Baseline toxicity data of different insecticides against the fall armyworm *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) and control failure likelihood estimation in Burkina Faso

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ABSTRACT

The fall armyworm (*Spodoptera frugiperda*) is a worldwide maize pest originating from the American continent. It invaded Africa during 2016, causing important economic damages, forcing African countries to take urgent actions to tackle this new invasive pest. In Burkina Faso, several chemical insecticides were promoted, but farmers have quickly and repeatedly reported control failures. In this work, we collected seven fall armyworm populations in as many maize producing areas of Burkina Faso. Following the approved IRAC leaf bioassay protocole, we evaluated the susceptibility of third instar larvae to seven commercially available insecticide formulations, including various modes of action: methomyl and chlorpyriphos-ethyl (acetylcholinesterase inhibitors), deltamethrin and lambda-cyhalothrin (sodium channel modulators), emamectin benzoate and abamectin (chloride channel activators) and *Bacillus thuringiensis* (a microbial disruptor of insect midgut membranes). Lethal concentrations (LC_{50}), resistance ratios (RR50) and relative toxicity were calculated for each population and active ingredient. LC_{50} values for all *S. frugiperda* populations were, in order of importance: emamectin benzoate (0.33–0.38 µg/l), methomyl (18–73 mg/l), abamectin (58–430 mg/l), chlorpyrifos-ethyl (199–377 mg/l), deltamethrin (70–541 mg/l) and lambda-cyhalothrin (268–895 mg/l). LC_{50} of the *B. thuringiensis* formulation ranged from 430 to 614 MIU/l. Lambda-cyhalothrin was the least efficient of the tested chemical pesticides, and emamectin benzoate the most efficient (relative toxicity × 2,712,969). Methomyl (× 49), abamectin (× 5), deltamethrin (× 13), chlorpyriphos-ethyl (× 4) were also more toxic than lambda-cyhalothrin.

Based on these results, we conclude that emamectin benzoate, methomyl and chlorpyriphos-ethyl insecticides are the most efficient for the control of the fall armyworm in Burkina Faso. We discuss the importance to implement a national-level resistance survey for this major pest, which would allow rapid and efficient adaptation of the control strategy.

Key words: chlorpyriphos-ethyl, emamectin benzoate, fall armyworm, methomyl, pyrethroids, resistance, Burkina Faso

INTRODUCTION

The fall armyworm, *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) is a major insect pest of various crops, but mainly maize. Native to America, *S. frugiperda* was first reported on the African continent in January 2016 (Goergen *et al*. 2016). From West Africa, it rapidly spread across the continent (Prasanna *et al*. 2018) and currently continues spreading to Asia (Maino *et al.* 2021; Sharanabasappa *et al.* 2018). Besides its main host plant, it is reported to develop on rice, sorghum, sugarcane, cabbage, beet, groundnut, soybean, onion, cotton, millet, tomato, and potato (Goergen *et al*. 2016), threatening nutritional security of millions of agricultural households in Africa (Prasanna *et al*. 2018). For instance, the estimated national mean loss of maize in Ghana was 22–67%, in Zambia 25–50% (Day *et al*. 2017), in Ethiopia and Kenya 32–47% (Kumela *et al*. 2019).

Due to the widespread and sometimes indiscriminate use of insecticides in the Americas, *S. frugiperda* populations rapidly developed resistance to organochlorines, organophosphates, carbamates and pyrethroids (Diez-Rodriguez & Omoto, 2001; Young & McMillian, 1979; Yu, 1991, 1992; Yu *et al.* 2003). Resistance to *Bacillus thuringiensis* maize have also been reported in Brazil, Puerto Rico and the U.S.A. (Flagel *et al.* 2018). As a result, farmers have increased frequencies and doses of insecticide applications, leading to field control failures in Brazil, Puerto Rico and Mexico (Carvalho *et al*. 2013; Gutiérrez-Moreno *et al*. 2019; León-García *et al*. 2012).

