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Influence of feeding-damaged plants on the oviposition responses within a community of female moths

Eric Siaw Ntiri · Paul-Andre Calatayud ·
Boaz Musyoka · Johnnie Van den Berg ·
Bruno Pierre Le Ru

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Abstract Competitive or facilitative interactions characterise phytophagous insect communities that utilise the same resources. These interactions are often mediated by the host plant. Plant mediation influences the oviposition choices that a community of insects, sharing the same host plant make. In this context, the oviposition choices of females within a community of lepidopteran cereal stemborers namely *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus* were studied in plant choice-experiments under laboratory and field conditions. Gravid females of each species were presented with a choice between maize plants infested by conspecific or heterospecific larvae and uninfested maize plants. The number of eggs and egg batches laid on plants were used to quantify oviposition. Results showed that none of the three stemborer species avoided oviposition on infested maize plants. In some cases a significant preference for infested maize plants were observed. Similarly, data from field trials under natural stemborer infestation, with *B. fusca* as the only species, showed that the wild ovipositing moths were not avoiding infested plants. Host plant mediation may influence the incidence of multi-species infestations by stemborer species often found in the field. The potential roles of herbivore-induced and egg-deposited-induced plant volatiles in this mechanism are discussed.

Keywords *Busseola fusca* · *Chilo partellus* · Herbivore-induction · Lepidoptera · *Sesamia calamistis* · Oviposition

Introduction

The structure and function of ecological communities are maintained by direct and indirect interactions between species (Wootton and Emmerson 2005). In phytophagous insect communities, these interactions often occur through the utilisation of the same host plants, with the outcome being negative (e.g. competition), positive (e.g. facilitation) or neutral (Denno et al. 1995; Bruno et al. 2003; Speight et al. 2008). These interactions can be directly intraspecific or interspecific (Memmott et al. 2007) or indirectly through the mediation of the host plant they share (Faeth 1986; Fisher et al. 2000; Kaplan and Denno 2007). Plant-mediated interactions are common and are also the dominant factors which influence interactions between phytophagous insects (Faeth 1986; Ohgushi 2005; Denno and Kaplan 2007).

E. S. Ntiri · P.-A. Calatayud · B. Musyoka · B. P. Le Ru
International Centre of Insect Physiology and Ecology (icipe),
P.O. Box 30772-00100, Nairobi, Kenya

E. S. Ntiri (✉) · J. Van den Berg
IPM Program, Unit for Environmental Sciences and Management,
North-West University, Potchefstroom, South Africa
e-mail: ensiaw@gmail.com

P.-A. Calatayud · B. P. Le Ru
UMR IRD 247 Laboratoire Evolution, Génomes, Comportement
et Ecologie, Diversité, Ecologie et Evolution des Insectes
Tropicaux, CNRS, 91198, Gif-sur-Yvette, Paris, France

P.-A. Calatayud · B. P. Le Ru
Université de Paris-Sud, 91405, Orsay, Paris, France

Plant mediation play out in processes such as oviposition - a form of resource utilisation by insects which establishes their relationship with host plants (Thompson and Pellmyr 1991; Bernays and Chapman 1994; Singer 2004). For most phytophagous insect species, especially Lepidoptera, oviposition is an important form of resource use, as the choice of host plants by a female determines the fitness of its offspring (Thompson and Pellmyr 1991; Renwick and Chew 1994). Generally, the physical and chemical properties, as well as the physiological state of the host plant (e.g. infested or non-infested) determine its final acceptability for the female. The final oviposition choices of the different species within a given community can be influenced by induced resistance or susceptibility of a host plant as a result of prior use by one species (Denno and Kaplan 2007). Thus, competition for, or facilitation of the use of the same host plant for final oviposition, can indirectly be mediated by the host plant (Awmack and Leather 2002). For example, some insect species are attracted to feeding-damaged plants for oviposition (Anderson and Alborn 1999; Viswanathan et al. 2005; Facknath 2012), while others are deterred from these plants (Sato et al. 1999; De Moraes et al. 2001; Wise and Weinberg 2002).

