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ORIGINAL PAPER

Cannibalism and intraguild predation involved in the intra- and inter-specific interactions of the invasive fall armyworm, *Spodoptera frugiperda*, and lepidopteran maize stemborers

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Abstract

Cannibalism and intraguild predation can play important roles in determining spread and survival or death of organisms which share the same resource. However, the relationship between cannibalism and intraguild predation, and the costs and benefits of such behaviours, is difficult to establish within insect communities, and little is known about how such behaviours are affected by invasive species. The present study was aimed at assessing the interactions between larvae of fall armyworm (*Spodoptera frugiperda*) and maize stemborers (native to Africa, *Busseola fusca*, and *Sesamia calamistis* and native to India, *Chilo partellus*) in relation to cannibalism and intraguild predation when they utilize the same resource. Experiments involving treatments with either single species of *S. frugiperda* or any of the stemborers or pairwise species combinations with *S. frugiperda* were conducted under laboratory conditions. The experimental insect larvae were reared on maize leaves and monitored until the last developmental stage where cannibalism and/or intraguild predation, larval survival, and relative growth rate were recorded. Results of the intraspecific interaction indicated that *S. frugiperda* exhibited cannibalism to a larger degree than the stemborers species, especially at the late instars. The higher cannibalism trait in *S. frugiperda* turned, however, to competitive advantage as it led to a higher degree of intraguild predation when they cohabit with stemborer species and allowed FAW to gain a greater relative growth rate. Overall, interactions with FAW are detrimental for stemborer species and may be an important factor to explain the invasive success of *S. frugiperda*. Such knowledge is essential to understand the mechanisms behind ecological interactions between pests with overlapping niches in the field and in designing successful integrated pest management strategies.

Keywords *Spodoptera frugiperda* · Cannibalism · Stemborers · Intraguild predation · Intra- and interspecific interactions

Key message

- Intraguild interactions of overlapping niches pest species determine their population evolutionary.
- Invasive fall armyworm (FAW) co-inhabits maize with stemborer species in maize cropping systems.
- In the presence of stemborer species
- FAW prefers to feed on stemborers rather than their conspecifics.
- FAW gains more weight when it feeds on stemborer species than when it feeds on their conspecifics.
- The higher intraguild predation of FAW on stemborers might control their population in the field

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Introduction

Resource availability varies spatially and temporally either within or across developmental stages and competitive exclusion should result when resources are limited. Such exclusion depends on the biological characteristics of the interacting organisms, where some species may have better competitive abilities. Intra- and interspecific competitions play an important role in determining survival/death and spread of organisms which share the same niche (Gurevitch et al. 1992; Cameron et al. 2007). The interaction between organisms can be expressed as either exploitative (as use of the resource by one species reduces the availability for the other) or interference competition (when one species behaviourally restricts the other species from access to limited resources). In the most extreme form of interference competition, the interaction leads to the death of one of the involved organisms either through wounds or through being eaten by its competitor and is thus defined as either cannibalism or intraguild predation.

Cannibalism, also called intraspecific predation, is known as killing and consumption of a conspecifics and is a widespread behaviour in phytophagous insects, mostly in lepidopteran species (Richardson et al. 2010). It is often more pronounced under high population densities (Sokame et al. 2022) and when resources are limited (Elgar and Crespi 1992) but can occur even when food is not limited (Polis 1981). Intraguild predation (IGP) occurs between different species within the same trophic level (Bentivenha et al. 2016a). Polis and Holt (1992) reported that although combining elements of predation and competition, intraguild predation is distinct from competition because one participant (the predator) accrues immediate energetic gains. It is also distinct from classical predation, because the act reduces potential competition besides the actual energetic gains. Intraguild predation can act as a mechanism of population regulation or as a determinant of community structure in phytophagous insect communities (Holt and Polis 1997; Bentivenha et al. 2016a; 2017). Irrespective of whether it is cannibalism or intraguild predation, these behaviours are often costly in terms of energy, time, risk of injury and death (Kelly and Godin 2001; Briffa and Elwood 2004) for competing individuals, and this may have repercussions for an individual's fitness. The balance between cannibalism and intraguild predation depends on involved species. For instance, it was reported that when cannibalism was compared to intraguild predation in the feeding on conspecific and heterospecific eggs among three predators, the coccinellids *Coccinella septempunctata* L. and *Hippodamia convergens* Guerin-Meneville and the predatory bug *Geocoris bullatus* Say, intraguild predation was less common than cannibalism for the coccinellid species, whereas it was more common than cannibalism for the predatory bug (Takizawa and Snyder 2011). Furthermore, Rasekh and Osawa (2020) reported that when *Harmonia axyridis* and *H. yedoensis* were exposed to either cannibalism or IGP, *H. axyridis* had longer development time while *H. yedoensis* presented shorter development and lighter adult weight. Therefore, the relationship between cannibalism and intraguild predation, and the costs and benefits of such behaviours is complex. Moreover, there is still little known about how such behaviours are affected by invasive species and how they could affect the dynamics of crop pests that share the same resources.

