



Do the invasive Fall Armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), and the maize lepidopteran stemborers compete when sharing the same food?

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Abstract In insect communities, the outcome of intra- and inter-specific competitions for food utilisation depend primarily upon density and duration even inter-specific competitions can occur when they are not sharing the same feeding niche such as between foliar feeders and stemborers. Experimental manipulations of larval densities and the durations of common diet feeding of fall armyworm (FAW), *S. frugiperda*, and the African lepidopteran stemborers, *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus*, were conducted to determine how the density

and the duration of resource utilization affected larval survival and the relative growth rate (RGR) in intra- and inter-specific interactions. The results showed both intra- and interspecific competitions were observed among all the four species and interspecific competition was significantly stronger between the stemborers than between the FAW and the stemborers. The results showed that multiple infestations of cereal plants with low larval densities of each species at optimum conditions will very likely prolong the coexistence between FAW and stemborers. In addition, the time partitioning of the resource use significantly influenced this coexistence.

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Introduction

The noctuid stemborers, *Busseola fusca* (Fuller) and *Sesamia calamistis* Hampson and crambid stemborer *Chilo partellus* (Swinhoe) are the key pests that attack cereal crops in eastern and southern Africa (Kfir et al., 2002; Seshu Reddy, 1998). They occur as single species or mixed multi-species communities depending on the areas altitude infesting maize and sorghum crops (Van den Berg et al., 1991; Krüger et al., 2008; Ong'amo et al., 2006; Tefera, 2004). Within these pest communities sharing the same

resource, competitive interaction frequently occurred. It has been reported that *C. partellus* competitively displaced *B. fusca* in the maize fields in South Africa (Kfir, 1997; Rebe et al., 2004). Interspecific competitions were demonstrated in artificial diet between *B. fusca*, *S. calamistis* and *C. partellus* with stronger competition recorded between the noctuids and the crambid than between the two noctuids (Ntiri et al., 2016). This community of stemborers might be disturbed by the recent introduction of the fall armyworm (FAW), *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) from America into sub-Saharan Africa, where it has invaded most countries causing severe damage in maize fields (Goergen et al., 2016; Rwomushana et al., 2018; Sisay et al., 2018). Recent field observations from Uganda highlight the potential for displacement of stemborer populations from maize to other cereals such as Sorghum by FAW (Hailu et al., 2021). This indicates that although, on vegetative maize plants before tasseling, stemborers feed mainly into plant stems whereas FAW mainly on leaves, stemborer larvae get chance to interact with FAW larvae at young developmental stages before they migrate from the leaves to stems (Sokame et al., 2021). Sokame et al. (2020) have already reported an advantage of *C. partellus* over other species under temperature increases but an overall weak competition between fall armyworm and stemborers. This was attributed to a different mode of feeding compared to stemborers. The fall armyworm only fed on the diet surface avoiding boring and feeding inside the diet as compared to stemborers. However, this can change if the insect's density and the duration of feeding increase.

Both insect's density and duration of feeding have been well investigated and have been shown to be important factors regulating the growth of insect populations since they are leading to increase the interspecific interactions (Connell, 1983; Teng and Apperson, 2000; Agrew et al., 2002; Miner et al., 2005; Fordyce, 2006; Muriu et al., 2013; Delong et al., 2014).

Ntiri et al. (2017) showed on artificial diet that the interspecific competition between the stemborers, *B. fusca*, *S. calamistis* and *C. partellus*, increased when both the insect's density and the time of resource utilization increased. From this work done by Ntiri et al. (2017) using only stemborers, there is a need to update this study by adding this new pest (FAW) into

the system in order: (i) to determine the larval density effect on the intraspecific interaction outcomes within FAW and its interspecific interactions with *B. fusca*, *S. calamistis* and *C. partellus* when they utilize the same resource in a restricted space and (ii) to assess whether these interactions outcomes varied with time partitioning.

Materials and methods

Insects

The stemborers (*B. fusca*, *S. calamistis* and *C. partellus*) and fall armyworm larvae of second instar (L2) were provided by Animal Rearing and Containment Unit (ARCU) at *icipe*, Nairobi, Kenya for the use of the experiments. For stemborers, larvae were continuously reared on the artificial diet of Onyango and Ochieng'-Odero (1994) filled in plastic jars (16.5 × 9 cm) with about 200 ml per jar. For FAW, the neonates and first instars were first reared on maize leaves and then transferred into the same set up and artificial diet as for stemborers, where second instar was used for the experiment. After inoculation, the plastic jars were tightly sealed using perforated lids with galvanized mesh after covered them with tissue paper and kept them in the rearing room at 26 ± 1 °C, $60 \pm 5\%$ RH., and L12 and D12 photoperiod. Each colony was rejuvenated two times a year with larvae directly collected from the field. The diet of Onyango and Ochieng'-Odero (1994) was composed of vitamins mix, maize leaf powder, brewer's yeast, bean powder, sucrose, ascorbic acid, sorbic acid, methylparaben formaldehyde. Agar ingredient was added to solidify the medium and hold the moisture.