Final acceptance for oviposition however, can also be influenced by the state of the gravid female, such as her egg load (quantity), learning through experience and the interplay between these factors (Minkenberg et al. 1992; Bernays and Chapman 1994; Cunningham et al. 1998). Furthermore, final acceptance may also be influenced by the presence or absence of natural enemies (Ballabeni et al. 2001; Wiklund and Friberg 2008).

The lepidopteran cereal stemborers *Busseola fusca* (Fuller) (Noctuidae), *Sesamia calamistis* Hampson (Noctuidae) and *Chilo partellus* (Swinhoe) (Crambidae) are among the major pests of cereals in sub-Saharan Africa (Kfir et al. 2002). In East and Southern Africa, where they co-exist, they occur as communities of single or mixed species infesting cereals in crop fields (Van den Berg et al. 1991a; Tefera 2004; Ong'amo et al. 2006a; Krüger et al. 2008). Several studies have been conducted to understand the host plant selection and preference mechanisms of these stemborer species (Päts and Ekbom 1994; Van den Berg 2006; Van den Berg et al. 2006; Calatayud et al. 2008a). *Busseola fusca* and *C. partellus* have been identified as oligophagous, while *S. calamistis* was found to be polyphagous on wild grasses (Le Ru et al. 2006a, b; Moolman et al. 2014). In Kenya, these three stemborer species occur as mixed communities in maize fields at the mid-altitudes co-infesting maize stems, but with variation in species dominance with respect to location and season (Guofa et al. 2001; Ong'amo et al. 2006a, b). Despite the spatial and temporal variations in the structure of their communities, there is little information on the type of intraspecific and interspecific interactions that characterise their use of the same host plant during oviposition.

The objective of this study was to address whether the maize host plant plays a mediating role in the establishment of a multi-species community of stemborer pests.

Materials and methods

Plants and insects

Maize plants of the hybrid variety, H513 (Simlaw, Kenya Seed Company, Nairobi, Kenya) were grown in plastic pots (12 cm in height × 13 cm in diameter) in a greenhouse at the Duduville campus of the International Centre of Insect Physiology and Ecology (*icipe*), Nairobi, Kenya. Mean temperatures were approximately 31/17 °C (day/night) with a L12:D12 photoperiod. Plants were used in experiments when they were between 4 and 6 weeks old (6–7 leaf stage, 65–70 cm height and 8–9 mm stem diameter).

Because wild insects are more responsive to plants compared to laboratory-reared insects as shown for *B. fusca* (Calatayud et al. 2008b), only field-collected insects of *B. fusca* (Bf), *S. calamistis* (Sc) and *C. partellus* (Cp) were used in this experiment. For each species, fourth to fifth instar larvae were collected from maize fields. They were then reared on an artificial diet as described by Onyango and Ochieng'-Odero (1994) for *B. fusca* and *S. calamistis,* and Ochieng et al. (1985) for *C. partellus*, until pupation. Pupae were sexed and kept separately in plastic containers (21 × 15 × 8 cm) until adult emergence. A cotton pad moistened with water was placed inside the container, to maintain relative humidity at >80%. The insects were kept in a rearing room at a temperature of 25 ± 0.05 °C, RH of 58.5 ± 0.4%, and photoperiod of L12:D12.

Adult males and females of each species were put together in mating cages (40 × 40 × 63 cm – one for each species), at the onset of the scotophase. Thereafter, the mating status was checked at hourly intervals until end of the scotophase. Pairs of moths that were mating were collected in plastic jars (8 cm high × 5 cm in diameter).

The gravid females were used in experiments during the following night. After each experiment, all used females were dissected to check for the presence of spermatophores in the *bursa copulatrix*, which in Lepidoptera indicates successful mating (Lum 1979). Only the results of females bearing spermatophores were included in the analysis.

For plant infestations, the larvae of *B. fusca, C. partellus* and *S. calamistis* were obtained from colonies reared at the Animal Rearing and Containment Unit (ARCU) at *icipe*, Nairobi, Kenya. Colonies were rejuvenated twice a year with field-collected larvae.

