



The fall armyworm *Spodoptera frugiperda* (J.E. Smith), a new pest of maize in Africa: biology and first native natural enemies detected

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ABSTRACT

The fall armyworm (FAW), *Spodoptera frugiperda* is a real threat to food security. It is able to totally destroy the cereal crops in a country. It can cause famine in Sub-Saharan Africa where cereals are subsistence crops. Reported in Africa in 2016, the FAW succeeded to colonize 47 countries in one year. Its migration capacities which are of around 100 km per night can allow it to have fully infested a country like Senegal (ca 200 000 km²) in less than a week. The FAW is very difficult to fight because resistant to several insecticides. Invasive species often invade a new environment without their natural enemies, which promotes their multiplication and damage to crops. To estimate the generation number per year and evaluate the impact of biological control of indigenous natural enemies on the FAW, larvae were collected in maize fields and monitored in the laboratory. The results show that the development cycle of *S. frugiperda* takes 25 days on average, that is to say fifteen (15) generations per year. The study confirms the presence of three species of native natural enemies, a nematode *Hexameris* sp. and two Hymenopterans *Chelonus* sp. and *Campoletis* sp. detected for the first time in West Africa on FAW larvae. The overall parasitism rate is 25.8%. These native natural enemies are a very promising means of control against FAW populations. The introduction of agricultural techniques to promote the maintenance and the proliferation of the FAW auxiliaries is an alternative to the use of pesticides.

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INTRODUCTION

In sub-Saharan Africa, food security is a development issue. Cereals remain the main subsistence food for people mostly poor (OCDE/FAO, 2016). Cereal production is threatened by several factors, namely climatic variability and invasive pests including *Spodoptera frugiperda* (Lepidoptera Noctuidae) (Day et al., 2017). The fall

armyworm, *S. frugiperda* is a dangerous pest of cereals detected in Africa in 2016 (Goergen et al., 2016). Since then, *S. frugiperda* has been invading Sub-Saharan Africa countries. The larvae of this pest can totally destroy the cereal crops. This pest invasion seems fast and efficient thanks to a great migratory capacity of up to 100 km per night (FAO, 2017). In Senegal, the species *S. frugiperda* has been

reported by (Brévault et al., 2018). During the same period our surveys have helped find *S. frugiperda* in Casamance, in southern Senegal (pers.comm E.TENDENG, September, 2017.). A study of its previously unrecognized bioecology in Africa is carried out to estimate the annual generation number. The difficulty of managing the pest related to a misunderstanding of its biology and associated auxiliary fauna is a real challenge to rise up. According to (Nagoshi et al. 2017) , the invasion of *S. frugiperda* in Africa has two major consequences. The pest is found in a new area where its natural enemies are absent, which would favor an initial period of rapid population growth and dispersal, with negative impacts on agriculture. The pest may have new resistance traits in its new environment, which puts the crops at risk. The incertitude related to the behavior of the insect in a new environment and the absence of phytosanitary treatments of major crops in Senegal, especially for maize, make that chemical control remains ineffective. In addition, *S. frugiperda* can easily develop resistance to insecticides (organophosphates, pyrethroids, carbamates, etc.) (Yu, 1991). Conservation biological control, which fosters the optimal use of indigenous natural enemies, is a promising way for reducing pesticide reliance (Labou et al., 2016b). Biological control would be an alternative to manage *S. frugiperda*.

The purpose of this study was to contribute to the control of the invasive pest *S. frugiperda*. Specifically, we evaluated the duration of the development cycle of *S. frugiperda* and also determined the parasitism rate by natural enemies.

MATERIELS AND METHODS

Biology of *Spodoptera frugiperda*

Sampling and determination of the duration of the development cycle of S. frugiperda

The sampling was done every 15 days in a maize field located at Boudialabou in Casamance (Senegal). The sampled larvae are returned to the laboratory, isolated in boxes and fed with fresh corn leaves until nymphosis. Nymphs obtained are individually

isolated in boxes and followed until the emergence of an adult of *S. frugiperda*, a parasitoid or parasite.

The eggs laid were monitored daily to know their hatching day. The neonate larvae were also followed until nymphosis to determine the duration of the development of the larval phase. The duration of the nymphal phase was determined by daily monitoring of nymphs until the emergence of adults. The lifetime of adults was shown by following newly emerged adults until they die.

Identification of developmental stages of S. frugiperda

The main development stages (egg, larvae, nymph and adult) were observed using a binocular magnifying glass equipped with a graduated scale. The photos were taken with the "Dinolite" to better visualize individuals. Eggs were measured and counted. Young larvae were described and the size of the cephalic capsule were measured. The size of neonate larvae and that of late larval stages were measured. Pupae were observed and described. Their size was measured. The emerged adults were killed with ethyl acetate and then spread to measure their wingspan.