Surrogate stems

Previous studies comparing entire maize plants with surrogate stems for stemborer larval rearing including the fall armyworm larvae showed that the surrogate stems gave higher survival rates (Ntiri et al., 2016; Sokame et al., 2020). In addition, the entire maize plants kept in the incubator deteriorated after only 5 to 7 days (Ntiri et al., 2016). Therefore, surrogate stems were justified as a better set-up to be used as well in this present study. The surrogate stem of Ntiri et al. (2016) is constituted of a piece of polymerizing

vinyl chloride (PVC) pipe with dimensions of 5 cm in internal diameter and 30 cm of length. Each pipe was divided into two halves (to facilitate later on the opening of the pipe for the recording of alive larvae) and then tight together using masking tape. An end of the surrogate stem was sealed using parafilm and then tight with masking tape. From that end of the pipe, the whole surrogate stem was wrapped in the aluminum foil but with the other end opened and then attached using rubber band to avoid the outflow of the hot liquid medium when dispensed later into the stems. The stems were filled through the opening end with stemborers diet (Onyango and Ochieng'-Odero, 1994) as a common diet for either stemborers or fall armyworm (Sokame et al., 2020) up to half level, leaving about 300m³ free space in the pipe. The following day when the diet had solidified in the stems, three quarters of aluminum foil wrapping the pipes and masking tapes were removed from the open to close end direction of the pipe and kept the remaining to later avoid the contamination of the diet from the bottom of the surrogates in contact of the holding containers. The same experimental procedure of Ntiri et al. (2016) and Sokame et al. (2020) was used to measure the influence of larval density and duration of interactions on the outcomes of the interactions between FAW and the stemborers, *B. fusca*, *S. calamistis* and *C. partellus*.

Influence of the larval density

Larval density effects on survival and growth rates either in single- or multiple-species infestations of stemborers (*B. fusca*: Bf, *S. calamistis*: Sc and *C. partellus*: Cp) and fall armyworm (*S. frugiperda*: FAW) larvae was evaluated. During this experiment, the aforementioned surrogate stems were each infested with four (4), eight (8) or twelve (12) second instar

larvae involving either single-species or multi-species combinations (Table 1) giving a total of 24 treatments, replicated 15 times each. Similar to Ntiri et al. (2017), for each species the wet mass of the tested group of larvae was assessed before infestation since a second instar larva is too small to determine confidently its individual mass.

After infestation, cotton wood was used to plug the open end of each surrogate stem tied with rubber band. The surrogate stems loaded were placed upright in an incubator of mark of "Sanyo MIR 554, Tokyo-Japan" at 25 °C, 70±10% RH, and L12:D12 photoperiod. This temperature was shown to be optimum temperature for development of stemborer species insects (Khadioli et al., 2014a, 2014b). After fifteen (15) days, the same timing used by Sokame et al. (2020), the surrogate stems were opened for the number and wet mass of live larvae recovery of each species.

Influence of the duration of the interactions

This experiment was conducted to evaluate whether the duration of the interactions influences survival and growth rates of stemborers (*B. fusca*: Bf, *S. calamistis*: Sc and *C. partellus*: Cp) and fall armyworm (*S. frugiperda*: FAW) larvae in either single- or multiple-species infestations. Following the study of Sokame et al. (2020), the single-species treatments (considered as control experiments) consisted of the use of 8 s instar larvae of either *C. partellus*, *B. fusca*, *S. calamistis* or fall armyworm. The multi-species treatments consisted of infesting each artificial stem with 4 s instar larvae of each species in each following pairing: FAW + Bf, FAW + Sc, FAW + Cp and 2 s instar larvae of each species involved in this combination: FAW + Sc + Bf + Cp. Each treatment was replicated fifteen (15) times. The experiment

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

Densities	Single-species				Multi-species			
	Bf	Sc	Cp	FAW	FAW+Bf	FAW+Sc	FAW+Cp	FAW+Bf+Sc+Cp
4 larvae	4	4	4	4	2+2	2+2	2+2	1+1+1+1
8 larvae	8	8	8	8	4+4	4+4	4+4	2+2+2+2
12 larvae	12	12	12	12	6+6	6+6	6+6	3+3+3+3

FAW = *S. frugiperda*, Bf = *Busseola fusca*, Sc = *Sesamia calamistis*, Cp = *Chilo partellus*

was conducted in an incubator with the same conditions as for larval density experiments. According to the duration, the experiment was terminated, and the pipes were opened 5, 10, 15 or 20 days after the infestation and the number of larvae alive and their wet mass were recorded in each artificial stem.

