Insecticide resistance in *Bemisia tabaci* Gennadius (Homoptera: Aleyrodidae) and *Anopheles gambiae* Giles (Diptera: Culicidae) could compromise the sustainability of malaria vector control strategies in West Africa

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A B S T R A C T

Insecticides from the organophosphate (OP) and pyrethroid (PY) chemical families, have respectively, been in use for 50 and 30 years in West Africa, mainly against agricultural pests, but also against vectors of human disease. The selection pressure, with practically the same molecules year after year (mainly on cotton), has caused insecticide resistance in pest populations such as *Bemisia tabaci*, vector of harmful phytopathogens on vegetables. The evolution toward insecticide resistance in malaria vectors such as *Anopheles gambiae sensus lato* (s.l.) is probably related to the current use of these insecticides in agriculture. Thus, successful pest and vector control in West Africa requires an investigation of insect susceptibility, in relation to the identification of species and sub species, such as molecular forms or biotypes. Identification of knock down resistance (*kdr*) and acetylcholinesterase gene (*Ace1*) mutations modifying insecticide targets in individual insects and measure of enzymes activity typically involved in insecticide metabolism (oxidase, esterase and glutathione-S-transferase) are indispensable in understanding the mechanisms of resistance. Insecticide resistance is a good example in which genotype–phenotype links have been made successfully. Insecticides used in agriculture continue to select new resistant populations of *B. tabaci* that could be from different biotype vectors of plant viruses. As well, the evolution of insecticide resistance in *A. gambiae* threatens the management of malaria vectors in West Africa. It raises the question of priority in the use of insecticides in health and/or agriculture, and more generally, the question of sustainability of crop protection and vector control strategies in the region. Here, we review the susceptibility tests, biochemical and molecular assays data for *B. tabaci*, a major pest in cotton and vegetable crops, and *A. gambiae*, main vector of malaria. The data reviewed was collected in Benin and Burkina Faso between 2000 and 2010 under the Corus 6015 research program. This review aims to show: (i) the insecticide resistance in *B. tabaci* as well as in *A. gambiae*; and (ii) due to this, the impact of selection of resistant populations on malaria vector control strategies. Some measures that could be beneficial for crop protection and vector control strategies in West Africa are proposed.

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1. Introduction

Most pesticides used in West Africa are for crop protection on cotton, especially in Sudano-Saharan countries. Six liters of insecticide per hectare are distributed on credit each year to cotton farmers by ginning companies (Martin et al., 2005). But these insecticides are also sold on the informal market, and used on other crops such as vegetables (Ahouangninou et al., 2011). They belong mainly to the pyrethroids (PY) and organophosphates (OP) chemical families. The whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) is one of the major pests of cotton and vegetable crops worldwide. This pest causes damage both directly by feeding and indirectly through the excretion of honeydew (Jones, 2003). *B. tabaci* is also a vector of *Tomato yellow leaf curl virus* (TYLCV), a complex of geminiviruses infecting tomato cultures worldwide (Berlinger, 1986). At present, invasions of virus-bearing *B. tabaci* continues to be a critical barrier to establishment of tomato crops in open fields (Berlinger, 1986). There is a considerable genetic and biological variability of *B. tabaci* leading to the opinion that *B. tabaci* is in fact a complex of morphologically indistinguishable species/biotypes (Perring, 2001; Simon et al., 2003; Pascual and Calleja, 2004; Boyo et al., 2007; McKenzie et al., 2009; De Barro and Ahmed, 2011; De Barro et al., 2011). We have retained the commonly used term ‘biotype’ here to link this study with previous studies. To date, approximately 30 *B. tabaci* biotypes have been identified that differ with regard to various characteristics as host range, fecundity, ability to transmit plant viruses, endosymbionts diversity and insecticide resistance (Dittrich et al., 1990; Byrne and Toscano, 2002; Otoioboga et al., 2002; Horowitz et al., 2003, 2005; Musa and Ren, 2005; Gnankiné et al., 2002, 2007; Xu et al., 2010). PYs and OPs were introduced in agriculture for the control of cotton pests about 30 years ago. They exerted a huge selection pressure on *B. tabaci* populations, which resulted to the selection of insecticide resistant populations from Burkina Faso (Houndé et al., 2010). In Burkina Faso, the resistance to insecticides is found to be resistant to cypermethrin, methamidophos and omethoate (Houndé et al., 2010). Sub-Saharan Africa Silverleafing (ASL) and Q1 biotypes were identified on cotton plants, tomatoes, and okra by *Cytochrome Oxidase* I (COII) (Gnankiné et al., 2013a). Generally, Q1 biotypes are found predominantly and preferentially on cotton plants. ASL biotype is found in sympatry with Q1 on vegetable crops. A recent report done by Gnankiné et al. (2013b) showed the presence of the mutations that are responsible for the *kdr* and *ace-1* resistance. These results clearly indicate that different biotypes/genetic groups co-exist in West Africa and exhibit variations in insecticide resistance. Regarding resistance, F331W mutation in the acetylcholinesterase gene (*ace-1*) was closed to fixation in Q1 and ASL individuals, but all Q3 individuals were susceptible. For *kdr*, the LI251 mutation was observed only in Q1 populations. Thus, insecticide treatments rapidly selected for resistant individuals of Q biotypes; for instance, B biotype is known to be more susceptible to several chemical compounds than the Q biotype explaining why it sometimes displaces the B biotype (Horowitz et al., 2005; Chu et al., 2010).