Identification of natural enemies of *Spodoptera frugiperda* and determination parasitism rate

Parasitoids and parasites identification of S. frugiperda

The main stages of development of parasitoids and parasites are identified. For parasitoids, the total length of the body, wings, antennas and abdomen is measured. Identification keys proposed by Van Achterberg (1990) and Braet et al.(2012) were used to identify parasitoids. Parasitic nematodes were spread out and their length measured. The determination keys proposed by Nickle (1972) and Baker and Capinera (1997) were used for their identification.

Determination of parasitism rate of parasitoids and parasites of S. frugiperda

The parasitism rate was determined by relating the number of auxiliaries (parasitoids and parasites) to the total number of larvae collected and monitored. The percentage of

parasitism was calculated using Mc Cutcheon's formula (1987)

$$\text{Parasitism rate} = \left[\frac{\text{Number of parasitized larvae}}{(\text{NLC} - \text{NDL})} \right] \times 100$$

NLC: Number of Larvae Collected

NDL: Number of Dead larvae without parasitism

RESULTS

Biology of *Spodoptera frugiperda*

Duration of the development cycle of *S. frugiperda* in laboratory

In laboratory, the total duration cycle of *S. frugiperda* is between 22 and 28 days at 25 °C with an average of 25 days. The number of generations per year is between 13 and 17 generations per year with an average of 15 generations (Table 1).

The incubation of the eggs last in 5 days (± 1 d). The duration of development of the larval phase is between 13 and 15 days with an average of 14 days while that of the nymphal phase is 7 days on average. The lifetime of adults is 31 days on average.

Identification of the development stages of *S. frugiperda*

The eggs, 400 in number, measure between 0.3 and 0.4 mm. They form a mass consisting of two layers (Figure 1b). The young larvae are light in color. The black cephalic capsule measures 0.15 mm on average (Figure 1c) and has a dark cervical shield. Sidebands appear gradually from the third larval stage of neonates. In the last larval stage, the size of larvae is variable. The average size is 0.6 mm for neonate larvae. The average size of larvae of last larval stage is 43.9 mm (Figure 1d). The pupae are brown in color with a very pronounced shine. The length of the pupae varies between 14 to 18 mm (Figure 1f). Size of adults vary between 32 to 40 mm wings pan (Figure 1a).

Emerging adults were sexed. Sexage was based on the color of the wings. The female has anterior wings colored gray-brown with indistinct whitish spots. In the male the gray-brown color is more contrasted with whitish spots.

Identification and rate of parasitism of the natural enemies of *Spodoptera frugiperda* Parasitoids and parasites identified on the moth

Despite its recent introduction into West African territory, *S. frugiperda* already has a large number of parasites such as nematodes and hymenopterans (Table 2).

The Nematodes

Nematodes of genus *Hexameris* (Figure 2c-e) emerged from the *S. frugiperda* larvae collected in the field. Out of a total of 290 larvae of *S. frugiperda* collected, 35 larvae died without parasitoids emerging. A total of 35 individuals were obtained from a total of 255 larvae. This gives a rate of parasitism estimated at 13.7%. For nematodes, the emergence of 2-4 individuals per host has sometimes been observed. In this case, the parasitism calculation considers only one individual. Adult nematodes have a length which ranges from 100 to 120 mm (Table 2).

The Hymenopterans

Hymenopterans of the genus *Chelonus* and *Campoletis* were obtained from larvae of *S. frugiperda*. These two hymenoptera are solitary parasitoids. A total of 28 individuals of the parasitoid *Chelonus* sp. was obtained on a number of 255 larvae of the pest. Its rate of parasitism was calculated, giving a percentage of 10.9. For the species *Campoletis* sp., only three (3) individuals emerged from the 255 larvae of the *S. frugiperda* sampled. Its rate of parasitism is 1.2% (Table 2).

Adults of the parasitoid *Chelonus* sp. that have emerged have a size that ranges from 8 to 9 mm (Figure 3f). They are characterized by the presence of two white spots in the anterior part of the abdomen. The relationship between antenna length and the body length and that of the wing and body are respectively 0.8 mm and 0.75 mm.

The species *Campoletis* sp. has long antennae (Figure 4a). They are longer than the body and vary from 7 to 8 mm. The length of the body varies from 6 to 7 mm. The forewings are between 5.7 to 5.9 mm

Table 1: Size and Life span of the main stages of development of *S. frugiperda* elevated in laboratory at $25 \pm 1^\circ\text{C}$, HR $65 \pm 5\%$, Photoperiod 12h.