In Africa, barely any alternatives to insecticides are being used. Most African countries had no insecticide formulations specifically recommended or registered for the protection of maize against this new pest (Sisay *et al*. 2019). Farmers were advised to apply formulations despite their questionable and unproven efficacy (Harrison *et al*. 2019; Sisay *et al*. 2019), including emamectin benzoate, imidacloprid, lindane, chlorpyriphos-ethyl, acetamiprid, cypermethrin, lambda-cyhalothrin (Kuate *et al*. 2019). In Burkina Faso for instance, more than

12,000 l of synthetic insecticides were sprayed on 14 000 ha of *S. frugiperda* infested fields, during the 2018–2019 crop season (MAAH 2018). However, many farmers complain about the ineffectiveness of some of these products for controlling *S. frugiperda* (Sisay *et al*. 2019).

In this context, we decided to conduct an acute toxicity assay on *S. frugiperda*, using insects collected in all maize production areas of Burkina Faso, and using most of the available active substances. With this information, we hope to provide the authorities with valuable information to communicate to farmers, and the scientific community with the resistance status of this pest in a newly invaded area.

MATERIALS AND METHODS

Insects

Spodoptera frugiperda larvae were collected from maize fieds located in two provinces of the country: Houet (collected in October 2019) and Kadiogo (collected in December 2019) (Fig. 1). Between 100 and 200 larvae were collected from each location: Samendeni, Tolotama, Toussiana, Sambla Toukoro (Houet), Nongana, Nakamtenga and Pabré (Kadiogo). They are referred hereafter to as Sam, Tol, Tou, STo, Non, Nak and Pab populations, respectively. Maize, tomato, cabbage and other vegetable crops are grown year-around in the province of Kadiogo. Maize, sorghum and other cereals are typically grown in the province of Houet.

Larvae were placed in plastic boxes with fresh maize leaves and shipped to the laboratory at the Training and Research Centre of the University Nazi Boni (UNB) in Bobo Dioulasso, Burkina Faso (Fig. 1). They were confirmed to be fall armyworm after morphological examination of the larvae and subsequent observation of the forewings of adult moths after emergence. Larvae were reared on maize leaves in the laboratory at 25 ± 2 °C, 60 ± 15% relative humidity, and under a 12:12 photoperiod. Insect development was checked every other day and fresh leaves were replaced after 24 h until pupation. Pupae were collected daily and placed in a cage (60 × 40 × 40 cm). The bottom of the cage was covered with white paper for female egg-laying. They were fed with a sugar water solution (100 g/l) throughout their life. The white paper was removed after oviposition, and cut to individualise each egg mass in separate boxes. Eggs were maintained under the same environmental conditions. Populations were reared in the laboratory and the progeny from the F1 generation was used for all bioassays.