Data analysis

The response variables calculated as interaction outcomes were survival and relative growth rate (RGR). The survival rate was evaluated as the number of larvae alive at the end of the experiment and expressed as percent of initial number of larvae inoculated. Survival data were analysed using a generalised linear model (GLM) with a binomial error distribution due to the binary nature of this parameter (survival vs. mortality) (Warton & Hui, 2011). Odds ratios (OR) with a 95% confidence interval (95% CI) were calculated for each treatment from the GLM results obtained. The RGR for each species was calculated using the following equation (Ojeda-Avila et al., 2003):

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

RGR for a group of species was calculated as the sum of RGRs of each species in that community. RGRs of treatments were analyzed via analysis of variance (ANOVA) because RGR data are continuous data and they were first tested for normality of their distribution using Shapiro–Wilk test and for homogeneity of variance using Bartlett test. The ANOVA was performed by constructing a general linear model with the *lm* function at 5% of level of significance. Significant differences were separated using Tukey's multiple comparisons tests performed using the R package "lsmeans" (Lenth, 2016) with *p* value adjustment method = false discovery rate (FDR) as addressed by Verhoeven et al. (2005). All analyses were performed with R software version 3.5.1 (R Core Team, 2018).

Results

Intraspecific interaction of fall armyworm and stemborers at different densities

For each species, the survival rate decreased significantly when the larval density increased (Fig. 1A, Supplementary Table S1). Between species, FAW had the lowest survival rate as compared to stemborer species among each density (Fig. 1A, Supplementary Table S1). Likewise, the RGR of each species decreased significantly when the larval density increased and the FAW exhibited the lowest RGR as compared to those of stemborer species among each density (Fig. 1B, Supplementary Table S2).

Interspecific interaction between fall armyworm and stemborers at different densities

In two species combinations, FAW had higher survival than that of *B. fusca* at all densities (Fig. 2A, Supplementary Table S3) and dominated *S. calamistis* only at 8 larval density (Fig. 2B, Supplementary Table S3) while the survival of *C. partellus* was higher than that of FAW at all densities (Fig. 2C, Supplementary Table S3). In four species combination, *C. partellus* had higher survival than those of other species at all densities (Fig. 2D, Supplementary Table S3).

In two species combinations, the RGR of FAW was higher than that of *B. fusca* at 4 and 8 larvae densities (Fig. 3A, Supplementary Table S4) and higher than that of *S. calamistis* at 4 larvae density (Fig. 3B, Supplementary Table S4) while *C. partellus* had the higher RGR than that of FAW only at 12 larvae density (Fig. 3C, Supplementary Table S4). In four species combination, the RGR of *C. partellus* was lower than those of other species at 4 larvae density while it was reversed at 8 and 12 larvae densities (Fig. 3D, Supplementary Table S4).

Comparison of survival and RGR between single species and communities at different densities

The survival rates of FAW under single-species were no significantly different to the survival rates of FAW under multi-species combinations at all densities (Fig. 4A, Supplementary Table S5). In contrast, except the comparison of Sc vs FAW + Sc, the single species survival rates of stemborer were

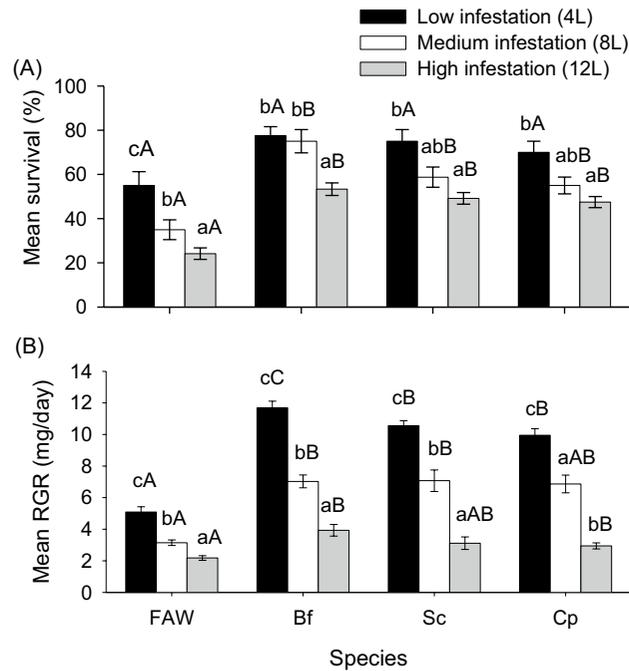


Fig. 1 Mean (\pm SE, $n=15$) survival (%) (A) and relative growth rate (RGR: mg/day) (B) of single species conditions of fall armyworm (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc) and *Chilo partellus* (Cp) at three different larval densities (4, 8 or 12 larvae). Survival data were analyzed using generalized linear model (GLM) with binomial distribution while RGRs were analyzed via analysis of variance (ANOVA) after

contracting general linear model with the *lm* function at 5% of level of significance. Means were separated using Tukey's multiple comparisons test with *lsmeans* R package and those with different letters were significantly different. Small letters were used to compare means between densities for each species and capital letters to compare means between species for each density

significantly higher than those of their multi-species combination counterparts with FAW (Fig. 4A, Supplementary Table S5).

The RGR of FAW larvae under single-species condition was significantly lower than the FAW larvae under multi-species combinations at all densities, except for FAW + Bf + Sc + Cp combination at 4 larvae density (Fig. 4B, Supplementary Table S6). For stemborer species, at 4 larvae density, no significant difference was revealed between the RGRs of single-species as compared to two species combinations with FAW (Fig. 4B, Supplementary Table S6). However, at 8 larvae density, there was no difference between RGR of stemborer single-species and those of their multi-species combination counterparts with FAW while at 12 larvae density, the RGRs of each stemborer species under single-species conditions were significantly higher than those of their multi-species

combination counterparts with FAW (Fig. 4B, Supplementary Table S6).

