

## Behaviour and biology of *Chilo partellus* (Lepidoptera: Pyralidae) on maize and wild gramineous plants

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**Abstract.** The ovipositional response, larval orientation, larval settling, feeding, food assimilation, growth and development of maize stemborer *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) on a susceptible maize (*Zea mays* L.) genotype (Inbred A) was compared to five wild plant species of the family Poaceae (Gramineae) in the laboratory and greenhouse. The intensity of oviposition differed among the test plants. *Pennisetum purpureum* Schumach was the most preferred test plant for oviposition when offered in a two-choice situation with maize. Likewise, *P. purpureum* and *Sorghum versicolor* Anderss were the most preferred test plant for oviposition when offered in multiple-choice tests. In no-choice tests *C. partellus* responses to the test plants were not significantly different. The number of first instar larvae that settled on leaf cuts of test plants in Petri dishes was significantly higher on maize and *S. versicolor* than on the other test plants at 24 h after infestation in a multiple-choice test. No significant differences were observed in larval settling among wild grasses at 4 h and 24 h after infestation in a no-choice test. In a two-choice test there was no significant difference in the number of neonate larvae that settled on maize and *S. versicolor* at 1 h and 24 h after infestation. Feeding by fourth-instar larvae was significantly higher on maize than on *Echinochloa pyramidalis* (Lam.) and *Hyparrhenia rufa* (Nees) Stapf. Larvae fed on maize assimilated significantly more food than those fed on *E. pyramidalis*, *Panicum maximum* Jacq. or *H. rufa*. Larval growth and development was significantly faster on maize and *S. versicolor* in comparison to other test plants.

**Key words:** alternate hosts, stemborer, host preference, feeding and food assimilation, growth and development, oviposition preference, *Chilo partellus*

**Résumé.** Les paramètres d'évaluation du degré d'infestation d'une variété de maïs (*Zea mays* L.) génotype A, sensible au foreur de tige, *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae), ont été déterminés en conditions de laboratoire et de serre. Ainsi, l'activité de ponte des adultes, l'orientation et la distribution des larves, le degré de consommation et d'assimilation des aliments, la vitesse de développement et de croissance de ces larves, ont été évalués sur le maïs, puis comparée à cinq espèces de plantes hôtes sauvages de la famille des Poaceae, maintenues dans les mêmes conditions. L'intensité d'oviposition est variable en fonction des plantes hôtes testées. Cependant, en situation de choix entre l'une des graminées et le maïs, la réponse de *C. partellus* est préférentiellement orientée vers *Pennisetum purpureum* Schumach pour l'oviposition. En absence de choix ou en situation de choix multiples, aucune différence significative n'a été observée entre les plantes testées. En situation de choix multiples 24 h après l'infestation, le nombre de larves de 1<sup>er</sup> stade observées sur les feuilles coupées des différentes plantes est sensiblement plus élevé

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sur le maïs et le sorgho (*Sorghum versicolor*, Anderss) que sur les autres plantes, toutes maintenues en boîte de Pétri. Cependant entre 4 et 24 h après l'infestation, aucune différence notable du nombre de larves n'a été observée entre les plantes sauvages en absence de choix. Au cours d'un essai avec deux plantes hôtes, aucune différence significative du nombre de larves néonates n'a été enregistrée entre le maïs et le sorgho, et ceci pendant une période comprise entre 1 et 24 h après l'infestation. La consommation alimentaire des larves de stade IV est plus élevée sur le maïs que sur *Echinochloa pyramidalis* (Lam.) et *Hyparrhenia rufa* (Nees) Stapf. Les larves nourries sur le maïs ont semble-t-il assimilé plus d'aliment que celles nourries sur *E. pyramidalis* et *Panicum maximum* Jacq., ou sur *H. rufa*. Le développement et la vitesse de croissance sont sensiblement plus rapides sur le maïs et sur *S. versicolor* que sur les autres plantes testées.

**Mots clés:** hôtes alternatifs, foreur, préférence alimentaire, consommation et assimilation nutritionnelle, croissance et développement, préférence ovipositionnelle

## Introduction

Cereal stem borers are ubiquitous and major pests of maize and other cereal crops throughout Africa (Khan *et al.*, 1997). In addition to *Chilo partellus* (Swinhoe), several indigenous stem borers are found in Africa (Overholt *et al.*, 1997). *Chilo partellus* is indigenous to Asia and became established in eastern Africa in early 1930s (Tams, 1932). *Chilo partellus* is now considered to be one of the most important pests of maize and other cereal crops in eastern and southern Africa. Most cereal stem borers, including *C. partellus*, are polyphagous and have several gramineous and other non-cultivated wild host plants (Ingram, 1958; Seshu Reddy, 1983; Harris, 1990; Khan *et al.*, 1991).

In Africa, the bulk of cereal crops are grown on small plots surrounded by land occupied by wild plants, of which many species are natural host plants of cereal stem borers. Because crop plants and wild hosts exist in the same area, a prerequisite for the development of a pest management package is an understanding of the multiple interactions among cultivated crops, wild hosts, various stem borer species and natural enemies, all of which may affect the dynamics of pest populations and pest status. Although some basic information on wild gramineous hosts of cereal stem borers in Africa is available (Ingram, 1958; Bowden, 1976; Seshu Reddy, 1983), their suitability as host plants has neither been studied in detail nor compared to maize plants. Many host range records also do not take into account how the plant–insect interaction was determined.

In nature an insect locates a host plant through a sequence of behavioural and biological responses. Six main categories of insect behavioural and physiological responses are considered important during insect establishment on plants: (i) Orientation and settling; (ii) feeding; (iii) metabolism of

ingested food; (iv) growth; (v) survival and fecundity; and (vi) oviposition (Saxena, 1969; Saxena *et al.*, 1974). Interruption of one or more of these insect responses due to unfavourable plant characters would render the plant unsuitable for insect establishment. The extent of insect establishment depends on an interaction of insect responses to various plant characteristics (Saxena, 1969).

As part of an effort to manage cereal stem borers in eastern Africa, we investigated the establishment of *C. partellus* on selected wild gramineous plants, commonly present in and around maize fields. Such information will aid in better understanding of the role of wild gramineous plants, in the population dynamics of stem borers in the field, aiding in the development of an improved areawide *C. partellus* management programme.