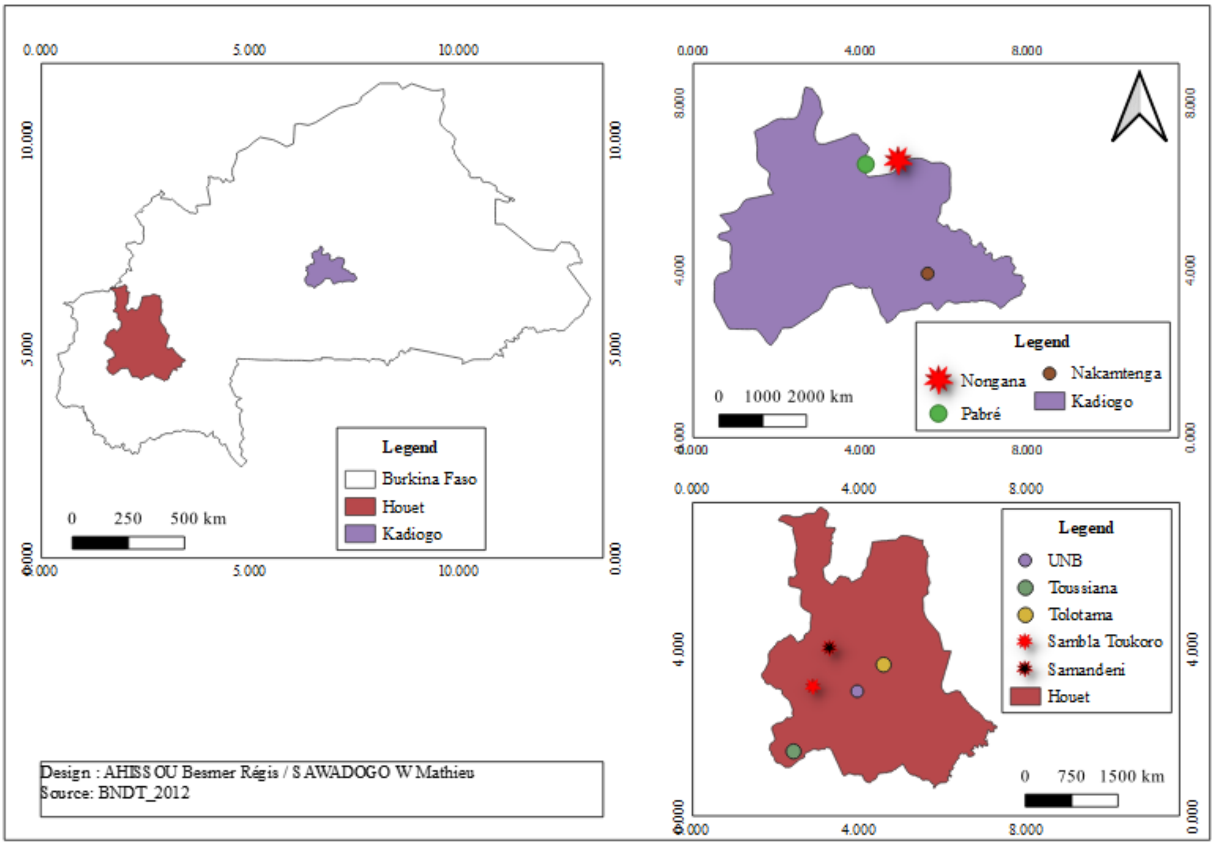

Fig. 1. Sampling locations of *S. frugiperda* populations. Left: Insects were collected from the two provinces of Houet and Kadiogo. Top right: collection sites in Kadiogo. Bottom right: collection sites in Houet.

Insecticides

According to the global list of pesticides authorized by the Sahelian Pesticides Committee (CSP) of November 2019, there is no insecticide registered for control of *S. frugiperda* in maize (CSP 2019). All insecticides used in this study are registered and officially intended for controlling lepidopteran larvae and other insect pests in vegetable crops. We selected the most widely used active substances: methomyl (250 g a.i./kg, Savahaler, Savana, France), chlorpyriphos-ethyl (480 g a.i./l, Pyrical 480EC, Arysta Lifescience, France), deltamethrin (25 g a.i./l, Tamega, Savana, France), lambda-cyhalothrin (25 g a.i./l, Sunhalothrin 2,5% EC, Wynca Sunshine, Mali), emamectin benzoate (19 g a.i./l, Emacot 019EC, Savana, France), abamectin (18 g a.i./l, Acarius, Savana, France) and *Bacillus thuringiensis* var. *kurstaki* (16 000 IU/mg, Bio K 16, Savana, France). The seven active ingredients tested, their IRAC group and modes of action are listed in Table 1.

Insecticide assay

Insecticide assays were conducted with F1 third-instars by following the IRAC standard leaf bioassay protocol (http://www.irac-online.org/). Maize leaves were washed with tap water and dried before being immersed for 10 sec in the insecticide solution. They were then allowed to dry for 1 h. Each insecticide solution was freshly prepared with distilled water and Triton X-100 (0.2 g/l). A distilled water solution containing Triton X-100 (0.2 g/l) was used as control. The leaves were placed in individual Petri dishes (9 cm in diameter) containing blotting paper. A minimum of five different concentrations of the tested insecticide solution were included in the assay. A total of 40 larvae were observed per tested concentration. They were placed individually in a Petri dish, and maintained at 25 ± 2 °C, 60 ± 15% relative humidity, and 12:12 photoperiod. Morbidity was assessed after 48 h of exposure to insecticides (72 h in the case of *B. thuringiensis*, because mortality was only observed on the third day after inoculation). Individuals were considered dead if they failed to move when touched with a small brush, or when they showed severe intoxication symptoms such as severe growth inhibition, halted molting, and feeding cessation.

