


SHORT COMMUNICATION

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Preliminary results on effects of planting dates and maize growth stages on fall armyworm density and parasitoid occurrence in Zambia

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Abstract

Fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith), has become one of the main invasive species on earth since it was first found outside its native range in Africa in 2016. Integrated pest management (IPM) is a comprehensive tool that can help farmers managing pests while reducing the need of synthetic pesticides. Within an IPM strategy, proper time of planting is a critical management decision for farmers as planting too early or too late can lead to complete loss of the crop. Commonly, planting early to avoid peak infestation of FAW is recommended to farmers, however, no empirical data in Africa is available to sustain the advice. We studied the effects of planting dates of maize as well of maize growth stages on FAW density and on its local parasitoids in a field study. Three plots were setup (early, intermediate and late planting) and data was collected weekly in each plot. Plots were 20 m × 20 m to avoid small-plot effects, but the relatively large size of the plots was resource intensive and prevented replication. As such, this paper presents preliminary results due to the lack of true replicates across locations and years. Generalized Linear Models were used to model FAW density and parasitoids abundance and diversity. Our results showed an increase of egg masses over time from early to late planting. Additionally, parasitism probabilities were lower in the early planting treatment than for the intermediate and late plantings and decreased with increased maize maturity. Results on biodiversity of parasitoids show a less even trend for early and late whorl stages which are dominated by one or two species while maize reproductive stages show a more even distribution of species. Our preliminary research is the first to provide empirical evidence that planting early helps to avoid the peak activities of FAW moths. These findings provide important information for the sustainable management of FAW in Zambia with the aim to reduce chemical inputs and increase farmers' incomes and livelihood.

Keywords *Spodoptera frugiperda*, Parasitoid, Integrated pest management, Maize growth stages

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Background

Biotic and abiotic factors such as rainfall, temperature, altitude, vegetation, natural enemies and agronomic management practices, play pivotal roles in influencing the occurrence, infestation rate and damage caused by pests (Wolda 1978; Conte et al. 2007; Savopoulou-Soultani et al. 2012; Thakur and Rawat 2014; Marchioro and Foerster 2016). For smallholder farmers with limited resources, the timing of planting, as part of an integrated pest management (IPM) approach, is one of the most important tools for pest control as planting too early or too late can result in complete crop loss. Time of planting can impact pest density, and therefore, damage incurred to crops. For instance, research on the maize stalk borer *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) has shown that late planting is associated with higher infestation rates, higher damage, and subsequently increased yield losses (Gebre-Amlak et al. 1989; Ebenebe et al. 1999). Understanding the population dynamics of insect pests and the community composition of local natural enemies can help develop a comprehensive pest management strategy centred on ecosystem services and cultural practices.

Indeed, a good understanding of the pest dynamics and tri-trophic interactions over the crop season can help avoid high infestation rates and yield losses by pests, and unnecessary pesticide applications. Furthermore, natural enemy populations can be conserved and enhanced at specific crop growth stages if diversity and abundance are known over time (Durocher-Granger et al. 2021). Just like insect pests, parasitoids are also affected by biotic and abiotic factors. Temperature, rainfall, landscape characteristics, seasonality, host density, host stages and herbivore-induced plant volatiles are known to influence diversity, abundance, and parasitism rates in the field (Bernasconi Ockroy et al. 2001; Tschardt and Brandl 2004; D'Alessandro et al. 2009; Mailafiya et al. 2010). As being dependent on their hosts for development, parasitoids would obviously benefit to synchronize their emergence as adults with the presence of susceptible host stages (Godfray 1994). This is especially important in tropical regions where a long dry season is observed and depending on whether the insect hosts have one or a few generations a year. Therefore, good knowledge of the parasitoid complex and dynamics under these climatic conditions is even more essential for developing a targeted IPM approach.

Globally, the adoption of IPM remains alarmingly low, particularly in low- and middle-income countries (Parsa et al. 2014; Alwang et al. 2019). IPM, especially the bio-control component, is often implemented and adopted only as a last resort to exit a crisis. A pesticide treadmill is observed around the world which is characterized by

overuse of synthetic insecticides (frequent applications, high dosages and limited range of active ingredients and/or mode of actions) leading to the development of pesticide resistance, pest resurgence, emergence of secondary pests and the depletion of beneficial insect populations (Bakker et al. 2020). This cycle, therefore, aggravates dependencies on pesticides for pest management. Fall armyworm [FAW, *Spodoptera frugiperda* (J.E. Smith)] (Lepidoptera: Noctuidae) management does not escape these major problems and collective efforts to develop sustainable and low-impact practices have already created extensive knowledge to develop best management practices for smallholder farmers in Africa and Asia (reviewed by Kenis et al. 2023). Smallholder farming systems need to become more resilient for the upcoming decades as pest invasions are likely to increase with change in climatic patterns and increasing trade routes (Early et al. 2016).

FAW has become a major maize pest worldwide after its invasion and establishment on the African and Asian continents since 2016 (Kenis et al. 2023). In Africa alone, the yield loss is estimated to be USD 9.4 billion (Eschen et al. 2021). In Zambia, farmers have reported maize yield losses ranging between 21 and 77% in 2017 (national average of 40%) (Day et al. 2017), and 10% and 58% (national average of 35%) in 2018 (Rwomushana et al. 2018), showing a wide variation between agroecological regions. FAW has not been observed yet in Africa undergoing diapause, but studies suggest its potential regional migration (Nagoshi et al. 2018, 2022). As maize monocropping is found across Africa at different periods of the year, regional migrations alongside resident local populations persisting on wild hosts and irrigated maize are likely to colonize maize fields at the onset of the rain.

Early planting is commonly recommended to smallholder farmers to avoid the peak infestation of FAW (Ayala et al. 2013; Harrison et al. 2019; Deshmukh et al. 2021). However, empirical data are missing to support this advice. This study aimed at identifying optimal planting time for maize by evaluating FAW density, parasitism probabilities and parasitoid abundance and diversity for early, intermediate and late planting. We also investigated maize growth stages effect on FAW density, parasitism probabilities and parasitoid abundance and diversity.

Materials and methods

Experimental design

Field studies were carried out during the rainy season from December 2021 to April 2022. An irrigation system was used once the rains stopped after mid-March 2022 to maintain the late planting plot until cob maturity. The site was located in Zambia's Lusaka province; Chalimbana (15°21'33.9"S, 28°29'18.9"E; altitude: 1130 m).

