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**Abdou Azaque Zouré, Athanase Badolo
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Resistance to insecticides in *Anopheles gambiae* complex in West Africa: A review of the current situation and the perspectives for malaria control

Abdou Azaque Zouré^{1,2} · Athanase Badolo³ · Frédéric Francis¹

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Abstract

In West Africa, the *Anopheles gambiae sensu lato* (s.l.) complex mosquitoes are the main malaria vectors. Malaria control relies mainly on long-lasting insecticide-treated nets (LLINs) and to a lesser extent on indoor residual spray (IRS) of insecticides. Important progress has been made in terms of malaria morbidity and mortality in these past decades. Resistance to insecticides in *An. gambiae* s.l. was first attributed to their use in agriculture. Further, their use in public health increased selection pressure. Resistance has been recorded to the four main classes of insecticides used in public health in West Africa. However, the spread of insecticide resistance in West Africa is persistent due to the lack of management of resistance monitoring. Resistance to insecticides involves different mechanisms. Resistance to pyrethroids and organochlorines was caused by target modification such as some sodium channel mutations in addition to metabolic changes. Reduction of sensitivity to organophosphates and carbamates was caused by acetylcholinesterase mutations. Therefore, efforts should be made as quickly as possible to develop novel vector control techniques. Furthermore, it is also suggested to combine environmental, chemical, and biological management. In this review, we outline the insecticide resistance of *Anopheles* in West Africa and the current alternative tools for effective mosquito vector control.

Keywords Malaria · Insecticide resistance · Biological control-West Africa · *Anopheles gambiae*

Introduction

In West Africa, *An. gambiae* s.l. complex mosquitoes are the main malaria vectors (Darriet 2007; Dadzie et al. 2013). According to the *World Malaria Report 2018*, malaria is still a public health concern with an estimated 219 million cases of

malaria occurred worldwide in 2017, compared with 217 million cases in 2016 and 239 million cases in 2010 (WHO 2018). The WHO (World Health Organization) African region is the most affected by malaria, whose most malaria cases (200 million or 92%) and accounted for 93% of malaria deaths in 2017 (WHO 2018). Several efforts for malaria control have been made in the last decade. Between 2000 and 2015, 17 countries worldwide (only two in Africa – Egypt and Morocco) eliminated malaria (zero indigenous cases for 3 years or more). Of these, only six countries worldwide, including only Morocco (in 2010) in Africa, have been certified as malaria-free by the WHO (2016).

The national malaria control programmes in sub-Saharan Africa rely mainly on long-lasting insecticide-treated nets (LLINs) and to a lesser extent on indoor residual spray (IRS) of insecticides for control of malaria (Ranson et al. 2011). The active ingredients of IRS formulations recommended by WHO belong to four insecticides classes: pyrethroids, organochlorines, organophosphates, and carbamates (WHO 2015a), whereas only pyrethroids are recommended as active

✉ Abdou Azaque Zouré
abdouazaque@gmail.com; entomologie.gembloux@ulg.ac.be

¹ Functional and Evolutionary Entomology, Gembloux Agro-Bio Tech, TERRA, University of Liège, Passage des Déportés 2, 5030 Gembloux, Belgium

² Institute of Health Sciences Research, Department of Biomedical and Public Health, IRSS/CNRST, Ouagadougou 03 BP 7192, Burkina Faso

³ Laboratoire d'Entomologie Fondamentale et Appliquée, Unité de Recherche et de Formation en Sciences de la Vie et de la Terre (UFR/SVT), Université Joseph KI-ZERBO, Ouagadougou 03 BP 7021, Burkina Faso

ingredients of LLINs (Prato et al. 2012). The scaling up of insecticide-based measures for vector control coupled with artemisinin-based combination therapies (ACTs) have significantly reduced malaria mortality in sub-Saharan Africa (OMS 2014). The *World Malaria Report 2018* highlighted disparities in sub-Saharan Africa, with an increase in malaria morbidity of 3.5 million in 2017 compared to 2016 in the 10 most affected countries in sub-Saharan Africa (WHO 2018). If low level and inadequacy of malaria investment is one of the main reason for this situation, the resistance of malaria vectors to insecticides has compromised the chance of these strategies to achieve successful malaria elimination (Ranson et al. 2009). WHO is targeting a 90% reduction of malaria cases and malaria mortality as part of the 2016–2030 pre-eradication agenda (WHO 2015b). Resistance to insecticides in malaria vectors was first linked to their use in agriculture (Diabate et al. 2002). Further, recent studies highlighted public health vector control tools including insecticide-treated bednets and insecticide spray as factors of selection pressure (WHO 2012). Nevertheless, resistance to insecticides is well established in malaria vector populations of West Africa. However, this insecticide resistance in *An. gambiae* s.l. has become a serious matter for malaria control and is a major challenge for malaria control programmes (Liu 2015). Resistance to carbamates and organophosphates has increased and may rise further in areas where IRS programmes have replaced pyrethroids with other active ingredients in response to a rise in resistance to pyrethroids (Ranson et al. 2011).

A systematic review of insecticide resistance of malaria vectors, *An. gambiae* s.l. complex mosquitoes, in countries in West Africa was performed, focussing on the mechanisms of malaria control in the region and their implications.

Status of insecticide resistance of malaria vectors in West Africa

Between 2007 and 2011, the distribution and use of LLINs and IRS increased significantly in West Africa (Coetzee and Koekemoer 2013). LLINs and IRS were effective against *An. gambiae* s.l., resulting in significant reductions in malaria transmission (WHO 2012) (Karunamoorthi and Sabesan 2013). Unfortunately, according to bioassays using the standard WHO protocol, resistance to all four classes of insecticide (pyrethroids, organophosphates, carbamates and organochlorines) has been reported in several countries of western Africa (Namountougou et al. 2012; WHO 2015a). *An. gambiae* s.l. strains resistant to DDT was recorded in several countries of West Africa mainly due to its use in agriculture (Ranson et al. 2009) (Table 1).