The evolution toward insecticide resistance in malaria vectors such as *Anopheles gambiae* Giles (Diptera: Culicidae) is partly related to the current use of these insecticides in agriculture (Corbel et al., 2007; Djogbéhoué et al., 2010; Yadouleton et al., 2011). The residues in plots known to contain mosquito-breeding sites, resulting in delayed growth rates and development of resistance in larvae (Akogbeto et al., 2006). To date, malaria vector control has predominantly focused on targeting the adult mosquito through house spraying and long lasting insecticide net (LLIN) use (Kelly-Hope et al., 2008; Raghavendra et al., 2011). Unfortunately, OPs and PYs currently used in control of agricultural pests as *B. tabaci* are also the same ones used for vector control increasing the potential for resistance selection in mosquitoes as *An. gambiae*.

*An. gambiae* is also a complex, with seven sibling species that are closely related and morphologically indistinguishable from each other by routine taxonomic methods (Gillies and Coetzee, 1987). It includes some of the most important malaria vector species of sub-Saharan Africa i.e. *An. gambiae* s.s. and *An. arabiensis*, Patton. Genetic differentiation also occurs within the highly polymorphic *An. gambiae* s.s. species subdivided into five cytoforms: Forest, Savanna, Bamako, Mopti, and Bissau. They differ in their arrangement of chromosomal inversion and appear more or less genetically isolated in the field (Colluzzi et al., 1985, 2002). In addition, studies using molecular markers such as X-linked ribosomal DNA revealed the presence of two distinct molecular forms within *An. gambiae* s.s: the M and S forms that co-exist in West Africa (Della Torre et al., 2005). In the dry savannas of West Africa, the S form preferentially breeds in temporary aquatic habitats and is found during the rainy seasons, whereas the M form is present all year round, breeding in man-made permanent aquatic habitats (Simard et al., 2009). In Burkina Faso, genes conferring resistance to insecticides display large frequency differences in M and S forms and also within *An. arabiensis* (Dabiré et al., 2012). Resistance of *An. gambiae* s.l. to DDT and pyrethroids is especially conferred in West Africa by mutation of the sodium channel target site, the L1014F *kdr* (Martinez-Torre et al., 1998; Diabaté et al., 2002a,b;
2. Insecticide resistance in *B. tabaci* populations

2.1. Susceptibility tests

Most techniques exist and are used to assess insecticide susceptibility of *B. tabaci* populations. A leaf dip bioassay method performed on the basis of previous studies (Rowland et al., 1991; Cahill et al., 1995), has been used to evaluate the resistance status in western Africa (Houndé et al., 2010). A few insecticides from different chemical families (OP, PY, neonicotinoids) were used. Using this technique, Houndé et al. (2010) demonstrated that populations from Burkina Faso (BF) showed higher resistance to all insecticides tested than populations from Benin and frequently from Togo. In the absence of a susceptible strain, the population that exhibits a low value was used as reference strain. For instance, the highest resistance to deltamethrin and bifenthrin (PY) was observed in the Tiaré (BF) population, which exhibited respectively, a 4.7- and 36-fold resistance. Soumoussou (BF) populations showed greater resistance to dimethoate, (8.4-fold) than populations from Lomé (Togo) (1.6-fold). The populations from Bobicon (Benin) and Lomé (Togo) have been used to calculate the resistance ratio (RR) for other field populations. To follow the phenotypical resistance during the season and for a rapid survey of resistance, the glass vial technique is recommended. This technique was used to determine the susceptibility of *B. tabaci* field populations to insecticides (OP, PY, carbamates) in the USA (Plapp et al., 1987; Sivasupramaniam et al., 1997). This technique is more suitable than the leaf-disk assay because it is less time consuming.