Stages	Length	Duration
Eggs	$0.4 \pm 0.1\text{mm}$	5 ± 1 days (Incubation)
Larvae	$0.6 \pm 0.2\text{mm}$ (neonate stage) 43.9 ± 0.2 mm (Last stage)	14 ± 1 day (Larval phase)
Pupae	14 ± 0.1 mm	7 ± 1 days (Nymphal phase)
Adults	31 ± 2 mm	16 ± 1 days (Adult phase) 26 ± 3 days (Total duration of the cycle)

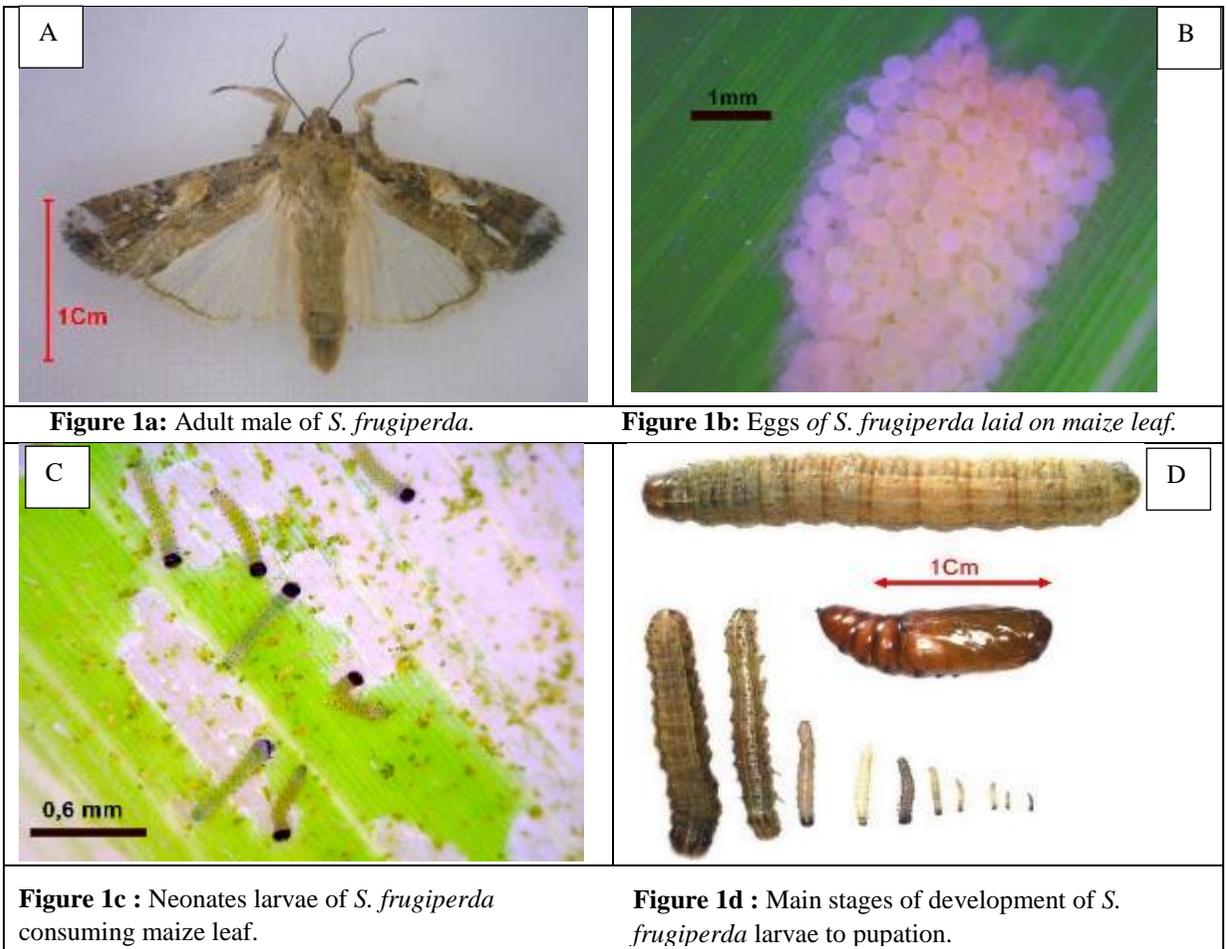




Figure 1e : Nymph of *S. frugiperda* from a loose soil maize field.

Figure 1g: Nymphs of *S. frugiperda* measured in the laboratory.



Figure 1f: Pinaculas of *S. frugiperda* larva arranged as a square.

Figure 1h: Cephalic capsule of *S. frugiperda* larvae with a lighter inverted "Y".

Table 2: Life span and parasitism rates of the main parasitoid hymenopterans and parasite nematodes observed on *S. frugiperda* monitored at the laboratory at $25 \pm 1^\circ\text{C}$, HR $65 \pm 5\%$, Photoperiod 12h.