In Benin, studies showed high levels of permethrin resistance in an agricultural area and an urban area (Djouaka et al. 2008). In southern Benin, strong resistance to permethrin and

DDT was found in *An. gambiae* s.l., which might be due to L1014F kdr (Yadouleton et al. 2010) (Djègbè et al. 2011). Deltamethrin resistance was widespread and significant increase in CYP6P3, CYP6M2, GSTD3 expression was observed after a three-year implementation of LLINs (Yahouédo et al. 2016). In Burkina Faso, resistance to pyrethroids has increased in recent years (Toé et al. 2014) due to increased frequencies of 1014F kdr mutation and ace-1R (Badolo et al. 2012; Dabiré et al. 2014). In Ivory Coast, resistance to carbamates was detected in the 1990 and resistance to pyrethroids was first reported in 1993 (Edi et al. 2012). More recently, higher levels of resistance to pyrethroids, organochlorines, and carbamates (Zoh et al. 2018) and increased kdr and ace-1 gene frequencies were reported (Koffi et al. 2012).

In Gambia, two studies revealed 1014F kdr mutation was strongly associated with the first report to DDT resistance (Betson et al. 2009) and both DDT and deltamethrin resistance (Opondo et al. 2016).

In Ghana, resistance to pyrethroids, the most widespread insecticides in LLINs and IRS, is mostly linked with kdr mutation in *An. gambiae* s.s. (Baffour-Awuah et al. 2016). High resistance to pyrethroids, carbamates, and DDT, and high frequency of L119F-GSTe2 with A296S-RDL associated with up-regulation of CYP6P9a, CYP6P9b, CYP6M7, and GSTe2 genes was observed (Riveron et al. 2016). In Guinea, resistance to all insecticides were associated with widespread L1014F kdr-west mutation and low levels of ace-1R mutation (Keita et al. 2017). In Liberia, resistance to deltamethrin but full susceptibility to bendiocarb (carbamate) and fenithrothion (organophosphate) was associated with high frequency of the 1014F kdr allele (Temu et al. 2012). Likewise, in Niger, susceptibility to bendiocarb and malathion (organophosphate) but resistance to pyrethroids and DDT was associated with L1014F kdr mutation (Soumaila et al. 2017).

In Mali, high levels of resistance to DDT, increased resistance to pyrethroids (deltamethrin and lambda-cyhalothrin) were associated with elevated metabolism of oxidase, glutathione S-transferases (GSTs), and esterase detoxification. Also, high frequencies of kdr and relatively low frequencies of ace-1R were found (Cisse et al. 2015; Keita et al. 2016). In Nigeria, high resistance to organochlorines (DDT and dieldrin) and permethrin was reported (Oduola et al. 2012; Habibu et al. 2017) and was associated with L1014F and L1014S kdr mutations (Habibu et al. 2017), but full susceptibility to organophosphates and carbamates was found (Okorie et al. 2015). Furthermore, high frequencies of L119F-GSTe2 and dieldrin resistance were associated with A296S-RDL mutation (Djouaka et al. 2016b). In Senegal, widespread resistance to DDT and pyrethroids (Niang et al. 2016) was associated with high and widespread distribution of kdr-West L1014F mutation and low distribution of kdr-East L1014S mutation (Dia et al. 2018). Lambda-cyhalothrin resistance

Table 1 Available insecticides and resistance level of the *Anopheles gambiae* in western Africa (2008–2018)