In East and Southern Africa, the native noctuid stemborers, *Busseola fusca* (Fuller) and *Sesamia calamistis* Hampson, and the invasive crambid *Chilo partellus* (Swinhoe) are key pests of maize and sorghum (Seshu-Reddy 1998; Kfir et al. 2002). Depending on altitude, they occur as single species or mixed multi-species communities (van den Berg et al. 1991; Tefera 2004; Ong'amo et al. 2006; Krüger et al. 2008). In addition to these maize pests, fall armyworm (FAW), *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) native to the Americas, has recently been reported in the region as an additional pest in maize cropping system (De Groote et al. 2020; Kassie et al. 2020; Sokame et al. 2020). FAW shares the same maize plant-feeding guild as the pre-existing lepidopteran stemborers (Goergen et al. 2016; De Groote et al. 2020; Sokame et al. 2020). The stemborer larvae feed on young leaves until the third instar, then bore into the maize stems where they complete their development (Holloway 1998; Polaszek 1998). FAW larvae, in contrast, feed preferentially on leaves throughout their development, especially the central leaves in plant whorl (Morrill and Greene 1973; Van den Berg 1997; Montezano et al. 2018). However, in maize fields at tasseling stage, the FAW larvae could be found feeding on the tassels and subsequently on the ear, silk, cob, and even in stemborer holes in the plant stem (Morrill and Greene 1973; Cruz and Turpin 1983; CAB International 2017) leading them to share the same ecological niche with possible intraguild competition. A previous study reported competition among these four maize pests when they utilize the same resource in a restricted space (Sokame et al. 2020) and the decrease in stemborer density at maize reproductive stage in maize fields following the invasion of FAW in the system (Sokame et al. 2021a) suggests competitive exclusion by FAW since its introduction in Africa. However, the potential of cannibalism and intraguild predation to play a role for the ecological species dynamics within the community is not well known.

Hypothetically, intraguild predation could contribute to the rapid establishment of FAW in new areas, and however, the benefits may be balanced by costs of cannibalism and the exact outcome depends on the interactions within the specific lepidopteran pest communities in maize. In the native range of FAW, cannibalism has been reported (Chapman et al. 1999a,b; Andow et al. 2015) as well as intraguild predation between FAW and *Helicoverpa zea* (Bentivenha et al. 2016a). Cannibalism has also been reported in *C. partellus*, but only at high larval densities (Bonhof and Overholt 2001). Nevertheless, there is still much to be clarified about the behaviour of other stemborer species, and about the interspecific interactions between FAW and these stemborers when they co-occur, and to understand the mechanisms behind species dynamics in the field. A better understanding of the intra- and interspecific interactions will be useful to understand how competitive displacement occurs between those pest species sharing a given ecological niche, and consequently facilitating the design of new successful integrated pest management strategies (Benelli 2015). In this context, the present study aimed at assessing the potential of cannibalism and intraguild predation of the four lepidopteran maize pests species when they are constrained to utilize the same resource, and the consequences for the interacting species.

Materials and methods

Insects

All stemborer and FAW larvae were provided by the Animal Rearing and Containment Unit (ARCU) at *icipe*, Nairobi, Kenya. Larvae were reared on artificial diet in cylindrical plastic jars (16.5 cm high and 9 cm in diameter) with about 200 ml of diet per jar. For the stemborers, the diet consisted of a vitamin mix, maize leaf powder, brewer's yeast, bean powder, sucrose, ascorbic acid, sorbic acid, and methylparaben formaldehyde (Onyango and Ochieng'-Odero 1994). For rearing FAW larvae, the diet was complemented with wheat germ, milk and Suprapen powder, whereas sucrose was removed. Agar was added to each type of diet to solidify the medium and preserve moisture. After inoculation, the plastic jars were tightly sealed using perforated lids with galvanized mesh. They were covered with tissue paper and kept in a rearing room at 26 ± 1 °C, 60 ± 5% RH., and L12 and D12 photoperiod. Twice a year, each colony was rejuvenated with field-collected stemborer or FAW larvae.

Experimental set-up

Experiment 1: cannibalism and intraguild predation in communities of fall armyworm and stemborer species during larval development

The experiment was conducted to evaluate the potential for cannibalism and intraguild predation of fall armyworm in single- and multi-species communities with stemborer species and whether individuals that have fed on conspecifics gain any advantages. Single-species experiments with FAW or one of the stemborers (*B. fusca*: Bf, *S. calamistis*: Sc, and *C. partellus*: Cp) or pairwise species combinations between FAW and each of the stemborer species were conducted in plastic containers (16 cm × 10 cm × 7 cm) lined with a paper towel to absorb excess moisture. The single-species infestation treatments consisted of 20 neonates, while the pairing-species combination involved 10 neonates of each species per container and enough food constituted of six pieces of freshly cut maize leaves (10 cm × 6 cm) were supplied in each container with two days interval until the experiment terminated. Survival, relative growth rate, and cannibalism coupled with intraguild predation were evaluated from neonate to the last instar larvae for pupation with four (4) days interval (corresponding to the mean time from one instar to another until L5 for FAW) and after five (5) days from L5 to L6, the last instar before pupation (Malusi P. pers. Observation). Cannibalism and intraguild predation were recorded either when a partial corpse of a dead larva found or when a larva had disappeared from the closed container. Dead larvae found in full corpse were attributed to other mortality reasons, were removed from the containers and were not considered for analysis.

Experiment 2: larval age-dependent cannibalism and intraguild predation in fall armyworm and stemborer communities

To compare cannibalism of FAW and intraguild predation on stemborer species and how this may differ with larval age, an experiment was performed with three larval age-groups: neonate to second as small size, third to fourth as medium size and, fifth and sixth instar as large size. Larvae of each age group were transferred to a container (as above), and six pieces of freshly cut maize leaves (10 cm × 6 cm) were supplied in each container as food on day 1 and day 3 of the experiment. The single-species infestation treatments consisted of 40, 20 and 10 larvae for small, medium, and large size groups, respectively. The densities were chosen as they correspond to densities often encountered in the field (Sokame BM. Pers. Obs.). Similar to the method of Bonhof and Overholt (2001), the pairing-species combination for multi-species communities was performed with 20, 10 and 5 larvae per container of each species for FAW + Bf, FAW + Sc and FAW + Cp pairings for each small, medium and large size group, respectively (Table 1). The cannibalism coupled with intraguild predation (dead larvae found in partial corpse or disappeared corpse) was recorded on the fourth (4) day of the experiment (corresponding to the mean time from one instar to another).