Table 1. Insecticides used against fall armyworm populations

Active ingredient	IRAC group	Mode of action	Label concentration (mg a.i./l)
Methomyl	1A	Acetylcholinesterase (AChE) inhibitors	937.50
Chlorpyriphos-ethyl	1B	Acetylcholinesterase (AChE) inhibitors	1 600.00
Deltamethrin	3A	Sodium channel modulators	37.50
Lambda-cyhalothrin	3A	Sodium channel modulators	83.33
Emamectin benzoate	6	Chloride channel activators	31.66
Abamectin	6	Chloride channel activators	63.00
Bacillus thuringiensis	11A	Microbial disruptors of insect midgut membranes	8×10^7 *

*Label rate expressed in IU/l; IRAC : Insecticide Resistance Action Committee (http://www.irac-online.org/).

Statistical analysis

The Abbott (1925) formula was used to correct the mortality. Concentration-mortality were subjected to probit analysis (Finney 1971) using SPSS software, to calculate values of slope, lethal concentration (LC_{50}), and fiducial limits (95%) for each population. Populations responses were considered equal when the confidence limits overlapped (Robertson & Preisler 1992). Resistance ratios (RR50) were determined by dividing the LC_{50} value of a given population by the LC_{50} of the most susceptible population. Control failure likelihood (CFL) was calculated by multiplying the achieved mortality percentage (to the label concentration) by 100, dividing the product by the minimum required efficacy (%) and subtracting the result from 100 (Guedes 2017). If the achieved mortality was higher than the required efficacy of the commercial formulation, CFL values < 0% suggest a negligible risk of control failure. The required efficacy was set at 80%, because it is the minimum efficacy threshold required to allow registration of a synthetic insecticide (Silva *et al.* 2011). The same reasoning was used for the biopesticide tested in this study, but with consideration of a minimum efficacy thresholds of 70% (Guedes 2017).

$$\text{CFL} = 100 - \frac{\text{Achieved mortality (\%)} \times 100}{\text{Required efficacy (\%)}}$$

RESULTS

LC_{50} values are presented in Table 2, along with resistance ratios, for all active substances and *S. frugiperda* populations.

For the acetylcholinesterase inhibitors, the LC_{50} values ranged from 18 to 73 mg/l for methomyl, and from 199 to 377 mg/l for chlorpyrifos-ethyl. Two populations (STo and Non) were slightly less susceptible to methomyl, since they had higher LC_{50} values, leading to resistance ratios (RR50) of 1.79 and 4 fold. For chlorpyrifos-ethyl, 6 out of 7 populations of *S. frugiperda* had similar susceptibility, with RR50 between 1.34 to 1.89 fold. The fall armyworm collection from Non was less susceptible to chlorpyrifos-ethyl.

For sodium channel modulators, the LC_{50} values ranged from 70 to 541 mg/l for deltamethrin, and from 268 and 895 mg/l for lambda-cyhalothrin. Three populations (STo, Tol, Tou) were less susceptible than the others to deltamethrin, with RR50 between 5 to 7 fold. Similar susceptibility to lambda-cyhalothrin was observed among the tested populations.

Table 2. Acute toxicity of some insecticides formulations against different populations of the fall armyworm from Burkina Faso