Table 1 Schedule of the three planting date treatments

Treatment	Date planted	First sampling date	Last sampling dates	Number of samplings
Early planting	20th December 2021	31st December 2021	11th April 2022	15
Intermediate planting	10th January 2022	21st January 2022	11th April 2022	12
Late planting	1st February 2022	11th February 2022	11th April 2022	9

Three fields of maize (variety MRI624; Syngenta Seeds Zambia), measuring 20 m × 20 m, were planted at three-week intervals from the start of the rains (planting-date schedule shown in Table 1). A 75 cm gap between maize rows was maintained, and 30 cm between maize plants. Standard agronomic practices for maize fields were adopted as recommended by the Ministry of Agriculture to smallholder farmers in Zambia. Neighbouring fields were planted with maize crops like every rainy season as maize is mainly rainfed in Zambia. Pseudoreplicates were used in order to avoid an effect of small plots on FAW density by increasing the size of each plot at 20 m × 20 m. The large size of the plots was resource intensive and prevented replication. Data were also collected during the rainy season 2019–2020, however, due to covid lockdown in March 2020, the data collection was ended prematurely, and the late planting treatment was not completed. Therefore, this study presents preliminary results due to lack of replications across sites, years and treatments.

Data collection

From maize germination (90%), 100 random plants were sampled weekly from each field using a random sampling method. Plants were assessed thoroughly for egg masses and larvae in a non-destructive manner to allow continuous collection over the crop cycle. During each assessment, the number of egg masses and larvae were recorded for each maize plant. A paintbrush was used to extract the hidden larvae in whorls or between the leaves to minimise damage to the maize plants. Date and growth stage of the maize plant were recorded for each sampling date in each of the planting date treatments.

Rearing and identification of the samples

Egg masses and larvae collected from the maize fields were placed individually in Petri dishes and given a unique sample ID number. Larval stage was determined for each larva collected based on head capsule width as described in Durocher-Granger et al. (2021). Larvae were reared on beet armyworm F9219B artificial diet (Frontier Scientific Services, Newark, DE, USA), with antibiotics (aureomycin) in the laboratory, and kept at 27 ± 2 °C and 50 ± 5% RH. Egg masses and larvae were observed every

day until emergence of the parasitoids or adult moths and the development of parasitoids or FAW moths was recorded. Dead FAW larvae and pupae were dissected to record absence or presence of parasitoid larvae. If parasitoid larvae were found, their presence was recorded as “Hymenoptera-related mortality”.

All emerged adult parasitoids were morphologically identified by two of the authors (LDG and MK) using various identification keys and collections of insects gathered during previous studies on *S. frugiperda* parasitoids (Durocher-Granger et al. 2021). Seven parasitoid larvae which emerged from FAW larvae but were unable to pupate in the Petri dishes were identified with molecular analyses using the mtDNA barcode gene (mtDNA) cytochrome c oxidase subunit 1 (COI), following the method described in Durocher-Granger et al. (2021) to compare them with verified sequences from the Barcode of Life Data System (BOLD; <http://www.boldsystems.org/>) (Ratnasingham and Hebert 2013) and supplementary sequences from the GenBank® database (<http://www.ncbi.nlm.nih.gov/genbank/>) (Benson et al. 2018).

Data analysis

Fall armyworm density

To estimate the effects of planting date (early, intermediate and late planting) and maize stage groups (VE-V7,

Table 2 Maize stage categories

Maize stage groups	Maize growth stages
VE-V7	Emergence to seventh leaf collar
V8-V14	Eighth to fourteenth leaf collar
VT-R6	Tasseling to maturity

V8-V14, VT-R6; Table 2) on the number of FAW (larvae and eggs separately), we modelled FAW density using Generalized Linear Models (GLM). We used a negative binomial distribution to model the count data and account for overdispersion. We used a Bayesian approach to fit the model because there are conditions with zero FAW, for which confidence intervals cannot be estimated using classical frequentist approaches. In addition,

the Bayesian approach is robust because it uses Markov chain Monte Carlo resampling (MCMC), a non-parametric method (Gelman et al. 2013). We ran eight chains of 10,000 iterations (50% for warm up) for a total of 40,000 iterations with the default adaptive priors. The model was validated by inspecting convergence diagnostics (presence of divergence(s), chain mixing, effective number of iterations). We used the posterior distributions to estimate the magnitude of the differences among treatments, as well as to approximate the degree of certainty for the direction of the differences.

Parasitism probabilities

GLMs were used to analyse parasitism probabilities as a function of maize stage groups (VE-V7, V8-V14, VT-R6) and planting date (early, intermediate and late planting). We specified a binomial distribution to model the proportion of FAW parasitized while taking into account the number of FAW sampled on each date. We fitted the model using a Bayesian approach for the reasons mentioned above. Parasitism probabilities were tested for larval parasitoids and egg parasitoids separately and then together. Parasitoid species were categorized into functional groups of host stages attacked (egg or larva) as shown in Table 3. We use the R package brms (Bürkner 2017), which provides an R style wrapper for the Stan Hamiltonian Monte Carlo sampler (Stan Development Team 2023).

Parasitoid biodiversity

GLMs were used to model the relative abundance (proportion) versus species rank relationship for planting date (early, intermediate and late planting), and for different maize stage groups (VE-V7, V8-V14, VT-R6). The slope is a proxy for species evenness, where a steeper slope corresponds to a less even distribution of species (Whittaker 1965). We fitted the relationships on the log–log scales to

allow a linear relationship and compare the fitted slopes among planting dates and maize stage groups.

All analyses and graphical representations were conducted in R (R Core Team 2022) using the aforementioned R packages.

Results

Fall armyworm density

FAW larvae

The expected density of FAW larvae ranges from 0.10 to 0.69 per plant across treatments. Fewer larvae were found in the early planting date treatment than in the other treatments, but the difference was not clear (certainty < 75%). However, we found a clear effect of maize stage groups (Fig. 1): VE-V7 < V8-V14 (odds ratio = 17.9:1, certainty = 95%), VE-V7 > VT-R6 (odds ratio = 5.8:1, certainty of 85%), V8-V14 > VT-R6 (odds ratio = 222:1, certainty > 99.9%).

