the day (Yee et al., 2012). It seems undeniable that the phenotypic plasticity of these traits contributes to the invasive potential of the mosquito, allowing it to be maintained in different environments. However, the standard of response, which is the magnitude of possible phenotypes from the same genotype, may exhibit adaptive variability, that is, the result of a selected genetic polymorphism in different environments (Lande, 2015).

The only known examples of adaptation, favoring the invasion of *Ae. albopictus*, are the seasonal diapause and resistance of eggs at negative temperatures, which are selected from populations in temperate environments (Hawley, 1988; Denlinger & Armbruster, 2014).

In the tiger mosquito, seasonal diapause is induced, only in susceptible populations, by the reduction of photoperiod as winter approaches. It is the adult female who perceives these signals and then produces a more resistant egg, having in particular important lipid reserves, and whose embryo will stop (or at least slow down strongly) its development at the stage of larva pharate (first stage) inside the chorion (Denlinger & Armbruster, 2014). The incidence of diapause, which corresponds to the proportion of eggs laid that actually initiate this alternative development, is then determined genetically and is correlated with the geographical origin of the populations. Hawley et al. (1988) have shown, for example, that under the same short-day diet, only populations from Japan, China, Korea and the United States, located at more than 25 ° north latitude, were able to lay eggs while tropical populations, closer to the equator (in Asia or the Indian Ocean), are unable to do so.

The same goes for acclimating eggs to the cold: exposing eggs to temperatures between 5˚C and 10˚C makes them more resistant when they are subsequently subjected to negative temperatures. However, this treatment does not have the same impact depending on the geographical origin of the populations, and unlike the temperate populations, eggs from tropical populations cannot survive at temperatures below -8˚C despite their acclimatization. (Hawley et al., 1988; Hanson & Craig, 1994).

Diapause and cold acclimatization can be considered independent: the first is induced in adults, the second in the egg stage, and acclimation of adults does not influence the cold resistance of their eggs (Hanson & Craig, 1994). However, the cold resistance of *Ae. Albopictus* eggs are maximized when these two processes are successively induced (Hanson & Craig, 1994).

While in Diptera local adaptation is often associated with the observation of clines along latitudes for features such as wing size, body mass or egg volume, only the incidence of diapause has been observed and clearly demonstrated in *Ae. albopictus* (Urbanski et al., 2012; Denlinger & Armbruster, 2014). The critical photoperiod, i.e. the daytime at which 50% of induced eggs enter diapause, is notably positively correlated with latitude and altitude in temperate *Ae. albopictus* populations (Focks et al., 1994).

Diapause can also be crucial when egg resistance limits are reached by quiescence, which can occur during long trips via shipping. Indeed, compared to *Ae. aegypti* in whom diapause is absent, non-diapausing eggs of *Ae. albopictus* are less resistant to desiccation-related stress (Sota & Mogi, 1992).

Recent high-throughput transcriptomic (RNAseq) analyzes have identified some of the molecular mechanisms involved in establishing and maintaining diapause at *Ae. albopictus* (Poelchau et al., 2013; Huang et al., 2015). Genes associated with the cytoskeleton, cubicular proteins, cell cycle or lipid metabolism thus have strong differences of expression between individuals induced or not for diapause. Another gene, pepck (phosphophenol pyruvate carboxykinase), involved in the transition from aerobic metabolism to anaerobic, appears as central in the diapause process (Poelchau et al., 2013). However, if these mechanisms begin to be elucidated, the genetic polymorphism (s) responsible for adaptive variation within populations remains unknown.

7. Control measures for *Aedes albopictus*:

The effectiveness of vector control depends essentially on the global consideration and the systematic elimination of all factors favoring the development of the vector. Thus, it is necessary to set up an integrated device to tackle all stages (aquatic and aerial) of the mosquito. For *Ae. albopictus*, a key element is the search and destruction of potential breeding sites. Indeed, an adequate development of the living environment can significantly reduce the population of this mosquito, particularly in urban areas (Delatte et al., 2008). It is therefore imperative to remove all elements that may contain stagnant water, both inside and outside the home. It is also important to ensure the proper flow of rainwater and wastewater and regularly clean gutters, manholes, and gutters. Finally, when necessary, the water tanks must be covered with a mosquito net.

However, it is often impossible to remove all lodgings. It is then necessary to use larvicidal or adulticidal insecticides. Larvicides will, of course, be applied to potential breeding sites while adulticides may be sprayed over a much larger area. The intensive use of these products quickly leads to the emergence of resistance in the larvae (Pinheiro & Tadei, 2002), leading to decreasing efficacy. Thus, many mutations in the acetylcholinesterase sequence are able to inhibit the mode of action of organophosphate insecticides.

Generally, it is still necessary to spray adulticide insecticides, because this is the only method allowing rapid and massive elimination of adults. It is most often an emergency measure during an epidemic. For this method to be effective, it is recommended to perform treatments every two to three days in ten days. In addition, in order to limit the appearance of resistance, it is recommended to use insecticides from different families alternately.

Despite these recommendations, the development of resistance is inevitable (Hamdan et al., 2005), such as the recent demonstration of the kdr mutation, which gives *Ae. albopictus* resistance to pyrethroids (Sawabe et al., 2010). These resistances are found all over the world, hinder the fight against vector and hinder the development of new insecticides. It, therefore, becomes urgent to develop alternative control methods.

Several avenues are under study, with encouraging results for some of them. The technique of the sterile insect consists of producing *Ae. albopictus* males and releasing them massively into the environment after having sterilized them with mutagenic agents. Since each female is fertilized only once, the copulation of these sterile males with females of wild phenotype results in the laying of unfertilized eggs (Oliva et al., 2013). This technique is currently being tested in the state of Bahia in Brazil on the species *Ae. aegypti* (Le monde, 2014) but could be easily adapted to *Ae. albopictus* because of a greater capacity of the latter to be produced in the laboratory (Carvalho et al., 2014).

Other techniques are still being studied, such as the use of an endosymbiont mosquito of the genus *Aedes*: Wolbachia. This bacterium is naturally present in certain mosquitoes and is known to manipulate the reproduction of *Aedes*. The presence of this bacterium in the salivary glands of mosquitoes has been associated with a decrease in the transmission of dengue virus (Bian et al., 2010; Mousson et al., 2012) and chikungunya (Slatko et al., 2014) by these insects. This would be a way to limit the transmission of arboviruses to humans without the vector population being affected. However, investigations should continue to better clarify the interrelationships between bacteria, vectors, and viruses before considering the use of this endosymbiont in the fight against arbovirus transmission.

Corresponding Author:
Ahmed Tabbabi, Ph.D.
Department of Hygiene and Environmental Protection, Ministry of Public Health, Tunis, Tunisia.
E-mail: tabbabiahmed@gmail.com

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