

Geographical Distribution of Arboviruses, *Aedes aegypti* and *Aedes albopictus* Vectors and Their Resistance to Insecticides in Africa: A systematic Review

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Abstract

Background & Objectives: Epidemics of arboviruses such as Dengue, Chikungunya and Zika have been recorded in recent years indicating that *Aedes aegypti* and *Aedes albopictus* are both important and very active vectors in Africa. For vector control, insecticides are on the front line, unfortunately, reported resistance jeopardizes the effectiveness of this strategy. The objective of this review was to determine the geographical distribution and insecticide resistance mechanisms of *Ae. aegypti* and *Ae. Albopictus* in Africa. **Methods:** A systematic review of the literature in scientific databases (PubMed, Google Scholar, ScienceDirect, Hinari) allowed us to identify relevant articles on the geographical distribution of *Aedes aegypti*, *Aedes albopictus* and arboviral diseases. On the other hand, studies related to insecticides used in vector control against *Aedes*, associated resistances and their molecular and metabolic mechanisms. **Results:** A total of 94 studies met the inclusion criteria for this search. *Aedes aegypti* is reported in most of Africa, and *Aedes albopictus* in part. There is a re-emergence and outbreak of Arbovirus epidemics in West and Central Africa. The insecticides used were organochlorines, carbamates,

organophosphates and pyrethroids. In *Aedes*, target site insensitivity and metabolic resistance would be the 2 main mechanisms of resistance to these insecticides. **Interpretation & Conclusion:** Resistance has been recorded in all four major classes of insecticides recommended by WHO for vector control and eradication. New vector control methods such as the use of plant extracts with larvicidal and adulticidal activities, advanced modern biotechnology techniques, and nanobiotechnology need to be developed.

Keywords

Aedes, Arbovirus, Insecticide Resistance, Molecular and Metabolic Mechanisms, Africa

1. Introduction

Worldwide, more than 5 billion people live in areas at risk of arbovirus infection [1]. These arboviral diseases are transmitted by hematophagous mosquitoes such as *Aedes aegypti* (Linnaeus, 1762) and *Aedes albopictus* (Skuse 1894) which are the major vectors involved in the transmission of arboviruses such as dengue virus, yellow fever virus, Zika virus, chikungunya virus and Rift Valley fever virus [2]. In Africa, *Aedes aegypti* remains the main vector of arboviruses, some of which are now re-emerging viral diseases [3]. *Aedes aegypti* is characterized by diurnal and twilight activity. It is also most often identified in the larval stage in breeding sites such as water containers like buckets, cans, pots, barrels and used tires [4]. The dengue virus (DENV), belongs to the genus *Flavivirus*, and to the family *Flaviviridae*. It has four distinct serotypes: DENV-1, DENV-2, DENV-3 and DENV-4. Chikungunya and Rift Valley fever viruses belong to the *Alphavirus* (*Togaviridae*) and *Phlebovirus* (*Bunyaviridae*) genera respectively. The Zika and yellow fever viruses are *Flaviviruses* [5].

Worldwide, according to the WHO, nearly 4 billion people are at risk of dengue infection, 96 million of whom present clinical manifestations per year [6]. In addition, 500,000 dengue carriers with warning signs or severe dengue should be hospitalized. Dengue causes nearly 20,000 deaths every year [6] [7]. Dengue has been recorded in 34 countries in Africa over the past decades [8]. West Africa has been identified as a potential dengue hotspot because of the rapid growth of urban areas without proper sanitation that creates large areas in which *Aedes aegypti* vector proliferates [2] [9].

Concerning yellow fever, each year nearly 200,000 cases and 30,000 to 60,000 deaths are recorded around the world. Yellow fever cases have increased over the past two decades due in part to deforestation, urbanization, population movements and climate change [10].

Arbovirus infections are usually asymptomatic and have similar clinical symptoms (fever, nausea, vomiting, joint pain, rash, headache) [11]. However, there are cases of severe or haemorrhagic dengue characterized by nosebleeds, and vomiting

of blood [12]. People infected with the yellow fever virus can develop severe visceral disease with a mortality rate of 20% - 60% [13]. Severe cases of Zika virus infection and death are rare, but microcephaly in babies born to women infected during pregnancy [14]. Rift Valley fever virus infection can lead to a bleeding syndrome.

There are no specific prophylaxis options for these diseases; treatment is often symptomatic. Thus vaccination could be one of the ideal methods of prevention but vaccines are not available for all these viruses. Only the yellow fever vaccine (YF-Vax, Stamaril) has been available and widely used for years. Progress has been made in the development of vaccines against dengue viruses [15]. For example, the first licensed dengue vaccine, CYD-TDV (Dengvaxia[®]), has been registered in several countries but is not yet widely used. Furthermore, transmission is not interrupted during the human infection phase. For this reason, control and prevention programs have been set up to stop the chain of development and propagation of vectors [16]. Hence the use of insecticides in vector control is one of the preventive measures [17]. Unfortunately, the use of agrochemicals can contribute to the emergence of vector resistance to insecticides [18]. A good knowledge of the bio-ecology of vector species is essential for the implementation of a vector control strategy. In addition, control cannot be successful without adequate information on the susceptibility of vectors to insecticides.