FAW egg masses

The expected density of FAW egg masses ranges from 0.0002 to 0.17 per plant across treatments (Fig. 2). We found relatively clear differences among planting dates: Early < Intermediate (odds ratio = 12.8:1, certainty = 93%), Early < Late (odds ratio = 1211:1, certainty > 99.9%), Intermediate < Late (odds ratio = 34:1, certainty > 97%). Among maize stage groups, only one difference was clear: VE-V7 < V8-V14 (odds ratio = 69:1, certainty = 98.5%), the other differences having degrees of certainty below 80%.

Parasitism probabilities

All parasitoids

The expected parasitism probabilities for all species varied between 2 and 39% depending on the planting date and maize stage group (Fig. 3). The early planting treatment had lower parasitism probabilities than both the intermediate planting (odds ratio = 291:1, certainty = 99.7%) and the late planting (odds ratio = 2665:1,

Table 3 Functional groups of parasitoids by stage of FAW attacked

Functional groups by stage attacked	Order	Family	Sub-family	Species
Egg parasitoids	Hymenoptera	Scelionidae		<i>Telenomus remus</i> (Nixon)
		Braconidae	Cheloninae	<i>Chelonus bifoveolatus</i> Szépligeti <i>Chelonus curvimaaculatus</i> Cameron
Larval parasitoids	Hymenoptera	Braconidae	Agathidinae	<i>Coccygidium luteum</i> Brullé
			Microgastrinae	<i>Cotesia icipe</i> Fernández-Triana & FiaBoe <i>Parapanteles</i> sp.
		Ichneumonidae	Campopleginae	<i>Diadegma</i> sp.
			Cremastinae	<i>Pristomerus</i> sp.
	Diptera	Tachinidae	Exoristinae	<i>Drino quadrizonula</i> (Thomson)

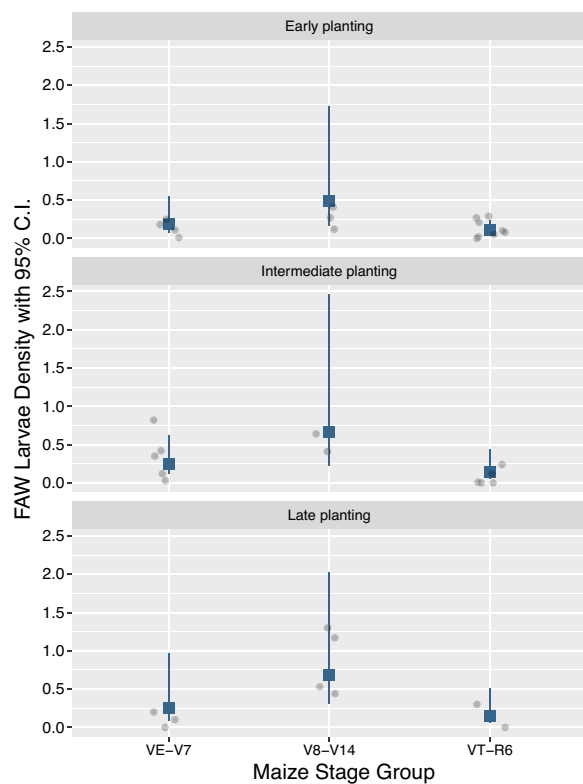


Fig. 1 Estimated fall armyworm larval density (number of larvae/number of plants sampled) by planting date and maize stage group. The squares show the estimated density and the whiskers, the 95% confidence intervals (CI) for each maize stage group and treatment combination

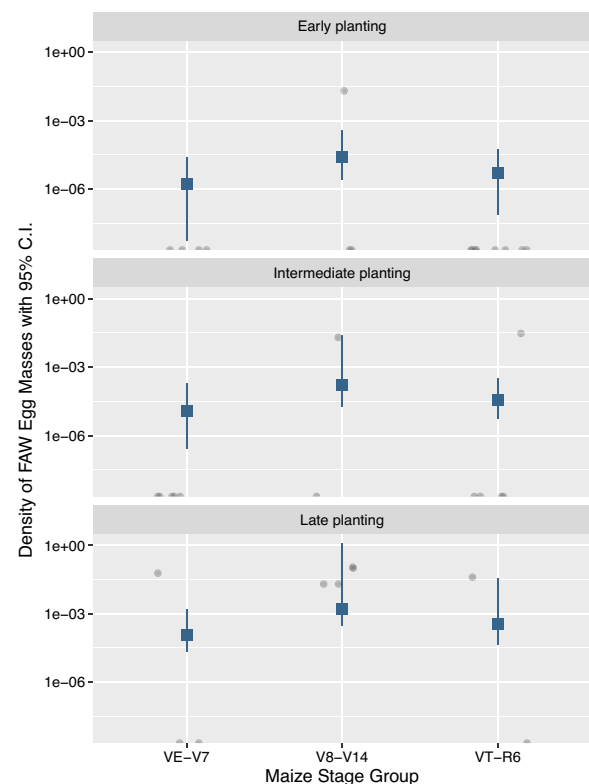


Fig. 2 Estimated fall armyworm egg masses density (number of egg masses/number of plants sampled) by planting date and maize stage group. The densities are plotted on the \log_{10} scale with zeros placed at the lower edge of the graph. The squares show the estimated density and the whiskers, the 95% CI for each maize stage group and treatment combination

certainty > 99.9%). There was no clear difference in the parasitism probabilities between the intermediate and late planting treatments (certainty of only 74%). Parasitism probabilities decreased with increasing maize growth stages. VE-V7 stages had higher probabilities of parasitism than V8-V14 (odds ratio > 40,000:1, certainty > 99.9%) and VT-R6 (odds ratio > 40,000:1, certainty > 99.9%), and V8-V14 had a slightly higher probabilities than VT-R6 (odds ratio > 410:1, certainty 99.8%).

Larval parasitoids

The expected parasitism probabilities for larval parasitoids varied between 1 and 26% depending on the planting date and maize growth stage (Fig. 4). Parasitism probabilities tended to be lower for the early planting date than for the intermediate (odds ratio = 11.4:1, certainty = 92%) and late planting dates (odds ratio = 7.7:1, certainty = 89%), but the difference between intermediate and late planting dates was not clear at all (odds ratio = 1.08:1, certainty = 52%). Maize growth stages had a clear effect: VE-V7 stages had higher probabilities of parasitism than V8-V14 (odds ratio > 40,000:1,

certainty > 99.9%) and VT-R6 (odds ratio > 40,000:1, certainty > 99.9%), and V8-V14 had a very slightly higher probabilities than VT-R6 (odds ratio = 89:1, certainty = 98.9%).