Insecticides	Location	*n*[a]	Fit of probit line				LC$_{50}$ (95% FL) mg/l[c]	RR50[d]
			Slope ± SE[b]	X^2	ddl	*P*		
Methomyl	Sam	200	3.27 ± 0.41	3.66	3	0.30	25.91 (21.80–30.45)	1
	Tol	200	3.55 ± 0.45	3.46	3	0.33	25.23 (21.49–29.45)	1
	Tou	200	3.05 ± 0.38	0.71	3	0.87	26.16 (21.81–30.96)	1
	STo	200	3.04 ± 0.36	3.26	3	0.35	32.69 (27.51–38.69)	1.79
	Non	240	1.45 ± 0.18	2.78	4	0.60	73.34 (54.56–97.45)	4.01
	Nak	200	2.23 ± 0.35	5.32	3	0.15	31.87 (21.73–41.09)	1
	Pab	200	2.22 ± 0.30	2.83	3	0.42	18.27 (13.35–23.19)	1
Chlorpyriphos –ethyl	Sam	280	8.86 ± 1.21	4.34	5	0.50	267.64 (252.92–283.42)	1.34
	Tol	200	5.64 ± 0.81	3.74	3	0.29	280.39 (255.63–316.57)	1.41
	Tou	200	6.85 ± 0.93	1.13	3	0.77	333.04 (306.40–365.98)	1.67
	STo	200	5.78 ± 0.70	0.73	3	0.87	294.62 (263.97–333.61)	1.48
	Non	200	5.46 ± 0.59	4.69	3	0.20	199.23 (179.44–220.40)	1
	Nak	200	4.41 ± 0.57	0.76	3	0.86	324.04 (286.02–371.84)	1.63
	Pab	240	3.47 ± 0.41	7.63	4	0.11	377.32 (329.57–435.42)	1.89
Deltamethrin	Sam	200	3.59 ± 0.45	3.99	3	0.26	69.95 (60.86–80.12)	1
	Tol	200	4.22 ± 0.58	7.28	3	0.06	385.88 (336.76–443.24)	5.52
	Tou	200	4.22 ± 0.58	7.28	3	0.06	358.88 (336.76–443.24)	5.13
	STo	240	11.00 ± 1.15	7.38	4	0.12	540.65 (516.43–567.42)	7.73
	Non	240	2.57 ± 0.29	4.89	4	0.30	118.02 (99.67–139.86)	1
	Nak	240	3.65 ± 0.41	3.39	4	0.50	90.86 (79.25–103.80)	1
	Pab	200	3.26 ± 0.47	5.26	3	0.15	184.39 (160.09–218.49)	2.64
Lambda– cyhalothrin	Sam	240	2.14 ± 0.34	9.05	4	0.06	268.35 (223.32–329.25)	1
	Tol	200	8.55 ± 1.08	2.79	3	0.43	674.10 (637.42–713.87)	2.51
	Tou	200	6.61 ± 1.04	6.98	3	0.07	387.69 (355.63–414.55)	1.44
	STo	240	2.58 ± 0.38	8.70	4	0.07	513.72 (439.01–611.66)	1.91
	Non	240	5.23 ± 0.60	7.78	4	0.10	895.28 (814.41–977.15)	3.34
	Nak	240	4.55 ± 0.47	3.85	4	0.43	536.40 (479.66–596.44)	2.00
	Pab	200	3.31 ± 0.51	5.01	3	0.17	486.86 (419.32–555.71)	1.81
Emamectin benzoate	Sam	360	2.83 ± 0.32	1.53	7	0.98	0.00036 (0.00029–0.00043)	1
	Tol	240	2.93 ± 0.33	1.29	4	0.86	0.00037 (0.00031–0.00044)	1
	Tou	240	3.00 ± 0.35	0.75	4	0.95	0.00033 (0.00028–0.00039)	1
	STo	200	2.89 ± 0.34	1.14	3	0.77	0.00035 (0.00029–0.00042)	1
	Non	240	3.67 ± 0.43	8.34	4	0.08	0.00033 (0.00028–0.00038)	1
	Nak	240	3.65 ± 0.43	8.92	4	0.06	0.00033 (0.00029–0.00038)	1
	Pab	240	4.26 ± 0.53	8.01	4	0.09	0.00038 (0.00033–0.00043)	1
Abamectin	Sam	200	3.12 ± 0.52	6.02	3	0.11	58.49 (49.39–67.13)	1
	Tol	200	3.75 ± 0.45	7.13	3	0.07	69.91 (61.66–79.73)	1
	Tou	200	4.81 ± 0.56	4.79	3	0.19	67.41 (60.59–74.95)	1
	STo	200	2.93 ± 0.51	7.11	3	0.07	62.34 (52.64–72.16)	1
	Non	320	4.79 ± 0.51	10.56	6	0.10	429.88 (391.02–475.24)	7.35
	Nak	240	4.19 ± 0.49	1.67	4	0.80	245.83 (220.71–277.07)	4.20
	Pab	280	4.38 ± 0.45	3.68	5	0.60	302.43 (272.70–338.09)	5.17
Bacillus thuringiensis	Sam	240	3.97 ± 0.47	3.61	4	0.46	430283534 (379409870–488993314)	1
	Tol	240	3.34 ± 0.40	1.39	4	0.85	424782228 (369261848–492489955)	1
	STo	240	4.55 ± 0.51	5.05	4	0.28	399646077 (355362294–448381180)	1
	Non	240	4.01 ± 0.48	2.23	4	0.69	443448757 (391262200–503492947)	1
	Nak	280	3.75 ± 0.47	1.94	5	0.86	614514737 (544525234–698128872)	1.54

[a] *n* = number of larvae tested; [b] SE = standard error; [c] LC$_{50}$ expressed in IU/l for *B. thuringiensis*; [d] RR50 = resistance ratio 50, LC$_{50}$ value of a given population by the LC$_{50}$ of the more susceptible population.

