

## Life tables, key factor analysis and density relations of natural populations of the spotted maize stemborer, *Chilo partellus* (Lepidoptera: Crambidae), under different cropping systems at the Kenyan coast

C.A.O. Midega<sup>1,2\*</sup>, C.K.P.O. Ogol<sup>1</sup> and W.A. Overholt<sup>3</sup>

<sup>1</sup>Department of Biological Sciences, Kenyatta University, PO Box 43844, Nairobi, Kenya; <sup>2</sup>International Centre of Insect Physiology and Ecology (ICIPE), PO Box 30772, Nairobi, Kenya; <sup>3</sup>Indian River Research and Education Centre, University of Florida, 2199 South Rock Road Fort Pierce, FL 34981, USA

(Accepted 22 March 2005)

**Abstract.** Studies were conducted at Mtwapa, in the coastal area of Kenya, during the long and short rains of 1999 and 2000 to evaluate interaction of mortality factors in lowering *Chilo partellus* (Swinhoe) populations in diverse agroecosystems. Treatments consisted of hedgerows of leucaena only, gliricidia only, alternating rows of leucaena and gliricidia, and three plots without trees. During the cropping seasons, maize was planted between the hedgerows while a row of cowpea was planted between the rows of maize. One of the plots without trees was planted to an intercrop of maize and cowpea. The remaining two plots without trees were planted to maize alone, one of which was mulched. The treatments were laid out in a randomized complete block design with four replications. There was no evidence of enhanced mortality in the more diverse systems indicating that the vegetation structure and cultural treatments studied did not enhance activity levels of *C. partellus* mortality factors. The highest mortality occurred in the early and medium larval stages in all treatments. This mortality was attributable to 'disappearance', which represented mortality from sources other than parasitism. The total real generation mortality showed that from the initial cohort of first and second instar larvae, less than 10% of *C. partellus* survived to adult stage under field conditions in all the treatments. Mortality by *Cotesia sesamiae* Cameron and *Cotesia flavipes* (Cameron) was very minimal, indicating the parasitoids were not important mortality factors of *C. partellus* under the cropping systems studied. Their effects were also not influenced by the cropping systems studied.

**Key words:** agroecosystem, life tables, mortality, *Chilo partellus*, *Cotesia sesamiae*, *Cotesia flavipes*

**Résumé.** Des expérimentations ont été conduites à Mtwapa, sur la côte kényane, pendant les longues et courtes saisons des pluies de 1999 et 2000 afin d'évaluer comment les différents facteurs de mortalité agissent sur la réduction des populations de *Chilo partellus* (Swinhoe) dans différents agrosystèmes. Les dispositifs ont consisté en des haies de leucaena seule, de gliricidia seule, des rangs alternés de leucaena et de gliricidia, et trois parcelles sans arbres. Pendant les périodes culturales, le maïs a été planté entre les haies et

du niébé a été planté entre les rangs de maïs. L'une des parcelles sans arbre a été plantée en associant maïs et niébé. Les deux autres parcelles sans arbre ont été plantées avec du maïs seul, l'une d'entre elles avec du paillage. Les traitements ont été arrangés en blocs aléatoires complets avec quatre répétitions. Nous n'avons observé aucune augmentation de la mortalité suggérant que les différents dispositifs cultureux étudiés n'ont pas augmenté les différents facteurs de mortalité de *C. partellus*. La mortalité la plus élevée a été observée sur les stades larvaires jeunes et intermédiaires pour tous les traitements. La mortalité a été attribuée principalement à la «disparition» des larves autrement dit à des facteurs autres que le parasitisme. La mortalité totale réelle par génération montre que moins de 10% des jeunes stades larvaires atteignent le stade adulte dans les conditions naturelles pour tous les traitements. La mortalité liée à *Cotesia sesamiae* Cameron et à *Cotesia flavipes* (Cameron) est très faible indiquant que les parasitoïdes ne sont pas des facteurs importants de mortalité de *C. partellus* dans nos conditions expérimentales. En outre, leurs actions n'est pas influencée par les conditions culturelles.

**Mots clés:** agrosystème, table de vie, mortalité, *Chilo partellus*, *Cotesia sesamiae*, *Cotesia flavipes*

### Introduction

Cereal stemborers are a major constraint to efficient production of maize and sorghum in eastern and southern Africa. Several species have been recovered, but the predominant and most economically important stemborer species in the low and mid elevations is *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae). It was accidentally introduced from Asia into Africa sometime before 1930 (Tams, 1932). Reports showed that this invasive species was displacing some indigenous stemborer species in the region (Kfir, 1997; Overholt, 1998; Kfir *et al.*, 2002). Estimates of yield losses due to stemborers range from 4 to 73% of the potential yield (Seshu Reddy and Walker, 1990). Recommended control strategies are often not practical for small-scale subsistence farmers, while the effectiveness of some cultural methods is questionable (van den Berg *et al.*, 1998). As a result, a large number of farmers do not actively control stemborers (Chitere and Omolo, 1993; Grisley, 1997; Ebenebe *et al.*, 2001). Therefore, biological control by releasing natural enemies and habitat management are more feasible and beneficial for the farmers to reduce stemborer populations in the fields (Bonhof, 2000).

*Cotesia sesamiae* Cameron (Hymenoptera: Braconidae), an indigenous larval parasitoid of stemborers, has not been able to maintain the pest population density at a level acceptable to farmers (Oloo, 1989; Overholt *et al.*, 1994a; Midega *et al.*, 2004). *Cotesia flavipes* (Cameron) (Hymenoptera: Braconidae), which has been used successfully in other parts of the world (Overholt, 1998), was introduced into Kenya against *C. partellus* from Pakistan in 1993 in an attempt to reduce the severity of the stemborer problem (Overholt *et al.*, 1994b). Establishment of this parasitoid has been reported

(Omwege *et al.*, 1995; Overholt, 1998). Field recoveries show that it has expanded its host range to include the native stemborer species (Zhou *et al.*, 2003). However, its impact alongside indigenous natural enemies under different cropping systems has not been evaluated.