Egg parasitoids

The expected mean parasitism probabilities by egg parasitoids were very low across planting dates and maize stage groups and varied only from 0.6% to 5% (Fig. 5). Parasitism probabilities tended to increase with later planting dates: lower in the early planting date than in the intermediate (odds ratio = 10.7:1, certainty = 91.5%) or late (odds ratio = 36.8:1, certainty = 97.4%) dates, but there was no clear difference between intermediate and late planting dates (odds ratio = 2.6:1, certainty = 73%). Parasitism probabilities tended to decrease with later maize stage groups: lower for VT-R6 than for V8-V14 (odds ratio = 9.5:1, certainty = 90.5%) or VE-V7 (odds ratio = 12.2:1, certainty = 92.4%), but the difference

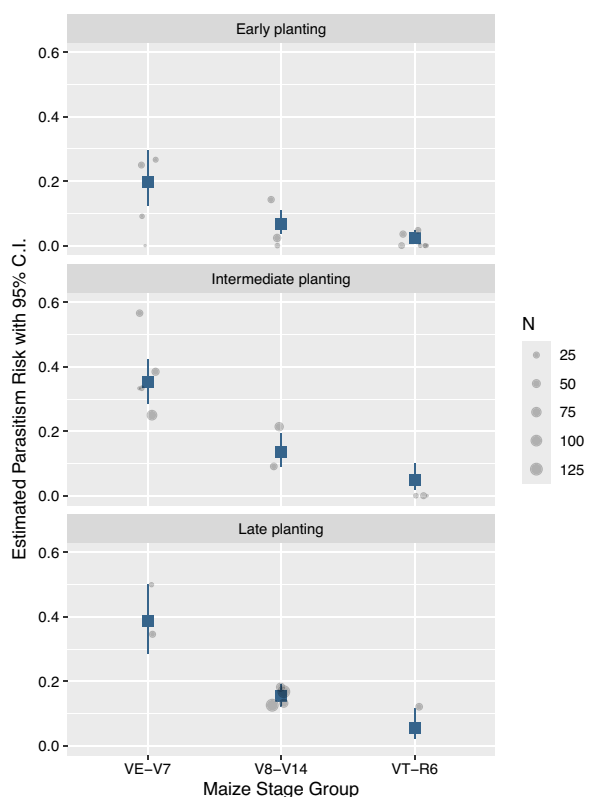


Fig. 3 Parasitism probabilities across the different planting date treatments and maize stage groups for all parasitoids. The squares show the estimated density and the whiskers, the 95% CI for each maize stage group and treatment combination. The size of the points is proportional to the number of FAW larvae sampled (N)

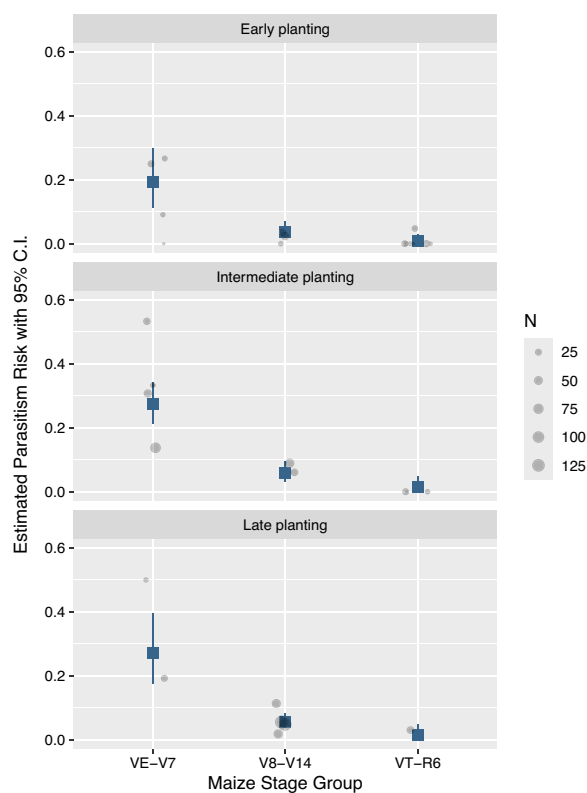


Fig. 4 Parasitism probabilities across the different planting date treatments and maize stage groups for larval parasitoids. The squares show the estimated density and the whiskers, the 95% CI for each maize stage group and treatment combination. The size of the points is proportional to the number of FAW larvae sampled (N)

between VE-V7 and V8-V14 was rather small and uncertain (odds ratio = 1.6:1, certainty = 61%).

Parasitoid biodiversity

Analysis of evenness by planting date treatments

Parasitoid abundance showed that *C. luteum* was the most abundant species followed by *Ch. curvimaaculatus* for early planting (66% and 17%), intermediate planting (55% and 17%) and late planting (47% and 18%) (Fig. 6). The slopes, and therefore species evenness, were very similar for all three planting dates. Species evenness tended to increase slightly with planting dates but there was a lot of uncertainty. Species abundances tended to be more even for the late planting date than for the intermediate planting date (odds ratio = 8.2:1, certainty = 89%) and early (odds ratio = 11.7:1, certainty = 92%) planting dates. The difference between early and intermediate dates was less clear (odds ratio = 2.5:1, certainty = 71%).

Analysis of evenness by maize stage groups

The rank-abundance plot shows that species evenness was higher for the latest maize stage group (VT-R6) than

the other two maize stage groups (VE-V7 and V8-V14), as shown by the differences in slopes (Fig. 7). The odds that this difference was real is over 160:1, or over 99% certainty. Results showed that VE-V7 and V8-V14 maize stages were dominated by one or two species while reproductive stages (VT-R6) showed a more even distribution of species with *Ch. bifoveolatus* (25%), *Ch. curvimaaculatus* (25%), *C. luteum* (25%) and *D. quadrizonula* (25%). At VE-V7 stages, *C. luteum* was the most abundant species (40%), followed by *C. icipe* (14%) whilst at V8-V14 stages, *C. luteum* was dominating (54%) followed by *Ch. curvimaaculatus* (18%).