For chloride channel activators, very low LC_{50} values were obtained for emamectin benzoate, ranging from 0.33 to 0.38 µg/l. We found no difference among the tested populations (the fiducial limits 95% overlap). Abamectin LC_{50} values ranged from 58 to 430 mg/l, with the Houet populations less susceptible than the Kadiogo population (F = 34.26; ddl = 6; P < 0.00001).

Table 3. Control failure likehood (%) of populations of the fall armyworm using insecticides in Burkina Faso

	Houet				Kadiogo			
Insecticides	Sam	Tol	Tou	STo	Non	Nak	Pab	Mean
Methomyl	–25.0	–25.0	–25.0	–25.0	–25.0	–25.0	–25.0	–25.0
Chlorpyriphos–ethyl	–25.0	–25.0	–25.0	–25.0	–25.0	–25.0	–22.5	–24.64
Deltamethrin	77.5	100.0	100.0	100.0	87.5	90.0	98.75	80.54
Lambda–cyhalothrin	81.25	100.0	100.0	97.5	100.0	100.0	100.0	96.96
Emamectin benzoate	–25.0	–25.0	–25.0	–25.0	–25.0	–25.0	–25.0	–25.0
Abamectin	33.75	46.25	45.0	37.5	100.0	100.0	100.0	66.07
Bacillus thuringiensis	100.0	100.0	—	100.0	100.0	100.0	—	100.0

Among the seven insecticides tested, *B. thuringiensis* var. *kurstaki* (BIO K 16) was the only biopesticide (a microbial disruptors of insect midgut membranes). Larval mortality was recorded on the third day after inoculation. The LC_{50} ranged from values were closed for all tested populations, ranging from 399 and 614 MIU/l. The overlapping fiducial limits at 95% indicate that the susceptibility levels of the Sam, Tol, STo and Non populations were not statistically different, while Nak population showed level of resistance to *B. thuringiensis* (1.54 fold) in comparison to the other populations.

Control failure likelihood (CFL) was assessed by considering a minimum efficacy threshold of 80% for synthetic insecticides and 70% for the biopesticide (Table 3). Three active ingredients have negligible risks of control failure (i.e. their CFL values are below 0%): methomyl, chlorpyriphos-ethyl and emamectin benzoate. This risk is higher for the other compounds, with CFL values ranging from 77 to 100% for pyrethroids and reaching 100% for *B. thuringiensis*, for all populations. This probability for abamectin was moderate for Sam, Tol and Tou populations (33.75 to 46.25) and very high for Non, Nak and Pab populations (100%).

To calculate the relative toxicities among the tested chemical insecticides, lambda-cyhalothrin was set at a value of 1, since it was the least efficient. On the basis of LC_{50} values, the relative toxicity was the highest for emamectin benzoate (relative toxicity: × 2,712,969). Methomyl (× 49), abamectin (× 15), deltamethrin (× 13), chlorpyriphos-ethyl (× 4) were also more toxic than lambda-cyhalothrin.

DISCUSSION

Our study was performed in a context of absence of registered insecticides against the fall armyworm in West Africa. We decided to perform this study with as many active molecules as possible, to be representative of what farmers are likely to apply in their fields. We selected old and newer insecticides belonging to four modes of action: AChE inhibitors (methomyl, chlorpyriphos-ethyl), sodium channel modulators (deltamethrin, lambda-cyhalothrin), chloride channel activators (emamectin benzoate, abamectin), and microbial disruptors of insect midgut membranes (*B. thuringiensis*). Although some slight differences were observed among the tested populations, they were all in the same range of susceptibility. This could probably be explained by a limited number of introductory pathways of this pest to Burkina Faso (Early *et al*. 2018; Otim *et al*. 2018), the relatively short period of establishment in the country (Tizie & N'Guessan 2017) and the similarity among the areas the populations were sampled in terms of control methods (MAAH 2018).