Infestation of plants for use in laboratory and field trials

Each potted maize plant was manually infested with 12 (third and fourth instar) larvae of the respective stemborer species. These advanced larval instars were used to ensure a high degree of feeding damage within 24 h before release of gravid females to lay eggs on these plants. Moreover, the larvae at this stage can co-occur with adult moths in the field during the maize cropping season as suggested by previous studies (Félix et al. 2011; Ndjomatchoua et al. 2016).

Oviposition experiments

Laboratory trials

This experiment was carried out to compare the oviposition preferences of females between uninfested and infested maize plants. For each experiment, a larvae-infested maize plant was offered together with an uninfested maize plant in an oviposition cage (70 × 50 × 50 cm). These cages were kept in a room at a temperature of 25 ± 0.05 °C, RH of $58.5 \pm 0.4\%$, and photoperiod of L12:D12. One gravid female was released into the middle of each cage, between the two plants. Each gravid female and maize plant (uninfested and infested) was used only once in the cage. The number of egg batches and the total number of eggs laid on each plant were recorded after two nights (Calatayud et al. 2007). For each species, the following treatment combinations, replicated 20 times, were used:

1. uninfested maize vs *B. fusca* (named Bf)-infested maize plant
2. uninfested maize vs *C. partellus* (named Cp)-infested maize plant
3. uninfested maize vs *S. calamistis* (named Sc)-infested maize plant.

Field trials

Field trials were also conducted to confirm the responses obtained from the experiments in the laboratory. These trials were conducted under field conditions in maize fields in the Makuyu village in Murang'a county, Kenya (S 0°55.387, E 37°09.004), where the three species regularly occur together (B. Le Ru, Pers. Obs.). The trials were conducted between May and July 2014, October to December, 2014 and from May to July 2015 (i.e. a total of 15 weeks of field trials). These periods corresponded with the rainfall seasons in Kenya.

Five potted maize plants forming a group were each infested with 12 (third and fourth instar) larvae of *C. partellus, B. fusca* or *S. calamistis*, 24 h before taking them to the field. In all, there were four groups of treatments for each trial field (3 groups of 5 potted plants with infestation of each species and one group of 5 potted uninfested plants as the control). Three farmer fields were selected for placement of pot groups. Each field had all the treatment groups (with five plants in each group) distributed along a straight line along the edge of the field. The arrangement of these treatments alternated in each trial field. Three different pheromone traps (Pherobank BV, Wageningen) each specific to *B. fusca*, *S. calamistis* and *C. partellus* sex pheromones, respectively were placed in nearby fields to monitor the male moth flight activity period of each stemborer species in the trial fields. The number of males and their species identification in each pheromone trap was recorded weekly after seed emergence till harvesting. Each potted plant was inspected for the presence of eggs of the different borer species one week after placement in the fields. The experiment was repeated 15 times. The number of egg batches and the total number of eggs were counted and recorded. Eggs were collected and allowed to hatch to identify the species.

Data analysis

The number of egg batches and total number of eggs on un-infested and infested plants from the oviposition response experiment in the laboratory were analysed using the quasi-Poisson generalised linear model with logarithmic link to cater for overdispersion in the data. Since the quasi-Poisson model was fitted for each of the

9 trials, Bonferroni correction was used to avoid type I error at $P = 0.05$. Thus statistical results were considered significant only if they reach a probability threshold of $p < 0.05/9 = 0.006$. All analyses were carried out in R version 3.1.0 (R Development Core Team 2017).

Results

Laboratory trials

Egg batches and total number of eggs oviposited by Busseola fusca

Busseola fusca laid significantly more egg batches and eggs on *Sc*-infested plants than on uninfested maize plants ($F = 3.42$, $P = 0.001$ for egg batches; $F = 2.31$, $P = 0.02$ for total number of eggs (Fig. 1a, Table 1).

Egg batches and total number of eggs oviposited by Sesamia calamistis

For all parameters evaluated, there were no significant differences between uninfested and infested plants either with conspecific's or heterospecific's infestation (Fig. 1b, Table 1).

Egg batches and total number of eggs oviposited by Chilo partellus

The mean number of batches laid by *C. partellus* was not significantly different between uninfested plants and plants infested either with conspecific or heterospecifics (Fig. 1c, Table 1). The mean number of eggs laid on plants by *C. partellus* was significantly higher on plants infested by *C. partellus* ($F = 2.14$, $P = 0.03$), but not in the other infested treatments.