Discussion

Our study showed an effect of planting dates on FAW density with an increase of FAW egg masses from early to late planting. However, no clear effect of planting dates was detected on FAW larvae density. Nevertheless, the increase in the number of egg masses reflects the buildup of FAW adult populations and therefore, supports the recommendation that early planting helps to avoid the peak of moth flight activity (Harrison et al. 2019;

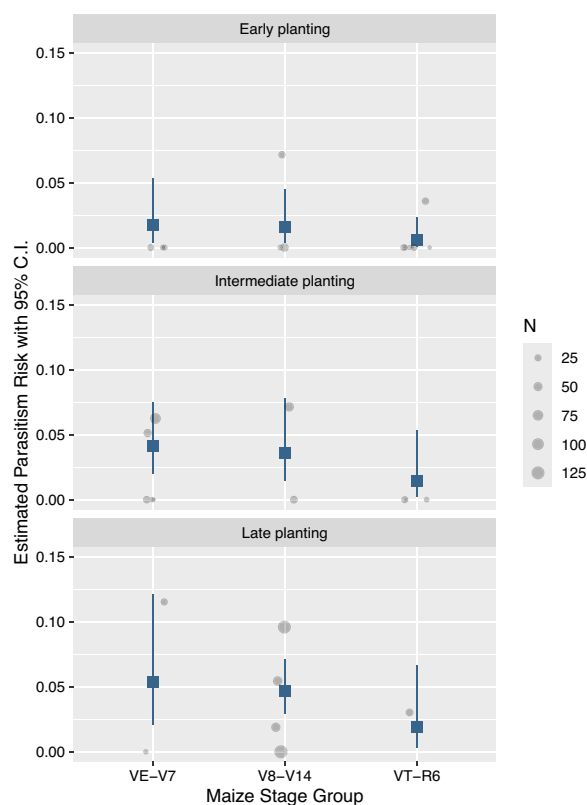


Fig. 5 Parasitism probabilities across the different planting date treatments and maize stage groups for egg parasitoids. The squares show the estimated density and the whiskers, the 95% CI for each maize stage group and treatment combination. The size of the points is proportional to the number of FAW larvae sampled (N)

Deshmukh et al. 2021). It is important to interpret these results with caution and compare them with similar agro-ecological zones where a short rainy season is followed by a long dry season. However, due to the lack of true replication, we are unable to extend the interpretation of the results to other regions or to extrapolate to further years. In Zambia, maize is largely rainfed and a sole rainy season occurs from November to March. Therefore, our results suggest that local populations of FAW persisting on irrigated crops surrounding the research field during the dry season seem to be the main source of infestation at the onset of the rain leading to a buildup of the population over the rainy season. This is also consistent with FAW larval development models developed from the same research field and other research sites in Zambia from previous years showing that eggs and young larvae were present in the fields soon after maize emergence (Lowry et al. 2022). Farmers using irrigation systems establish new maize crops once the rainfed maize is harvested. Therefore, the buildup of FAW population at the end of the rainy season is likely to migrate on irrigated

maize and to persist during the dry season. These persisting local FAW populations are then ready to reinvade maize crops at the beginning of the rainy season. In addition, smallholder farmers prefer to use staggered planting techniques for maize crops due to lack of mechanisation, to reduce risk of erratic early rains or to spread labour peaks (planting, weeding, applying inputs, etc.) (Harrison et al. 2019), which result in an increase of pest incidence as the rainy season progresses. Furthermore, FAW eggs and larvae were found during maize reproductive stages (VT-R6) but at lower rates than during early and late whorl stages. As the cropping season progresses, the availability of the preferred maize stage (i.e., young vegetative maize leaves) becomes limited. However, reproductive structures such as silk, closed tassels and early cob stages are still suitable food for FAW larval development (Pannuti et al. 2016; Mohamed et al. 2023). This outcome has implications for farmers' incomes as damage to silk, tassels or cobs can lead to kernel abortion, reduction in grain formation, fungal infection, aflatoxin contamination and loss of grain quality (Anjorin et al. 2022; FAO and CABI 2019). Farmers generally use chemicals to control FAW in the early to late whorl stages, however research on safe cultural practices to reduce damage to reproductive structures should also be explored to avoid losing income due to a poor-quality harvest.

Our study also shows higher probabilities of parasitism for FAW eggs and larvae on intermediate and late planting compared to early planting for both larval and egg parasitoids. The lower parasitism probabilities on early planting maize are likely due to the generally lower availability of parasitoids early in the season. Parasitoids attacking FAW from our research study probably undergo a diapause or quiescence period even if diapause has not been observed for FAW, which, in Africa, is present all year-round on various rainfed and irrigated crops. Synchronization of adult parasitoid emergence with the presence of specific host stages is particularly important for species parasitizing hosts with one or few generations per year (Godfray 1994). As studied by Seymour and Jones (2000), diapause in tropical parasitoid species is induced by humidity due to the limited annual variations in daylength, the main cue inducing insect diapause in temperate regions. In their study on *Microplitis demolitor* (Wilkinson), a solitary braconid parasitoid of *Helicoverpa armigera* (Hübner) and *Helicoverpa punctigera* Wallengren (Noctuidae: Lepidoptera), the adult parasitoids emerged roughly 38 days after diapause was terminated. While its hosts use temperature as an environmental cue to terminate diapause, *M. demolitor* uses increased humidity. In Lusaka, annual variation in daylength ranges between 11 h and 15 min, and 13 h and 4 min (WorldData.info 2015), which is a small variation