2.2. Biochemical assays

Biochemical assays permit to detect enzymes associated with mechanism of resistance like elevated esterases, P-450s and glutathione-S-transferases. These include electrophoretic gels. The advantages of biochemical testing include the ability to carry out multiple assays on a single insect to look for multiple insecticide resistance rapidly (Brogdon, 1989). We have no data in Africa but in Greece, *B. tabaci* resistance to pyrethroids has been associated with both target-site modifications and enhanced detoxification of insecticidal compounds (Roditakis et al., 2009). Oxidative and hydrolytic pathways associated with elevated carboxylesterases (COE) and cytochrome P450-dependent monooxygenase activities have been reported (Ditrich et al., 1990; Bloch and Wool, 1994; Shchukin and Wool, 1994). A significant correlation was observed between α-cypermethrin resistance levels and COE activity with α-naphthyl acetate (Roditakis et al., 2009).

The resistance to OPs and carbamates might involve enhanced detoxification of the insecticides by non-specific COE and cytochrome P450-dependent monooxygenases (Bloch and Wool, 1994), but also target site modifications (Byrne and Devonshire, 1997; Anthony et al., 1998; Alon et al., 2006). Cytochrome P450 activity was strongly correlated with resistance to imidacloprid (Karunker et al., 2008). It has been demonstrated that overexpression of CYP6CM1 is associated with high levels of imidacloprid resistance in *B. tabaci*.

2.3. Molecular assays

The PCR procedure was performed to determine *B. tabaci* biotypes (Gnankiné, 2011) associated to the identification of *kdr* and ace-1R mutations (Tsagkaroukou et al., 2009). Thus, genomic DNA was extracted from each individual adult of *B. tabaci* in 26 μL of Nonidet P-40 extraction buffer. Biotypes were identified using a PCR-RFLP (restriction fragment length polymorphism) based diagnostic assay. Briefly, in this method, a fragment of the mitochondrial marker CO1 (cytochrome oxidase 1 gene sequences, *mtCOI*) gene was amplified by PCR (Frohlich et al., 1999), using universal COI primers C1-J-2195 (5′-TGATTITTTTGTCATCAGAAAT-3′) and TL2-N-3014 (5′-TCCAATGCACATTCTCCATATA-3′) (Khasdan et al., 2005). The PCR products were then digested by the restriction endonucleases Xap1 (Fermentas) and/or Bfml (Fermentas), which generates a clear polymorphism between biotypes B, MS, Q and Q1, Q2 or Q3 genetic groups. The PCR products are incubated with 10 U/μL Xap1 (Fermentas) at 37 °C for 3 h before loading onto agarose gel (Gnankiné, 2011).

For identification of various *kdr* and ace-1R mutations, genomic DNA of samples was also used to amplify a ~0.145 kb DNA fragment from the ISS4-6 region of the *B. tabaci* sugar channel, using primers Bt-kdr-F1 (5′-GCCAAATCTGTCGCAACT-3′) and Bt-kdr-Rlnr1 (5′-GAGACAAAGTCTGTAGC-3′). For ace-1R, primers Bet-ace-F (5′-TAGGGATCTGGCAGACC-3′) and Bet-ace-R (5′-TGCAACCGCTCCGTGACT-3′) were used to amplify a ~0.25 kb DNA fragment from AChE gene of *B. tabaci*.

Tsagkaroukou et al. (2009) developed a PCR-RFLP method to detect mutations on Vgsc (Voltage-gated sodium channel) and ace-1R allele. This method checks the genotypes resistance for a high
number of samples from populations. It requires a two-step procedure PCR amplification and subsequent digestion by restriction enzymes. PCR and gel electrophoresis-based detection methods, including PCR-RFLP, are difficult to employ for high-throughput screening. Recently, an oligonucleotide microarray was developed for the detection of the M918V, L925I and T929V mutations in the voltage-gated sodium channel gene (vgsC) associated with PY resistance, and the F331W ace1 mutation associated with OP resistance (Chung et al., 2011). The oligonucleotide microarray was then applied to detect the resistance allele frequency in B. tabaci adults collected in areas of Korea, Japan, China and Greece in which OPs and PYs have been widely applied for pest control.