Vectors have developed resistance to most insecticides used in public health [19] [20]. This has created problems in vector control programs in many countries. Information on insecticide resistance is, therefore, of paramount importance when considering tools or approaches for the control of arboviral diseases, but data for Africa are patchy. In addition, arboviruses pose an increasing threat to public health in low- and middle-income countries, in endemic areas, and place a strain on health systems in affected countries in the event of an epidemic. Epidemics occur worldwide but are mainly in tropical and subtropical areas, especially in crowded urban and semi-urban areas.

Thus, the aim of this review was to determine the geographical distribution of *Aedes aegypti* and *Aedes albopictus*, and of arboviruses transmitted to humans, and then to identify the different types of insecticides used and the possible resistance (metabolic or molecular) linked to their use in Africa.

2. Methodology

2.1. Data Search Strategies

A systematic review of the literature was conducted during the period from 2000 to 2021. The search was performed in English and/or French in the databases: Pubmed, Google Scholar, ScienceDirect, Web of Science, and Hinari. The key search terms used were “*Aedes aegypti*” AND/OR “*Aedes albopictus*” AND “Names of all African countries”. We also searched for studies that focused on arboviral diseases by associating the names of these arboviruses. Articles on the mechanism of resistance of *Aedes* to insecticides were also searched using:

“Aedes” AND “insecticide” AND “resistance”. A filter was used to limit the search to keywords in the title and/or abstract of the articles [PubMed: (tiab); Google Scholar: Allintitle and Science Direct: TITLE-ABSTR-KEY].

2.2. Data Processing

The data were exported into Endnote software, duplicates were eliminated. A review of the titles by two independent reviewers resulted in a first selection of eligible articles. The reading of the abstracts of these eligible articles constituted the second level of selection and the articles without abstracts or presenting irrelevant data were then eliminated. The review of the full texts finally allowed the final selection of the studies included in this review. Differences between the two independent reviewers were resolved by the intervention of a third person or through discussions to reach a consensus. **Figure 1** presents the data selection strategy.