## Materials and methods

### Plants

The test plants were five wild gramineous plants commonly present in and around maize cropping environments in eastern Africa – *Sorghum versicolor* Anderss *Pennisetum purpureum* Schumach, *Panicum maximum* Jacq, *Echinochloa pyramidalis* (Lam.) and *Hyperrhenia rufa* (Nees) Stapf. Root splits of wild grasses were obtained from the field and transplanted in pots. All plants were used in the experiments four weeks after transplanting. Four-week old, stem borer-susceptible maize plants of Inbred A variety were used as a control, for all tests. The plants were maintained in an insect-proof screen house at the Mbita Point Field Station (MPFS) of the International Centre of Insect Physiology and Ecology (ICIPE), near the shores of Lake Victoria in Western Kenya (latitude between 0°25' S and 0°30' S and longitude between 34°10' E

and 34°15' E and elevation 1240 m above sea level). All plants selected for use in experiments were approximately of same biomass. All experiments were conducted at a mean temperature of  $25 \pm 5^\circ\text{C}$ .

### *Insects*

The test insects were reared in a laboratory on an artificial diet (Ochieng *et al.*, 1985) at MPFS. The founder colony in the culture came from maize and sorghum stubble and collected locally in farmers' fields. First, third and fourth instar larvae and one-day-old, mated females of *C. partellus* were used in the different tests of this study.

### *Ovipositional response*

To determine the ovipositional response of mated female moths, three laboratory reared, one-day-old mated, gravid female moths of *C. partellus* were released into an oviposition cage of nylon mesh (20-cm diameter, 80-cm high) containing a four-week-old test plant. The experiment was conducted in a screen house and was replicated six times. The female moths were allowed to oviposit for 48 h, after which the plants were removed and the number of eggs laid on each host plant was counted.

### *Ovipositional preference*

Two-choice and multiple-choice tests were conducted to compare ovipositional preference of *C. partellus* gravid female moths on test plants and maize. Two-choice tests were conducted in a screen house under a nylon mesh cage (20-cm diameter, 80-cm high) to compare ovipositional preference of *C. partellus* on maize with each wild plant species. Six mated females were released at the centre of the oviposition cage containing one pot of maize and one pot of a test plant. The female moths were allowed to oviposit for 48 h, after which the total number of eggs laid was counted for each host. The experiment was replicated six times. The multiple-choice tests were also conducted in a screen house under nylon mesh chambers (60-cm diameter, 80-cm high). One pot of each wild host plants, along with one pot of a maize plant, was arranged randomly but equidistantly in a circle within the chamber. Eighteen, laboratory-reared, mated females moths were released at the centre of the cage. The plants were removed after 48 h and the total number of eggs laid was counted for each host plant. The experiment was replicated six times.

### *Larval orientation and settling preference*

First instar larvae were provided with a choice of 6-cm-long leaf cuts of test plants in separate two-choice and multiple-choice experiments. For the

two-choice tests, two leaf cuts of each wild host and two leaf cuts of maize, were arranged equidistantly, along the edge of a Petri dish (9-cm diameter) and lined with moist filter paper. Twenty, first instar larvae of *C. partellus* were released in the centre of the Petri dish. The Petri dish was covered with a lid to avoid the escape of the larvae and sealed with parafilm. The Petri dish was placed in a dark room, at 27°C and relative humidity of 70%. The number of larvae found on or under the leaf cuts were recorded at intervals of 1, 4 and 24 h after release. The experiment was replicated six times.

For multiple-choice tests, leaf cuts of different host plants were arranged randomly and equidistantly, with their adaxial sides up, along the edge of a Petri dish (15-cm diameter) lined with moist filter paper. One hundred first instar larvae were released at the centre of the Petri dish. The rest of the procedure was the same as that described for the two-choice test experiments. The experiment was replicated six times.

### *Arrest and dispersal of first-instar larvae on leaf cuts*

A 6-cm long fresh leaf cut of maize or the test wild plant was placed singly, in the centre of a 9-cm diameter Petri dish lined with moist filter paper. Ten first instar neonate larvae were released on each leaf cut and the Petri dish was covered with a lid to prevent larvae from escaping and sealed with a piece of Parafilm membrane. The number of larvae remaining on or under the leaf cut was recorded at 1, 4 and 24 h after release. The experiment was conducted in a dark room, at 27°C and a relative humidity of 70%. The experiment was replicated six times.

### *Arrest and dispersal of first-instar larvae on whole plants*

The test plants, planted in pots (25-cm diameter), were thinned to one plant per pot, and arranged in a randomized complete block design (RCBD) in a screen house. When the plants were 4 weeks old, 10 neonate larvae of *C. partellus* were released on the outermost leaf of each plant and covered with nylon mesh cage (20-cm diameter, 80-cm high). Seventy-two hours after infestation all the plants were dissected. The number of larvae recovered on each host plant was recorded to reflect the arrest of larvae on the plant. The experiment was replicated six times.

### *First-instar larval feeding on leaf discs in no-choice tests*

Leaf feeding experiments with excised leaves of different host plants were conducted in the laboratory. The experiment was conducted in glass vials, lined with moist filter paper to prevent plant tissue from wilting. Leaf tissue in the vials was

presented to 10 neonate *C. partellus* larvae in the form of discs measuring 1.2 cm in diameter ( $r = \text{Ø}/2$ ;  $1.2/2 = 0.6$ . Area =  $r^2 \times \pi$ ;  $(0.6)^2 \times 3.14 = 1.13 \text{ cm}^2$ ). The vials containing leaf tissues from different host plants were covered with lids, arranged in a RCBD and kept in a dark room at 27°C and 70% relative humidity. The experiment was replicated six times. After 24 h of feeding, the area of the leaf disc, fed by the larvae (out of  $1.13 \text{ cm}^2$ ) was measured again using graph paper, indicating the larval feeding on leaf disc of different test plants.

#### *Fourth-instar larval feeding on stem cuts in no-choice tests*

Feeding experiments with excised stems were conducted in the laboratory. A pre-weighed, 6 cm long stem cut ( $W_1$ ) of a host plant was offered to a newly moulted fourth instar *C. partellus* larva in a vial. Vials containing stem segments from different host plants were covered with plastic lids and arranged in a RCBD, with six replications. The larvae were allowed to feed for 48 h. Thereafter, the uneaten stems were weighed again ( $W_2$ ) after removing all frass. A control of five stem segments of each host plant was placed alongside the experiment to determine the weight loss from evaporation. The differences between ( $W_1$ ) and ( $W_2$ ) after adjustment for weight loss from evaporation indicated stem feeding by the fourth instar larvae.