Countries	WHO susceptibility tests ¹ Resistance level	Insecticide resistance report	Studies
Benin	-Permethrin 0.75% (PY), (S, R) -Deltamethrin 0.05% (PY), (R) -DDT 4% (OC), (R) -Bendiocarb 0.1% (C), (S, R) -Malthion 5% (OP), (S) -Deldrin 4% (OC), (S) -Propoxur 0.1% (C), (R, PR) -Pirimiphos methyl 0.25% (OP), (S) -Fenitrothion 1% (OP), (PR) -Carbosulfan 0.4% (R) -Chlorpyrifos-methyl 0.4% (R, PR, S)	-High levels of permethrin resistance in an agricultural area and an urban area -High levels of kdr-W mutation. -High levels of two P450s, CYP6P3, and CYP6M2 and significant increase of CYP6P3, CYP6M2 GSTD3 expression after a three-year implementation of LLINs. -Resistance to pyrethroids and DDT. -Increased frequency of kdr L1014 F, 1014S, and 1575Y. -ace-1R at very low frequency (0.01%). -Low mortality to carbamates and organophosphates. -ace-1 mutation could not entirely explain resistance to carbamates and organophosphates. -Full susceptibility and strong resistance to bendiocarb. -Full susceptibility to chlorpyrifos-methyl. -Low resistance to carbosulfan. -High resistance levels to permethrin. -ace-1 R mutation present in <i>An. gambiae</i> s.s., but absent in <i>An. coluzzii</i> . -High deltamethrin resistance, suspected resistance to bendiocarb and susceptible to pirimiphos methyl and fenitrothion. -Widespread deltamethrin resistance. -Multiple insecticide resistance in rice growing area. -Pyrethroid resistance increased in intensity in recent years. -Resistance to DDT and pyrethroids in the south-west of Burkina. -Resistance of DDT and permethrin in all four sites (Goundry, Koupela, Kuinima, Soumouso). -Carbamate and organophosphate resistance relatively rare and largely confined to the south-west. -Low resistance to bendiocarb in <i>An. gambiae</i> s.s. but not in <i>An. coluzzii</i> . -High kdr mutation (L1014F) (0.92%) in <i>An. gambiae</i> s.s. -Increased of frequency of kdr L1014 F mutation in <i>An. gambiae</i> s.s. and spread in <i>An. coluzzii</i> . -ace-1R mutation prevailed predominately in <i>An. gambiae</i> s.s. -Moderate frequency of ace-1R mutation in the Sudan and Sudan-Sahel regions and absent in the Sahel region. -Detection of GABA V327I mutations. -First report of Ace.1G119S mutation in <i>An. arabiensis</i> . -ace-1R mutation in both <i>An. coluzzii</i> . (0.04 to 0.13) and <i>An. gambiae</i> s.s. (0.25 to 0.5), but absent in <i>An. arabiensis</i> .	(Djouaka et al. 2008; Djogbénou et al. 2011; Aïzoun et al. 2013; Padonou et al. 2012; Djègbè et al. 2014; Aikpon et al. 2014; Sovi et al. 2014; Nanguenon et al. 2015; Yahouédo et al. 2016)
Burkina Faso	-Permethrin 0.75%, (R, RP) -Deltamethrin 0.05% (PY), (R, PR) -Bendiocarb 0.1%, (PR, R, S) -Fenitrothion 0.05%, (PR) -DDT 4% (OC), (R, PR) -Fenitrothion 1% (OP), (PR, S)	-Resistance to DDT and pyrethroids in the south-west of Burkina. -Resistance of DDT and permethrin in all four sites (Goundry, Koupela, Kuinima, Soumouso). -Carbamate and organophosphate resistance relatively rare and largely confined to the south-west. -Low resistance to bendiocarb in <i>An. gambiae</i> s.s. but not in <i>An. coluzzii</i> . -High kdr mutation (L1014F) (0.92%) in <i>An. gambiae</i> s.s. -Increased of frequency of kdr L1014 F mutation in <i>An. gambiae</i> s.s. and spread in <i>An. coluzzii</i> . -ace-1R mutation prevailed predominately in <i>An. gambiae</i> s.s. -Moderate frequency of ace-1R mutation in the Sudan and Sudan-Sahel regions and absent in the Sahel region. -Detection of GABA V327I mutations. -First report of Ace.1G119S mutation in <i>An. arabiensis</i> . -ace-1R mutation in both <i>An. coluzzii</i> . (0.04 to 0.13) and <i>An. gambiae</i> s.s. (0.25 to 0.5), but absent in <i>An. arabiensis</i> .	(Dabiré et al. 2008; Djogbénou et al. 2008; Badolo et al. 2012; Namountougou et al. 2012; Dabiré et al. 2009, 2012, 2014; Toé et al. 2014)
Ivory Coast	-Permethrin 0.75%, (R, PR) -Deltamethrin 0.05%, (R, PR, S) -Alpha-cypermethrin 0.05%, (R) -Lambda-cyhalothrin 0.05%, (R) -DDT 4%, (R) -α-cypermethrin 0.05%, -Pirimiphos-methyl 1% -Bendiocarb 0.1%, (PR, R) -Malathion 5%, (S) -Carbosulfan 0.4% (C), (R) -Propoxur 0.4% (C), (R) -Chlorpyrifos-methyl 0.4% (OP), (PR, S) -Fenitrothion 1% (OP), (R, PR, S) -Alphacyperméthrine (0.1%), (RP)	-Resistance to all insecticide classes. -High resistance levels to pyrethroids, organochlorines, and carbamates were widespread. -Various levels of resistance to pyrethroids (deltamethrin, permethrin, and lambda-cyhalothrin). -Strongly resistant to deltamethrin, bendiocarb, and DDT. -Probable resistance to malathion. -Elevated activity of insecticide detoxifying enzymes (esterases and glutathione S-transferases [GSTs]). -Resistance to carbosulfan and propoxur. -Suspected resistance to chlorpyrifos-methyl. -Low resistance to fenitrothion. -Frequency of L1014F kdr mutation varied from 0.37 in the site without agricultural insecticide to 0.95 in the site with intense use of insecticides. -High frequency of kdr L1014F (91%–96%). -High allelic frequencies of kdr L1014F mutation in <i>An. gambiae</i> s.s. (85.9–99.8%) and <i>An. coluzzii</i> (81.7–99.6%). -Low frequencies of ace-1R (below 0.5%) in <i>An. gambiae</i> s.s. (25.6–38.8%) and <i>An. coluzzii</i> (28.6–36.7%). -First report of the East African 1014S kdr mutation. -G119S mutation in both <i>An. coluzzii</i> and <i>An. gambiae</i> s.s. -High resistance to pyrethroids, DDT, and carbamates. -First detection of N1575Y mutation in resistance to pyrethroids. -L1014F kdr (0.33 in 2012 compared to 0.05 in 2002). -Resistance to pyrethroids and DDT. -Resistance to DT and deltamethrin. -1014F kdr mutation strongly associated with both DDT and deltamethrin. -First report of DDT resistance.	(Ahoua Alou et al. 2010; Konan et al. 2011); Edi et al. 2012; Koffi et al. 2012; Ahoua Alou et al. 2012; Tia et al. 2017; Chouaïbou et al. 2017; Edi et al. 2017; Sadia-Kacou et al. 2017; Zoh et al. 2018; Camara et al. 2018)
Gambia	-Deltamethrin 0.05%, (R, RP) -DDT 4%, (R, RP) -Permethrin 0.75% (PY) (PR)	-Resistance to DT and deltamethrin. -1014F kdr mutation strongly associated with both DDT and deltamethrin. -First report of DDT resistance.	(Betson et al. 2009; Opondo et al. 2016)