Intraspecific interaction of fall armyworm and stemborers at different durations of infestation

For all the four species, survival of all the four species tended to decrease with the duration of infestation. This was less pronounced for *C. partellus* (Fig. 5A, Supplementary Table S7). In contrast, the RGR tended to increase with the duration of infestation and then decreased at the highest duration of infestation (20 days) (Fig. 5B, Supplementary Table S8).

Interspecific interactions between fall armyworm and stemborers at different durations of infestation

In pairing species combinations, FAW survived better than either *B. fusca* or *S. calamistis* at 15

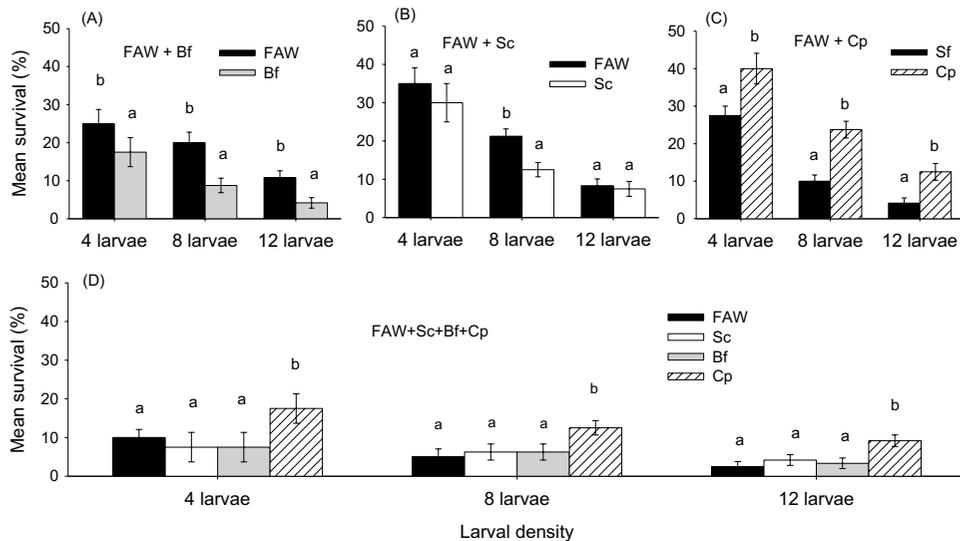


Fig. 2 Mean (\pm SE, $n=15$) of survival (%) of fall armyworm (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc) and *Chilo partellus* (Cp) in (A–C) two- and (D) four-species combinations at three different larval densities (4, 8 or 12 larvae) in artificial stem and media. Data were analyzed using gener-

alized linear model (GLM) with binomial distribution. Means were separated using Tukey's multiple comparisons test with lsmeans R package and those with different letters were significantly different

and 20 days after infestation (Fig. 6A&B, Supplementary Table S9) while *C. partellus* had higher survival than that of FAW at all durations of infestation (Fig. 6C, Supplementary Table S9). In four species combination, only *C. partellus* had higher survival at 10, 15 and 20 days of infestation (Fig. 6D, Supplementary Table S1).

In pairing species combinations, the RGR of FAW was higher than that of *B. fusca*, at 5 days and 15 days after infestation (Fig. 7A, Supplementary Table S10), while it was higher than that of *C. partellus* only at 5 days of infestation (Fig. 7C, Supplementary Table S10). No significant difference was revealed in FAW+Sc combination (Fig. 7B, Supplementary Table S10). In four species combination, *C. partellus* had the highest RGR than those of other species at 15 days of infestation while the RGR was significantly higher for all stemborer species than that of FAW at 20 days of infestation (Fig. 7D, Supplementary Table S10).

Comparison of survival and RGR between single species and communities at different durations of infestation

Although the survival rates of FAW were significantly lower as compared to the survivals of stemborers under single-species conditions, they were similar to those registered under multi-species combinations regardless of the duration of infestation (Fig. 8A, Supplementary Table S11). In contrast, the RGRs of FAW tended to increase from single-species to multiple-species conditions regardless of the duration of infestation (Fig. 8B, Supplementary Table S12).