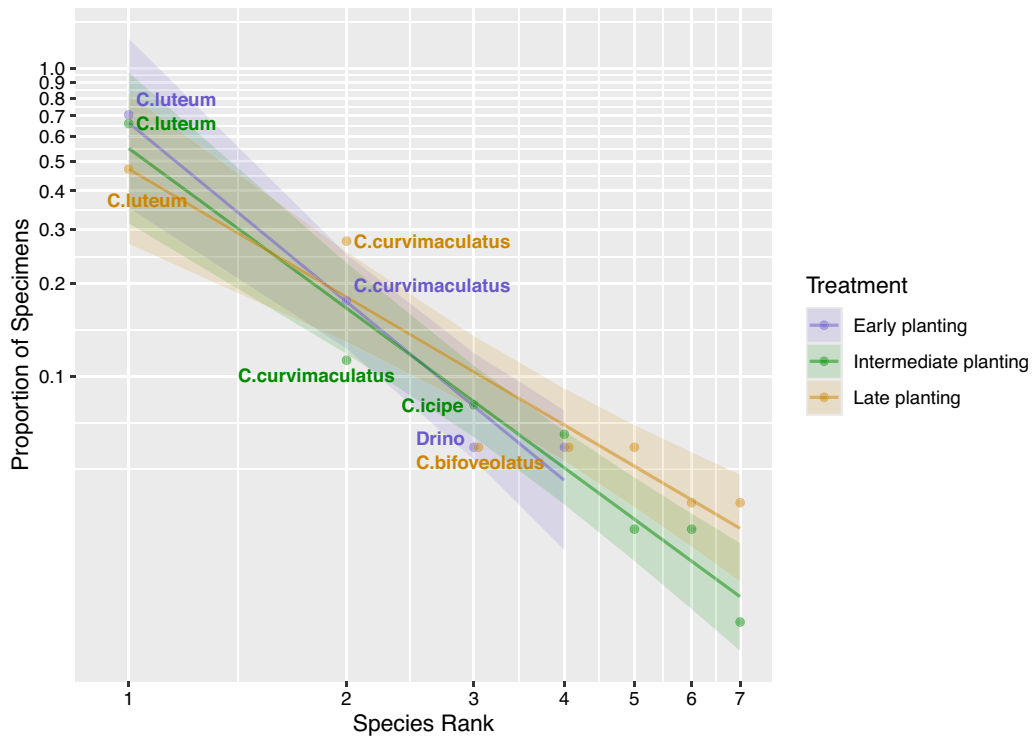


Fig. 6 Relative abundance of parasitoid species (evenness of species abundances) by planting dates

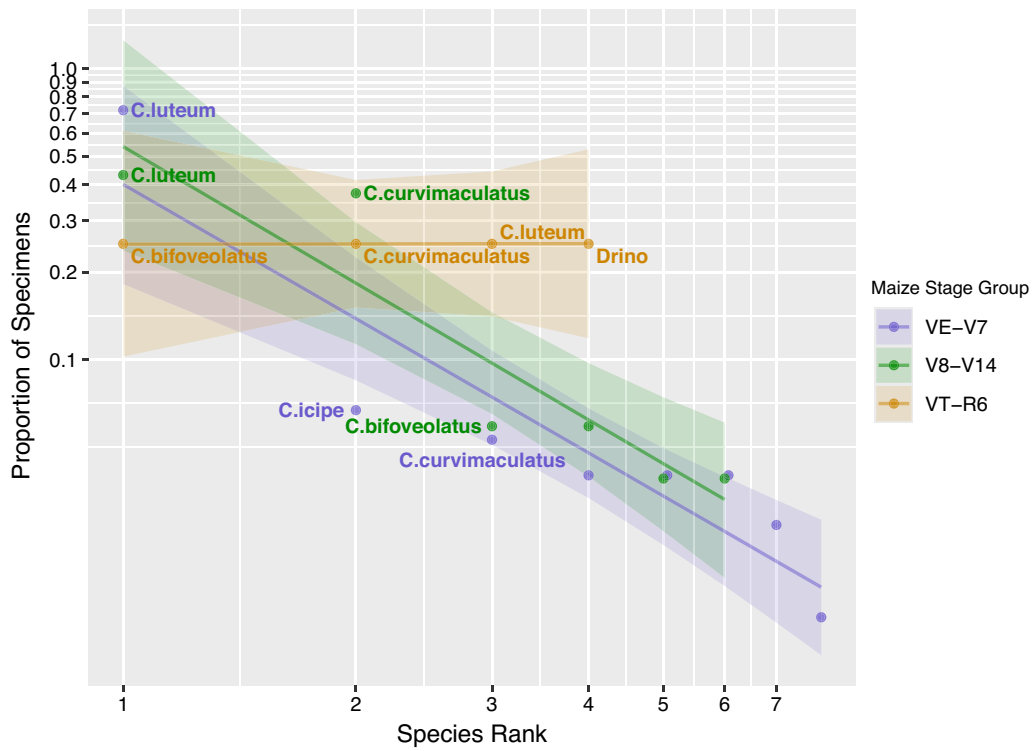


Fig. 7 Relative abundance of parasitoid species (evenness of species abundances) by maize stage groups

compared to temperate climates. Furthermore, Lusaka province, where the research experiment was conducted, the daily temperature ranges from 25 to 32 °C and exhibits a long dry season from usually early to mid-March until November to December, with a variation in relative humidity between 40 and 80%. Therefore, humidity variation in our research study is likely to play a role in the abundance of local parasitoids at the onset of the rains and throughout the rainy season.

We also found an effect of maize growth stages on parasitism probabilities. These results suggest that the probabilities of an event of parasitism is higher during early whorl stages than late whorl or reproductive stages, and that late whorl stages are also more likely to have parasitized FAW larvae than during reproductive stages. These results are important considering recommendations to farmers to spray chemical insecticides during the early and late whorl stages against FAW. As part of an integrated pest management approach, spraying chemical insecticides early can be counter-productive alongside the simultaneous recommendation to farmers to conserve natural enemies. As higher parasitism probabilities occur in the early whorl stages, broad-spectrum chemical insecticides have the potential to reduce the populations of natural enemies attacking FAW in the field, which can lead to a resurgence of the pest. Instead, the focus should be on conserving and enhancing local natural enemies found during the VE-V7 stages as these are the stages where parasitism is more likely to occur and there is an opportunity to build up their populations for the next maize stages.

As found in the rainy season 2018–2019 (Durocher-Granger et al. 2021), maize growth stages affect the parasitoid abundance and diversity; early and late whorl stages have higher diversity but are dominated by one or two species. According to our results, *C. luteum* is the dominating species during early and late whorl stages. As found across African countries, this parasitoid species is one of the most common and abundant FAW parasitoids (Kenis et al. 2023). *C. icipe* was the second most abundant parasitoid during early whorl stages. This parasitoid prefers first and second instar larvae of FAW (Mohamed et al. 2021), therefore its high abundance in early whorl stages is expected. *Ch. curvimaeculatus*, being an egg-larval parasitoid, requires eggs to be available for oviposition. However, it kills its host larva when the parasitoid larva emerges to build a cocoon. Therefore, the peak of adult emergence may be seen only during the late whorl stages as its cycle spreads over two host stages. The trend of parasitoids diversity and abundance on the reproductive stages of the maize is interesting as no species is dominant in these stages but there is rather an equal distribution of four species. This is consistent with

our previous study where diversity and abundance of parasitoids decreased as the maize matured (Durocher-Granger et al. 2021). *Ch. curvimaeculatus* seems to be one of the parasitoids colonizing the fields in the early season alongside *C. luteum*, *C. icipe* and *Parapanteles* sp. Results on *D. quadrizonula*, a tachinid fly, are also consistent with our previous study where this species was recorded from late whorl stages, when late FAW instar larvae had increased in abundance.