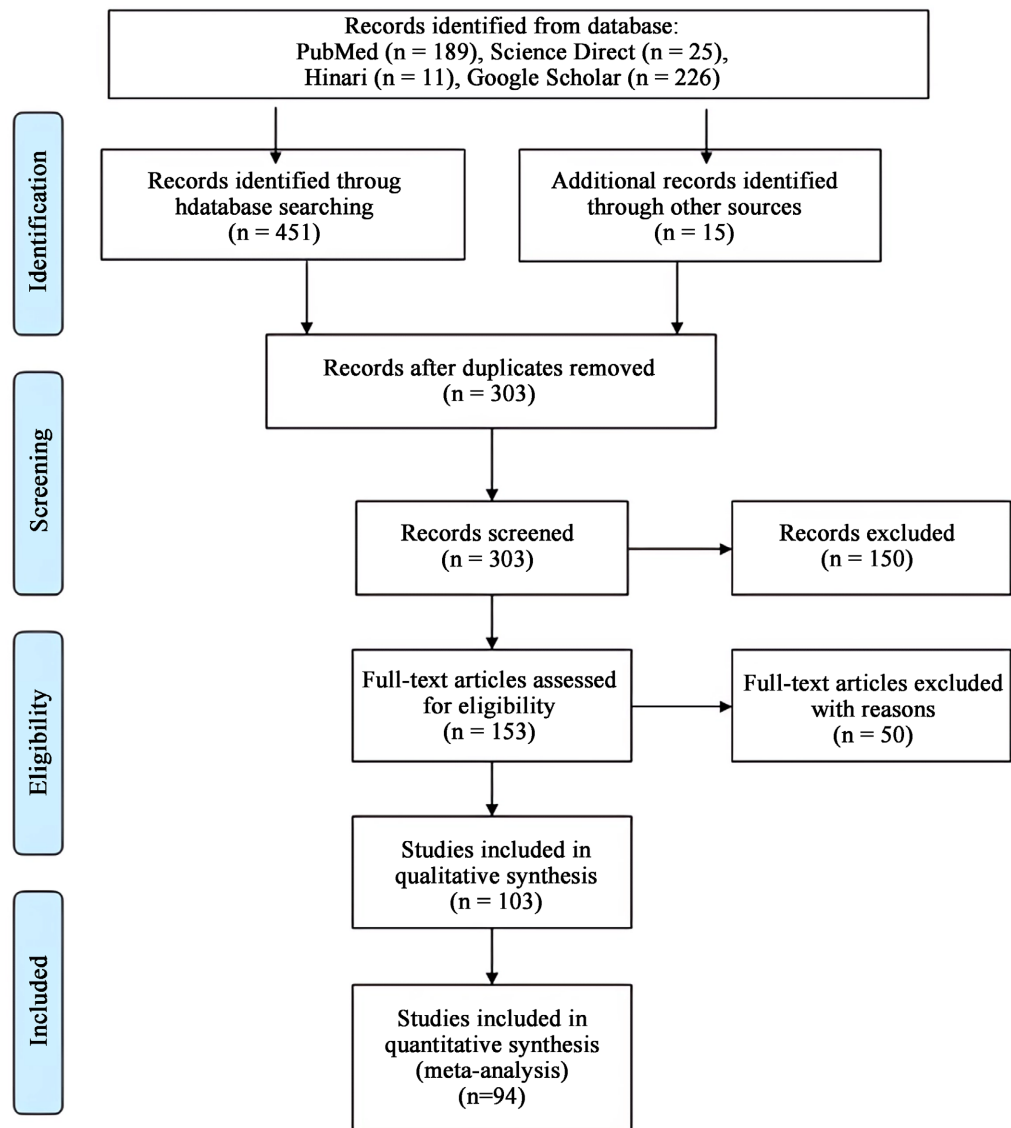


Figure 1. PRISMA.

2.3. Data Extraction and Analysis

Information such as author, country, years of arboviral disease outbreaks, insecticide susceptibility or resistance, and resistance mechanisms were extracted from the articles selected for review.

3. Results

3.1. Search Results in Figure 1

Figure 1 shows a flow diagram of the process for selecting studies included in the systematic review according to PRISMA.

3.2. Geographical Distribution of *Aedes* in Africa

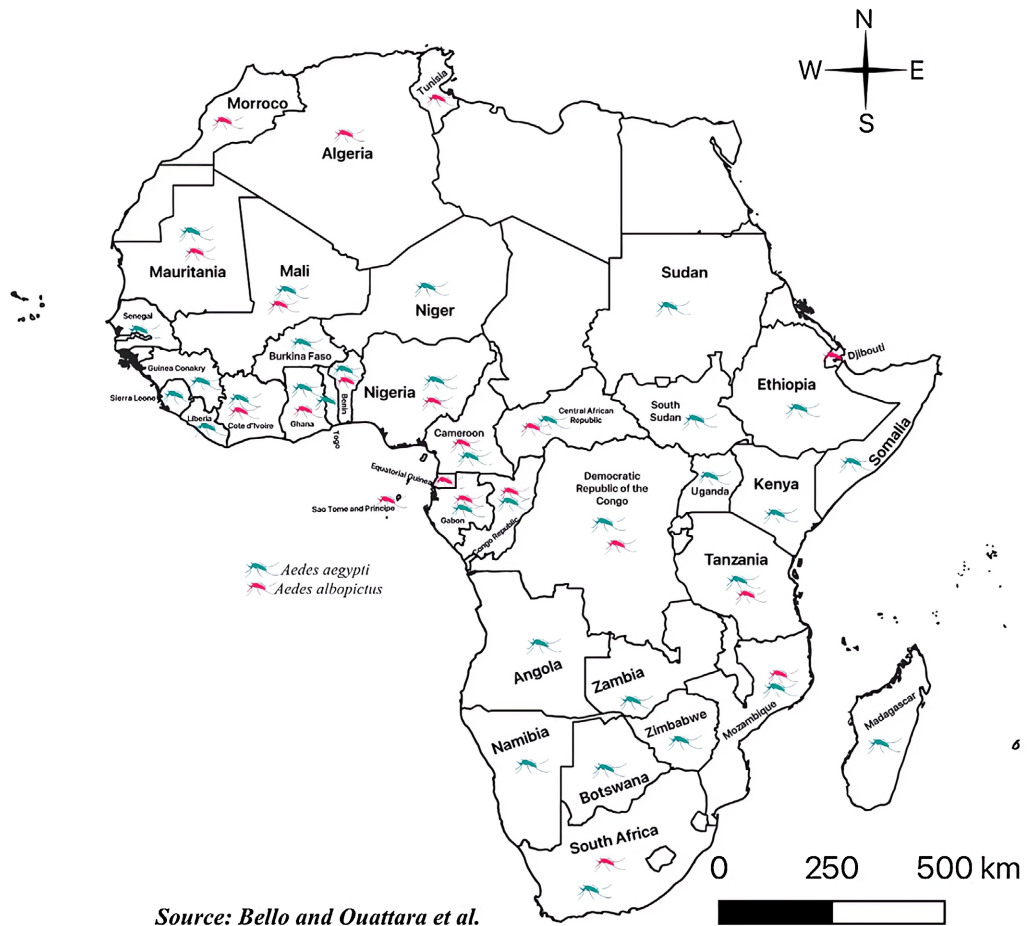
The vectors *Aedes aegypti* and *Aedes albopictus* are two major vectors of arboviruses [21]. *Ae. aegypti*, is native to sub-Saharan Africa from a wild and zoophilic ancestral species named *Ae. aegypti formosus* [22]. *Aedes albopictus* is native to Southeast Asia, the Indian Ocean islands and the Western Pacific and has subsequently spread to Africa through human activities and transportation [23]. Both species are well represented on almost the entire African continent with high density in West and Central Africa due to the tropical and subtropical climate [2]. **Figure 2** shows the geographical distribution map of *Aedes aegypti* and *Aedes albopictus* in Africa.