Discussion

Similar to Ntiri et al. (2017), our results indicated that direct competition in the form of interference competition characterized also the interactions between FAW and a community of maize stemborers using the same resource. Although interference competition occurs when one or two competing species feed on the same resource (Denno et al., 1995; Duyck et al., 2004; Schoener, 1983), in our case, as highlighted by Sokame et al. (2020), the FAW is occupying a

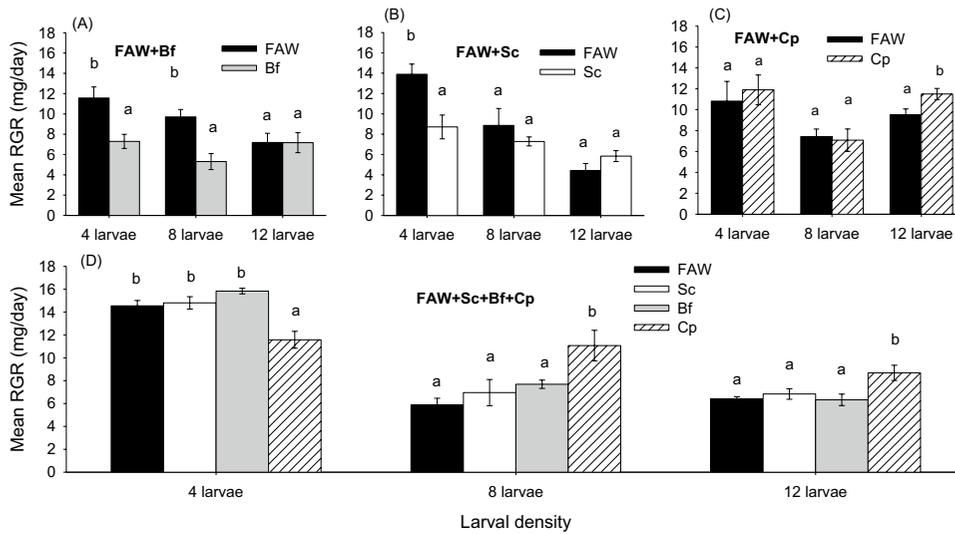


Fig. 3 Mean (\pm SE, $n=15$) of relative growth rate (RGR: mg/day) of fall armyworm (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc) and *Chilo partellus* (Cp) in (A–C) two- and (D) four-species combinations at three different larval densities (4, 8 or 12 larvae) in artificial stem and media. Data were analyzed using analysis of variance (ANOVA)

different niche than maize stemborers. For FAW larvae, foliar and corn feeders but not feeding inside the plant stems, remained generally on the surface whereas borer larvae penetrated the diet, where after the direct competition ended between FAW and stemborer larvae. However, under higher density with a limited resource, the species might expand and then overlap their niches and then are faced with challenges in food acquisition and simultaneous allocation of derived limited nutrient to necessary life-history traits such as survival, growth, and reproduction.

Under intraspecific interactions, with the same species sharing the same niche the larval survival and RGR of either FAW or stemborers were higher at low larval density and decreased with increase larval density, and FAW exhibited the lower values. Density-dependent intraspecific competitions is well reported in the literature on Lepidoptera for which increased density generally decrease the insect's survival and growth (Van Hamburg, 1980; Van Hamburg and Hassel, 1984; Teng and Apperson, 2000; Coulson et al., 2000; Agrew et al., 2002; Gibbs et al., 2004; Fantinou et al., 2008; Ntiri et al., 2017). DeLong et al. (2014) reported an inverse relationship between population density and metabolic rate of species. On the other

after contracting general linear model with the *lm* function at 5% of level of significance. Means were separated using Tukey's multiple comparisons test with *lsmeans* R package and those with different letters were significantly different

hand, the lower survival and RGR with increased larval density for FAW, might be also due to the cannibalistic behaviour of FAW as already reported from field observations (Sarmiento et al., 2002; Farias et al., 2001; Chapman et al., 2000; Da Silva, 1999) as well as under laboratory conditions (Bentivenha et al., 2017; Da Silva and Parra, 2013; De Polanía et al., 2009; Goussain et al., 2002; Chapman et al., 1999a, 1999b) which led to a stronger cannibalism for FAW when the larval density increase.

Under interspecific interactions, *C. partellus* dominate the other species in survival and RGR at all densities when significant, while the competitions between FAW and other noctuids are less and sporadic across the densities. These results confirm the asymmetry of interspecific competition outcomes in phytophagous insects (Denno et al., 1995; Inbar, 1995; Kaplan and Denno, 2007). Asymmetrical competition between noctuids, *B. fusca* and *S. calamistis* and the crambid, *C. partellus* has already been reported by Ntiri et al. (2016, 2017) and between FAW and stemborers by Sokame et al. (2020). The dominance of *C. partellus* in interactions with the noctuid species at all densities indicates that it is a superior competitor in the use of resource. The reason