Table 1 Number of larvae used for each species in the single- and multiple-species combinations tested for each of the three densities of infestation

Combinations	Larval sizes		
	Small	Medium	Large
FAW	40	20	10
Bf	40	20	10
Sc	40	20	10
Cp	40	20	10
FAW + Bf	20 + 20	10 + 10	5 + 5
FAW + Sc	20 + 20	10 + 10	5 + 5
FAW + Cp	20 + 20	10 + 10	5 + 5

FAW Spodoptera frugiperda, *Bf Busseola fusca*, *Sc Sesamia calamistis*, *Cp Chilo partellus*

For both Experiments 1 and 2, the plastic containers were closed with perforated plastic lids and kept in a rearing room at a temperature of 25 ± 0.05 °C, RH of 58.5 ± 0.4%, and a photoperiod of L12:D12 for 4 days. Each treatment was replicated twenty times. The cannibalism (C) in single-species communities and both cannibalism and intraguild predation (C&IGP) in multi-species communities were calculated as follows:

$$Cor(C\&IGP) = N - (Ns + Nd)$$

where N denoted the initial number of larvae in each container, Ns number of surviving larvae and Nd number of dead larvae.

The relative growth rate (RGR) for each species was calculated using the following equation (Ojeda-Avila et al. 2003):

$$\text{RGR} = \frac{\text{Mass per surviving larva} - \text{Initial mass per larva}}{\text{Number of days after pairing species}}.$$

Data analyses

The number of surviving larvae and the number of larvae that have been consumed (cannibalism and intraguild predation) from either experiment 1 or experiment 2 were analysed using a generalized linear model (GLM) with negative binomial regression procedure. Significant differences were separated using Tukey's multiple comparison test performed using the R package "lsmeans" (Lenth 2016). The relative growth rate (RGR) of the larvae from the two experiments was analysed using Kruskal–Wallis nonparametric procedure with dunn.test R package after being tested for normality and homogeneity of variance using Shapiro–Wilk and Bartlett tests, respectively. All analyses were performed with R software version 3.5.1 (R Core Team 2018).

Results

Cannibalism and intraguild predation, survival, and relative growth rate in pairing-species combinations and single-species communities of fall armyworm and stemborer species during larval development

In pairing-species combinations, cannibalism coupled with intraguild predation on stemborers in each combination (Fig. 1A1–A3) was higher than those on FAW throughout the entire larval development ($\chi^2 = 54.21$; df = 3; $P \leq 0.0001$). Furthermore, none of the stemborer species survived until the last instar in any of the combinations (Fig. 1B1–B3). The survival rate of either FAW or stemborers decreased along larval development instars ($\chi^2 = 42.52$; df = 5; $P = 0.001$) and the survival of FAW was higher than those of stemborers in each combination ($\chi^2 = 57.13$; df = 3; $P = 0.004$). Whenever the stemborers were finished, the cannibalism within FAW increased exponentially (Fig. 1A1–A3). The growth rate of the survived stemborer did not reach the optimum before they disappeared in the treatments with species pair combinations (Fig. 1C1–C3). The optimum of FAW growth rate ranged from 40 to 50 mg/day across the different combinations, and it decreased after stemborer species were no longer present in the combinations (Fig. 1EC1–C3).

In single-species communities, cannibalism rate (Fig. 1D) was higher in FAW than in stemborer species from third to last instar, L3 ($\chi^2 = 56.7$; df = 3; $P = 0.01$), L4 ($\chi^2 = 34.92$; df = 3; $P = 0.002$) L5 ($\chi^2 = 95.78$; df = 3; $P = 0.03$) and L6 ($\chi^2 = 123.54$; df = 3; $P \leq 0.0001$). Across larval instars, the three stemborers species presented similar survival and even higher than those of FAW species from third to sixth instar (Fig. 1E, $\chi^2 = 308.17$; df = 5; $P = 0.0001$). FAW presented the greater relative growth rate as compared to those of stemborers at third and fourth instars with an optimum of 30 mg/day (Fig. 1F). However, the optimum is lower compared to when it could feed on stemborer species (Fig. 1C1, C2).

Larval age-dependent cannibalism and intraguild predation in fall armyworm and stemborer communities and their comparison in single- versus pairing-species combinations communities

In the treatments with combinations of fall armyworm and stemborer species, the number of stemborer larvae that was consumed was higher than the number of fall armyworm larvae consumed in all combinations and at all larval size groups: FAW + Bf (Fig. 2A, small: LR = 82.47; df = 1; $P \leq 0.0001$, medium: LR = 49.11;