Auxiliaries	Number *	Life span of adults	Parasitism (%)
HYMENOPTERA PARASITOID			
Ichneumonidae	3	7 ± 2 days	1.2
<i>Campoletis</i> sp.			
HYMENOPTERA PARASITOID			
Braconidae	28	$8d \pm 1$ day	10.9
<i>Chelonus</i> sp.			
NEMATODE PARASITE			
Mermithidae	35	120 ± 5 days	13.7
<i>Hexamermis</i> sp.			
Total parasitism			25.8

*: On a total of 255 larvae of *S. frugiperda* collected.

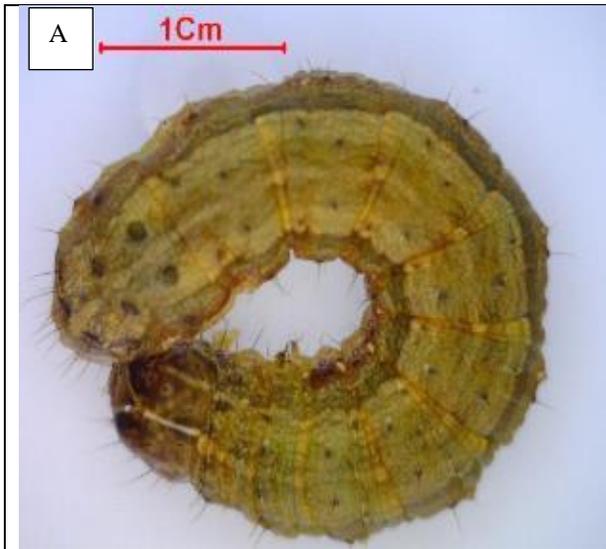


Figure 2a : Non-parasitized *S. frugiperda* larva.

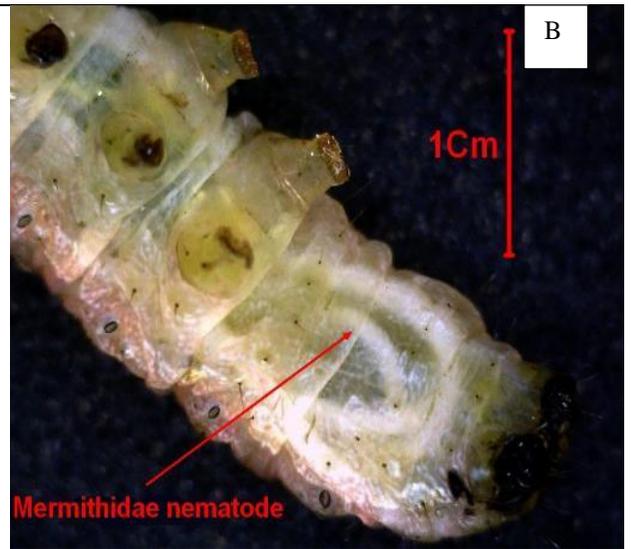


Figure 2b: Parasitic nematode (*Hexamermis* sp.) inside the body cavity of *S. frugiperda* larva.



Figure 2c-d : Active emergence of Mermithidae nematodes (*Hexamermis* sp.) from the body cavity of *S. frugiperda* larvae (either at the level of the cephalic capsule or at the level of the false legs).



Figure 3a: *Spodoptera frugiperda* larva.

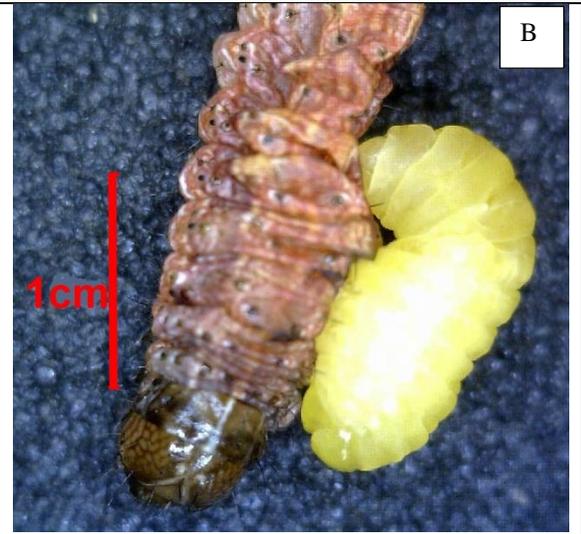


Figure 3b: Parasitoids larva (*Chelonus* sp.) sucking the hemolymph from *S. frugiperda* larva.