Emamectin benzoate was, by far, the most efficient insecticide to control *S. frugiperda*. The fall armyworms were also relatively susceptible to the older insecticides methomyl (carbamate) and chlorpyriphos-ethyl (organophosphaste), confirming previous reports from other countries (Gutiérrez-Moreno *et al*. 2019; Ríos-Díez & Saldamando-Benjumea 2011). Based on our results, low risk of control failure are expected for these three insecticides. *Spodoptera frugiperda* were less susceptible to deltamethrin and lambda-cyhalothrin, despite the high doses included in our assays. Previous evidences of high resistance levels of deltamethrin and lambda-cyhalothrin were reported in Mexico, Brazil and Colombia (Carvalho *et al*. 2013; León-García *et al*. 2012; Ríos-Díez & Saldamando-Benjumea 2011). In this context, failure to control fall armyworm would be very likely, as the doses required are higher than those authorised by the manufacturers, and therefore would be of serious health and environmental risk. In Benin, Adeye *et al*. (2018) reported the ineffectiveness of the binary Lambdace 25 EC (lambda-cyhalothrin 15 g/l and acetamiprid 10 g/l) on fall armyworm. In the absence of a susceptible fall armyworm population in this study, resistance factor to different insecticides were only calculated by comparing LC_{50} values and fiducial limits at 95% to identify a significantly more susceptible population. No difference of susceptibility level to emamectin benzoate was recorded in all seven tested populations. In addition, no spatial dependence to insecticides was observed for the majority of the products tested, with exception of abamectin.

Contrasted susceptibility levels to different active substances may be observed within a pest population as the result of several factors, alone or in combination: 1) differences in crop management approaches among the regions, 2) climatic conditions (seasonal or tropical), 3) the mode of action of the insecticide, 4) the *S. frugiperda* original strain (maize or rice strains) and 5) the methods used to assess susceptibility and development of resistance to the chemicals (Ríos-Díez & Saldamando-Benjumea 2011). Several previous studies clearly demonstrated differences of susceptibility to various insecticides among field strains of *S. frugiperda* in Mexico and Puerto Rico (Gutiérrez-Moreno *et al*. 2019), Brazil (Campos *et al*. 2011; Carvalho *et al*. 2013), Colombia (Ríos-Díez & Saldamando-Benjumea 2011), Venezuela (Morillo & Notz 2001), USA (Yu 1991, 1992).

In general, the resistance ratios were higher for pyrethroids than organophosphates and carbamates (Carvalho *et al*. 2013; León-García *et al*. 2012; Morillo & Notz 2001). Resistance ratio (RR50) of the lambda-cyhalothrin selected strain in Venezuela varied from 19.4–41.9 fold between P0 and F9 generation, whereas in a methomyl selected strain the RR50 ranged from 3.1–22.1 fold in P0 to F9 (Morillo & Notz 2001). Subsequent experiments with a population of *S. frugiperda* from Mexico also showed high resistance ratios: 1002.2 fold, 204.5 fold and 183.0 fold for deltamethrin, lambda-cyhalothrin and methomyl, respectively (León-García *et al*. 2012). In another study, the resistance to lambda-cyhalothrin increased 10-fold in 6.5 generations compared to 11.5 generations for methomyl, which has a similar mode of action to diazinon (i.e. AChE inhibitors). Heritability of resistance was therefore higher for lambda-cyhalothrin, making methomyl a better option for control of fall armyworm from Colombia (Ríos-Díez & Saldamando-Benjumea 2011), similarly to our results. Genetic bases of pesticide resistance are essential to better understand the evolution of resistance and to refine resistance management strategies (Mckenzie 2000). The heritability of *S. frugiperda* resistance to lambda-cyhalothrin has been identified as autosomal and recessive, which tends to delay inheritance (Diez-Rodriguez & Omoto 2001). Previous evidences of the inefficiency of some pyrethroid insecticides were reported around the globe, for example in Brazil and Puerto Rico (Carvalho *et al*. 2013; Gutiérrez-Moreno *et al*. 2019).