By means of these techniques, three biotypes AnSL (Sub-Saharan Africa Non-Silverleafing), ASL and Q have been detected in 3 West African countries (Gnankiné et al., 2013a). These biotypes display a specific pattern of geographic distribution influenced by the host plant species. In Benin and Togo, the ASL and AnSL biotypes were predominant. In Burkina Faso the Q biotype was dominant, with two sub-groups, Q1 and Q3 (recorded to date only in this country), and ASL individuals found in sympathy with Q1 individuals in some localities (Gnankiné et al., 2013b). In addition, the data indicated that the biotype seemed to be linked to the kind of mutations detected in all samples. F331W mutation (ace1) gene was closed to fixation in Q1 and ASL individuals tested (e.g. Western BF) (Fig. 2). In the para-type voltage gated sodium channel gene (kdr), the L925I mutation was observed only in Q1 populations with the exception of Q1 individuals from Bitou (middle-East BF), where no mutation was detected (Gnankiné, 2011) and no M918T and T929V mutations have been observed in all populations tested. In northern Benin, no kdr gene was detected but ace-1R gene has been recorded. In Q3 individuals none of F331W (ace1 gene) and L925I (kdr gene) mutations were found in all individuals.

3. Insecticide resistance in Anopheles gambiae populations

3.1. Molecular forms

PCR tests revealed two “molecular” forms (M and S), which are morphologically identical and largely sympatric throughout West Africa (Della Torre et al., 2001, 2005, Touré et al., 1998), but show molecular differences in the intergenic spacer (IGS) of the ribosomal DNA (Favia et al., 2001). Although a strong deficit of M/S hybrids is observed in the field (Diabaté et al., 2003) the forms interbreed in the laboratory and their offsprings are viable and fertile.
3.2. Insecticide susceptibility tests

Susceptibility tests involve the use of WHO (World Health Organization) test kits, a specially designed plastic container lined with insecticide-impregnated papers (WHO, 1998, 2011). Susceptibility tests were performed on 2–3-day-old An. gambiae s.l. females provided by larval collection, using the WHO standard vertical tube protocol. Bioassays with WHO diagnostic test kits were carried out using PY, carbamate and OP insecticides. Mortality control was carried out by exposing wild populations from each site to non-insecticidal impregnated paper. After 1 h exposure, mosquitoes were transferred into insecticide-free tubes and maintained on sucrose solution. Final mortality was recorded 24 h after exposure. The threshold of susceptibility was fixed at 98% for the active molecules according to the WHO protocol (WHO, 1998). The resistance/susceptibility status was evaluated according to WHO criteria (WHO, 2011) considering mortality above 97% and below 90% representative of susceptibility and resistance, respectively. But between the two values, resistance was suspected. Dead and surviving mosquitoes were grouped separately and stored on silica gel at −20°C for further molecular characterization.

In Benin, WHO diagnostic tests showed high frequency of resistance in both M and S forms of An. gambiae s.s. to permethrin, bendiocarb, fenitrothion and DDT (Corbel et al., 2007; Djègbè et al., 2008). That raises the question of their taxonomic status.

(Diabaté et al., 2007).
Resistance may occur by other physiological mechanisms such as metabolic detoxification through increased enzyme activities (monoxygenase, esterase or glutathione S-transferase) (Hemingway, 1998). In Benin, Corbel et al. (2007) have carried out a study using biochemical assays suggesting that detoxification enzymes could be involved in the resistance of An. gambiae to permethrin, DDT, dieldrin and carbosulfan. An. gambiae s.l. mosquitoes from Malanville and Ladji showed significantly higher mixed function oxidase (MFO) content than the susceptible reference strain Kismu. The level of esterase activity (using α-naphthyl acetate as a substrate) in Ladji population was significantly higher than that measured for Kismu strain and other field populations (Corbel et al., 2007). Differences in the levels of GST activity were also observed in populations collected in Malanville and Aséca compared with Kismu strain and populations collected in Ladji and Parakou. However, An. gambiae s.l. mosquitoes from Cotonou and Malanville showed higher oxidase activity compared to the Kismu susceptible strain in 2009, whereas the esterase activity was higher in Bohicon mosquitoes in both 2008 and 2009 (Djégbé et al., 2011).