Table 1 (continued)

Countries	WHO susceptibility tests ¹ Resistance level	Insecticide resistance report	Studies
Ghana	-Propoxur 0.1% (C), (R) -Bendiocarb 0.1% (C), (R) -Cyfluthrin 0.15% (PY), (R, S) -Deltamethrin 0.05% (PY), (R, S) -Lambda-cyhalothrin 0.05% (PY), (R, S) -Pirimiphos-methyl 0.25% (OP), (S) -Permethrin 0.75% (PY), (R) -DDT 4% (OC), (R) -Dieldrin 4% (OC), (R) -Malathion 5% (OP), (S) 𐄂-Etofenprox 0.5% (R)	-Suspected resistance to permethrin and deltamethrin. -Resistance to all classes of insecticides except organophosphates. -Organophosphates are considered appropriate for IRS. -Highest level of resistance to pyrethroids. -Lowest knockdown resistance mutant gene. -Higher frequency of ace-1 119S in <i>An. gambiae s.s</i> than <i>An. coluzzii</i> , exceeding 90%. -ace-1 G119S strongly associated with resistance. -High frequency of L119F-GSTe2 and A296S-RDL. -Upregulation of CYP6P9a, CYP6P9b, CYP6M7, and GSTe2 genes.	(Anto et al. 2009) (Essandoh et al. 2013; Baffour-Awuah et al. 2016; Riveron et al. 2016; Dery et al. 2016)
Guinea	-Deltamethrin 0.05%, (R) -Permethrin 0.75%, (R) -Alphacypermethrin 0.1%, (R) -Lambda-cyhalothrin 0.05%, (R) -DDT 4%, (R) -Bendiocarb 0.1%, (R) -Deltamethrin 0.05%, (R) -Bendiocarb 0.1%, (S) -Fenitrothion 0.05%, (S)	-Resistance to all insecticides (deltamethrin, permethrin, alphacypermethrin, lambda-cyhalothrin, DDT, and bendiocarb) -kdr-west mutation (60% or more) was widespread. -Low levels of ace-1R mutation.	(Keita et al. 2017)
Liberia	-Deltamethrin 0.05%, (R) -Bendiocarb 0.1%, (S) -Fenitrothion 0.05%, (S)	-Resistance to deltamethrin but full susceptibility to bendiocarb and fenitrothion.	(Temu et al. 2012)
Mali	-Lambda-cyhalothrin 0.05%, (R, RP) -DDT 4%, (R, RP) -Permethrin 0.75%, (R, RP) -Deltamethrin 0.05%, (R, RP) -Bendiocarb 0.1%, (S) -Fenitrothion 1.0%, (S)	-High frequency of the 1014F kdr allele (90.5%). -Susceptible but suspected resistance. 𐄂-High levels of resistance to DDT. -Increased resistance to deltamethrin and lambda-cyhalothrin. -Low resistance to fenitrothion and bendiocarb. -High allelic frequencies of <i>kdr</i> in all sites. -Relatively low allelic frequencies of <i>ace-1R</i> . -Elevated insecticide metabolism of oxidase, GSTs, and esterase detoxification.	(Cisse et al. 2015; Keita et al. 2016)
Niger	-Permethrin 0.75%, (R) -Deltamethrin 0.05%, (R, RP) -Lambda-cyhalothrin 0.05%, (R, RP) -Etofenprox 0.5%, (R, RP) -Alpha-cypermethrin 0.05%, (R) -DDT 4%, (R) 𐄂-Bendiocarb 0.1%, (S) -Malathion 5%, (S)	-Susceptible to bendiocarb and malathion but resistant to pyrethroids and DDT. -L1014F kdr mutation present (frequency of 58%).	(Soumaila et al. 2017)
Nigeria	-Dieldrin 4% (OC), (R) -DDT 4% (OC), (R) -Permethrin 0.75% (PY), (R) -Deltamethrin 0.05% (PY), (PR) -Bendiocarb 0.1% (C), (PR) -Malathion 5%, (S) -Lambda-cyhalothrin 0.05%, (R) -Cyfluthrin 0.15% (S) -Etofenprox 0.5%, (R)	-Very low resistance to deltamethrin and propoxur. -High resistance to DDT. -High frequencies allelic kdr-west mutation. -Absence of ace-1R point mutation in population resistant to carbamates. -High resistance to DDT and permethrin. -Suspected resistance to bendiocarb. -Insecticide resistance associated with L1014F and L1014S kdr mutations. -Resistance to pyrethroids and DDT but full susceptibility to organophosphates and carbamates. -1014F kdr detected at a frequency of 5.8%-24.52%. -High frequency of kdr-West L1014F mutation (89.53%). -Low of kdr-East L1014S (10.24%). -Widespread resistance to DDT and pyrethroids. -Widespread distribution of the 1014F kdr.	(Oduola et al. 2012; Okorie et al. 2015; Habibu et al. 2017)
Senegal	-Permethrin 0.75%, (R) -Deltamethrin 0.05%, (RP, S) -Lambda-cyhalothrin 0.05%, (R) -DDT 4%, (R) -Bendiocarb 0.1%, (S) -Malathion 5%, (S)	-1014F kdr detected at a frequency of 5.8%-24.52%. -High frequency of kdr-West L1014F mutation (89.53%). -Low of kdr-East L1014S (10.24%). -Widespread resistance to DDT and pyrethroids. -Widespread distribution of the 1014F kdr.	(Niang et al. 2016; Dia et al. 2018)
Togo	-Permethrin 0.75%, (R) -DDT 4%, (R)	-First report of L1014S kdr (66–100%). -High resistance to DDT and permethrin. -kdr N1575Y frequency was 10–45%. -ace-1 G119S frequency was 4–16%.	(Djègbè et al. 2018)