The present study also shows that fall armyworm populations in Burkina Faso are highly susceptible to AChE inhibitors (methomyl, chlorpyrifos-ethyl). These old molecules showed better efficacy and lower probability of treatment failure compared to abamectin, one of the newest molecules available on the market in Burkina Faso. This is contradictory with the results recently obtained by Gutiérrez-Moreno *et al.* (2019), which reported that AChE inhibitors, displayed lower potencies against fall armyworm populations from Puerto Rico and Mexico than newer molecules. For abamectin, we showed a variation in susceptibility of fall armyworm populations depending on the cropping system of the sampled area. Fall armyworm populations collected from the province of Kadiogo (with vegetable crops associated with maize) were less susceptible than those collected from the province of Houet (mainly producing cereals). This difference in susceptibility may be related to the frequency of insecticide applications, higher in vegetable crops than in cereals; maize was not treated with insecticides before the arrival of the fall armyworm in 2016 (Caniço *et al.* 2020). Now, abamectin is becoming increasingly important in tomato production to control major pests such as mites and leafminer *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) in Burkina Faso (Sawadogo *et al*. 2020; Son *et al*. 2017, 2018).

Emamectin benzoate was found to be highly effective against all sampled fall armyworm populations. Emamectin benzoate came out to be an effective insecticide for most armyworm species: it exhibited low or very low levels of resistance in *S. litura* (Fabricius) (Lepidoptera: Noctuidae) (Karuppaiah & Srivastava 2013; Motaphale *et al*. 2018; Sharma & Pathania 2014), and *S. exigua* (Hübner) (Lepidoptera: Noctuidae) (Saeed *et al*. 2012; Zhang *et al*. 2014). In a recent study, emamectin benzoate also proved to be very effective against the fall armyworm, with a low level of resistance, comparable to abamectin (Gutiérrez-Moreno *et al*. 2019). As observed in our assays, previous works reported that abamectin was less toxic for *S. litura* than emamectin benzoate (Ahmad & Mehmood 2015; Thodsare & Srivastava 2014). In the case of *S. exigua*, genetic studies have shown that inheritance of emamectin benzoate was autosomal, incompletely dominant, and polygenic (Che *et al.* 2015). Consequently, continued and intensive application of this compound has contributed to rapid evolution of high resistance in field populations from China (Che *et al*. 2013; Su & Sun 2014). Due to their similar mode of action, *S. exigua* selected with emamectin benzoate had a high level cross-resistance to abamectin (Che *et al*. 2015).

Biological control should become a more important part of fall armyworm management in Africa (Kenis *et al.* 2019). Biopesticides are emerging, with *B. thuringiensis* among the most promising solutions (Deravel *et al*. 2014). However, the number of resistant species has been increasing worldwide (Tabashnik *et al*. 2013). In the present study, some *S. frugiperda* populations were less susceptible than others to the biopesticide *B. thuringiensis* var. *kurstaki*. The exposure duration of 3 days may have limited the expression of the full potential of this relatively slow-acting insecticide. Several studies have shown that the susceptibility to synthetic insecticides depends on the level of resistance to *B. thuringiensis*. For example, strains of *Helicoverpa armigera* (Hübner) and *H. punctigera* (Wallengren) (all Lepidoptera: Noctuidae) resistant to Cry2Ab showed small increases in susceptibility to AChE inhibitors such as methomyl and chlorpyrifos (Bird & Downes 2014). Higher susceptibility to insecticides derived from the bacterium abamectin and spinosad was reported with a laboratory selected strain of *H. armigera* that was resistant to Cry1Ac (Xiao *et al*. 2016). This may also be the case for the fall armyworm for which improved susceptibility to chlorpyrifos-ethyl and methomyl has been recorded with populations showing low susceptibility to *B. thuringiensis*.

Finally, the implementation of an efficient control strategy against this pest can only be achieved through a continuous survey of its susceptibility to insecticides, to be deployed in all maize-producing regions of the country. Such a monitoring is a fundamental element of any resistance prevention program: detecting susceptibility evolution in the laboratory allows the adaptation of the control methods before the problem becomes too serious. The establishment of a network of laboratories for insecticide susceptibility monitoring of *S. frugiperda* is essential for designing regional integrated management programmes, and to preserve the efficacy of the available active ingredients.

ACKNOWLEDGEMENTS

This research was funded by the Academy of Research and Higher Education-Commission Development Cooperation (ARES-CDD) as part of the PRD AGRO-ECO project.

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