As compared to our previous surveys on FAW parasitism in 2018–2019 (Durocher-Granger et al. 2021) one additional species of egg parasitoid, *T. remus*, was found. Interestingly, egg mass parasitism was low (0.6% to 5%) and did not contribute significantly to FAW mortality across maize stages and over the rainy season. Egg parasitoids, having a much shorter life cycle than larval parasitoids and being more exposed to drought in host eggs on plants than larval parasitoids in their cocoons, may suffer even more from long dry seasons as those experienced in Central Zambia.

Conclusions

In conclusion, the results from this study provide preliminary field evidence that early planting helps avoiding high peak activities of moths. Furthermore, important insights in parasitoids seasonal activity, diversity and abundance can also support the development of a comprehensive IPM strategy around cultural and biological control. However, it is important to note that the trend observed from our study is year- and location-specific and cannot be extrapolated to other years or regions in Zambia considering the difference in agroecological zones and variability in climatic conditions, especially regarding the rainfall patterns.

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Author contributions

LDG, AL and MK conceived and planned the experiments. LDG collected the field and laboratory data. MB, YTY and LO performed the molecular identification of the parasitoid larvae. GMW and EF performed the analysis and interpretation of the results. LDG took the lead in writing the manuscript with support from MK and MD, and all authors provided critical feedback and helped shape the research, analysis and manuscript.

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Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations**Ethics approval and consent to participate**

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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References

- Alwang J, Norton G, Larochele C. Obstacles to widespread diffusion of IPM in developing countries: lessons from the field. *J Integr Pest Manag.* 2019;10(1):10. <https://doi.org/10.1093/jipm/pmz008>.
- Anjorin FB, Odeyemi OO, Akinbode OA, Kareem KT. Fall armyworm (*Spodoptera frugiperda*) (J. E. Smith) (Lepidoptera: Noctuidae) infestation: maize yield depression and physiological basis of tolerance. *J Plant Prot Res.* 2022;62(1):12–21. <https://doi.org/10.24425/jppr.2022.140294>.
- Ayala OR, Navarro F, Virla EG. Evaluation of the attack rates and level of damages by the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), affecting corn-crops in the northeast of Argentina. *Rev Fac Cienc Agrar UNCuyo.* 2013;45(2):1–12.
- Bakker L, van der Werf W, Tittonell PA, Wyckhuys KA, Bianchi FJ. Neonicotinoids in global agriculture: evidence for a new pesticide treadmill? *Ecol and Soc.* 2020;25(3):26. <https://doi.org/10.5751/ES-11814-250326>.
- Benson DA, Cavanaugh M, Clark K, Karsch-Mizrachi I, Ostell J, Pruitt KD, Sayers EW. GenBank. *Nucleic Acids Res.* 2018;46:D41–7. <https://doi.org/10.1093/nar/gkx1094>.
- Bernasconi Ockroy ML, Turlings TC, Edwards PJ, Fritzsche-Hoballah ME, Ambrosetti L, Bassetti P, Dorn S. Response of natural populations of predators and parasitoids to artificially induced volatile emissions in maize plants (*Zea mays* L.). *Agric For Entomol.* 2001;3(3):201–9. <https://doi.org/10.1046/j.1461-9555.2001.00107.x>.
- Bürkner PC. brms: an R package for Bayesian multilevel models using Stan. *J Stat Softw.* 2017;80(1):1–28. <https://doi.org/10.18637/jss.v080.i01>.
- Conte A, Goffredo M, Ippoliti C, Meiswinkel R. Influence of biotic and abiotic factors on the distribution and abundance of *Culicoides imicola* and the Obsoletus Complex in Italy. *Vet Parasitol.* 2007;150(4):333–44. <https://doi.org/10.1016/j.vetpar.2007.09.021>.
- D'Alessandro M, Brunner V, von Mérey G, Turlings TC. Strong attraction of the parasitoid *Cotesia marginiventris* towards minor volatile compounds of maize. *J Chem Ecol.* 2009;35:999–1008. <https://doi.org/10.1007/s10886-009-9692-7>.
- Day R, Abrahams P, Bateman M, Beale T, Clotey V, Cock M, et al. Fall armyworm: impacts and implications for Africa. *Outlooks Pest Manag.* 2017;28(5):196–201. https://doi.org/10.1564/v28_oct_02.
- Deshmukh SS, Prasanna BM, Kalleshwaraswamy CM, Jaba J, Choudhary B. Fall armyworm (*Spodoptera frugiperda*). In: Omkar, editor. Polyphagous pests of crops. Singapore: Springer; 2021. p. 349–72. <https://doi.org/10.1007/978-981-15-8075-8>.
- Durocher-Granger L, Mfune T, Musesha M, Lowry A, Reynolds K, Buddie A, Giovanni C, Offord L, Chipabika G, Dicke M, Kenis M. Factors influencing the occurrence of fall armyworm parasitoids in Zambia. *J Pest Sci.* 2021;94(4):1133–46. <https://doi.org/10.1007/s10340-020-01320-9>.
- Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, Blumenthal DM, Gonzalez P, Grosholz ED, Ibañez I, Miller LP, Sorte CJB, Tatem AJ. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat Commun.* 2016;7:12485. <https://doi.org/10.1038/ncomms12485>.
- Ebenebe AA, Van den Berg J, Van der Linde TC. Effect of planting date of maize on damage and yield loss caused by the stalk borer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) in Lesotho. *S Afr J Plant Soil.* 1999;16(4):180–5. <https://doi.org/10.1080/02571862.1999.10635007>.
- Eschen R, Beale T, Bonnini MJ, Constantine KL, Duah S, Finch EA, Makale F, Nunda W, Ogunmodede A, Pratt CF, Thompson E, Williams F, Witt A, Taylor B. Towards estimating the economic cost of invasive alien species to African crop and livestock production. *CABI Agric Biosci.* 2021. <https://doi.org/10.1186/s43170-021-00038-7>.
- FAO, CABI. Community-based fall armyworm (*Spodoptera frugiperda*) monitoring, early warning and management, training of trainers manual. 1st ed. Rome: Food and Agriculture Organization of the United Nations; 2019. p. 112.
- Gebre-Amlak A, Sigvald R, Pettersson J. The relationship between sowing date, infestation and damage by the maize stalk borer, *Busseola fusca* (Noctuidae), on maize in Awassa, Ethiopia. *Int J Pest Manag.* 1989;35(2):143–5. <https://doi.org/10.1080/09670878909371343>.
- Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. Bayesian data analysis. 3rd ed. Boca Raton: CRC Press; 2013.
- Godfray HCJ. Parasitoids: behavioral and evolutionary ecology. Princeton: Princeton University Press; 1994.
- Harrison RD, Thierfelder C, Baudron F, Chinwada P, Midega C, Schaffner U, Van Den Berg J. Agro-ecological options for fall armyworm (*Spodoptera frugiperda* JE Smith) management: providing low-cost, smallholder friendly solutions to an invasive pest. *J Environ Manage.* 2019;243:318–30. <https://doi.org/10.1016/j.jenvman.2019.05.011>.
- Kenis M, Benelli G, Biondi A, Calatayud PA, Day R, et al. Invasiveness, biology, ecology, and management of the fall armyworm *Spodoptera frugiperda*. *Entomol Gen.* 2023. <https://doi.org/10.1127/entomologia/2022/1659>.
- Lowry A, Durocher-Granger L, Oronje M, Mutisya D, Mfune T, Gitonga C, et al. Optimizing the timing of management interventions against fall armyworm in African smallholder maize: modelling the pattern of larval population emergence and development. *Crop Prot.* 2022;157:105966. <https://doi.org/10.1016/j.cropro.2022.105966>.
- Mailafiya DM, Le Ru BP, Kairu EW, Calatayud PA, Dupas S. Factors affecting stem borer parasitoid species diversity and parasitism in cultivated and natural habitats. *Environ Entomol.* 2010;39:57–67. <https://doi.org/10.1603/EN09196>.
- Marchioro CA, Foerster LA. Biotic factors are more important than abiotic factors in regulating the abundance of *Plutella xylostella* L., Southern Brazil. *Rev Bras Entomol.* 2016;60(4):328–33. <https://doi.org/10.1016/j.rbe.2016.06.004>.
- Mohamed SA, Wamalwa M, Obala F, Tonnang HE, Tefera T, Calatayud PA, Ekese S. A deadly encounter: alien invasive *Spodoptera frugiperda* in Africa and indigenous natural enemy, *Cotesia icipe* (Hymenoptera, Braconidae). *PLoS ONE.* 2021;16(7):e0253122. <https://doi.org/10.1371/journal.pone.0253122>.
- Mohamed HO, Dahi HF, Awad AA, Gamil WE, Fahmy BF. Damage symptoms, development, and reproductive performance of the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) on fodder maize and cob. *Acad Biol.* 2023. <https://doi.org/10.20935/AcadBiol6073>.
- Nagoshi RN, Goergen G, Tounou KA, Agboka K, Koffi D, Meagher RL. Analysis of strain distribution, migratory potential, and invasion history of fall armyworm populations in northern Sub-Saharan Africa. *Sci Rep.* 2018;8:3710. <https://doi.org/10.1038/s41598-018-21954-1>.
- Nagoshi RN, Goergen G, Koffi D, et al. Genetic studies of fall armyworm indicate a new introduction into Africa and identify limits to its migratory behavior. *Sci Rep.* 2022;12:1941. <https://doi.org/10.1038/s41598-022-05781-z>.
- Pannuti LER, Baldin ELL, Hunt TE, Paula-Moraes SV. On-plant larval movement and feeding behavior of fall armyworm (Lepidoptera: Noctuidae) on reproductive corn stages. *Environ Entomol.* 2016;45(1):192–200. <https://doi.org/10.1093/ee/nwv159>.