In western Burkina Faso, a higher level of esterases was observed in the predominant molecular S form of An. gambiae from Banfora, Orodara and in M and S forms from Tiéfòra (Namoundougou et al., 2012). A significantly high level of GSTs was observed in An. gambiae populations from all sample sites compared with Kismu strain, except from those collected in Dédougou.

3.4. Molecular analysis

Genomic DNA was extracted from individual mosquitoes according to a procedure described by Collins et al. (1987). After quantification of the extracted DNA, adults of An. gambiae tested in the bioassay were processed by PCR for molecular identification of species complex and molecular forms according to Scott et al. (1993) and Favia et al. (2001), respectively. For kdr detection the frequency of the L1014F mutation in the same samples was determined by allele-specific PCR as described by Martinez-Torres et al. (1998). Ace-1R mutation was detected using the procedure based on the PCR-RFLP assay described by Weill et al. (2004) with minor modification. Specific primers, Ex3A3Gdir (GATCGTGGACACCGTTTCG) and Ex3A3Grev (AGATGGCCGCGTMAACAG) were used in PCR reactions. Fifteen microliter of PCR product was digested with 5 U of Alul restriction enzyme (Promega, France) in a final volume of 25 μl at 37 °C for 3 h. Products were then analyzed by electrophoresis on a 2% agarose gel stained with ethidium bromide and visualized under UV light. By means of these techniques, many authors could detect the prevalence of target site mutations molecular M and S forms of An. gambiae in several geographical areas, either alone or in sympatry (Fig. 3).

The establishment of frequencies of kdr and ace-1R mutations on a map in connection with the molecular forms represents an overview of the resistance situation in Burkina Faso (Dabiré et al., 2012). An. gambiae form S was predominant in the west, which is also the cotton belt area, except in VK5 and VK7 localities near rice-growing areas. This form was also found in majority of eastern areas. In the middle part of Burkina Faso (Yamtena and Koubri), M-forms were found with a moderate prevalence. The frequency of L1014F kdr allele implied in pyrethroid-resistance in cotton-growing areas was highest and ranged between 0.79 and 0.99 and was assumed to be selected by the intensive use of insecticides in agriculture (Chandre et al., 1999; Diabaté et al., 2002a). It was far more frequent in the S form than in the sympatric M form (Djogbéno et al., 2008a,b). Even though the ace-1R mutation was spread across two climatic zones, it was recorded mostly in the cotton growing areas (Dabiré et al., 2009b). Ace-1R mutation was less spread than kdr mutation within the An. gambiae s.s (Fig. 3).

In Benin, M and S forms were also detected either alone or in sympatry (Yadoulet et al., 2011; Djégbé et al., 2011). A higher frequency of L1014F kdr allele was also detected in An. gambiae mosquitoes collected in urban areas compared to those collected in cotton growing areas (Yadoulet et al., 2011). The expansion of vegetable growing within urban and cotton treated areas probably contributed to selection pressure on mosquitoes (Corbel et al., 2007; Yadoulet et al., 2011; Djogbéno et al., 2011). Another L1014S kdr mutation was found recently in An. arabiensis in Benin (Djégbé et al., 2011). Up to now, the situation of OP and carbamates is not worrying. Nevertheless, less than 1% of An. gambiae showed the presence of the ace-1R mutation (Yadoulet et al., 2011).

4. Impact of selection of resistant insect populations on malaria vector control strategies

Although it is known that selection for resistance in mosquitoes occurs at the adult stage as a consequence of household insecticide use, or public health including treated bed nets it cannot be ignored that the indirect selection pressure from the agricultural use of insecticides on breeding sites is a noteworthy consideration (Mouchet, 1988).

The highest frequencies of L1014F mutation in An. gambiae are found in cotton growing regions of Burkina Faso, including the old and the new cotton belts (Namoundougou et al., 2013; Dabiré et al., 2009c). The expansion of vegetable growing within urban areas in Benin probably contributed to selection pressure on mosquitoes (Corbel et al., 2007). In old cotton areas, insecticides, may have selected resistance in S form and not M form. Indeed, the S form occurred in relative important proportion toward the end of the rainy season with a maximum peak in October (Diabaté et al., 2002a; Dabiré et al., 2009a). Then, L1014F mutation may have been transferred from S form to M form by introgression in sympatric populations (Diabaté et al., 2002b).