3.3. Diseases Transmitted by *Aedes* Mosquitoes According to Geographical Areas

Africa is the ancestral home of yellow fever, chikungunya and Zika viruses and probably of dengue virus, although this is less clear [3]. An African origin of yellow fever has been confirmed after molecular analyses of the virus genome dating back at least 1500 years [24]. CHIKV was first isolated in Tanzania in 1952 [25] and has spread widely in Asia [26]. As for Zika virus, it was first isolated in Uganda in 1947 from a monkey and *Aedes africanus* in the Zika forest near Entebbe [27]. Rift Valley Fever virus was first isolated in 1931 from sheep on a farm in the Rift Valley of Kenya. In recent years a re-emergence and outbreak of chikungunya, dengue, yellow fever, and Zika viruses have been reported in West and Central Africa [28]. Mathematical models can be used to predict dengue epidemics [29]. **Table 1** shows the countries where sporadic cases and epidemics have been reported.

3.4. Status of Insecticide Resistance in *Aedes* Mosquitoes in Africa

The most common chemical methods used in vector control are indoor residual spraying (IRS), larvicides, space treatments and long-lasting insecticide-treated nets [76]. The four classes of insecticides recommended in vector control by WHO are pyrethroids, organophosphates, carbamates and organochlorines [77]. These insecticides can be used for indoor residual treatments [78]. Pyrethroids



Source: Bello and Ouattara et al.

Figure 2. Map showing the distribution of *Aedes aegypti* and *Aedes albopictus* in Africa.

Table 1. African countries where arboviral diseases have been reported in recent years.

Virus	Countries	Years	Authors
Zika	Angola	2017	[30]
	Cape Verde	2015, 2016	[31]
	Gambia	2007	[32]
	Gabon	2007	[33]
	Mali	2011	[32]
	Senegal	2007, 2011, 2012	[32]
Chikungunya	Ethiopia	2019	[34]
	Cameroun	2006	[35] [36]
	Congo	2011, 2019-2019	[37] [38]
	Djibouti	2019	[39]
	Gabon	2007, 2010	[40] [41]
	Kenya	2004, 2006, 2018	[42]

Continued

	Sierra Leone	2012	[43]
	Senegal	2009, 2010, 2015	[44]
	Soudan	2005	[45]
Dengue	Angola	2013, 2015, 2016	[46] [47] [48]
	Benin	2019	[49]
	Burkina Faso	2016, 2017	[50] [51]
	Ivory Coast	2017, 2019	[52] [49]
	Ethiopia	2018, 2019	[53]
	Gabon	2007, 2010	[54]
	Kenya	2011, 2013, 2014, 2017	[55] [56]
	Mali	2019, 2020	[49]
	Mauritania	2019	[49]
	Mozambique	2014	[57]
	Senegal	2009, 2017, 2018	[58]
	Seychelles	2015, 2020	[53]
	Soudan	2004, 2015	[59] [60]
	Tanzania	2014, 2018-2019	[61]
Yellow Fever	Angola	2015-2016	[62]
	Cameroun	2017-2021	[63]
	Congo	2015-2016	[62]
	Ivory Coast	2001-2003, 2010, 2011	[64]
	Ethiopia	2013	[65]
	Ghana	2021	[66]
	Guinea	2000-2001, 2008, 2009	[67] [68]
	Liberia	2004	[69]
	Nigeria	2018, 2020, 2021	[70]
	Senegal	2020	[71]
	Sierra Leone	2011	[72]
	Soudan	2005, 2011, 2012	[45] [73] [74]
	Uganda	2010, 2011, 2016, 2019	[49]
	Togo	2020	[75]

are used for the treatment of nets [76] as well as adult mosquito populations [79] [78]. Organophosphates, temephos, metrophene and *Bacillus thuringiensis israelensis* (Bti) are used for larvae control and space treatment [80]. The different uses of these insecticides have allowed to slow down the proliferation of *Aedes*

mosquitoes, to protect populations against arboviral diseases and to reduce their incidence. Unfortunately, in the last few years an outbreak and re-emergence of these diseases have been observed [81]. This upsurge could be explained by the resistance of vectors to certain classes of insecticides reported worldwide. Strains of *Ae. aegypti* and *Ae. albopictus* have become resistant to certain insecticides such as DDT, probably because the latter has been used for a long time as a pesticide in agriculture [82] and this resistance is a serious problem [83]. In Africa, after research on insecticide bioassays in accordance with the standard WHO protocol, it has been reported that mosquitoes are resistant to insecticides of the pyrethroid, organophosphate, carbamate and organochlorine classes [84] [85]. Insecticide use and induced mutations vary from country to country (Table 2).