#### *Food assimilation*

To determine the amount of food assimilation on different hosts, third instar larvae were starved (but water-satiated) for 2 h, and weighed individually on a microbalance. Thereafter larvae were introduced singly into glass vials lined with moist filter paper, and provided with a 6-cm long stem cut from a test plant. The larvae were allowed to feed for 24 h in a no-choice situation and then starved again for 2 h so that the green matter was excreted out of the

gut. The individual weights of the insect and uneaten food were recorded. The experiment was replicated six times. To assess the loss in insect body weight due to catabolism, a control was similarly established, in which the larvae were given access to a moist cotton swab to prevent desiccation. The amount of food assimilated by the larvae was determined using the formula previously used by Khan and Saxena (1985) as follows:

$$\text{Food assimilated} = \frac{W_1 \times (C_1 - C_2)}{C_1} + W_2 - W_1$$

where  $W_1$  = initial weight of larvae;  $W_2$  = final weight of larvae;  $C_1$  = initial weight of control larvae;  $C_2$  = final weight of control larvae.

#### *Larval growth and development*

To understand the effect of host plants on the growth and development of the larvae, host plants were established in plastic pots (20-cm high, 12-cm diameter) in a screen-house. After four weeks of emergence, each test plant was infested with 10 first instar larvae. At 15 days after infestation, potted plants of each host were dissected. The number of *C. partellus* larvae recovered from each host and their respective stage of development at the time of dissection were recorded. The larvae were allowed to pupate on stem cuttings of the same host plants in which they developed. Fresh stem cuttings were offered on every alternate day. The day on which a larva pupated was recorded. The experiment was replicated six times; each replication consisted of five pots of plants. Larval development was measured as a growth index (G. I.) which was the ratio of percent larvae becoming pupae to the developmental period in days (Saxena, 1969; Khan and Saxena, 1985).

$$\text{G.I.} = \frac{\% \text{ larvae pupation}}{\text{larval period}}$$

**Table 1.** Ovipositional response/preference of *Chilo partellus* female moths to different host plants in no-choice and multiple-choice tests

Hosts	No. of eggs laid on different hosts in no-choice test <sup>1</sup> ± SE	No. of eggs laid on different hosts in multiple-choice test <sup>2</sup> ± SE
Maize	191 ± 25 a	102 ± 13 ab
<i>Sorghum versicolor</i>	180 ± 22 a	149 ± 22 a
<i>Pennisetum purpureum</i>	113 ± 17 a	140 ± 12 a
<i>Echinochloa pyramidalis</i>	157 ± 20 a	80 ± 11 b
<i>Panicum maximum</i>	138 ± 18 a	79 ± 10 b
<i>Hyparrhenia rufa</i>	127 ± 19 a	61 ± 11 b

Means in column followed by the same letters are not significantly different at ( $P = 0.05$ ) by Tukey's Studentized Range test (for no-choice) and Student–Newman–Keuls (SNK) (for multiple-choice).

<sup>1</sup> Three *Chilo partellus* female moths per test plant, in a separate cage.

<sup>2</sup> Eighteen *Chilo partellus* female moths, for all the six test plants in one cage.

### Statistical analysis of data

All experiments were replicated six times in a RCBD. Data in Tables 1, 3, 5–9 were subjected to statistical analysis system (SAS) programme (SAS Institute, 1994), and mean were compared with Tukey's Studentized Range test. Tables 2 and 4 were analysed using the *t* test. Ryan's *Q* test (REGWF) was used for analysis in Table 10.

### Results

No significant difference was observed among the plant species in the number of eggs laid in 48 h by *C. partellus* female in no-choice test (Table 1). In two-choice oviposition test, the only significant difference was observed in the number of eggs laid by *C. partellus* female moths on maize versus *P. purpureum*. Significantly more eggs ( $P = 0.05$ ;  $df = 5$ ) were laid on *P. purpureum* as compared to maize (Table 2). In multiple-choice tests, significantly high numbers of *C. partellus* female eggs were laid on *S. versicolor* and *P. purpureum* as compared to the other test plants (Table 1).

In no-choice, larval arrest and dispersal tests on leaf cuts, significantly more larvae settled on leaf cuts of maize than on *E. pyramidalis* and/or *H. rufa* at 1 h after infestation (Table 3). Four hours after

infestation, significant differences were also observed in larval settling among the different host plant leaf cuts. Significantly ( $df = 45$ ,  $P = 0.05$ ) more larvae settled on maize than on *P. maximum*, *H. rufa* and *E. pyramidalis* (Table 3). Twenty-four hours after infestation, significantly ( $df = 45$ ,  $P = 0.05$ ) more larvae settled on maize than on *P. maximum* and *E. pyramidalis* (Table 3). In two-choice larval orientation test on leaf cuts, larval settling was significantly higher, at 1 h after infestation on maize than on *P. purpureum* ( $df = 5,5$ ,  $P > F' = 0.0314$ ) and *H. rufa* ( $df = 5,5$ ,  $P > F' = 0.0360$ ) (Table 4). However, there were no significant differences between the number of larvae settled on maize and *S. versicolor* ( $df = 5,5$ ,  $P > F' = 0.9916$ ), *P. maximum* ( $df = 5,5$ ,  $P > F' = 0.9248$ ), *E. pyramidalis* ( $df = 5,5$ ,  $P > F' = 0.4676$ ). Four hours after infestation, there was no significant difference between the number of larvae settled on leaf cuts of susceptible maize cultivar Inbred A and all wild test plants *H. rufa* ( $df = 5,5$ ,  $P > F' = 0.1201$ ), *E. pyramidalis* ( $df = 5,5$ ,  $P > F' = 0.5923$ ), *P. purpureum* ( $df = 5,5$ ,  $P > F' = 0.9705$ ), *P. maximum* ( $df = 5,5$ ,  $P > F' = 0.9565$ ), and *S. versicolor* ( $df = 5,5$ ,  $P > F' = 0.8305$ ) (Table 4). Twenty-four hours after infestation, the pattern of the larval settling on paired leaf cuts remained almost the same as for

**Table 2.** Ovipositional preference of *Chilo partellus* female moths to susceptible maize cultivar (Inbred A) and wild host plants in two-choice tests

Host plants		No. of eggs laid on inbred A vs each wild host		Degree of freedom, Prob. > F' =
A	B	A	B	
Maize	<i>Sorghum versicolor</i>	814 ± 233	372 ± 97 ns	df = (5,5), F' = 0.0792
Maize	<i>Pennisetum purpureum</i>	424 ± 153	966 ± 140 ns	df = (5,5), F' = 0.8577
Maize	<i>Echinochloa pyramidalis</i>	555 ± 215	421 ± 118 ns	df = (5,5), F' = 0.2139
Maize	<i>Panicum maximum</i>	245 ± 139	127 ± 74ns	df = (5,5), F' = 0.1966
Maize	<i>Hyparrhenia rufa</i>	361 ± 73	241 ± 82 ns	df = (5,5), F' = 0.8035

Average of six replications, means ± SE. Means value followed by ns is not significant different from the corresponding mean value in the same row at each df, and F' by *t*-test.