Recently in Cameroon, Fosso et al. (2012) showed phenotypic resistance in An. gambiae larvae to deltamethrin. Highest resistance ratio (RR = 325) was observed in larvae from cultivated areas as compared to polluted (RR = 195) by wastes or organic products in decomposition or non-polluted areas (RR = 205). According to

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Nazni et al. (2005) resistance at larval stages is extremely high compared to adult stages. Mosquitoes may develop different resistance mechanisms through different metabolic pathways in the larval and adult stages (Kawada et al., 2011).

In Burkina Faso and Benin, there is some evidence that the process of insecticide selection begins in fields, in treated areas, as most of the criteria listed by Georghiou (1982) were already observed. Among these criteria, one can retain: (i) Appearance of vector resistance prior to application of chemicals against the vector; (ii) higher resistance of vectors in agricultural areas than in non-agricultural; (iii) correlation between intensity of insecticide use on crops and degree of resistance vectors; (iv) fluctuations in resistance of vectors in parallel with periods of agricultural spraying; (v) correspondence between the spectrum of resistance of vectors and types of insecticides applied to crops; (vi) temporary suppression of mosquito population densities following application of agricultural sprays.

At the same time, use of PY and OP in agriculture has caused resistance in the tomato bollworm Helicoverpa armigera to PYs (Martin et al., 2000, 2002), the whitefly B. tabaci to PYs, OPs and neonicotinoids (Houndété et al., 2010) and the aphid Aphis gossypii to PYs and OPs (Carletto et al., 2010). To manage these resistant populations, the cotton protection strategy has been modified, reducing the use of PY and OP and re-introducing (Martin et al., 2005). PY and OP are still used, not only for cotton protection, but also in protection of vegetables in peri-urban areas (Ahouangninou et al., 2011) despite the resistance of these same pest species.

Fig. 3. Distribution of the frequency of kdr and Ace1R in An.gambiae s.l. populations in two countries of West Africa.
A: unidirectional incompatibility

B: Bidirectional incompatibility

Fig. 4. Wolbachia-induced cytoplasmic incompatibility in insects.

We have detected the presence of high frequency of ace-1R allele in ASL biotypes of B. tabaci in northern Benin (Fig. 2). This shows the permanent selection pressure of OP on B. tabaci and other pests, and may selected rapidly individual mosquitoes in the breeding sites in the future. In western Burkina Faso, Q1 and ASL biotypes of B. tabaci exhibit a higher level of ace-1R (Fig. 2). The ace-1R mutation prevalence is fixed in some western cotton and vegetable areas (range between 0.9 and 1). This also indicates that the farmers currently use OPs against B. tabaci. In the same areas, Dabiré et al. (2012) showed a rather high level of ace-1R frequency in An. gambiae populations (<0.4). This level could increase more if farmers do not stop the OP treatments against agricultural pests.

In some areas, the level of adult resistance may be higher than larvae. A similar case was previously reported regarding the malathion resistance of An. arabiensis in Sudan (Hemingway, 1983) where the authors attributed the absence of larval resistance to the house spraying as the major source of selection pressure rather than agricultural spraying.

Nevertheless, alternatives to PYs and OPs are registered on cotton in most West African countries and some of them are already in use. Spinosad and indoxacarb have been tested with success against H. armiger (Ochou and Martin, 2003). Low quantities of spinosad are regularly used on cotton and growers appreciate this product because of its effectiveness in protecting vegetables against caterpillars. Neonicotinoids are used on cotton in Burkina Faso to control the sucking pests, B. tabaci and A. gossypii. But the resistance recently detected in B. tabaci field populations (Houndété et al., 2010), raises concerns of their impact on the selection of Q biotype.

5. A selection of sustainable insect pest and vector management measures

5.1. Impact of transgenic cotton on resistance: The case of Burkina Faso

Implementation of transgenic cotton gave rise to hope, because pesticides belonging to OP and PY are not used in fields of Bt-cotton. Only, neonicotinoids are used at the end of the cotton phenological stages. It is probable that this technology allows homozygous and heterozygous ace-1R pests and vectors, which survive in the presence of insecticide, to be rapidly outcompeted in the absence of insecticide. In Culex pipiens, there is direct and indirect evidence that the resistance allele (ace-1R) entails a large fitness cost, probably due to the mutated AChE1 having a much lower level of activity (Berticat et al., 2008). However, the recent observation of Ace1 duplicated alleles (i.e. the presence of a resistant and a susceptible allele on the same chromosome) in An. gambiae populations from West Africa should reduce the fitness cost associated with resistance and slow its regression (Djobéno et al., 2008a, 2010).