¹ OC, organochlorines; OP, organophosphates; C, carbamates; PY, pyrethroids; WHO: World Health Organisation

According to WHO recommendations, 98–100% mosquito mortality indicates full susceptibility (S), 80–97% indicates potential resistance (PR) that needs to be confirmed, and <80% mortality indicates resistance (R) (MR4 2014)

This table shows that resistance to all four classes of insecticides (organochlorines, pyrethroids, organophosphate, and carbamate) used in LLINs and IRS has increased from 2008 to 2018 in West Africa. The mechanisms of metabolic resistance and target site resistance have been investigated in these studies

was mostly conferred by overexpressed CYP6M7 (Samb et al. 2016). In Togo, strains that were highly resistant to DDT and permethrin were observed with high frequencies L1014S kdr N1575Y (Djègbè et al. 2018).

Despite this resistance, populations susceptible to organophosphates still exist (Coetzee and Koekemoer 2013). *An. gambiae* s.l. were sensitive to pyrethroids until 2015 (Ranson and Lissenden 2016). (Table 1). Therefore, before finding more viable alternatives, there is still the possibility of continuing to use insecticides through IRS and LLINs. But until when will this remain relevant?

Mechanisms involved in insecticide resistance

Target site resistance: mutations of ace-1, kdr, GABA, and GSTe2 genes

Resistance by target modification of *An. gambiae* includes mutations of acetylcholinesterase (AChE) and GABA receptors, voltage-gated sodium channels, and glutathione S-transferase epsilon 2 (GSTe2), and knockdown resistance (kdr) (Wondji et al. 2011; Platt et al. 2015). Several previous studies have been done on these mutations in western Africa and show that resistance is increasing.

Modification of acetylcholinesterase (ace-1)

Acetylcholinesterase (AChE), encoded by the ace-1 gene, is the target of organophosphates (OPs) and carbamates (Assogba et al. 2016). The G119S mutation has been associated with high levels of resistance to carbamates and organophosphates in *An. gambiae* s.l. (Assogba et al. 2014; Liebman et al. 2015) in West Africa. In 2012, multiple types of resistance with the concomitant presence of kdr L1014F and ace-1 G119S mutations in *An. gambiae* s.l. were found throughout Burkina Faso and most savannas of western Africa (Namountougou et al. 2012; Jones et al. 2012b). In Benin, the ace-1 mutation was less frequent (Yadouleton et al. 2010). At a larger scale, IRS could fade because this mutation is associated with resistance to only two (organophosphates and carbamate) of the four types of insecticides used in malaria control.

Modification of voltage-gated sodium channel (kdr)

The target of pyrethroids and organochlorine DDT is the voltage-gated sodium channel (VGSC) (Yang et al. 2016). A mutation of VGSC modifies its binding ability, resulting in knockdown resistance (kdr) (Karunamoorthi and Sabesan 2013). Four kdr mutations (L1014S, L1014P, L1014F, and N1575Y) are widely distributed in *An. gambiae* s.l. (Jones et al. 2012a). Previous studies showed that L1014F kdr was

most widely distributed among *An. gambiae* s.l. populations in West Africa. Recently the L1014S kdr, which was initially predominant in East Africa, was reported also in West Africa, particularly in Benin and Burkina Faso (Jones et al. 2012a; Namountougou et al. 2012). The L1014P and N1575Y mutations were also frequently found in *An. gambiae* s.l. (Ranson et al. 2011; Jones et al. 2012a). After 2001–2003, the prevalence of L1014F mutations seems to have increased in *An. coluzzii* and *An. Arabiensis* (Knox et al. 2014; Baffour-Awuah et al. 2016), but was low frequency in *An. gambiae* s.s. (Djègbè et al. 2011; Dabiré et al. 2014). This mutation could greatly affect the implementation of LLINs because it only causes resistance to pyrethroids.

Modification of the GABA receptor (rdl)

The γ -aminobutyric acid (GABA) receptor encoded by the rdl gene is the target of cyclodienes, organochlorines (lindane), and phenylpyrazoles (fipronil) (Casida and Durkin 2015). A302G and A302S mutations were associated with dieldrin resistance in *An. gambiae* s.l. (Wondji et al. 2011; Platt et al. 2015; Zhang et al. 2016). The V327I mutation associated with the A296S substitution in dieldrin resistance was detected in Burkina Faso and Benin (Coetzee and Koekemoer 2013; Djouaka et al. 2016a, b). This mutation was not yet widespread but strategies are still needed for its control. Due to resistance to organochlorines, the IRS may be non-operational.

Modification of glutathione S-transferase epsilon 2 (GSTe2)

The glutathione S-transferase gene, GSTe2, is implicated in resistance to the major classes of insecticides (mostly organophosphate and pyrethroids such as permethrin). The GSTe2 gene was found to be overexpressed in resistant strains of *An. gambiae* s.l. (Djadid et al. 2006; Djouaka et al. 2011). A single amino acid change L119F in upregulated GSTe2 conferred high levels of metabolic resistance to DDT (Djouaka et al. 2016b). In Benin and Nigeria, mutation of the resistant allele L119F-GSTe2 was present at high frequencies and was also frequently associated with the A296S-RDL mutation responsible for dieldrin resistance (Riveron et al. 2014). Glutathione S-transferase overexpression and A296S-RDL once again compromise the implementation of IRS and LLINs.