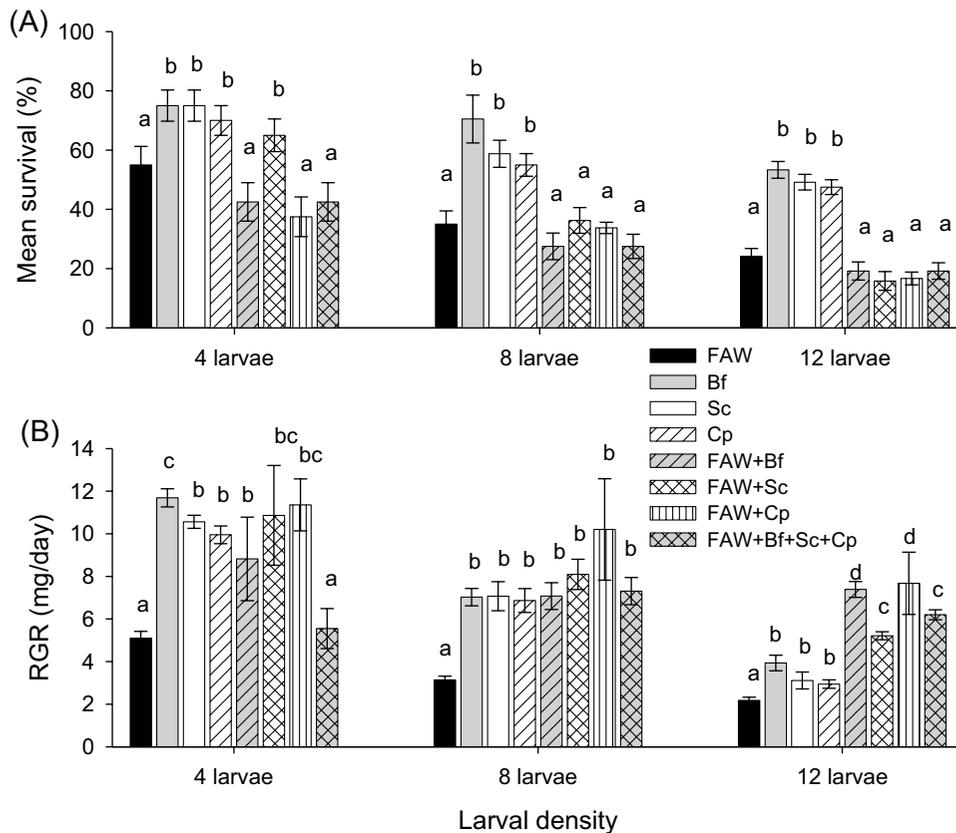


Fig. 4 Mean (\pm SE, $n=15$) survival (%) (A) and relative growth rate (RGR: mg/day) (B) of fall armyworm (FAW) with *Busseola fusca* (Bf), *Sesamia calamistis* (Sc) and *Chilo partellus* (Cp) in single-species conditions and in two- and four-species combinations at three different larval densities (4, 8 or 12 larvae). Survival data were analyzed using generalized lin-

ear model (GLM) with binomial distribution while RGRs were analyzed via analysis of variance (ANOVA) after contracting general linear model with the *lm* function at 5% of level of significance. Means were separated using Tukey's multiple comparisons test with *lsmeans* R package and those with different letters were significantly different

might be that *C. partellus* is not only a hardy species but also has a higher development rate than the noctuids (Khadioli et al., 2014a, 2014b). In addition, not surprisingly the results showed that at low density, interspecific competition between species is low and generally becomes stronger with increasing density as already reported in density-dependent population regulation (Flockhart et al., 2012; Underwood, 2010). Therefore, multiple infestations of cereal plants with low larval densities of each species at optimum conditions will very likely prolong their coexistence.

Concerning duration of competitions, this study showed that the intensity of intra- and inter-specific competition between FAW and the three stemborer

species was plastic over a given time period. Although survival rates decreased with time, RGRs increased with time up till 15 days following infestation after which it declined in either intraspecific or interspecific combinations. This temporal plasticity of competition between FAW and stemborers could be as a result of the fluctuations in food resources quality and availability as utilisation increased with time (Ayabe et al., 2015; Wissinger, 1989; Blanckenhorn, 1998). Therefore, there was an increased need for food for development with time, as larvae moulted into next instars and developed to pupae. This has been reported within a community of lepidopteran stemborer species (Ntiri et al., 2017). At early