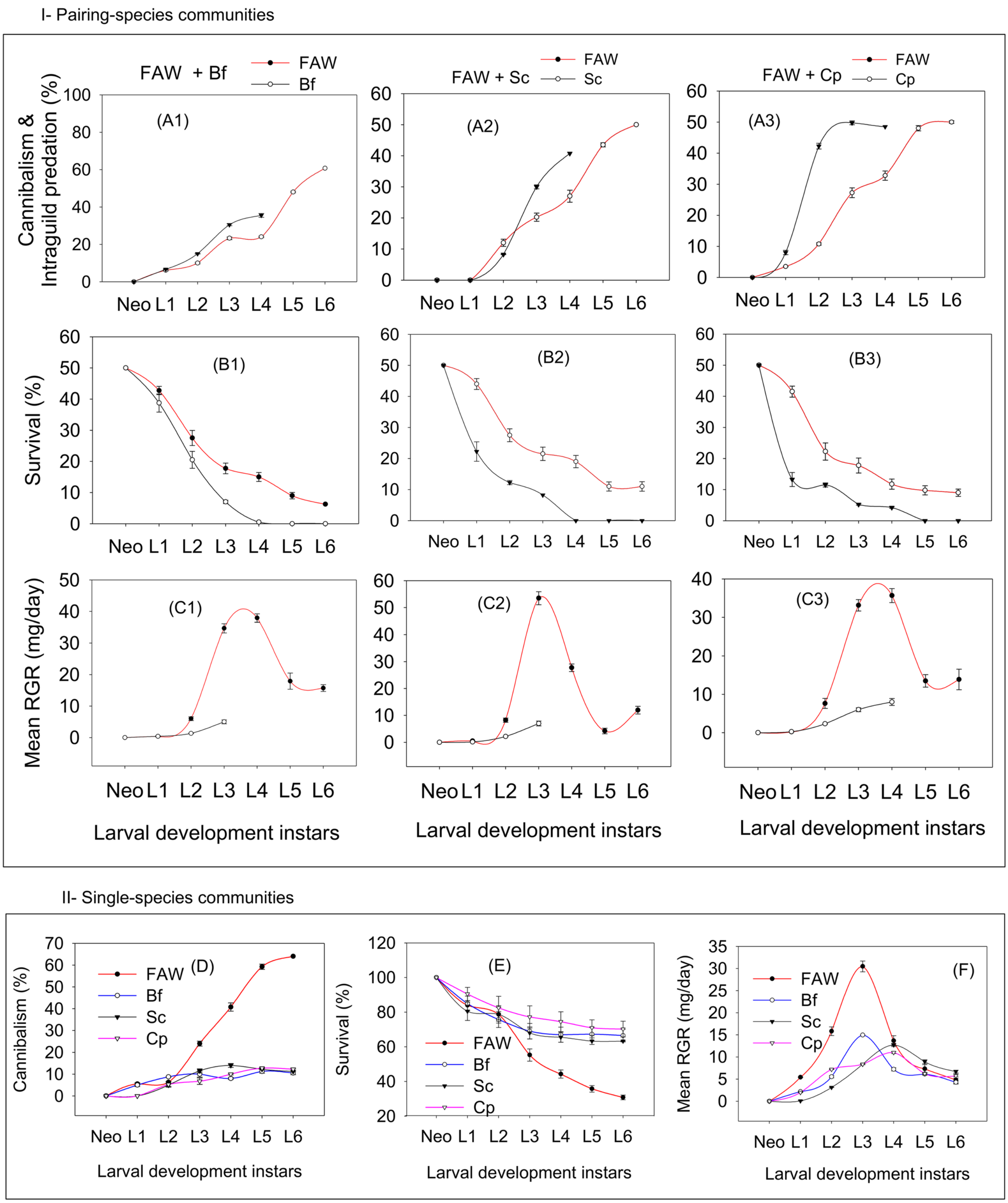

Fig. 1 Cannibalism and/or intraguild predation (**A1–A3**), survival (**B1–B3**) and relative growth rate (**C1–C3**) in pairing-species communities and the same parameters in single-species communities (**D**, **E**, and **F**, respectively) of *Spodoptera frugiperda* (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc), and *Chilo partellus* (Cp) across larval development instars