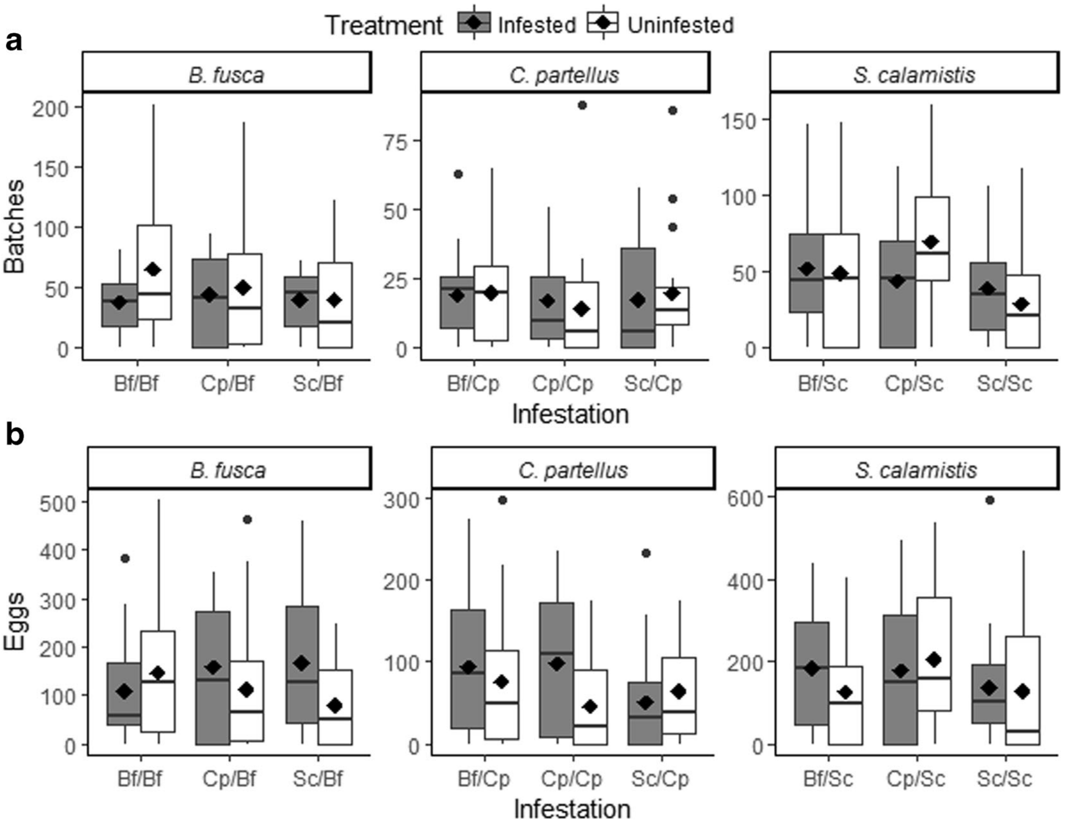

Fig. 1 **a** Boxplot of egg batches and (**b**) Total number of eggs oviposited on infested and uninfested maize plants by *Busseola fusca* (Bf), *Sesamia calamistis* (Sc) and *Chilo partellus* (Cp) moths. The mean for each boxplot is represented by the solid diamonds within each box. Solid circles represent the outliers for corresponding dataset. (x(y)/x: Moth species infesting/species ovipositing). Each treatment was replicated 20 times

Table 1 Statistical values indicating significance of differences between treatments of uninfested and infested maize plants by *Busseola fusca (Bf)*, *Sesamia calamistis (Sc)* and *Chilo partellus (Cp)* in each treatment