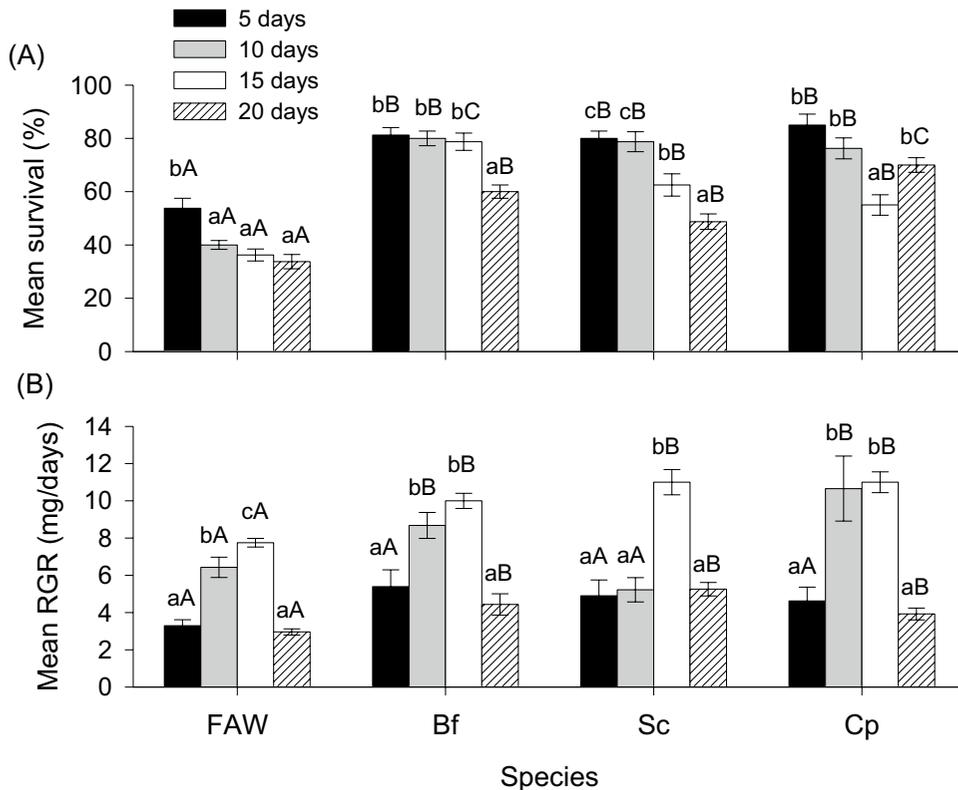


Fig. 5 Mean (\pm SE, $n=15$) survival (%) (A) and relative growth rate (RGR: mg/day) (B) of single species infestations of fall armyworm (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc) and *Chilo partellus* (Cp) at four different durations of infestation. Survival data were analyzed using generalized linear model (GLM) with binomial distribution while RGRs were analyzed via analysis of variance (ANOVA) after

contracting general linear model with the *lm* function at 5% of level of significance. Means were separated using Tukey's multiple comparisons test with *lsmeans* R package and those with different letters were significantly different. Small letters were used to compare means between densities for each species and capital letters to compare means between species for each density

development stages, the size of larvae enabled high survival and probably resulted in less contact between individuals. However, as body size increased with time, the increasing requirement and consumption of food increased the intensity of competition, and RGR started decreasing (Werner and Gilliam, 1984; Ntiri et al., 2017). This could be one underlying influence of duration of interactions on competition outcomes. The trade-off between high larval RGR and low survival that was observed as competition progressed is a phenomenon already reported in other species (Nylin and Gotthard, 1998), and may be a response to specific nutrient needs to meet the increasing stressful competitive environment (Boggs, 2009). The time partitioning of the resource use appears also as a key

factor of the coexistence of these competing insect species.

In conclusion, this study showed that larval density and duration of interaction between larvae of FAW and stemborers, *B. fusca*, *C. partellus* and *S. calamistis*, that utilise the same resource have a significant influence on the intra- and interspecific interactions outcomes within and between the species. It showed that multiple infestations of cereal plants with low larval densities of each species at optimum conditions will very likely prolong their coexistence. The time partitioning of the resource use appears also as a key factor of the coexistence of these competing insect species.

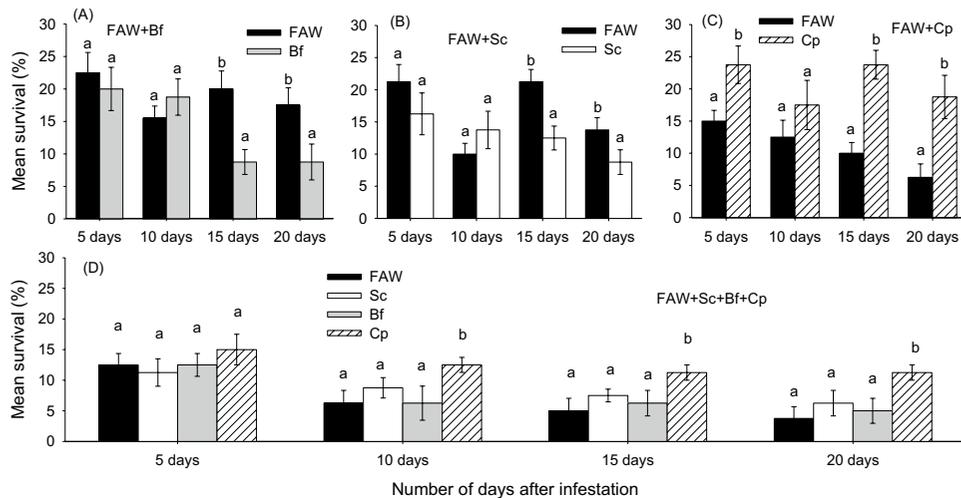


Fig. 6 Mean (\pm SE, $n=15$) of survival (%) of fall armyworm (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc) and *Chilo partellus* (Cp) in (A-C) two- and (D) four-species combinations at four different durations of infestation. Data were analyzed using generalized linear model (GLM)

with binomial distribution. Means were separated using Tukey's multiple comparisons test with lsmeans R package and those with different letters were significantly different