Six *Chilo partellus* female moths per comparison, for maize and one wild host plant, each at the time, in a separate cage.

**Table 3.** Settling response of *Chilo partellus* neonate larvae to leaf cuts of different host plants in no-choice tests

Host	Mean number of larvae recorded on leaf cuts at hours after infestation (HAI)		
	1 HAI	4 HAI	24 HAI
Maize	7.60 ± 0.79 ab	8.40 ± 0.75 a	6.00 ± 0.68 a
<i>Pennisetum purpureum</i>	7.80 ± 0.51 a	6.70 ± 0.55 ab	4.20 ± 0.82 ab
<i>Sorghum versicolor</i>	6.20 ± 0.66 abc	6.40 ± 0.77 ab	4.10 ± 0.43 ab
<i>Panicum maximum</i>	5.40 ± 0.65 bcd	4.80 ± 0.41 b	3.00 ± 0.55 b
<i>Hyparrhenia rufa</i>	5.00 ± 0.59 cd	5.70 ± 0.57 b	3.50 ± 0.65 ab
<i>Echinochloa pyramidalis</i>	3.70 ± 0.74 d	4.80 ± 0.75 b	2.70 ± 0.42 b

Average of six replications, means ± SE. Means in columns followed by the same letters are significantly different at ( $P = 0.05$ ) by Tukey's Studentized test.

HAI: hours after infestation.

**Table 4.** Comparison of settling preference of *Chilo partellus* neonate larvae on leaf cuts of susceptible maize and wild host plants in two-choice test

Host plants		Mean number of larvae settled at hours after infestation		Degree of freedom
A	B	A	B	
1 h after infestation				
<i>Pennisetum purpureum</i>	Maize	1.66 ± 0.66	10.83 ± 1.99 *	df = (5,5), <i>F</i> ' = 0.0314
<i>Panicum maximum</i>	Maize	3.66 ± 0.88	9.50 ± 0.92 ns	df = (5,5), <i>F</i> ' = 0.9248
<i>Sorghum versicolor</i>	Maize	6.00 ± 1.50	8.66 ± 1.49 ns	df = (5,5), <i>F</i> ' = 0.9916
<i>Echinochloa pyramidalis</i>	Maize	2.16 ± 0.79	8.50 ± 1.11 ns	df = (5,5), <i>F</i> ' = 0.4678
<i>Hyparrhenia rufa</i>	Maize	0.66 ± 0.49	9.33 ± 1.42 *	df = (5,5), <i>F</i> ' = 0.0360
4 h after infestation				
<i>Pennisetum purpureum</i>	Maize	3.50 ± 0.80	7.83 ± 0.79 ns	df = (5,5), <i>F</i> ' = 0.9705
<i>Panicum maximum</i>	Maize	3.00 ± 0.57	5.50 ± 0.56 ns	df = (5,5), <i>F</i> ' = 0.9565
<i>Sorghum versicolor</i>	Maize	4.16 ± 1.35	8.16 ± 1.22 ns	df = (5,5), <i>F</i> ' = 0.8305
<i>Echinochloa pyramidalis</i>	Maize	1.33 ± 0.95	7.66 ± 1.23 ns	df = (5,5), <i>F</i> ' = 0.5923
<i>Hyparrhenia rufa</i>	Maize	0.83 ± 0.47	8.66 ± 1.02 ns	df = (5,5), <i>F</i> ' = 0.1201
24 h after infestation				
<i>Pennisetum purpureum</i>	Maize	1.16 ± 0.47	4.83 ± 1.05 ns	df = (5,5), <i>F</i> ' = 0.1100
<i>Panicum maximum</i>	Maize	1.83 ± 0.60	4.50 ± 0.95 ns	df = (5,5), <i>F</i> ' = 0.3296
<i>Sorghum versicolor</i>	Maize	4.16 ± 0.54	5.00 ± 1.23 ns	df = (5,5), <i>F</i> ' = 0.0943
<i>Echinochloa pyramidalis</i>	Maize	2.00 ± 0.93	7.00 ± 1.09 ns	df = (5,5), <i>F</i> ' = 0.7297
<i>Hyparrhenia rufa</i>	Maize	1.00 ± 0.44	5.83 ± 0.70 ns	df = (5,5), <i>F</i> ' = 0.3431

Average of six replications, means ± SE. Means in rows followed by \* are significantly different from the corresponding mean value in the same row at each df, and *F*', respectively. ns = not significant, by *t*-test.

1 and 4 h after infestation. No significant differences were observed between maize and wild plants *P. maximum* (df = 5,5,  $P > F' = 0.3296$ ), *P. purpureum* (df = 5,5,  $P > F' = 0.1100$ ), *H. rufa* (df = 5,5,  $P > F' = 0.3431$ ), *E. pyramidalis* (df = 5,5,  $P > F' = 0.7297$ ) and *S. versicolor* (df = 5,5,  $P > F' = 0.0943$ ) (Table 4).

In multiple-choice larval settling test on leaf cut tests, 1 h after infestation, there were significant differences in the number of larvae settled on the leaf cuts of the test plants. Significantly (df = 45,  $P = 0.05$ ) more larvae settled on leaf cuts of susceptible maize cultivar Inbred A than on the other hosts (Table 5). Four hours after infestation, significantly more larvae settled on leaf cuts of

maize than on *E. pyramidalis*, *P. maximum* and *H. rufa* (df = 45,  $P = 0.05$ ). There was no significant difference between the number of larvae settled on any of the wild host plants (Table 5). Twenty-four hours after infestation, the tendency of the larval settling on leaf cuts of different test plants remained almost the same as in 1 h after infestation. After 24 h significantly (df = 45,  $P = 0.05$ ) more larvae settled on maize, and *S. versicolor* than on *P. purpureum*, *E. pyramidalis*, *P. maximum* and *H. rufa*. The lowest numbers of larvae were observed on (Table 5).