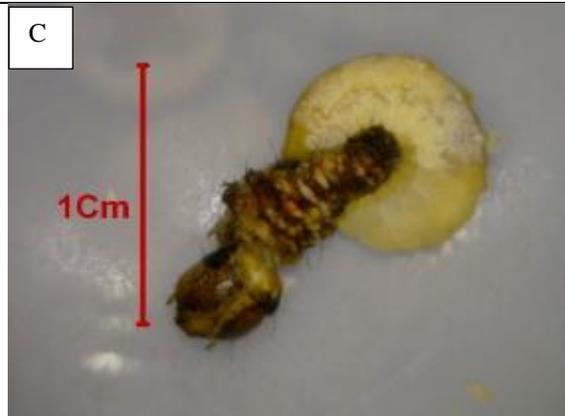


Figure 3c : Parasitoid larvae (*Chelonus* sp.) sucking the hemolymph from *S. frugiperda* larva.

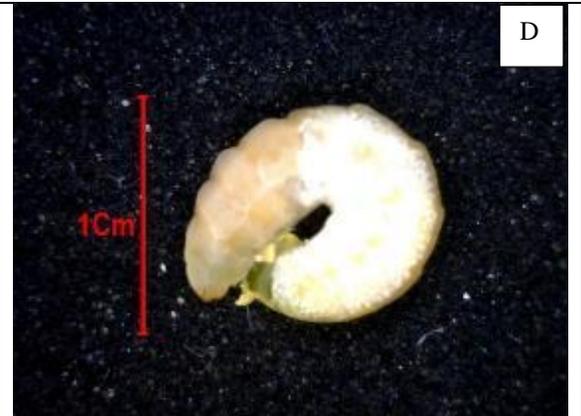


Figure. 3d: Parasitoids larva (*Chelonus* sp.) alone after sucking the hemolymph from *S. frugiperda* larva.

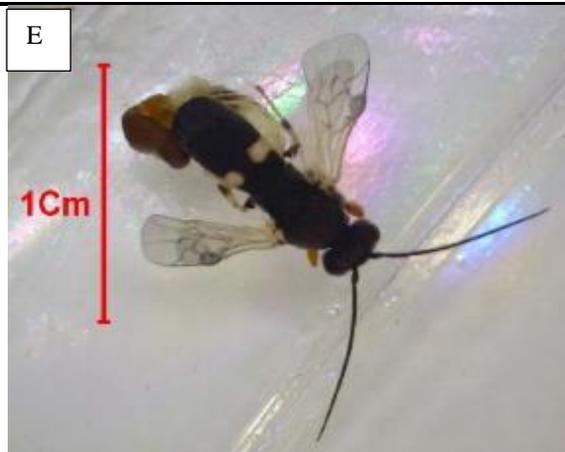


Figure 3e : Emergence of *Chelonus* sp. adult parasitoid.



Figure 3f: Adult *Chelonus* sp. able to parasitize *S. frugiperda* larva.



Figure 4a: Adult *Campoletis* sp. able to parasitize *S. frugiperda* larva.

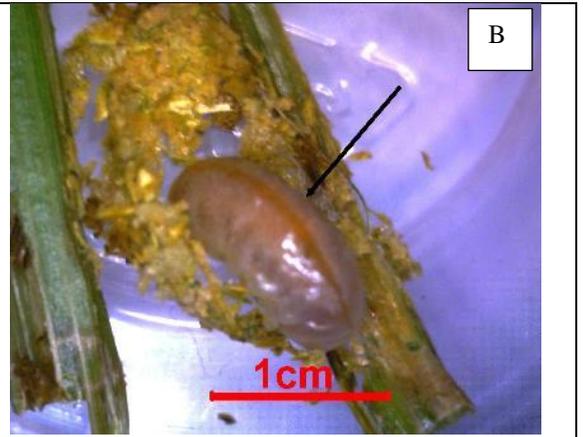


Figure 4b: Parasitoid larvae (*Campoletis* sp.) newly emerged from *S. frugiperda* larva.



Figure 4c: Cocoon of the parasitoid (*Campoletis* sp.) on maize leaf.

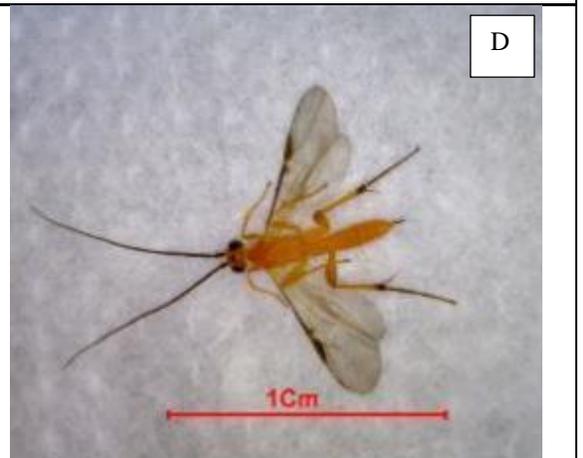


Figure. 4d: Adult of the parasitoid (*Campoletis* sp.) freshly taken out of the cocoon