For example, in South Africa, no *kdr* mutations were detected in the *Aedes* populations sampled, so (provisional) resistance to DDT and pyrethroids could be of metabolic origin or linked to another mechanism [86].

In Angola, a significant association between resistance phenotypes and genotypic frequencies for the V1016I and V410L mutations (located in domain I of segment 6 of VGSC) was found in Luanda but not for F1534C (domain IV of VGSC). The V1016I and V410L mutations significantly increase resistance to pyrethroids and deltamethrin [87].

In Benin, a study conducted in the North in the department of Atacora, which is an agricultural area where farmers use several types of pesticides without respecting the recommended doses [88] determined the effect of the following insecticides: permethrin, deltamethrin, lambda-cyhalothrin, DDT and bendiocarb on *Aedes*. This study, which was carried out in urban and rural areas, reported a resistance to DDT and pyrethroids, with an average mortality rate of 12% and 38% respectively, regardless of the mosquito's area of origin, but they remain sensitive to bendiocarb [89].

In Burkina Faso, studies have shown high levels of resistance to some insecticides. A study conducted in the capital city of Ouagadougou indicates that *Aedes*, an important vector of arboviruses, is resistant to pyrethroid and carbamate insecticides, but remains susceptible to organophosphates with the presence of the V1016I *kdr* mutation and a very high frequency of the F1534C *kdr* allele [90]. Other studies have also reported resistance of *Aedes aegypti* to deltamethrin (pyrethroids) and bendiocarb carbamates in other cities as well [91] [92]. These resistances were associated with high activity of non-specific esterases and glutathione-S-transferases, suggesting the existence of multiple resistance mechanisms [92]. Badolo *et al.*, reported pyrethroid resistance and high levels of *kdr* F1534C, V1016I mutations in urban and semi-urban sites with overexpression after analysis of P450 family genes [93].

In Cape Verde the strains tested were highly resistant to DDT [94]. Resistance to deltamethrin and temephos was reported, this was the first report of temephos resistance in an African population of *Ae. aegypti*. Enzymatic analysis performed in 2012 revealed a high metabolism of oxidase, glutathione S-transferases (GSTs)

and esterase detoxification but no significant changes in 2014. Resistance mutations at the target site were not detected [95].

In Cameroon, *Aedes aegypti* mosquitoes were resistant to DDT, permethrin and deltamethrin and three *kdr* mutations, F1534C, V1016G and V1016I were detected. The P450s genes, *Cyp9J28*, *Cyp9M6*, *Cyp9J32* and *GSTD4* were overexpressed [96]. It has been reported that GSTs as well as P450 genes are involved in pyrethroid resistance with the F1534C *kdr* mutation detected in locations where *Aedes* is resistant to pyrethroids [96] [97].

In the Central African Republic, possible resistance to deltamethrin and DDT was observed in *Ae. aegypti* and *Ae. albopictus*, although some strains were susceptible. No *kdr* mutations were detected in either species; however, detoxifying enzyme activity was higher in most populations than in the susceptible *Ae. aegypti* strain [98]-[100].

In Congo, resistance was observed against the organochlorine DDT, pyrethroids, and carbamates. The primary role of cytochrome P450 monooxygenases in resistance has been reported. None of the genotyped specimens of *Ae. aegypti* or *Ae. albopictus* possessed the 1534C allele, suggesting that this mutation is not currently involved in pyrethroid resistance in populations of these two species in Congo [100].

In Côte d'Ivoire, all *Ae. aegypti* populations showed probable resistance to propoxur and is associated with acetylcholinesterase (AChE) activity. The resistance to propoxur could be due to the intensive use of insecticide sprays containing this molecule as an individual and collective protection measure against mosquitoes [101]. White females have an ability to overproduce detoxifying enzymes to metabolize propoxur molecules before they exert a toxic effect on the target [102]. Three *kdr* mutations (V410L, V1016I, and F1534C) were present in the populations tested and some of the pyrethroid resistance can be attributed to the presence of mutations [103].

In Congo, all populations showed resistance to permethrin and propoxur but were sensitive to deltamethrin. Both *Ae. aegypti* and *Ae. albopictus* were also shown to be susceptible to organophosphates (temephos and fenitrothion). The *kdr* F1534C mutation was not detected in either species, the observed resistances would not be due to the *Kdr* mutations [100].

In Ghana, results showed high phenotypic resistance to Dichlorodiphenyltrichloroethane (DDT) and pyrethroids. Probable resistance to carbamates and organophosphates was also detected at some sites. A high frequency of point mutations in the voltage-dependent sodium channel (F1534C and V1016I) was detected in resistant and susceptible *Aedes aegypti* [104]. Resistance to DDT and pyrethroids in the Ghanaian population of *Ae. Aegypti* may be due to the F1534C mutation [105] [106].