In the experiment on larval arrest and dispersal from whole plants, significantly (df = 25,  $P = 0.05$ ) more larvae were arrested on the susceptible maize and wild sorghum *S. versicolor*, than on the other

**Table 5.** Settling preference of *Chilo partellus* neonate larvae to leaf cuts of different host plants in multiple-choice tests

Host	Mean number of larvae settled hours after infestation		
	1 HAI	4 HAI	24 HAI
Maize	24.40 ± 3.30 a	16.80 ± 1.92 a	20.20 ± 1.71 a
<i>Sorghum versicolor</i>	13.80 ± 2.20 b	11.50 ± 2.14 ab	19.10 ± 1.95 a
<i>Pennisetum purpureum</i>	12.40 ± 1.72 b	10.70 ± 1.36 ab	12.40 ± 1.19 b
<i>Echinochloa pyramidalis</i>	12.10 ± 2.21 b	8.00 ± 1.34 b	9.20 ± 1.29 b
<i>Panicum maximum</i>	10.50 ± 1.38 b	8.70 ± 1.73 b	8.50 ± 1.31 b
<i>Hyparrhenia rufa</i>	7.80 ± 1.13 b	7.50 ± 1.55 b	2.70 ± 0.81 c

Average of six replications, means ± SE. Means in columns followed by the same letters at 1 HAI 4 HAI and 24 HAI are significantly different in 1 and 24 HAI, but not in 4 HAI at ( $P = 0.05$ ) accordingly by Tukey's Studentized Range test. HAI: hours after infestation.

**Table 6.** Arrest of *Chilo partellus* neonate larvae on different host plants, 72 h after infestation

Host	No. of larvae arrested host on each host plant
Maize	10.00 ± 0.00 a
<i>Sorghum versicolor</i>	8.33 ± 0.91 a
<i>Echinochloa pyramidalis</i>	2.66 ± 1.02 b
<i>Panicum maximum</i>	1.50 ± 0.84 b
<i>Hyparrhenia rufa</i>	1.16 ± 0.79 b
<i>Pennisetum purpureum</i>	0.83 ± 0.40 b

Average of six replications, means ± SE. Means in columns followed by the same letter are significantly different at ( $P = 0.05$ ) by Tukey's Studentized Range test.

test plants (Table 6). Significant ( $df = 45$ ,  $P = 0.05$ ) differences were observed in larval feeding on leaf discs obtained from maize than on those from *P. purpureum*, *H. rufa* and *E. pyramidalis* (Table 7). The results showed that feeding of fourth instar *C. partellus* larvae on stem segments was significantly ( $df = 45$ ,  $P = 0.05$ ) higher on maize than on *E. pyramidalis* and *H. rufa* (Table 8). Larval feeding on maize, *S. versicolor*, *P. maximum* and *P. purpureum* was not significantly different. There was significantly ( $df = 45$ ,  $P = 0.05$ ) more food assimilation on susceptible maize than on *E. pyramidalis*, *P. maximum*

**Table 7.** Area of leaf disc fed by ten first instar *Chilo partellus* neonate larvae on different host plants

Host	Area (cm <sup>2</sup> ) of leaf disc fed by the larvae in each test plant
Maize	0.96 ± 0.29 a
<i>Sorghum versicolor</i>	0.65 ± 0.18 ab
<i>Panicum maximum</i>	0.33 ± 0.19 ab
<i>Pennisetum purpureum</i>	0.15 ± 0.11 b
<i>Hyparrhenia rufa</i>	0.15 ± 0.11 b
<i>Echinochloa pyramidalis</i>	0.03 ± 0.02 b

Average of six replications, means ± SE. Means in columns followed by the same letters are not significantly different at ( $P = 0.05$ ) by Tukey's Studentized Range test.

**Table 8.** *Chilo partellus* fourth instar larval feeding on stem segments of different host plants, 48 h after infestation

Host	Stem feeding (mg) larva/48 h
Maize	1.22 ± 0.09 a
<i>Sorghum versicolor</i>	1.06 ± 0.03 ab
<i>Pennisetum purpureum</i>	1.05 ± 0.04 ab
<i>Panicum maximum</i>	1.04 ± 0.02 ab
<i>Echinochloa pyramidalis</i>	1.02 ± 0.01 b
<i>Hyparrhenia rufa</i>	1.00 ± 0.02 b

Average of six replications, mean ± SE. Means in columns followed by the same letters are significantly different at ( $P = 0.05$ ) by Tukey's Studentized Range test.

**Table 9.** Food assimilation by *Chilo partellus* fourth instar larvae on different host plants, 24 h after infestation

Host	Food assimilated (mg) on different hosts
Maize	0.45 ± 0.06 a
<i>Sorghum versicolor</i>	0.25 ± 0.06 ab
<i>Pennisetum purpureum</i>	0.23 ± 0.11 ab
<i>Echinochloa pyramidalis</i>	0.15 ± 0.02 b
<i>Panicum maximum</i>	0.06 ± 0.02 b
<i>Hyparrhenia rufa</i>	0.03 ± 0.02 b

Means ± SE. Means in column followed by the same letters are significantly different at ( $P = 0.05$ ) by Tukey's Studentized Range test.

and *H. rufa* (Table 9). Assimilation of food was similar on maize *S. versicolor* and *P. purpureum*.

In larval growth and development experiment, among the plants dissected at 15 days after infestation, the larval period (from first instar to pupation) was significantly ( $df = 52$ ,  $P = 0.05$ ) shorter on susceptible maize (25 days) and wild sorghum *S. versicolor* (29 days) as compared to the other test plants, which was 41 days to 47 days. The percentage of larvae which pupated and the growth index were significantly higher on susceptible maize (95.7 and 3.8%, respectively) than on the wild host plants, which ranged from 32 to 10% for pupation and 1.1 to 0.1 for the growth index, at ( $df = 52$ ,  $P = 0.05$ ) and ( $df = 52$ ,  $P = 0.05$ ), respectively (Table 10).