Species	Treatment comparisons	Egg batches		Total eggs	
		F	*p* value	*F*	*p* value
Busseola fusca	*Bf*-infested vs uninfested	0.67	0.51	2.14	0.35
	Sc-infested vs uninfested	3.42	0.001	2.31	0.02
	Cp-infested vs uninfested	1.35	0.18	1.06	0.30
Sesamia calamistis	*Sc*-infested vs uninfested	0.38	0.71	0.19	0.85
	Bf-infested vs uninfested	0.95	0.35	1.30	0.20
	Cp-infested vs uninfested	0.16	0.87	0.50	0.62
Chilo partellus	*Cp*-infested vs uninfested	1.86	0.07	2.14	0.03
	Bf-infested vs uninfested	1.37	0.18	0.64	0.52
	Sc-infested vs uninfested	0.91	0.37	0.67	0.51

The *p* values in the table are compared with threshold $p = 0.006$ for Bonferroni correction

Field trials

The numbers of male moths captured inside pheromone traps differed largely between species (Fig. 2). A higher number of *B. fusca* moths (89% of total capture) were recorded than the other species. This suggests *B. fusca* to be the dominant species for the duration of the field experiments (Fig. 2).

Maize plants of each infestation treatment were oviposited on by wild moths in the field (16 in total). Of these, *B. fusca* oviposited on each plant with the different infestation treatment (14 plants), whereas *S. calamistis* oviposited on plants only infested by *C. partellus* (2 plants). Only 3 uninfested plants received eggs during the whole field trial period. No eggs from *C. partellus* were recorded.

Discussion

The results of this study provide an insight into one possible mechanism responsible for the incidence of multispecies larval infestations in field cereal crops, through the oviposition choices made by the adult females.

To the best of our knowledge this is the first report on the oviposition responses from a community of different stemborer species that co-infest maize plants. The results from the laboratory trials showed that none of the three female species avoided plants previously infested either with conspecific's or heterospecific's larvae. Similarly, despite the low presence of *C. partellus* and *S. calamistis* moths, data from the field trials, showed oviposition by the wild moths on infested maize plants either with conspecific's or heterospecific's infestation; indicating that the wild moths were not avoiding plants previously infested by larvae.

Although such enhancement of oviposition by *C. partellus* on maize plants by larval conspecific infestation has already been reported by Kumar (1986), the results for the other stemborer species contrast with the

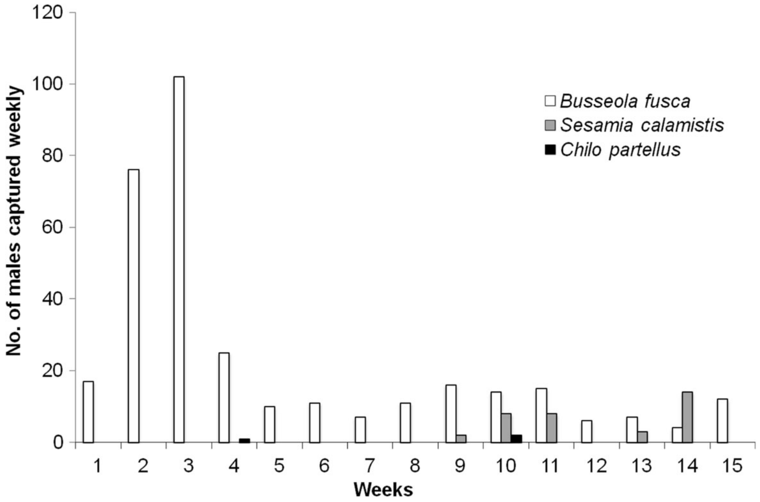

Fig. 2 Number of males of the different stemborer species captured per week with pheromone traps in maize farms. Trials were conducted between May–July 2014, October–December, 2014 and May–July 2015

observation made by Kfir (1997) who reported that *B. fusca* avoided ovipositing on maize already infested by heterospecifics and also with the suggestion by Ndemah et al. (2001) that *S. calamistis* did not oviposit on plants containing egg batches or that were damaged by borer larvae.

Studies on plant induced responses to insect herbivory have mainly reported on their defensive role (e.g. Kessler and Baldwin 2001; Arimura et al. 2005). The results of this study on the other hand, contributes to studies that have shown that prior feeding probably induces susceptibility (Ohgushi 2005; Denno and Kaplan 2007) in the maize host plant, facilitating oviposition by subsequent species (Agrawal and Sherriffs 2001; Horgan 2012). Induced plant defences affect the abundance of generalists more than specialists when these form a community that subsequently utilises the same host plant (Poelman et al. 2008). If plant mediation is a dominant factor in the oviposition selection process among the three stemborer species, induced susceptibility should promote the abundance not only of the oligophagous species (*B. fusca* and *C. partellus)*, but also the polyphagous *S. calamistis* (Sensu Le Ru et al. 2006b) to co-exist and utilise the same maize host plant.