DISCUSSION

The results show that the total duration of *S. frugiperda* cycle is between 22 and 28 days with an average of 25 days at 25 °C. Which give on average 15 generations a year. Castro and Pitre (1988) have shown that *S. frugiperda* development cycle is between 28 to 38 days when the pest is fed with sorghum and 35 to 45 days when fed with corn. The FAW is a formidable invasive pest as it has a fairly rapid development cycle that varies with temperature (Chapman et al., 2000; Barros et al., 2010b; Jeger et al., 2017). The optimum larval development temperature of *S. frugiperda* is 28°C, but may be lower for egg-laying and pupation (CABI, 2017). Depending on the host plant and weather

conditions, the cycle duration may be different. The pest also has a preference for poaceous, especially maize (Dumas et al., 2015). The results of Castro and Pitre (1988) showed a cycle of 45 days. The generation number per year is 8, much lower than the annually 15 generations obtained from the results of this study after rearing *S. frugiperda* in the laboratory from September 2017 to September 2018. The number of generations per year of the *S. frugiperda* has a big impact on yields. Indeed each generation can cause damage to the present crops. It is a pest with a very strong occurrence because of its wide spectrum of host plants. Indeed, larvae feed on leaves and stems of more than 80 plant species (CABI, 2017). This polyphagous

character can promote the increase in the number of generations observed annually in tropical countries. Depending on the host plant, there are different populations of the *S. frugiperda* with a "C" strain on corn and cotton and a dominant "R" strain on rice, millet and wild grasses (Groot et al., 2008).

For the larvae, our results showed that the average duration of larval phase development is 14 days whereas it is 21 days at 25 °C (Silva et al., 2017) and 11 days at 25 °C (Santos et al., 2003) for larvae fed with maize. The duration of the larval phase depends on the conditions and the host plant. The larval stage is the most dreaded stage of the pest *S. frugiperda*. The damages are caused by larvae that can cause enormous losses in yields that can go until the total destruction of crops. Human consumption of maize is expected to increase by 21% (28 Mt), especially in developing countries, especially those in Africa where white maize is an essential staple food in many countries (OCDE/FAO, 2016). In sub-Saharan Africa, famine will persist if no effective protective measures are taken to limit the expansion of the FAW. In other words, larvae cause countless damages to coarse grains such as rice and sorghum, but also cotton and vegetable crops (FAO, 2017). Indeed, the longer is the duration of the larval stage, the greater are the losses because the larvae consume a lot, especially during the last four days before pupation (Flanders et al., 2017). As soon as the eggs hatch, the larvae begin to consume the host plant until they pupate. All part of the plant can be consumed (leaf, stem, ear, bud...). The amount ingested increases with the growth of the larvae. The consumption of *S. frugiperda* larvae is most important from the 3rd larval stage and increases until the last one. This can lead to significant yield losses. The pest status of FAW is usually associated with specific developmental stages of the host plant (Barros et al., 2010a). Larvae prefer most often seedlings and young leaves that are more susceptible to damage. In an infested cornfield, older larvae are often housed in the bud of the plant. This position in the bud

protects this pest against some auxiliaries (predators and parasitoids) and even some chemicals. Producers have difficulty detecting the pest in these conditions. They only observe the damage. On the ground, the attack of plants with 6-10 leaves is more severe and has more harmful damages. The larva destroys the bud of young plants and prevents their normal development. Maize is more sensitive at the time of inflorescence (Kranz et al., 1981). Eggs are incubated in 5 days (± 1 day). This egg incubation duration depends on the temperature and is between 2 and 10 days (Jeger et al., 2017). For temperatures between 21 and 27 °C the incubation duration of eggs is between 2 and 4 days (Sparks, 1979).

For the identification of the main stages of development of *S. frugiperda* (egg, larva, nymph and adult), the results show that a female lays oblong eggs grouped on the leaves of the host plant. A spawn contains about near 300 to 400 eggs arranged in layer. Adult female of *S. frugiperda* can lay up to 1500 to 2000 eggs (Kumela et al., 2018). The eggs measure between 0.3 and 0.4 mm. They form a mass consisting of two layers. The egg mass is covered with a felted protective layer of silks from the abdomen of the female (Figure 1b). These observations corroborate those studies on the moth (Capinera, 1999; EPPO, 2015). Indeed, this protective layer makes it difficult to count eggs with a binocular magnifying glass in the laboratory.