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Declarations

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

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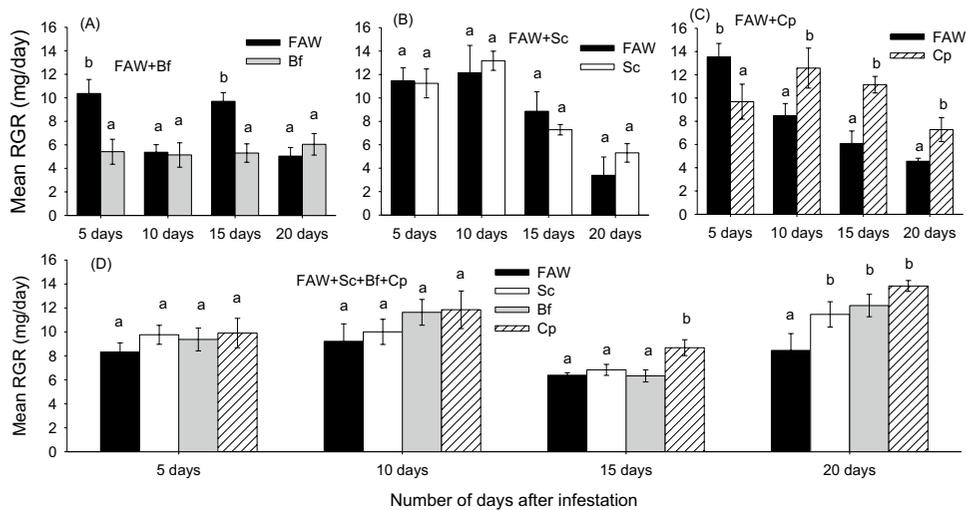


Fig. 7 Mean (\pm SE, $n=15$) of relative growth rate (RGR: mg/day) of fall armyworm (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc) and *Chilo partellus* (Cp) in (A–C) two- and (D) four-species combinations at four different durations of infestation. Data were analyzed using analysis of variance (ANOVA)

after contracting general linear model with the *lm* function at 5% of level of significance. Means were separated using Tukey's multiple comparisons test with *lsmeans* R package and those with different letters were significantly different

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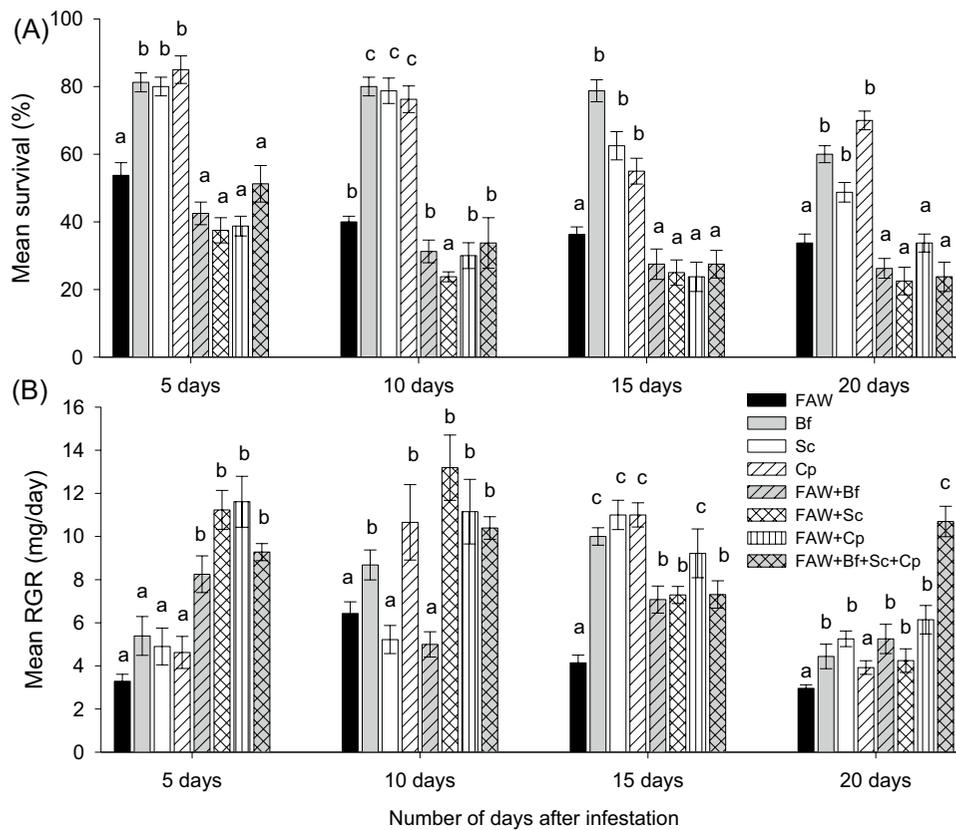


Fig. 8 Mean (\pm SE, $n=15$) survival (%) (A) and relative growth rate (RGR: mg/day) (B) of fall armyworm (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc) and *Chilo partellus* (Cp) in single species conditions and in two- and four-species combinations at four different durations of infestation. Survival data were analyzed using generalized linear model (GLM) with

binomial distribution while RGRs were analyzed via analysis of variance (ANOVA) after contracting general linear model with the *lm* function at 5% of level of significance. Means were separated using Tukey's multiple comparisons test with *lsmeans* R package and those with different letters were significantly different

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