In Gabon, studies have shown that one population of *Ae. aegypti* (Libreville) and two populations of *Ae. albopictus* (Buea) studied were resistant to DDT [98].

In Nigeria, the *Aedes aegypti* population in Lagos State, developed resistance to

DDT and permethrin, P450 and GST activities were implicated in DDT and permethrin resistance in this study [107]. The presence of *kdr* F1534C, S989P, and V1016G mutations was also determined among resistant populations using molecular methods. A high level of resistance to DDT and pyrethroids was recorded in *Aedes aegypti* in another study, although probable resistance to deltamethrin was reported in one site [108].

In Senegal all populations collected were resistant to DDT and carbamates [94]. This resistance is a direct consequence of previous vector control programs widely applied in the country. Pyrethroid resistance is due to significant overexpression of detoxification genes related to insecticide metabolism. Three cytochrome P450s genes (CYP6BB2, CYP9J26 and CYP9J32) were found to be significantly overexpressed [80].

In Tanzania, *Ae. aegypti* populations at most sites in Dar es Salaam are fully resistant to permethrin and lambda-cyhalothrin, while deltamethrin has shown probable resistance [109] [110] (Table 2).

Table 2. Susceptibility and resistance of *Aedes* species to insecticides in Africa.

Countries	Town	Species	Insecticide susceptibility and resistance	Studies
South Africa	Johannesburg	<i>Ae. Aegypti</i>	Bendiocarb (S, PR) DDT (PR, R) Deltamethrin (S, PR) Pirimiphos-methy (PR, R)	[86]
Angola	Louanda, Huambo	<i>Ae. aegypti</i>	Permethrin 0.75% (R, PR) Deltamethrin 0.05% (R, S)	[87]
Benin	Natitingou	<i>Ae. aegypti</i>	Pyretroid I (R) Deltaméthrine (R) Bendiocarb (S) Organosphates (R) Carb(S)	[89]
Burkina Faso	Ouagadougou Bobo-Dioulasso	<i>Ae. aegypti</i>	Permethrin 0.75% (R) Deltamethrin 0.05%, (R) Malathion 5% (S, R) Fenitrothion 1% (S) Bendiocarb 0.1% (S, R) Propoxur 0.1% (R) Chlorpyrifos-methyl 0.4% (S) Temephos (S)	[90]-[93]
Cape Verde	Praia,	<i>Ae. aegypti</i>	DDT 4% (R) Fenitrothion 1% (S) Propoxur 0.1% (PR) Deltamethrin 0.05% (S) Lambda-Cyhalothrin 0.05% (S) Permethrin 0.75% (S) Temephos (S, R) Bti (S)	[87] [94] [95]

Continued

Cameroun	Yaounde, Douala, Widespread	<i>Ae. aegypti</i> <i>Ae.</i> <i>albopictus</i>	PyretroidI (S) PyretroidII (S, R) DDT 4% (PR, R) Organosphates (S) Carb (R, S) Temephos (S) Bti (S) Deltamethrin 0.05% (R, S) permethrin 0.75% (R, S) Bendiocarb 0.1% (R, S)	[96]-[98] [112]
	Central African Republic	Bangui	<i>Ae. aegypti</i> <i>Ae.</i> <i>albopictus</i>	PyretroidIII (S, RS) DDT (R, PR) Organosphates (S) Carb(S) Temephos (S) Bti (S)
Ivory Coast	Abidjan	<i>Ae. aegypti</i>	PyretroidII (PR, S) DDT 4% (R) Deltamethrin 0.05% (S, PR) Permethrin 1% (S) Malathion 5% (S) Propoxur 0.1% (R, S) Fenitrothion 1% (R) Lambdacyalothrin 0.05% (S) Chlorpyrifos-methyl 0.8% (S)	[101]- [103]
Congo	Brazzaville, Lefini	<i>Ae. aegypti</i> <i>Ae.</i> <i>albopictus</i>	PyretroidI (R) PyretroidII (S) DDT 4% (R) Propoxur à 1% (S, R) Fénitrothion à 1%. (S) Temephos (S)	[100]
Gabon	Libreville	<i>Ae. aegypti</i> <i>Ae.</i> <i>albopictus</i>	PyretroidII (S) Organosphates (S) Carb(S) Temephos (S) Bti (S) Deltamethrin 0.06% (R) DDT 4% (R) Propoxur 0.3% (S) Fenitrothion 0.5% (S) Temephos (S)	[98]
Ghana	Accra, Widespread	<i>Ae. aegypti</i> <i>Ae.</i> <i>formosus</i>	PyretroidI (R, PR, S) PyretroidII (R) DDT 4% (R) Permethrin 0.75% (S, R)	[52] [105] [106] [113]
Senegal	Dakar	<i>Ae. aegypti</i>	DDT 4% (R) Fenitrothion 1% (S) Propoxur 0.1% (PR)	[94] [80]