## Discussion

There are plenty of examples illustrating the importance of wild hosts as a source of pests for adjacent crops. However, there is no general theory that predicts the role of uncultivated host plants in insect invasions and outbreaks of cultivated crops. The overall value of uncultivated land will have to be judged on a case-by-case basis depending on the ecological mechanisms underlying the various disadvantages and advantages. In uncultivated crops, most of which are short-lived in comparison to natural hosts, damage is typically caused by herbivores that migrate into fields from the outside (Usua, 1968; Joyce, 1976; Price, 1976). Wild habitats often harbour food sources for many pest insect species, and they may encourage insect invasion and outbreaks in neighbouring agro-ecosystems (van Emden and Way, 1971). On the other hand, wild hosts adjacent to cultivated crops can provide extremely important refugia for natural enemies as well as sources of nectar, pollen, and host/alternate prey (Altieri *et al.*, 1977; Altieri and Whitcomb, 1979; Altieri, 1981; Herzog and Funderburk, 1986). There are also several examples of adjacent wild habitat being used to suppress insect outbreaks by keeping

**Table 10.** Growth and development of *Chilo partellus* larvae on different host plants dissected 15 days after infestation with neonate larvae

Host	Larval period (days)	Percentage pupation	Growth index
Maize	25.6 ± 0.7 b	95.7 a	3.8 ± 0.1 a
<i>Sorghum versicolor</i>	29.0 ± 1.3 b	32.6 b	1.1 ± 0.2 b
<i>Panicum maximum</i>	41.4 ± 2.1 a	12.0 b	0.3 ± 0.0 b
<i>Echinochloa pyramidalis</i>	46.3 ± 0.7 a	10.0 b	0.2 ± 0.0 b
<i>Hyparrhenia rufa</i>	45.0 ± 0.0 a	10.0 b	0.2 ± 0.0 b
<i>Pennisetum purpureum</i>	47.0 ± 5.0 a	10.0 b	0.1 ± 0.0 b

Mean ± SE. Means in column followed by the same letters at 15 days after infestation, are significantly different at ( $P = 0.05$ ) by Ryan's  $Q$  test (REGWF).

the pest on the so-called wild trap plants (Watt, 1981; Altieri and Letourneau, 1984).

The present study on the suitability of wild gramineous plants as hosts of *C. partellus* in comparison to a susceptible maize variety provides the basis for considering the role of wild hosts in population dynamics of *C. partellus*. The ovipositional response of *C. partellus* showed that there were no significant differences in the number of eggs laid on the host plants in no-choice tests. This demonstrates that in the absence of maize plants, female moths tended to lay eggs on available host plants. Saxena (1993) reported high ovipositional responses of female moths both on resistant and susceptible maize cultivars in a no-choice situation. In a no-choice situation *C. partellus* female moths even oviposited on non-host plants as reported by Kumar and Saxena (1985). In field trials *C. partellus* female moths have been shown to oviposit eggs on non-host plants such as cowpea and cassava when they were intercropped with sorghum (Ampongo-Nyarko *et al.*, 1994).

The two-choice oviposition test results showed that *C. partellus* gravid female moths oviposited more eggs on susceptible maize cultivar Inbred A compared to *S. versicolor*, *E. pyramidalis*, *P. maximum* and *H. rufa*. There are reports that Inbred A maize variety, the least hirsute host plant, was the most preferred for oviposition (Ampofo, 1985). Roome *et al.* (1977) suggested the prevention of desiccation and dislodgment of the egg mass as a factor in the choice of smooth areas for oviposition by *C. partellus*. However this study showed that *C. partellus* female moth preferred to lay more eggs on *P. purpureum* than on maize in a two-choice situation. Similar results were obtained by Hutter (1996) who studied *C. partellus* oviposition on different varieties of *P. purpureum* as compared to maize. While in multiple-choice tests *C. partellus* female moth oviposited significantly more eggs on *S. versicolor* and *P. purpureum* than the other wild test plants, but not against maize.

More larvae settled on leaf cuts of maize than on *E. pyramidalis*, *P. maximum*, *H. rufa* and *P. purpureum*. This may be attributed to the suitability of plants, as

discussed by Ampofo and Nyangiri (1986). In the present study, low larval arrest on *E. pyramidalis*, *P. maximum*, *H. rufa* and *P. purpureum* may be due to larval non-preference. Newly hatched *C. partellus* larvae showed poor acceptance of resistant maize ICZ2-CM and subsequently dispersed (Ampofo and Nyangiri, 1986; Ampofo, 1986a). Kumar (1993) reported that low larval arrest on resistant MP 704 maize variety corresponded to its high level of resistance, whereas higher establishment of larvae on Inbred A reflects its susceptibility to *C. partellus*. Ampofo (1986b) reported a low level of larval establishment and high larval dispersal from resistant maize cultivars as the result of the presence of plant chemicals. Similar factors may also exist in wild host species used in this study where larval establishment was poor. Plant chemical characteristics are likely to condition the plants for acceptance or rejection by the larvae (Dethier, 1982), and hence require further investigation.

In larval arrest and dispersal studies with whole plants, the percentage of first instar larvae which could not be recovered on plants 72 h after infestation ranged from 76.6% to 87.7% on *P. maximum* and *P. purpureum*, respectively. Insect losses could be attributed to mortality factors, such as desiccation during movement, natural mortality and plant chemicals. Ampongo-Nyarko *et al.* (1994), reported that when first instar larvae of *C. partellus* were artificially infested on sorghum, about 30% of the larvae established in the whorl of the plant, 25% were recovered on the surrounding plants within 50 cm and 45% were lost. Berger (1992) reported a high level of larval dispersal, either by ballooning or crawling. Other workers (Van Hamburg, 1980; Chapman *et al.*, 1983; Pats and Ekbohm, 1992), have also reported this type of dispersal for lepidopterous larvae. Dispersal may have been due to the presence of plant chemicals and/or physical characters and/or poor nutrient quality, which stimulated the larvae of *C. partellus* to disperse away from the test plant.

Significantly more leaf feeding by first instar larvae on susceptible maize cultivar Inbred A could be due to its susceptibility to *C. partellus*. This is in

agreement with the previous observations by Saxena (1990) that the level of larval feeding on maize is due to their susceptibility to stem borer. The reduced feeding on leaves of wild grasses *P. maximum*, *P. purpureum*, *E. pyramidalis* and *H. rufa*, suggests that the wild hosts may have antibiosis properties, or be physically less suitable for feeding or lack nutrients necessary for optimal stem borer growth.