The non-avoidance of infested maize plants for oviposition may also suggest an egg aggregation mechanism employed by these communities of maize stemborer species for high egg and larval densities, possibly to dilute the risk of parasitoid attack (Williams et al. 2001; Rohlfs and Hoffmeister 2004), mortality from desiccation (Klok and Chown 1999; Prokopy and Roitberg 2001) or for social thermoregulation (Klok and Chown 1999) – some of the benefits of the Allee effect (Stephens and Sutherland 1999; Stephens et al. 1999). In fact, results from some field samplings have shown the presence of multiple egg batches of *B. fusca* on the same plant (Van Rensburg et al. 1987; Ndemah et al. 2001). Furthermore, field results have also shown a clustered distribution of these stemborer species among cereal host plants (Overholt et al. 1994; Ndemah et al. 2001; Gounou and Schulthess 2004). This phenomenon indicates a trait of adult female stemborer moths, (at least for *B. fusca*) to oviposit on plants already infested by conspecifics (Ndjomatchoua et al. 2016). For *B. fusca* and *C. partellus*, overcrowding on a host plant may not be a challenge to larval survival, due to the ability of early instar larvae to disperse to nearby plants (Van den Berg et al. 1991b; Ndemah et al. 2001; Erasmus et al. 2016). Generally, for most insect species, the ecological cost of ovipositing on an already infested host plant is smaller than in an enemy-dense host plant, as competition may only lower the fitness level of offspring, but enemy-dense space may result in death (Dicke and Loon 2000).

The results of this study also show that the behaviour of the three stemborer species deviates from that as proposed by the optimal oviposition theory, which predicts that an adult female would choose to oviposit on an unoccupied host plant and avoid infested host, to safeguard her offspring from competition (Thompson 1988; Scheirs and De Bruyn 2002; Gripenberg et al. 2010). Our results showed that females within the studied stemborer complex oviposited on and in some cases significantly preferred already infested plants on which their offspring could face competition from larvae already present. It is also an emerging knowledge that some insects oviposit on plants, not for the enhancement of offspring performance, but rather of the adults (Scheirs and De Bruyn 2002). Furthermore, aside properties of the host plants (Bernays and Chapman 1994; Awmack and Leather 2002), the short life span (3–5 days), as well as neural limitations of insect species (Larsson and Ekbom 1995; Bernays 2001), egg load of the female (Minkenberg et al. 1992) and learning through experience (Cunningham et al. 1999) can also explain this observation.

This study has shown that one possible mechanism responsible for the incidence of multi-species larval infestations in field cereal crops is through host plant mediation. The adult females prefer to oviposit on host plants with prior infestations. The other mechanism is through the movement of larvae from their initial host plant to nearby plants (Kaufmann 1983; Berger 1989; Van den Berg et al. 1991b; Erasmus et al. 2016). Although not considered in this study, induced plant volatiles from larvae feeding (HIPVs) (Dicke and Loon 2000; Bruce et al. 2005) and volatiles induced by insect egg deposition (OIPVs) on host plants (Hilker and Meiners 2002) have been identified to play influencing roles in the oviposition responses by phytophagous insects which utilise infested host plant. These induced plant volatiles may be involved in the oviposition choices made by stemborer females. Further studies to elucidate the roles of HIPVs and OIPVs from maize on the oviposition choices made by female stemborer community should deepen our understanding of the mechanisms responsible for the multi-species infestation in maize fields.

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Author contribution ESN, PAC and BPL conceived research.

ESN and BM conducted experiments.

ESN analysed data and conducted statistical analyses.

ESN, PAC BM, JVDB and BPL contributed to writing of manuscript.

BPL secured funding.

All authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare no conflicting interests with regard to the work as carried out and reported in this manuscript.

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