After egg hatch, neonate larvae feed on the upper surface of maize leaves without crossing the blade and the lower epidermis remains transparent (Figure 1c). This aspect of the leaves facilitates the recognition of the pest in the field. In laboratory, the similarity observed at the different larval stages is confusing as to their clear distinction (Figure 1d). Which explains the variation of the number of larval stages (5 to 6) found in the literature (Santos et al., 2003). As they develop, the larvae of *S. frugiperda*, present four pinaculas arranged in square at the level of the last segment (Figure 1g). Older larvae of this pest possess a « Y » inverted of lighter color in the cephalic capsule (Figure 1h). These characters are decisive for the

recognition of larvae according to a number of studies on *S. frugiperda* biology (Passoa, 1991; EPPO, 2015). The color of the larvae gets darker as they grow from light green to brown (EPPO, 2015). Nevertheless, the color of the larvae remains an unreliable criterion because it is often random. As for nymphosis, if it takes place in loose soil, the chrysalis is protected by a silk cocoon secreted by the larvae (Figure 1e). On a hard surface, the chrysalid is without a silk cocoon. The chrysalis has three segments at its posterior end. Adults are sexually dimorphic based on color contrast more accentuate in the male (Pogue, 2002). In the laboratory, recognition based only on the color of adults is a criterion that becomes obsolete with time because adults lose their color very quickly in contact with the wall of breeding cages. Moreover, this dimorphism is easily confused with that of other species of the same genus e.g., *S. exempta* or *S. littoralis* (Reddy, 2017; EPPO, 2015).

To manage the populations of the *S. frugiperda*, control strategies have been mainly adopted; chemical control by use of synthetic products, the genetic control with the use of genetically modified plants (GMOs) (Bernardi et al., 2014) and biological control through the use of organic extracts (Scapinello et al., 2014; Sosa et al., 2017). The control based into *B. thuringiensis* (Bt) with the formulation of maize-Bt hybrids was also been used for controlling the fall armyworm (Farias et al., 2014; Niu et al., 2017). However, these control methods have limitations because of the resistance developed by this pest (Adamczyk Jr et al., 1997; Bernardi et al., 2017).

Biological control appears as a serious alternative to enhance. As a result, it becomes relevant to exploit the action of the natural enemies of this pest in its environment. Our results show that, despite its recent introduction in West Africa, *S. frugiperda* already has a large parasite procession that goes from nematodes to hymenopterans. Indeed, nematodes of the genus *Hexameris* (Figure 2e) and hymenopterans of the genus *Chelonus* (Figure 3f) and *Campoletis* (Figure

4a) were obtained from the larvae of the *S. frugiperda* with an overall parasitism rate of 25.8%. This rate of parasitism is divided between nematodes (13.7%) and hymenopterans (12.1%). These hymenopterans belong to the family Braconidae (*Chelonus* sp.) and ichneumonidae (*Campoletis* sp.). With a parasitism rate of 10.9% for *Chelonus* sp. and 1.2% for *Campoletis* sp. These parasitoids and the parasite *Hexameris* sp. (13.7%) are a promising mean for the biological management of the pest. For the first time in West Africa a parasitic nematode and two parasitoid hymenoptera regulate *S. frugiperda* populations. In Africa, five species of parasitoids were recorded from the fall armyworm in three East African countries in 2017 (Sisay et al., 2018). For parasitism of nematodes, specimens up to more than 10 cm long have been observed inside the L4 stage larvae organism. This infestation would start from the young larvae (neonates) which, dispersing, spend a short time on the ground where they are often in contact with the juvenile nematodes. The latter infesting only during this phase (James et al., 2010; Campos-Herrera, 2015), parasitize the larvae through an active entrance through their cuticle. The germs of this nematode grow in the abdomen of the host larvae, which now leads a sluggish life with a marked decrease in its consumption. At maturity, the nematode actively leaves its host either by the cephalic capsule or most often by the false legs of the lower ventral (Figure 2c-2d). A record of four individuals of the parasite per host larvae were sometimes obtained. At the exit of the parasite, the larvae is in the form of a body lying on the place of emergence of the nematode (Figure 2d). After emergence, adult nematodes couple and intertwine to produce offspring that in turn actively seek other host larvae. This phenomenon was observed on isolated nematodes in boxes containing humid sand just after emergence. Adult nematodes have a life span that exceeds 90 days in the laboratory.

The species *Chelonus* sp. is an ovolarval parasitoid. The *Chelonus* Panzer genus

can attack several Lepidoptera including *Helicoverpa armigera*, *Plutella xylostella*, *Phthorimaea operculella*, and *Hellula undalis* (Yousuf and Ray, 2009). This genus is cosmopolitan and belongs to the subfamily of the Cheloniinae which includes solitary endoparasitoids koïnobiontes. Koïnobionte parasitoids do not immediately kill their hosts, which appear to follow normal development (Askew and Shaw, 1986). The parasitized larvae continue their development until the exit of the parasitoid. At the time of emergence, the host larvae becomes moribund and is unable to move or feed. Parasitoid, although located on the outside, remains attached to the larvae track and continues to suck the hemolymph (Figure 3b-3c). When the contents of the larvae are emptied, the parasitoid larvae is detached from it and continues its development by secreting a silk cocoon that protects it until the adult emerges. The larvae obtained are pearly white in color and vary in size from 8 to 10 mm. The lifetime of the larvae is 8 to 9 days after which emerges an adult.