A high silica content may be one of the factors responsible for stem borer resistance in wild grasses (McNaughton *et al.*, 1985; Setamou *et al.*, 1993). Plant chemicals, physical and/or anatomical characters such as hairiness or presence of high concentration of waxes on the leaf surface as discussed by Painter (1951) and Norris and Kogan (1979), may influence low larval feeding on wild host species. Another physical character, which was observed on some of the wild host plants, was the toughness of the leaf tissue, which could have influenced the feeding on *P. maximum*, *E. pyramidalis* and *H. rufa*. The results further indicated that larval feeding on leaf discs was significantly lower on wild host plants than on the susceptible maize cultivar Inbred A. Similarly stem feeding was significantly lower on *E. pyramidalis* and *H. rufa* than on the susceptible maize cultivar. This result agrees with that of Kumar *et al.* (1993) who reported percentage stem length tunnelled by *C. partellus* was significantly lower on resistant MP704, V37 and Poza Rica 7832 than on the susceptible Inbred A.

Low food assimilation and poor growth of *C. partellus* larvae, when fed on wild host plants *E. pyramidalis*, *P. maximum*, and *H. rufa* than on the susceptible maize, could be due to improper nutrient proportions. Soo Hoo and Fraenkel (1966) reported that even though all the necessary nutrients required for growth might be present, it is conceivable that the insect may still grow poorly as a result of improper nutrient proportions. The larval developmental rate was faster on the susceptible maize cultivar and wild sorghum than on the other hosts. The reason could be either the quality of the nutrient content or the presence of resistant factors in the other hosts. The resistant maize cultivars MP704, V-37, and Poza Rica 7832 retarded development of *C. partellus* larvae due to resistance through antibiosis (Kumar *et al.*, 1993). Lower development on *P. maximum*, *E. pyramidalis*, *P. purpureum* and *H. rufa* also could be due to poor and unbalanced nutrient contents. In that connection, Soo Hoo and Fraenkel (1966) reported that even though all the necessary nutrients required for growth may be present, it is conceivable that the insect may still grow poorly as a result of improper nutrient proportions. The duration of the larval period of *C. partellus* was shortest on the susceptible maize cultivar and wild sorghum compared to the other

wild host plants. Significantly longer larval periods were recorded on *P. maximum*, *E. pyramidalis*, *P. purpureum* and *H. rufa* suggesting that these plants are less suitable for insect development. Kumar *et al.* (1993) reported that the generation time of larvae feeding on resistant maize plants is longer than on susceptible cultivars. The higher the growth index, the more suitable the plant was for the insect's growth. The growth index was significantly higher on susceptible maize cultivar Inbred A than on the other test plants. This can be attributed to its suitability for the development of *C. partellus*.

Although *P. purpureum* was highly attractive to oviposition of *C. partellus* female moths, larval development on *P. purpureum* was significantly lower than on maize. Similar results were also reported by Hutter (1996), who compared ovipositional preference and development of *C. partellus* on different varieties of *P. purpureum*. This grass can act as a trap plant and provide natural control to *C. partellus*. In an effort to control cereal stem borers, ICIPE scientists have formulated a 'push-pull' or stimulo-deterrent diversionary strategy, which involves the combined use of trap and repellent plants (Khan *et al.*, 2000). In this strategy *P. purpureum* is being used as a trap plant for management of stem borers. Although stem borers oviposit heavily on this grass, only a few are able to complete their life cycles (Hutter, 1996; Khan *et al.*, 2000).

An increased understanding of the influence of wild host pest populations will lead to the development of recommendations for utilizing grass for stem borer management. Therefore, the ecological effects of wild host on population dynamics of *C. partellus* need to be studied in detail.

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#### References

- Altieri M. A. (1981) Weeds may augment biological control of insects. *Calif. Agric.* 35, 22–24.
- Altieri M. A. and Letourneau D. K. (1984) Vegetation diversity and outbreaks insect pests. *CRC Crit. Rev. Plant Sci.* 2, 131–169.
- Altieri M. A. and Whitcomb W. H. (1979) The potential use of weeds in the manipulation of the beneficial insects. *Hort. Sci.* 14, 12–18.
- Altieri M. A., van Schoonhove A. and Doll J. D. (1977) The ecological role of weeds in insect pest management systems: a review illustrated with bean (*Phaseolus vulgaris* L.) cropping systems. *PANs* 24, 185–206.