Metabolic and behavioural resistance

Increased metabolism of the pyrethroid deltamethrin was linked with upregulation of cytochrome P450 CYP9K1 (Vontas et al. 2018). Also, the cytochrome P450 genes (CYP4G), especially CYP4G16 and CYP4G17, were overexpressed in resistant strains of *An. gambiae* s.l., suggesting a possible link with cuticular-based resistance (Bass and

Jones 2016). Also, the cytochrome P450 monooxygenases, GSTs, and carboxylesterases (COEs) were responsible for metabolically based resistance to pyrethroids (PYs), organophosphates (OPs), organochlorines (OCs), and carbamates (Cs) (Prato et al. 2012; Baldet et al. 2014). Behavioural resistance was observed to DDT and permethrin. Exophily after IRS decreased, which suggested that mosquitoes were more likely to rest in houses with LLINs than in houses with IRS (Ossè et al. 2013). Increased exophagy (blood feeding outside of houses) by *An. gambiae* s.l. in response to LLINs has been reported in Kenya (Gatton et al. 2013).

Impact and management of insecticide resistance on malaria control

To measure the public health impact of insecticide resistance, it is critical to assess the changing malaria transmission dynamics in Africa and to mobilise resources against this resistance (Ranson and Lissenden 2016). In this context, new approaches to stop resistance are urgently needed (Ranson and Lissenden 2016; Churcher et al. 2016). The WHO Global Technical Strategy for Malaria Control 2016–2030 (GTS) target an elimination of malaria in at least 35 countries where there was transmission in 2015 (WHO 2015b). The goal of this strategy is, reduce malaria mortality rates at least 90% globally in 2030. The recommended package of core includes vector control, chemoprevention, diagnostic testing and treatment. Therefore, the best approach should be the development of integrated pest management (IPM) or integrated vector management (IVM) (Perveen 2011). These strategies aim to maintain the effectiveness of vector control despite the threat of resistance (Karunamoorthi and Sabesan 2013). Thus, this strategy could be an alternative for the effective management of insecticide resistance in West Africa. Then, control tools could integrate a combination of environmental management with physical, chemical, genetic, and biological controls, including entomophagous predators and entomopathogenic fungi (Bawin et al. 2015; Hemingway et al. 2016). Besides these proposals for innovative alternatives, countries in West Africa could synergise their efforts towards holistic management of malaria in this highly endemic region. This will allow early and coordinated responses to new resistance to limit it as much as possible as soon as possible.

Biocontrol using microorganisms

Use of entomopathogenic fungi

Entomopathogenic fungi such as *Metarhizium anisopliae* Metschn. and *Beauveria bassiana* (Bals.-Criv.) Vuill. have been advocated as biological control agents (Bawin et al. 2016). Recent studies have demonstrated the importance and

potentiality of the combination of permethrin and entomopathogenic fungi as vector control interventions against insecticide resistant *An. gambiae* s.l. (Seye et al. 2014; Mohammed et al. 2015). Transgenic *M. pingshaense* can be used to manage *An. gambiae* s.l. resistant to pyrethroids (Bilgo et al. 2018a). Interestingly, insecticide resistant strains of *An. gambiae* s.l. were more susceptible to entomopathogenic fungi than insecticide susceptible strain of *An. gambiae* s.l. (Karunamoorthi and Sabesan 2013). Bawin et al. (2016) showed that three pathogenic fungal strains of fungi (namely: *Aspergillus clavatus* Desm, *Aspergillus flavus* Link, and *M. anisopliae*) may be productive and virulent against mosquito larvae. Toxins from *M. anisopliae* have different modes of action that improve the utility of entomopathogens as alternative malaria control tools (Bilgo et al. 2017). *Lagenidium giganteum* Couch (formerly: *L. culicidum*) is also pathogenic to mosquito larvae (Bawin et al. 2015). *Metarhizium* spp. hold promise for future applications in transgenic biological control of mosquitoes (Bilgo et al. 2018b). Development of *Beauveria bassiana* s.l. in *Anopheles* mosquitoes was observed after inoculation through tarsus and proboscis routes. Proboscis route of infection is critical for early death of vector mosquitoes (Ishii et al. 2017). All these fungi offer possibilities for diverse biopesticide formulations. However, their use in vector control is still limited to *Bacillus* crystals alone (Bawin et al. 2015). Substantial hurdles and limitations exist due to current technical platforms; hence, the experimentation and use of this method, which requires bioreactors, could be quite tedious for West African countries. Also, unfortunately, the formulation, storage, and shelf life of these entomopathogenic fungi for large-scale use is not as easy as for conventional neurotoxic chemicals.

Mosquito microbiota and paratransgenesis

The microbiota has an impact on different aspects of mosquito biology, which could be another strategy for malaria control (Hegde et al. 2015). The microbiota plays an important role in mosquito longevity, reproductive fitness, and reduced susceptibility to malaria parasites (Sharma et al. 2013). Antibiotics in ingested blood enhance *Plasmodium* infection status of *An. gambiae* by disturbing their gut microbiota (Gendrin et al. 2015). In mosquitoes, *Wolbachia* can cause vector sterility by cytoplasmic incompatibility and can also inhibit the transmission of protozoa (*Plasmodium*) (Slatko et al. 2014). *Wolbachia* was also found to inhibit *Plasmodium* development and stimulate an immune response in *An. gambiae* (Kambris et al. 2010). This evidence of the effects of *Wolbachia* promoted further investigations on the possible use of natural *Wolbachia*-*Anopheles* associations to limit malaria transmission (Baldini et al. 2014; Bourtzis et al. 2014). Often, the use of *Wolbachia* to reduce *Aedes* vectorial capacity and fitness has been successful (Slatko et al. 2014). This

technology can be effectively transferred to *Anopheles* for malaria (Hemingway et al. 2016; Chavshin et al. 2014). *Enterobacter* was the predominant culturable gut bacterium that can block *P. falciparum* development (Cirimotich et al. 2011; Boissiere et al. 2012; Yadav et al. 2015). *Serratia* and *Asaia* interacted strongly with *Plasmodium* infection status and modified vector pathogenicity (Capone et al. 2013; Bando et al. 2013). Tchioffo et al. (2016) identified a correlation between the abundance of *Serratia* and *P. falciparum* infection both in the midgut and the salivary glands of mosquitoes. In addition, *Asaia* was found to act as an immune modulator of the expression of some anti-microbial peptides (AMPs), by releasing anti-*Plasmodium* effector molecules (Mitraka et al. 2013; Capone et al. 2013). Interestingly, in semi-field conditions, the application of transgenic *Asaia* as a tool for malaria control shows promising results (Mancini et al. 2016).