Continued

			Deltamethrin 0.05% (PR) Lambda-Cyhalothrin 0.05% (S, PR) Permethrin 0.75% (S, R) Malathion 5% (S) Temephos (S, R) Bti (S) PyretroidII (PR, S) DDT (R) Organosphates (PR, R) Carb(S)	[114]
Soudan	Port Soudan	<i>Ae. aegypti</i>		
Mayotte	Petit Terre	<i>Ae aegypti</i>	PyretroidII (S)	[115]
	Kaweni	<i>Ae albopictus</i>	Temephos (S) Bti (S)	[115]
Nigeria	Lagos, Kwara State	<i>Ae. aegypti</i>	PyretroidI (S)	[107]
			PyretroidII (PR, S)	[108]
			DDT 4% (R, S) Carb(R)	[116]- [118]
			Permethrin 0.75% (S, R)	
Tanzania	Dar es Salaam	<i>Ae. aegypti</i>	PyretroidI (R, PR) PyretroidII (R, PR)	
			Deltamethrin 0.05 (R)	[109]
			Permethrin 0.75% (S, R)	[110]
			Lambda-cyhalothrin 0.05% (S) Bendiocarb (R)	

According to WHO recommendations, mosquito mortality of 98% - 100% indicates full susceptibility (S), 80% - 97% indicates potential resistance (PR) that needs to be confirmed, and <80% mortality indicates resistance (R).

Aedes mosquitoes have developed resistance to several classes of insecticides commonly used in vector control programs. Among the organophosphates are malathion and temephos; among the pyrethroids are permethrin and deltamethrin; among the carbamates are bendiocarb and propoxur; and among the organochlorines is DDT (dichlorodiphenyltrichloroethane) [111].

3.4. Insecticide Resistance Mechanisms in *Aedes* Mosquitos

The resistance of the vectors to insecticides is due to some mechanisms that they develop to escape the effect of insecticides [111]. In the case of *Aedes*, target site mutations and metabolic resistance would be the 2 main mechanisms of resistance. These mechanisms are characterized by reduced penetration of insecticides into the mosquito, non-synonymous mutations affecting the proteins targeted by insecticides (target site mutations) or increased biodegradation or enzymatic sequestration (metabolic resistance) of insecticides [77]. In Africa, both mechanisms have been found in some countries (Table 3).

- **Resistance by mutation of the target site**

Target site mutation is the primary mechanism of resistance in insects [119]. This mechanism involves substitution/alteration of genes encoding insecticide target proteins affecting the binding property of the toxic compound. Mutations of conserved target sites have been reported in genes encoding the voltage-gated sodium channel (VGSC), the ryanodine receptor, the acetylcholinesterase AChE, the nicotinic receptor and the GABA [120].

Organophosphates and carbamates (acetylcholinesterase mutations).

The modification of the primary structure of AChE due to a mutation makes it insensitive to organophosphates and carbamates and gives the insect a certain level of resistance [121] [122]. Unlike *Anopheles spp.* and *Culex pipiens*, more than one mutation event is required to change glycine to serine at codon 119, the only position associated with resistance commonly detected in mosquitoes [123].

Pyrethroids and DDT (voltage-dependent sodium channel mutations).

Pyrethroids, pyrethrins and DDT act on VGSC and induce a modification of the triggering kinetics [119] [124]. In *Ae. aegypti*, mutations in VGSCs, also known as knock-down resistance mutations (kdr), are frequent. Among these mutations, the most widespread is 1534C which confers resistance to permethrin, deltamethrin, DDT [125]. The Kdr 1016I mutation has long been considered a major cause of pyrethroid resistance [126], but recent analyses, which also examined the F1534C position, showed that the 1016I/1534C haplotype is more strongly associated with pyrethroid resistance [127].

Cyclodienes (gamma-aminobutyric acid receptor mutation).

The GABA receptors are deactivated by gamma-aminobutyric acid, which leads to an inhibition of nerve impulses [128]. Resistance to the dieldrin mutation (Rdl), A302S, was detected in a strain of *Ae. aegypti* [129] resistant to cyclodienes and in wild populations of *Ae. albopictus* from Reunion and Java [130].

Resistance due to mutations in the target site has been reported in some African countries. In Burkina Faso, studies have reported mutations in the voltage-gated sodium channel VGSC, and kdr mutations F1534C and V1016I have been detected in *Aedes aegypti* [131]. In a population tested in Ivory Coast, three kdr mutations (V410L, V1016I, and F1534C) were present. Point mutations in the voltage-dependent sodium channel (F1534C and V1016I) were detected in resistant *Aedes aegypti* in Ghana101.