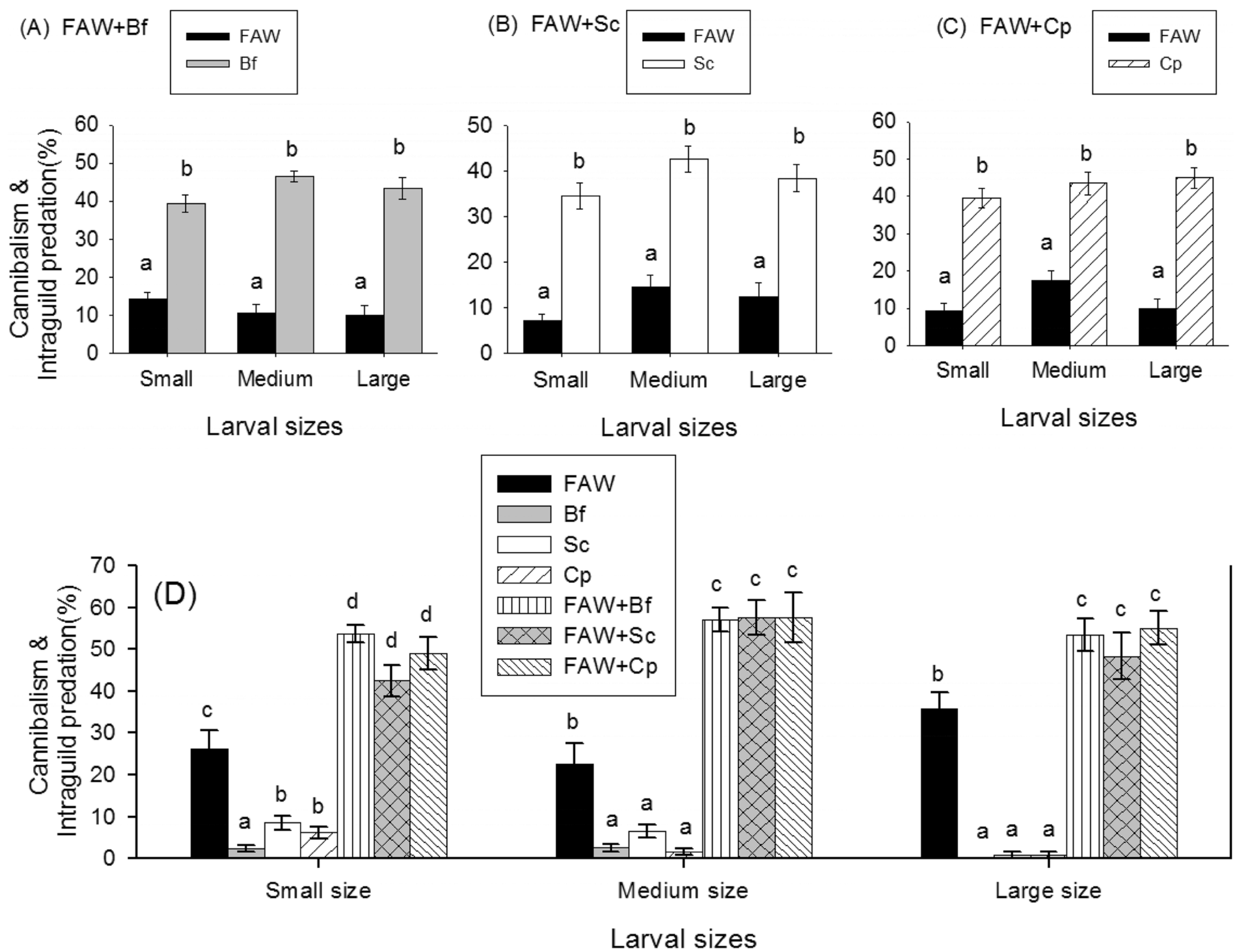

Fig. 2 Cannibalism and/or intraguild predation of *Spodoptera frugiperda* (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc), and *Chilo partellus* (Cp) in pairing-species combination communities (**A**–**C**) and their comparison with those in single-species communities (**D**) at different larval stages: small size (neonate to second instar), medium size (third to fourth instar) and large size (fifth to sixth instar). Statistical comparisons between single- and corresponding multi-species pairings are shown. Means (±SE) were compared using Tukey's comparisons tests performed using lsmeans R package, following generalized linear model (GLM) with negative binomial procedure

df = 1; $P \leq 0.0001$ and large: LR = 26.95; df = 1; $P \leq 0.0001$), FAW + Sc (Fig. 2B, small: LR = 62.41; df = 1; $P \leq 0.0001$, medium: LR = 28.73; df = 1; $P \leq 0.0001$ and large: LR = 10.35; df = 1; $P = 0.001$) and FAW + Cp (Fig. 2C, small: LR = 49.14; df = 1; $P \leq 0.0001$, medium: LR = 22.88; df = 1; $P \leq 0.0001$ and large: LR = 28.90; df = 1; $P \leq 0.0001$). Furthermore, the cannibalism coupled with intraguild predation in pairing-species combination was significantly higher as compared to cannibalism only in single-species communities at all larval size groups (Fig. 2D, small: LR = 349.81; df = 6; $P \leq 0.0001$, medium: LR = 356.83; df = 6; $P \leq 0.0001$ and large: LR = 246.41; df = 6; $P \leq 0.0001$).

Discussion

The polyphagous feeding (Montezano et al. 2018), the voracity (Wan et al. 2021), the high potential economic loss in crops (Wang et al. 2020) and the recent invasion in Africa (Goergen et al. 2016) of FAW have created a pressing situation to develop efficient and sustainable pest management. To take a holistic approach in protecting maize there is a significant value in understanding the interaction of FAW with stemborer species that also inhabit maize plants. Our results indicated that FAW could completely outcompete stemborers through intraguild predation when they cohabit the same resource. This behaviour increased in the larger instars because as the body size of the larvae increases, the larvae require more resource and need to eat more. The advantage for FAW was furthermore reflected in its growth rate, which ranged from 40 to 50 mg/day when they were reared with stemborer species while only 30 mg/day when FAW was reached alone. Although these numbers are in contrast with other studies (e.g. Ongaratto et al. 2021; Bentivenha et al. 2016a,b), where the weight of FAW reared alone as a single species was greater than when reared with other species, it would, for example, be interesting for further studies to address if the increased growth rates also generate positive effects on adult life and mating for FAW since female weight in Lepidoptera often is positively correlated with fecundity (Jimenez-Perez and Wang 2004; Rhainds 2015).

The reason for FAW having higher competitive ability through intraguild predation can be due to FAW being more prone to cannibalism than the stemborers. This cannibalistic behaviour of FAW has already been documented, both in laboratory and under field conditions (Chapman et al. 2000; Goussain et al. 2002), and was confirmed in our single-species treatment. That FAW readily switches to predatory behaviour might prepare the species for more aggressive behaviours with both actions of attack and defence. For example, Bentivenha et al. (2017a) studied intraspecific interactions of FAW larvae and reported that they exhibited either high attack (head touching) or defence (recoiling) as the prevalent movement and that the frequency of these movements increased with larval development because of their increased interaction with other larvae when they become bigger and more mobile. In situations of conspecific cannibalism, the costs of fight may thus be high to FAW since other individuals also have a high ability to attack and defend themselves. In interspecific competition, however, the predator–prey interactions may be asymmetric in favour of FAW since the stemborer species are not exhibiting predatory behaviour to the same degree. The stemborers thus probably go into defence behaviour rather than into attack and thus inflict lower fight costs to FAW. By reducing cannibalism on their conspecifics and instead concentrating on intraguild predation on the heterospecific species, FAW could gain the advantages from feeding on larvae with less energy invested. Previous studies have furthermore showed an advantage of FAW in interaction with *H. zea* due to morphological characteristics such as integument or mandible architecture (Bentivenha et al. 2016a), which also could explain the success of FAW during intraguild competition. In the present study, intraguild predation did, however, not seem to lead to a higher absolute survival rate of FAW, only a relatively better survival in comparison to the other species. This can be due to that FAW resorts to cannibalistic behaviour in later instars when the heterospecific species are eliminated from the system. Likely FAW (and other cannibalistic species) switches between cannibalism and intraguild predation depending on the species community, which may have substantial consequences for the involved species both at the individual and population level.