These first applications based on microbiota change pointed to the importance of characterising mosquito bacterial communities for paratransgenesis as an alternative approach to alter mosquito phenotype, which will block malaria transmission in malaria endemic areas such as in western Africa, as opposed to genetic modification of the insect itself (Tchioffo et al. 2016). Paratransgenesis in *Anopheles* was first described by Yoshida et al. (2001), who demonstrated that genetically modified *Escherichia coli* expressing a single-chain immunotoxin could reduce *Plasmodium berghei* oocyst development up to 58% in *An. stephensi* (Yoshida et al. 2001). Also, due to its worldwide ubiquity, *Pseudomonas* seemed to be another promising candidate for paratransgenesis to reduce and/or inhibit malaria transmission (Raharimalala et al. 2016).

However, some limitations need to be overcome. First, the field release of paratransgenic mosquitoes imposes a rigorous risk assessment framework coherent with a strict regulatory system appropriate to national and international guidelines. A thorough evaluation of the risks and benefits of this strategy is required. An investigation of hazards and safety related concerns is crucial (Mancini et al. 2016). Paratransgenesis could be applicable in western Africa, but first several studies to characterise the microbiota of *An. gambiae* in all agro-ecological areas will be needed to identify effector molecules and specific symbiotic bacteria refractory to *Plasmodium* in mosquitoes. More studies are needed to assess true effectiveness, risks, and benefits of paratransgenesis before general applications.

Bacteria used as insecticides

Bacillus thuringiensis serovar *israelensis* and *Lysinibacillus sphaericus* are two bacteria that act as larvicidal insecticides. They were successfully used in field conditions in Gambia and Ghana (Majambere et al. 2007; Nartey et al. 2013). *B. thuringiensis* serovar *israelensis* produces two different

toxins encoded by crystal protein (Cry) (Cry4A, Cry4B, Cry11A, and Cyt1A) and Cyt genes. Both toxins were able to degrade the midgut membrane causing larval mortality (Lacey 2007). Similarly, *L. sphaericus* contains the insecticidal Mtx and Bin toxins, which paralyse the digestive system and disrupt the nervous system of mosquitoes (Bawin et al. 2016). Among biological insecticides, commercial formulations based on *B. thuringiensis* are the most sold (Bawin et al. 2015). Microorganisms produce various groups of biologically active compounds known as biosurfactants. Biosurfactants from *Bacillus subtilis* A1 and *Pseudomonas stutzeri* NA3 lead to various physiological changes in *An. stephensi*. This allows further consideration of their development as biopesticides in the fight against malaria (Parthipan et al. 2018). Limitations similar to that of for entomopathogenic fungi production exist. Lack of bioreactors could be a handicap in the implementation of bacteria to control malaria in western Africa. In addition, the other limitation could be that bacteria vitality in mosquitoes and related ecological environments cannot be fully controlled.

Plant-based insecticides

Nanoparticles: future trends

Nanoencapsulation is a process by which nanoparticles retain and slowly but efficiently release diverse molecules by diffusion, dissolution, and biodegradation (Khater 2012). Previous studies highlight that *Zornia diphylla* L. and *Nicandra physalodes* Schreb. processed as silver nanoparticles (AgNPs) are a promising and eco-friendly tool against vector mosquito larvae (Govindarajan et al. 2016b). AgNPs are easy to produce, cheap, stable over time, and can be employed at low dosages to strongly reduce vector mosquito larvae populations (Govindarajan et al. 2016a). Other studies investigated the biosynthesis of AgNPs using a cheap ethanol extract of *Artemisia vulgaris* leaves and *Hypnea musciformis* Wulfen (Murugan et al. 2015; Roni et al. 2015). Limitations of nanoencapsulation are its very high costs and adaptability to resources used by developing countries in malaria control.

Repellents and essential oils

Insect repellents can be a complement to the use of insecticides through application on the skin for individual protection where early bites of malaria vectors have occurred. One of the widely used synthetic insect repellents is N,N-diethyl-metaltoluamide (DEET), which provides long-lasting protection of up to 8 h. Unfortunately, it has environmental and human health risks (Khater 2012). Most insect repellents are volatile terpenoids such as terpenen-4-ol. Today, the best-known repellent is citronella oil, which is obtained from various

Cymbopogon species (Gramineae) as *C. nardus* (Ajaiyeoba et al. 2008).