- **Metabolic resistance**

Metabolic resistance is caused by elevated activity via overexpression or conformational change of enzymes involved in the processes of insecticide metabolism, sequestration and excretion. Metabolic resistance is very common and has been reported against all insecticides used in public health as well as agricultural pesticides [132].

Pyrethroids

Overexpression of cytochromes P450 is frequently associated with pyrethroid resistance [77]. Several P450 genes, particularly members of the CYP6 and CYP9

subfamilies, have been linked to resistance via overexpression in transcriptomic studies of insecticide-resistant versus susceptible strains of *Aedes* [133].

Organophosphates

Quantitative mapping of trait loci suggests that the molecular basis of temephos resistance in *Ae. aegypti* is highly multivariate [134]. This is supported by the diversity of genes highlighted in transcriptomic studies related to temephos resistance, with several P450s, ECCs and GSTs identified as overexpressed [135].

High catalytic activity of glutathione S-transferases (GST) is correlated with insecticide resistance (Boyer *et al.*, 2007; Fragoso *et al.*, 2007). Similarly, high esterase activity is responsible for the detoxification of insecticides in resistant insect populations (Cambell *et al.*, 1997). Other detoxification genes are also involved in ribonucleic acid interference (RNAi) inactivation in *Ae. aegypti*, including GSTE2 and GSTE7 in deltamethrin resistance [136]. Overexpression after analysis of P450 family genes was reported in Burkina Faso by Badolo *et al.* P450s and GSTD4 genes were overexpressed in a study carried out in Cameroon [93]. In Nigeria, P450 and GST activities were implicated in the resistance of the *Aedes aegypti* population in Lagos State [104] (Table 3).

Table 3. Molecular and metabolic mechanism of *Aedes* resistance to insecticides.

Species	Countries	Mutations	Mechanism	Authors
<i>Aedes aegypti</i>	Angola	V410L, F1534C, V1016I	Kdr/Metabolic resistance	[87]
<i>Aedes aegypti</i>	Burkina Faso	F1534C, V1016I, V410L	Kdr/Metabolic resistance	[90] [93] [131] [137]
<i>Aedes aegypti</i>	Cape Verde	F1534C, V1016I	Kdr/Metabolic resistance	[87] [95]
<i>Aedes aegypti</i> , <i>Aedes albopictus</i>	Cameroon	F1534C, V1016G, V1016I Surexpression (genes P450s, Cyp9J28, Cyp9M6, Cyp9J32 GSTD4)	Kdr/Metabolic resistance	[96]-[99]
<i>Aedes aegypti</i>	Cote d'Ivoire	F1534C, V1016I, V410L	Kdr	[103] [102]
<i>Aedes aegypti</i> , <i>Aedes formosus</i>	Ghana	F1534C, V1016I	Kdr	[52] [104]-[106] [113]
<i>Aedes aegypti</i>	Nigeria	F1534C	Kdr	[108] [107]

3.5. Alternatives in the Face of Resistance

The use of insecticides in vector control programs has shown its limits because they induce resistance in *Aedes* and could even cause cancers and ecological disasters [138]. New methods of vector control have therefore been studied. Plant extracts with larvicidal activity can be used [139]. Also, the breeding and release

of genetically modified mosquitoes (GMOs) to eliminate or modify local populations of *Aedes aegypti* and *Aedes albopictus* could be the new strategy [140]. These vectors can be infected by *Wolbachia*, a bacterium that prevents *Aedes* from transmitting arboviruses. In addition, genetic engineering has made it possible to introduce lethal genes into *Aedes aegypti*, such as the OX513A strain [140] [141]. In addition, the advanced technology of CRISPR Cas9 [142] [143] coupled with the gene drive mechanism could generate only male mosquitoes unable to transmit arboviruses to humans [144] [145]. All these new attractive technologies should be framed by ethics and bioethics in order not to cause an imbalance and an ecological disaster. But the use and acceptance of this technology are not obvious because of the mistrust of some people towards genetically modified organisms [146]. To eliminate and reduce the impact of *Ae. aegypti* and *Ae. albopictus*, we need to prevent their proliferation by combining several strategies. Environmental management can be achieved by eliminating larval breeding sites and sanitizing localities. Biological control using larvivorous fish and *Bacillus thuringiensis israelensis* (Bti). Chemical control and public awareness sessions.

4. Conclusion

Recent outbreaks of DENV, CHIKV, and ZIKV indicate that both *Ae. aegypti* and *Ae. albopictus* are important vectors, and the risk appears to be concentrated in urban areas. Chemical methods used as insecticides in vector control have shown their limitations with *Aedes* resistance. Therefore, Africa should find new ways such as a good sanitation plan for houses by destroying all the larvae sites, the use of plant extracts with larvicidal activity, the use of modern advanced biotechnology such as CRISPR Cas9 and gene drive. Nanobiotechnology could also be used to fight efficiently against vectors and arboviruses. However, all this must be done under the governance of ethics and deontology while preserving biodiversity and the environment.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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