The higher intraguild predation of FAW on stemborer species when they inhabit the same resource indicates a clear competitive advantage of FAW and could be a factor partially explaining its success as an invasive pest species. The preference of intraguild predation over cannibalism of FAW in multi-species communities has been already reported for other maize pests (Song et al. 2021; Zhao et al. 2021) and intraguild predation may be an important factor during FAW invasion to decrease competition from other species. Although our study was performed in the laboratory and needs to be confirmed in the field, our results may reflect that intraguild predation could give FAW an advantage over the stemborer species by allowing them to colonize the niche used by these species (Bentivenha et al. 2016b; Bentivenha et al. 2017b), when they co-occur on maize plants. For example, Sokame et al. (2021a) observed in 2018 an overall reduction in stemborer density in maize fields in Kenya at the beginning of the season. In addition, historical data of stemborer infestations compared to the recent evaluations in maize and sorghum cropping systems in Uganda showed a significant decline of infestations on maize in detriment to sorghum fields from 2016, which suggests an early arrival of FAW in Uganda leading to displacement of stemborers in maize fields (Hailu et al. 2021). However, since FAW tends to feed on leaves and stemborers on plant stems in late instars surviving stemborers may thus escape FAW through niche partition, and this might result in co-existence to some extent between FAW and stemborer species in maize agroecological zones (Morrill and Greene 1973; CAB International 2017; Sokame et al. 2020, 2021a). To better understand these complex dynamics requires further studies at a larger scale because other parameters such as agricultural landscape (Bentivenha et al. 2016a), the food quality of the host plant, and larval behaviour (Dial and Adler 1990) may also influence intraguild interactions.

The invasion of FAW in Africa constitutes an additional pest in maize agroecosystems that needs to be considered within the context of integrated pest management (IPM) strategies. For example, the optimal control measures may differ depending on the lepidopteran pest community that is present, and stemborer control may need to include also other host plant species other than maize if FAW is invading the field. Our study in combination with the mentioned field observations (Morrill and Greene 1973; CAB International 2017; Hailu et al. 2021; Sokame et al. 2020, 2021a, b; Mutyambai et al. 2022) indicates that FAW can reduce the population density and impact of stemborers in maize fields. However, if whether FAW could contribute to the control of stemborer populations in the context of IPM programmes, is another interesting question to explore. Such impact needs to be reliably assessed at an appropriate ecological scale which allows the effects on the population dynamics to be quantified and integrated into the decision-making processes of the pest management.

Author contributions

BMS, P-AC, PA, and KKG designed the studies. BMS, and BM collected the data. BMS analysed the data and wrote the manuscript. All authors reviewed and approved the manuscript before submission.

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Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval This research complied with all local and national standards for ethical conduct in research. This research did not involve vertebrates or humans, and thus, no IRB approvals were needed.

References

Andow DA, Farias JR, Horikoshi RJ, Bernardi D, Nascimento AR, Celso O (2015) Dynamics of cannibalism in equal-aged cohorts of *Spodoptera frugiperda*. Ecol Entomol 40:229–236. https://doi.org/10.1111/een.12178

Arnott G, Elwood RW (2009) Assessment of fighting ability in animal contests. Anim Behav 77:991–1004. https://doi.org/10.1016/j.anbehav.2009.02.010

Benelli G (2015) Should I fight or should I flight? How studying insect aggression can help integrated pest management. Pest Manag Sci 71:885–892. https://doi.org/10.1002/ps.3974

Bentivenha JPF, Baldin ELL, Hunt TE, Paula-Moraes SV, Blankenship EE (2016a) Intraguild competition of three noctuid maize pests. Environ Entomol 45:999–1008. https://doi.org/10.1093/ee/nvw068

Bentivenha JPF, Paula-Moraes SV, Baldin ELL, Specht A, da Silva IF, Hunt TE (2016b) Battle in the New World: *Helicoverpa armigera* versus *Helicoverpa zea* (Lepidoptera: Noctuidae). PLoS ONE 11:e0167182. https://doi.org/10.1371/JOURNAL.PONE.0167182

Bentivenha JP, Montezano D, Hunt TE, Baldin EL, Peterson JA, Victor V, Pannuti LE, Velez AM, Paula-Moraes SV (2017) Intraguild interactions and behavior of Spodoptera frugiperda and Helicoverpa spp. on maize. Pest Manag Sci 73:2244–2251. https://doi.org/10.1002/ps.4595

Bentivenha José PF, Baldin ELL, Montezano DG, Hunt TE, Paula-Moraes SV (2017) Attack and defense movements involved in the interaction of *Spodoptera frugiperda* and *Helicoverpa zea* (Lepidoptera: Noctuidae). J Pest Sci 90:433–445. https://doi.org/10.1007/s10340-016-0802-3

Bonhof MJ, Overholt WA (2001) Impact of solar radiation rainfall and cannibalism on disappearance of maize stemborers in Kenya. Insect Sci Appl 21:403–407. https://doi.org/10.1017/s1742758400008523

Briffa M, Elwood RW (2004) Use of energy reserves in fighting hermit crabs. Proc Royal Soc B 271:379. https://doi.org/10.1098/RSPB.2003.2633

CAB International (2017) *How to identify fall armyworm. Poster. Plantwise*, http://www.plantwise.org/FullTextPDF/2017/20177800461.pdf (2017) (Date of access: 23/11/2018). https://www.cabi.org/isc/fallarmyworm