5.2. Bacteria in controlling pests and vectors

B. tabaci, like most phloem-feeding insects, hosts an obligatory primary endosymbiont, the bacterium Portiera aleyrodaridae, required for providing essential nutrients for its survival and development. B. tabaci is also infected by several facultative vertically-transmitted symbiotic bacteria called secondary endosymbionts (Gueguen et al., 2010). Interestingly, a specific symbiotic community infects each biotype or genetic group (Gnankéné et al., 2013b). The symbiotic Ricketta function as both maternal- and reproductive manipulators (Himler et al., 2011). In the laboratory, elimination of symbionts by the use of antibiotics is recommended.

Population transformation using the intracellular bacterium Wolbachia is particularly attractive because this maternally inherited agent provides a powerful mechanism to invade natural populations, through cytoplasmic incompatibility (CI) (Fig. 4). Trans-infected Wolbachia strains from Drosophila melanogaster introduced into the dengue vector Ae. aegypti successfully invaded two natural Ae. aegypti populations in Australia, reaching near-fixation in a few months following releases of male-infected Ae. aegypti adults (Hoffmann et al., 2011). Maternal transmission of Wolbachia to resulting progeny is dependent on establishing infections in the ovaries of adult females. Ultimately this barrier to germline infection must be overcome to establish stably infected lines that could be deployed for malaria vector control strategies. A recent study shows that Plasmodium falciparum development in An. gambiae is suppressed by transient somatic infections of wMelPop-CLA (Hughes et al., 2011). However, Anopheles species are naturally not infected by Wolbachia and then the control of malaria using Wolbachia-based methods is likely not achievable before a long term.

6. Conclusions

IPM strategies adopted against cotton pests lead to a reduction in the level of pest populations and could influence positively the management of mosquitoes. For conventional cotton adopted in all West African countries, two to four treatments with PY plus OP contribute to the selection of resistant B. tabaci ASL and Q biotypes, increasing ineffectiveness of the treatments and enhancing pest infestations. This is due to the increasing dosages and application
frequencies, which have a reverse effect of gradually reducing the natural enemy populations.

The Bt cotton strategy in Burkina Faso with one or two treatments of neonicotinoids, leads to the selection of B. tabaci Q biotype resistance. This technology have the same effects as conventional cotton, except the replacement of the local biotype (ASL) by Q biotype which could have a strong rate of recurrence in the transmission of viral diseases, particularly in solanaceous crops. In this strategy, suppression of PY and OP applications should result in reduction of selection pressure in An. gambiae, decreasing mainly OP resistance, thus increasing sensitivity of pyrethroids against mosquitoes (dominance and fixation of kdr mutation), in particular, their repulsive effects before the addition of enzymatic resistance mechanisms lead to their inefficiency.

Management of resistance can slow resistance spread in all insect populations, and perhaps cause a resistant population to “revert” to a more susceptible level. Tactics for management of resistance can include the following counter measures: (i) respecting the dose and frequency of pesticide application; (ii) using local rather than area wide application; (iii) spraying locally only when pests are present; (iv) using targeted and less persistent pesticides; and (v) using, as far as possible, non-chemical control methods, alone or in combination with chemical measures.

Meanwhile, with the development of durable tools such as vaccines, vector control has also been enhanced by the use of long lasting impregnated bed nets (LLINs) that are expected to improve the efficacy of classical impregnated nets. Globally, malaria prevention remains a long-term challenge and we must change our multidisciplinary concepts. The use of genetically modified mosquitoes and the perspective of the use of bacteria can now be properly envisioned, not exclusively but as part of a complete package in the current successful strategies used in the field.

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Conflicts of interest

The authors declare that they have no competing interests

Authors' contributions

OG and MT conceived and designed the study, OG, MT and INHB drafted the manuscript. MT, FC, MA, IG, RKD supervised and reviewed this manuscript. Each author approved the final manuscript.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.actatropica.2013.06.004. These data include Google maps of the most important areas described in this article.

References