Essential oils (EOs) may also act on mosquito larvae. The alkaloids isolated from *Annona squamosa* L. showed good larvicidal growth-regulating and chemosterilant abilities against *An. Stephensi* (Govil and Singh 2010; Khater 2012). Essential rhizome oil from *Curcuma longa* was found to be an efficient larvicide against *An. gambiae* (Solomon et al. 2012). Limonoids from neem oil and *Mentha piperita* L. oil may be an effective alternative to conventional synthetic insecticides for the control of *An. stephensi* (Govil and Singh 2010). EOs are volatiles with strong odour and soluble in organic solvents; they could be promising alternatives for malaria vector control. In tropical and Mediterranean countries, EOs are extracted from various aromatic plants generally by steam or hydro-distillation, and are an important part of the traditional pharmacopoeia (Govil and Singh 2010). EOs can also be synthesised by all plant organs and are found in several plant families. Some metabolites, such as monoterpenes (α -pinene, cineole, eugenol, limonene, terpinolene, citronellol, citronellal, camphor, and thymol) contribute to the repellent activity of essential oils (Nerio et al. 2010). β -caryophyllene, a sesquiterpene, is a repellent against *Aedes aegypti*. Phytol, a linear diterpene alcohol, is a repellent against *An. gambiae* (Price and Berry 2006; Govil and Singh 2010). Neem effects insects in several ways, including through feeding and oviposition deterrence, growth inhibition, and fecundity and fitness reductions. It was found to be effective against mosquitoes, and was considered a potential eco-friendly pesticide (Nicoletti et al. 2011). In Nigeria, traditionally 13 plants were used as insecticides, namely *Azadirachta indica* A. Juss., *Cymbopogon citratus* DC. Stapf, *Ossimum gratisimum* L., *Ageratum conyzoides* L., *Annona squamosa* L., *Hyptis suaveolens* L. Poit., *Tridax procumbens* L., *Citrus sinensis* L. Osbeck, *Lantana camara* L., *Solanum nigrum* L., *Ancardium occidentale* Limaneus, *Myrianthus arboreus* P. Beauv, and *Xylopia aethiopica* Dunal, and are effective against *An. gambiae* s.l. (Mohammed et al. 2015). *Lantana camara* L., *Hyptis suaveolens* Poit., *Ocimum canum* Sims., and *Hyptis spicigera* Lam. are natural and eco-friendly substances for the control of malaria vectors, and can be used as insecticides against malaria vectors resistant to pyrethroids (Wangrawa et al. 2015). *Lantana camara* L. showed higher effectiveness against *An. gambiae* adults, eggs, and larvae (Wangrawa et al. 2018). *Lantana camara* L. showed high oviposition deterrence in *An. gambiae* (Wangrawa et al. 2016). Since 2013, in Burkina Faso, an anti-mosquito soap (named Faso Soap) with repellent substances such as citronella and shea was tested. Faso Soap is based on microencapsulation technology. If sold at the price of an ordinary soap, 300 CFA francs or 50 cents euros, it will be accessible to the entire populations of poor countries, unlike current expensive anti-malarial products (Niyondiko et al. 2013). Almost all these

plants exist in West Africa. Reforestation programmes could make them easily available to large populations. Therefore, this method of control appears to be the most appropriate for lower income populations.

Biotechnological approaches

One of the biotechnological approaches is the “release of insects with dominant lethality” (RIDL). By releasing male transgenic mosquitoes carrying the dominant lethal gene, this approach introduces the expression of a dominant lethal gene in vector populations (Huang et al. 2017). It induces preferential breakdown of the X chromosome during male meiosis to get a bias of male gamete production (Benelli et al. 2016). Breakdown of the paternal X chromosome in *An. gambiae* prevents it from being transmitted to the next generation, resulting in fully fertile mosquito strains producing more than 95% male offspring (Galizi et al. 2014). A weekly release of 50 million sterile males permitted the elimination of the New World screwworm *Cochliomyia hominivorax* Coquerel in the United States (Huang et al. 2017). A daily release over a period of 12 days of several thousand sterile individuals reduced almost 99% of the indigenous population of *Culex quinquefasciatus* Say from a small island (< 1 km²) in Florida (Bawin et al. 2015).

The sterile insect technique (SIT) is based on the mass release of males sterilised by radiation. The sterile males are unable to fertilise eggs, thereby reducing the mosquito population. The SIT has been developed to successfully target *Aedes aegypti* for the control of dengue, chikungunya, and Zika virus (Phuc et al. 2007; Huang et al. 2017). In contrast, these techniques are still at the stage of field study for *Anopheles* spp. (Huang et al. 2017).

The gene drive mechanism is positioned as a innovative strategy for the control of vectors. This mechanism uses selective pressure on a given gene of interest to modify its genetic transmission in a population. A recent laboratory study used a CRISPR-cas9 gene drive targeting the doublesex gene (*Agdsx*), which caused a complete population suppression in *An. gambiae* mosquitoes (Kyrou et al. 2018).

Genetic forcing is currently being used in experiments on malaria vectors in West and East Africa. Target Malaria (<https://targetmalaria.org/where-we-operate/>) is conducting an experiment on genetically modified mosquitoes in Burkina Faso, Mali, and Uganda (Benelli and Beier 2017), with the goal of reducing the *An. gambiae* population. The purpose of genetic forcing is to disseminate a genetic trait that forces the sex ratio in favour of males (Wilke et al. 2018). This method could be an alternative for control of malaria in western Africa. The limited vectorial capacity of mosquito populations by genetic manipulation appears promising but poses ethical and legal problems. Thus, civil society organisations

fear that genetic forcing may become uncontrollable and have unintended consequences.

Conclusions

This review highlights the existence of insecticide resistance in *An. gambiae* s.l., the main vector of malaria in West Africa. This resistance must be continuously integrated in anti-vectorial campaigns against malaria. Control programmes must rely on the continuous monitoring of vector populations, taking into account any useful methods available, to measure the effectiveness of the fight. Therefore, a multidisciplinary approach that includes biological control techniques (focused on microbiote manipulation and transgenesis) as well as repellents and essential oils from indigenous vegetation of West Africa for malaria control is recommended as a potential alternative to synthetic insecticides. Unfortunately, the application of these new tools could be confronted with biological, technical, ethical and legal challenges.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests in the publication of this paper.

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