Cameron TC, Wearing HJ, Rohani P, Sait SM (2007) Two-species asymmetric competition : effects of age structure on intra- and interspecific interactions. J Anim Ecol 76:83–93. https://doi.org/10.1111/j.1365-2656.2006.01185.x

Chapman JW, Williams T, Escribano A, Caballero P, Cave RD, Goulson D (1999a) Age-related cannibalism and horizontal transmission of a nuclear polyhedrosis virus in larval *Spodoptera frugiperda*. Ecol Entomol 24:268–275

Chapman JW, Williams T, Escribanoc A, Caballero P, Cave RD (1999b) Fitness consequences of cannibalism in the fall armyworm, *Spodoptera frugiperda*. Behav Ecol 10:298–303. https://doi.org/10.1093/beheco/10.3.298

Chapman JW, Williams T, Martínez AM, Cisneros J, Caballero P, Cave RD, Goulson D (2000) Does cannibalism in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) reduce the risk of predation? Behav Ecol Sociobiol 48:321–327. https://doi.org/10.1007/s002650000237

Cruz I, Turpin FT (1983) Yield impact of larval infestations of the Fall Armyworm *Spodoptera frugiperda* (J. E. Smith) to Midwhorl Growth Stage of Corn1. J Econ Entomol 76:1052–1054. https://doi.org/10.1093/jee/76.5.1052

Dial CI, Adler PH (1990) Larval behavior and cannibalism in *Heliothis zea* (Lepidoptera: Noctuidae). Ann Entomol Soc Am 83:258–263. https://doi.org/10.1093/aesa/83.2.258

Elgar M, Crespi J (1992) Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, Oxford

Goergen G, Kumar PL, Sankung SB, Togola A, Tamò M (2016) First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in West and Central Africa. PLoS ONE 11:e0165632. https://doi.org/10.1371/journal.pone.0165632

Goussain MM, Moraes JC, Carvalho JG, Nogueira NL, Rossi EML (2002) Effect of silicon application on corn plants upon the biological development of the fall Armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae). Neotrop Entomol 31:305–310

Gurevitch J, Morrow LL, Wallace A, Walsh JS (1992) A Meta-Analysis of Competition in Field Experiments. Am Nat 140:539–572

Hailu G, Niassy S, Bässler T, Ochatum N, Studer C, Salifu D, Agbodzavu MK, Khan ZR, Midega C, Subramanian S (2021) Could fall armyworm, *Spodoptera frugiperda* (J. E. Smith) invasion in Africa contribute to the displacement of cereal stemborers in maize and sorghum cropping systems. Int J Trop Insect Sci 41:1753–1762

Holloway JD (1998) Noctuidae. In: Polaszek A (ed) African cereal stem borers: economic importance, taxonomy, natural enemies and control. Wallingford, UK, pp 79–86

Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. Am Nat 149:745–764

Jimenez-Perez A, Wang Q (2004) Effect of body weight on reproductive performance in *Cnephasia jactatana* (Lepidoptera: Tortricidae). J Insect Behav 17:511–522

Kassie M, Wossen T, De Groote H, Tefera T, Sevgan S, Balew S (2020) Economic impacts of fall armyworm and its management strategies: evidence from southern Ethiopia. Eur Rev Agric Econ 47:1473–1501. https://doi.org/10.1093/erae/jbz048

Kelly CD, Godin JJ (2001) Predation risk reduces male-male sexual competition in the trinidadian guppy (*Poecilia reticulata*). Behav Ecol Sociobiol 51:95–100

Kfir R, Overholt WA, Khan ZR, Polaszek A (2002) Biology and management of economicaly important lepidopteran cereal stem borers in Africa. Annu Rev Entomol 47:701–731. https://doi.org/10.1146/annurev.ento.47.091201.145254

Krüger W, van den Berg J, van Hamburg H (2008) The relative abundance of maize stem borers and their parasitoids at the Tshiombo irrigation scheme in Venda, South Africa. S Afr J Plant Soil 25:144–151. https://doi.org/10.1080/02571862.2008.10639910

Lenth RV (2016) Least-Squares Means: The R Package lsmeans. J Stat Softw 69:1–33

Montezano DG, Specht A, Sosa-Gómez DR, Roque-Specht VF, Sousa-Silva JC, Paula-Moraes SV, Peterson JA, Hunt TE (2018) Host Plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. Afr Entomol 26:286–300. https://doi.org/10.4001/003.026.0286

Morrill WL, Greene GL (1973) Distribution of fall armyworm larvae. 1. Regions of field corn plants infested by larvae. Environ Entomol 2:195–198

Mutyambai DM, Niassy S, Calatayud P-A, Subramanian S (2022) Agronomic factors influencing fall Armyworm (*Spodoptera frugiperda*) infestation and damage and its co-occurrence with stemborers in maize cropping systems in Kenya. Insects. https://doi.org/10.3390/insects13030266

Ntiri ES, Calatayud PA, Van Den Berg J, Schulthess F, Le Ru BP (2016) Influence of temperature on intra- and interspecific resource utilization within a community of lepidopteran maize stemborers. PLoS ONE 11:e148735. https://doi.org/10.1371/journal.pone.0148735

Ntiri ES, Calatayud PA, Van den Berg J, Le Ru BP (2017) Density dependence and temporal plasticity of competitive interactions during utilisation of resources by a community of lepidopteran stemborer species. Entomol Exp Appl 162:272–283. https://doi.org/10.1111/eea.12514

Ojeda-Avila T, Woods HA, Raguso RA (2003) Effects of dietary variation on growth, composition, and maturation of Manduca sexta (Sphingidae : Lepidoptera). J Insect Physiol 49:293–306. https://doi.org/10.1016/S0022-1910(03)00003-9