- Ampofo J. K. O. (1985) *Chilo partellus* (Swinhoe) oviposition on susceptible and resistant maize genotypes. *Insect Sci. Appl.* 6, 323–330.
- Ampofo J. K. O. (1986a) Effect of resistant maize cultivars on larval dispersal and establishment of *Chilo partellus* (Lepidoptera: Pyralidae). *Insect Sci. Appl.* 7, 103–106.
- Ampofo J. K. O. (1986b) Maize stalk borer *Chilo partellus* (Lepidoptera: Pyralidae) damage and plant resistance. *Environ. Entomol.* 15, 1124–1129.
- Ampofo J. K. O. and Nyangiri E. O. (1986) Maize resistance to *Chilo partellus* (Swinhoe); behaviour of newly hatched larvae and movement from oviposition site to feeding sites. *Appl. Entomol. Zool.* 21, 269–276.
- Ampongo-Nyarko K., Seshu Reddy K. V., Nyang'or R. A. and Saxena K. N. (1994) Reduction of insect pest attack on sorghum and cowpea by inter-cropping. *Entomol. Exp. Appl.* 70, 179–184.
- Berger A. (1992) Larval movement of *Chilo partellus* (Lepidoptera: Pyralidae) within and between plants: timing, density responses and survival. *Bull. Entomol. Res.* 82, 441–448.
- Bowden J. (1976) Stem borer ecology and strategy for control. *Ann. Appl. Biol.* 84, 107–111.
- Chapman R. F., Woodhead S. and Bernays E. A. (1983) Survival and dispersal of young larvae of *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae). *Bull. Entomol. Res.* 73, 65–74.
- Dethier V. B. (1982) Mechanisms of host-plant recognition. *Entomol. Exp. Appl.* 31, 49–56.
- Harris K. M. (1990) Biology and *Chilo* species. *Insect Sci. Appl.* 11, 467–477.
- Herzog D. C. and Funderburk J. E. (1986) Ecological basis for habitat management pest cultural control, pp. 217–250. In *Ecological Theory and Integrated Pest Management Practice* (Edited by M. Kogan). John Wiley and Sons.
- Hutter N. J. (1996) An assessment of the potential value of ten varieties of Napier grass (*Pennisetum purpureum*) with respect to their use as a trap crop for the spotted stem borer (*Chilo partellus*) attacking maize (*Zea mays*). MSc Thesis in Tropical Agriculture and Environmental Science, University of Newcastle-upon-Tyne, Newcastle, UK.
- Ingram W. R. (1958) Biological control of graminaceous stem borers and legume pod borers. *Insect Sci. Appl.* 4, 205–209.
- Joyce R. J. V. (1976) Insect flight in relation to problems of pest control, pp. 135–155. In *Insect Flight* (Edited by C. R. Rainey). Blackwell, Oxford.
- Khan Z. R. and Saxena R. C. (1985) Behavioural and physiological responses of *Sogatella furcifera* (Homoptera: Delphacidae) to selected resistant and susceptible rice cultivars. *J. Econ. Entomol.* 78, 1280–1286.
- Khan Z. R., Litsinger J. A., Barrion A. T., Villaneuva F. F. D., Fernandez N. J. and Taylor L. D. (1991) *World Bibliography of Rice Stem Borer: 1794–1990*. International Rice Research Institute, Los Banos, Laguna, Philippines. 415 pp.
- Khan Z. R., Ampongo-Nyarko K., Chiliswa P., Hassanali A., Kimani S., Lwande W., Overholt W. A., Pickett J. A., Smart L. E., Wadhams L. J. and Woodcock C. M. (1997) Intercropping increases parasitism of pests. *Nature* 388, 631–632.
- Khan Z. R., Pickett J. A., vanden Berg J., Wadhams L. J. and Woodcock C. M. (2000) Exploiting chemical ecology and species diversity: stem borer and striga control for maize and sorghum in Africa. *Pest Manage. Sci.* 56, 957–962.
- Kumar H. (1993) Responses of *Chilo partellus* (Lepidoptera: Pyralidae) and *Busseola fusca* (Lepidoptera: Noctuidae) to hybrids of a resistance and susceptible maize. *J. Econ. Entomol.* 86, 962–968.
- Kumar H. and Saxena K. N. (1985) Ovipositional response by *Chilo partellus* (Swinhoe) in relation to its mating, diurnal cycle and certain non-host surfaces. *Appl. Entomol. Zool.* 20, 218–221.
- Kumar H., Nyangiri E. M. O. and Asino G. O. (1993) Colonization responses and damage by *Chilo partellus* (Lepidoptera: Pyralidae) to four variably resistant cultivars of maize. *J. Econ. Entomol.* 86, 739–746.
- McNaughton S. J., McNaughton M. M. and Dav R. H. (1985) Silica as a defense against herbivore and growth promoter in African grasses. *Ecology* 66, 528–535.
- Norris D. M. and Kogan M. (1979) Biological and morphological basis of resistance in plants, pp. 23–26. In *Breeding Plants Resistant to Insects*. Maxwell and Jennings, John Wiley and Sons.
- Ochieng R. S., Onyango F. O. and Bungu M. D. O. (1985) Improvement of techniques for mass culture of *Chilo partellus* (Swinhoe). *Insect Sci. Appl.* 6, 425–428.
- Overholt W. A., Ngi-Song A. J., Omwega C. O., Kimani-Njogu S. W., Mbapila J., Sallam M. N. and Ofomata V. (1997) A review of the introduction and establishment of *Cotesia flavipes* Cameron in East Africa for biological control of cereal stemborers. *Insect Sci. Appl.* 17, 79–88.
- Painter R. H. (1951) *Insect Resistance in Crop Plants*. Macmillan, New York. 520 pp.
- Pats P. and Ekbom B. (1992) Infestation and dispersal of early instars of *Chilo partellus* (Lepidoptera: Pyralidae) at different densities. *Environ. Entomol.* 21, 1110–1113.
- Price P. W. (1976) Colonization of crops by arthropods: nonequilibrium communities in soybean fields. *Environ. Entomol.* 5, 824–835.
- Roome R. E., Chanda G. K. and Padghan D. (1977) Choice of oviposition site by *Chilo* the sorghum stalk borer. *Bull. SRO*, 115–121.
- SAS Institute (1994) *SAS/STAS Guide for Personal Computers*, version 6.10. SAS Institute, Cary, NC.
- Saxena K. N. (1969) Patterns of insect-plant relationship determining susceptibility or resistance of different plants. *Entomol. Exp. Appl.* 12, 751–766.
- Saxena K. N. (1990) Mechanism of resistance/susceptibility of certain sorghum cultivar to the stem borer *Chilo partellus* (Swinhoe): role of behaviour and development. *Entomol. Exp. Appl.* 59, 91–99.
- Saxena K. N. (1993) Larval development of *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) on artificial diet

- incorporating leaf tissue of sorghum lines in relation to their resistance or susceptibility. *Appl. Entomol. Zool.* 27, 325–330.
- Saxena K. N., Gandhi J. R. and Saxena R. C. (1974) Patterns of relationship between certain leafhoppers and plants. *Entomol. Exp. Appl.* 17, 303–318.
- Seshu Reddy K. V. (1983) Sorghum stem borers in Eastern Africa. *Insect Sci. Appl.* 4, 33–39.
- Setamou M., Schulthess F., Bosque-Prez N. A. and Thomas-Odojo A. (1993) Effect of plant nitrogen and silica on the bionomics of *Sesamia calamistis* (Lepidoptera: Noctuidae). *Bull. Entomol. Res.* 83, 405–411.
- Soo Hoo C. F. and Fraenkel G. (1966) The consumption and digestion and utilization of food plants by phytophagous insects; *Prodenia eridania* (Cramer). *J. Insect Physiol.* 12, 711–730.
- Tams W. H. T. (1932) New species of African Heterocera. *Entomologist* 65, 1241–1249.
- Usua E. J. (1968) The biology of *Busseola fusca* and *Sesamia* species in south-western Nigeria: distribution and population studies. *J. Econ. Entomol.* 61, 830–833.
- Van Emden H. F. and Way M. J. (1971) Host plants in the population dynamics of insects, pp. 181–199. In *Insect/Plant Relationships* (Edited by H. F. van Emden). Blackwell, Oxford.
- Van Hamburg H. (1980) The grain sorghum stalk borer *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae): Survival and location of larvae at different infestation level in plants of different ages. *J. Entomol. Soc. S. Afr.* 43, 71–76.
- Watt A. D. (1981) Wild grasses and grain aphid (*Sitobion avenae*), pp. 222–229. In *Pests, Pathogens, and Vegetation* (Edited by J. M. Tresh). Pitman, London.