- Parsa S, Morse S, Bonifacio A, Chancellor TCB, Condori B, Crespo-Pérez V, Hobbs SLA, Kroschel J, Ba MN, Rebaudo F, Sherwood SG, Vanek SJ, Faye E, Herrera MA, Dangles O. Obstacles to integrated pest management adoption in developing countries. *Proc Natl Acad Sci*. 2014;111(10):3889–94. <https://doi.org/10.1073/pnas.1312693111>.
- R Core Team. R: A language and environment for statistical computing computer program, version By R Core Team, Vienna, Austria. 2022.
- Ratnasingham S, Hebert PDN. A DNA-based registry for all animal species: the barcode index number (BIN) system. *PLoS ONE*. 2013;8: e66213. <https://doi.org/10.1371/journal.pone.0066213>.
- Rwomushana I, Bateman M, Beale T, Beseh P, Cameron K, Chiluba M, et al. Fall armyworm: impacts and implication for Africa. Evidence Note Update, CAB International. 2018. <https://www.invasive-species.org/wp-content/uploads/sites/2/2019/02/FAW-Evidence-Note-October-2018.pdf>.
- Savopoulou-Soultani M, Papadopoulos NT, Milonas P, Moyal P. Abiotic factors and insect abundance. *Psyche J Entomol*. 2012;2012:167420.
- Seymour JE, Jones RE. Humidity-terminated diapause in the tropical braconid parasitoid *Microplitis demolitor*. *Ecol Entomol*. 2000;25(4):481–5.
- Stan Development Team. Stan modeling language users guide and reference manual, 2.26.1. 2023. <https://mc-stan.org>. Accessed 2 Oct 2023.
- Thakur M, Rawat S. Effect of abiotic factors on population dynamics of insect pests and natural enemies in potato crop. *J Agrometeorol*. 2014;16(2):187–91. <https://doi.org/10.54386/jam.v16i2.1513>.
- Tscharntke T, Brandl R. Plant-insect interactions in fragmented landscapes. *Annu Rev Entomol*. 2004;49:405–30. <https://doi.org/10.1146/annurev.ento.49.061802.123339>.
- Whittaker RH. Dominance and diversity in land plant communities. *Science*. 1965;147(3655):250–60.
- Wolda H. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *J Anim Ecol*. 1978;47(2):369–81. <https://doi.org/10.2307/3789>.
- WorldData.info. Sunrise and sunset in Zambia. 2015. <https://www.worlddata.info/africa/zambia/sunset.php>. Accessed 5 May 2023.

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