Ongamo G, Le Rü B, Dupas S, Moyal P, Calatayud P-A, Silvain J-F (2006) Distribution, pest status and agro-climatic preferences of lepidopteran stem borers of maize in Kenya. Ann Soc Entomol Fr 42:171–177. https://doi.org/10.1080/00379271.2006.10700620

Ongaratto S, Baldin EL, Hunt TE, Montezano DG, Robinson EA, Santos MC (2021) Effects of intraguild interactions on *Anticarsia gemmatalis* and *Chrysodeixis includens* larval fitness and behavior in soybean. Pest Manag Sci 77:2939–2947. https://doi.org/10.1002/PS.6330

Onyango FO, Ochieng'-Odero, JER, (1994) Continuous rearing of the maize stem borer Busseola fusca on an artificial diet. Entomol Exp Appl 73(2):139–144. https://doi.org/10.1111/j.1570-7458.1994.tb01848.x

Polaszek A (1998) African cereal stem borers: economic importance, natural enemies and control. CAB International, Wallingford, Oxon

Polis GA (1981) The evolution and dynamics of intraspecific predation. Annu Rev Ecol Evol Syst 12:225–251

Polis GA, Holt RD (1992) Intraguild predation: The dynamics of complex trophic interactions. Trends Ecol Evol 7:151–154. https://doi.org/10.1016/0169-5347(92)90208-S

R Core Team (2018) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rasekh A, Osawa N (2020) Direct and indirect effect of cannibalism and intraguild predation in the two sibling *Harmonia* ladybird beetles. Ecol Evol 10:5899–5912. https://doi.org/10.1002/ece3.6326

Richardson M, Mitchell R, Reagel P, Hanks L (2010) Causes and consequences of cannibalism in noncarnivorous insects. Annu Rev Entomol 55:39–53.https://doi.org/10.1146/annurev-ento-112408-085314

Rhainds M (2015) Size-dependent realized fecundity in two lepidopteran capital breeders. Environ Entomol 44:1193–1200. https://doi.org/10.1093/ee/nvv075

Seshu-Reddy KV (1998) Maize and sorghum: East Africa. In: Polaszek A (ed) African cereal stem borers: economic importance, taxonomy, natural enemies and control. CAB International, Wallingford Oxon

Sokame BM, Rebaudo F, Malusi P, Subramanian S, Kilalo DC, Juma G, Calatayud PA (2020) Influence of temperature on the interaction for resource utilization between Fall Armyworm, Spodoptera frugiperda (Lepidoptera : Noctuidae), and a community of lepidopteran maize stemborers larvae. Insects 11:73. https://doi.org/10.3390/insects11020073

Sokame BM, Musyoka B, Obonyo J, Rebaudo F, Abdel-rahman EM, Subramanian S, Kilalo DC, Juma G, Calatayud PA (2021a) Impact of an exotic invasive pest, Spodoptera frugiperda (Lepidoptera : Noctuidae), on resident communities of pest and natural enemies in maize fields in Kenya. Agronomy 11:1074. https://doi.org/10.3390/agronomy11061074

Sokame BM, Tonnang HEZ, Subramanian S, Bruce AY, Dubois T, Ekesi S, Calatayud PA (2021b) A system dynamics model for pests and natural enemies interactions. Sci Rep 11:1–14. https://doi.org/10.1038/s41598-020-79553-y

Sokame BM, Malusi P, Subramanian S, Kilalo DC, Juma G, Calatayud PA (2022) Do the invasive Fall Armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), and the maize lepidopteran stemborers compete when sharing the same food? Phytoparasitica 50:21–34. https://doi.org/10.1007/s12600-021-00952-6

Song Y, Yang X, Zhang H, Zhang D, He W, Wyckhuys KAG, Wu K (2021) Interference competition and predation between invasive and native herbivores in maize. J Pest Sci 94:1053–1063. https://doi.org/10.1007/s10340-021-01347-6

Takizawa T, Snyder WE (2011) Cannibalism and intraguild predation of eggs within a diverse predator assemblage. Environ Entomol 40:8–14

Tefera T (2004) Lepidopterous stem borers of sorghum and their natural enemies in eastern Ethiopia. Trop Sci 44:128–130. https://doi.org/10.1002/ts.153

Van den Berg J, Van Rensburg JBJ, Pringle KL (1991) Comparative injuriousness of *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Pyralidae) on grain sorghum. Bull Entomol Res 81:137–142. https://doi.org/10.1017/S0007485300051191

Van den Berg J (1997) Economy of stem borer control in sorghum. ARC-Crop protection Series no 2, Potchefstroom, South Africa, pp-4

Wagner JD, Wise DH (1996) Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. Ecology 77:639–652. https://doi.org/10.2307/2265637

Wan J, Huang C, Li C, Zhou H, Ren Y, Li Z, Xing L, Zhang B, Qiao X, Liu B, Liu C, Xi Y, Liu W, Wang W, Qian W, Mckirdy S, Wan F (2021) Biology, invasion and management of the agricultural invader: Fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). J Integr Agric 20:646–663. https://doi.org/10.1016/S2095-3119(20)63367-6

Wang W, He P, Zhang Y, Liu T, Jing X, Zhang S (2020) The Population Growth of *Spodoptera frugiperda* on six cash Crop species and implications for its occurrence and damage potential in China. Insects 11:639. https://doi.org/10.3390/INSECTS11090639

Zhao J, Hoffmann A, Jiang Y, Xiao L, Tan Y, Zhou C, Bai L (2021) Competitive interactions of a new invader (*Spodoptera frugiperda*) and indigenous species (*Ostrinia furnacalis*) on maize in China. J Pest Sci 95:159–168. https://doi.org/10.1007/s10340-021-01392-1