The *Campoletis* sp. species is a larval endoparasitoid that plays an important role in regulating *S. frugiperda* (Molina-Ochoa et al., 2003; Dequech et al., 2005; Ordóñez-García et al., 2015). The FAW is a natural host of the parasitoid *C. flavicincta* (Neto et al., 2004; Zanuncio et al., 2013). The larvae of the parasitoid, just out of the larvae of *S. frugiperda* pest starts making his cocoon (9.5mm long) which allows it to continue his development until the emergence (Figure 4b-4c).

In addition to biological control, cultural method with a use of "push-pull" was experienced in East Africa and seems to effectively fight against the larvae of *S. frugiperda* (Midega et al., 2018). Indeed, the establishment of plants attracting the auxiliaries between the rows of the host culture and plants repelling the FAW at the border of the field acts both on the physical and chemical characteristics of the pest. The effectiveness of the "push-pull" can be attributed to the confusion of the pest to detect the host plant. On the other hand, depending

on the biology of *S. frugiperda*, the distance between the rows of the crop affects the efficiency of the dispersion of the larvae. Indeed, neonate larvae from hatching eggs disperse by moving on the leaves or hanging from a silk thread they secrete. This dispersion is all the more effective thanks to the action of the wind which causes their oscillation allowing the larvae to land on a nearby plant or on the ground. If the plant nearby differs from the host, the larvae proliferate with difficulty and die by loss of contact with their food. Young larvae are often parasitized by juvenile nematodes leading an active life free searching host. The larvae, by consuming maize leaves are contaminated by ingesting nematode eggs deposited by females. Indeed, the females adult of nematodes leave the ground and rise to the leaves to lay eggs. Active infestation of nematodes through the cuticle of larvae is also possible. Eggs can hatch in the soil and infective juveniles of mermithidae go back vegetation, where they discover and invade their host (Riga, 2004). In this case, nematode enters the digestive tract of the larvae by piercing the cuticle.

A good knowledge of the bio-ecology of the FAW seems necessary for its effective management. Indeed, its appearance in Senegal, the FAW constitutes a new threat to food security because of its high migration capabilities and its damages to corn crops. In Senegal, arthropod pest complex can cause damage in field-grown (Labou et al., 2016a; Diatte et al., 2018b). However, many ecosystems have a great diversity of entomological species that plays an important role in natural regulation (Labou et al., 2017; Tendeng et al., 2017; Diatte et al., 2018a). Very active during the night, adults of the FAW can move up to a distance exceeding 100 km (FAO, 2017). These migratory performances are manifested by his ability to colonize new environments. *S. frugiperda* adults from the United States migrated to Georgia from southern Florida over a distance about 600 km (Nagoshi et al., 2008). In Africa, Comparative molecular analyses of invasive fall armyworm in Togo reveal strong

similarities to populations from the eastern United States and the Greater Antilles (Nagoshi et al., 2017). Another study confirmed initial indications based on Togo populations of *S. frugiperda* that Florida and the Greater Antilles are the likely source of at least a subset of the African infestation and further suggest an entry point in western Africa (Nagoshi et al., 2018). This suggests that the specimens found in Casamance (in Senegal) in August 2017 would come from the same source. Comparative molecular analyses of the FAW are necessary to determine the origin of the strains found in Senegal.

Conclusion

Native natural enemies regulate *S. frugiperda* populations. The present study confirms the presence of indigenous natural enemies of the fall armyworm in West Africa. The results show a regulation rate of 25.8%. This natural regulation would be an alternative to the use of often ineffective chemicals against this pest. For the first time in West Africa, a parasitic nematode and two parasitoid hymenoptera regulate *S. frugiperda* populations. The results of this study allow us to conclude that these native natural enemies are a very promising means of control against FAW populations. The use of chemicals to control FAW can be a cause for economic loss due to their high price and inefficiency against *S. frugiperda*, and ecological waste by killing natural enemies and other useful insects. Control methods or agricultural practices that favor the maintenance of native natural enemies are necessary to fight *S. frugiperda*. More research is needed on local factors (crop management) and landscapes (crops and non-crop habitats) that favor parasitoid communities.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

ET contributed to the definition of experimental protocols, field data collection,

statistical data analysis and article writing. BL contributed to the definition of experimental protocols, statistical analysis of data and the writing of the article. MD contributed to the definition of the experimental protocols and the writing of the article. SD contributed to the definition of the experimental protocols and the writing of the article. KD contributed to the coordination of activities, the definition of experimental protocols, statistical data analysis and manuscript correction.

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