Bellows *et al.* (1992) described a method for evaluating the impact of natural enemies on their hosts that involved construction and analysis of life tables for the affected populations. Mortality caused by an agent and other sources of mortality acting on the population are compared and contributions of contemporaneous factors are separately quantified. Life tables are one of the most useful tools in the study of insect population dynamics (Harcourt, 1969; Southwood, 1978). They allow the ecological role a natural enemy plays in a particular system to be determined, i.e. whether it is a source of regulation contributing to stability or not. Life table studies by Oloo (1989), Oloo and Ogeda (1990) and Ogeda (1999) reported that mortality due to natural enemies lowers stemborer densities in western Kenya. They observed that less than 10% of the immature stages (small larvae) reached the adult stage. These studies were, however, restricted to maize monocrop systems.

Studies on agroecosystem diversification as a pest management strategy have revealed that increasing the vegetational diversity of agroecosystems may increase system stability and decrease the incidence of major insect pest outbreaks observed in some monocultures (reviewed by Cromartie, 1981; Andow, 1991). This has been explained in part by the enemies' hypothesis (Root, 1973) which predicts that population densities of natural enemies will be higher and insect pest populations lower in more diverse habitats due in large part to the availability of alternate prey, nectar sources and suitable

microhabitats. One of the most common practices to achieve agroecosystem diversity is intercropping (Päts *et al.*, 1997; Kogan, 1998; Abate *et al.*, 2000; Potting *et al.*, 2005). Studies in western Kenya revealed that the presence of cowpea (non-host) in an intercropping combination consistently reduced stemborer densities on cereals (Minja, 1990). Sköv-gard and Päts (1997) also concluded that intercrop-ping maize with cowpea significantly reduced stemborer infestation and enhanced crop yield. Similarly, studies by Khan *et al.* (1997, 2000, 2001) and Khan and Pickett (2004) revealed that intercropping maize with desmodium, *Desmodium uncinatum* Jacq., (Fabaceae) significantly decreased stemborer infestation and enhanced crop yields. There was, however, a shortage of information on the nature and role of various mortality factors associated with the decrease in the incidence of the major insect pests in such polycultures. The present studies were thus conducted to closely monitor the populations of *C. partellus* through intensive sampling and construction of life tables and key factor analysis to understand how mortality factors interact under agroforestry and intercropping systems.

## Materials and methods

### Study site

These studies were conducted at the Kenya Agricultural Research Institute (KARI) Regional Research Centre at Mtwapa, Coast Province, Kenya (3°56' S, 39°44' E and 15 m above sea level). Average rainfall is about 1200 mm per year, is bimodal and allows cultivation of two crops annually. Temperatures are generally high (25–30°C) throughout the year (Warui and Kuria, 1983). Agriculture in the coastal system is characterized by predominantly tree-based systems in which trees such as coconut palms (*Cocos nucifera* L.), cashews (*Anacardium occidentale* L.) and mangoes (*Mangifera indica* L.) are intercropped with cassava (*Manihot esculenta* L.) and/or maize (*Zea mays* L.) with or without livestock grazing.

### Experimental design and plot layout

Five-month-old seedlings of *Leucaena leucocephala* (Lam) De Wit and *Gliricidia sepium* Jacq. (Steud) (Fabaceae) were planted in hedgerows at Mtwapa during the long rains of 1999. Plots measured 16 m by 13 m and were separated by 4 m buffer strips. Trees were spaced 3.2 m between and 0.65 m within hedgerows. Hedgerows consisted of leucaena only, gliricidia only, and alternating rows of leucaena and gliricidia. One of the leucaena/gliricidia hedgerow plots had a row of cowpea (variety k80) planted between the rows of maize (but not between the

maize and trees) at an intra-row spacing of 0.1 m. Maize (Pwani 4 hybrid) was planted between the hedgerows at a spacing of 0.3 m within rows, 0.8 m between rows and 0.8 m between rows of maize and the tree hedgerows. There were two other treat-ments where maize was planted alone without trees or with cowpea. Two days before planting maize and cowpea, the leucaena and gliricidia trees were pruned to 0.3 m above the ground level and all prunings weighed and applied as mulch on the plots from which they were taken. Foliage from a separately developed leucaena and gliricidia plot was used to mulch plots without trees, except for one of the maize monocrop plots. This gave a total of seven treatments, which were laid out in a randomized complete block design and replicated four times. Plots were hand-weeded three times during each cropping season. The experiments were completed in the long and short rains of 1999 and 2000.

Weekly sampling for the life stages of *C. partellus* started two weeks after maize emergence and continued until harvest. During each sampling occasion, ten maize plants were randomly selected per plot. These plants were uprooted and checked for *C. partellus* egg batches and then dissected to recover the larvae and pupae. Both dead and live larvae and pupae were recovered. Live larvae were placed individually in vials with natural diet (pieces of maize stalk) until they pupated or died. Similarly, pupae were maintained until they emerged as adults or died. They were checked daily for parasitoid emergence. The parasitoids were preserved in 70% alcohol and representative samples sent to the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya, for identification.

The field samples did not yield sufficient numbers of eggs to account for the number of larvae and pupae recovered during subsequent sampling occasions. Therefore, the egg data were not used in the life table analysis. In addition, it was not easy to separate the various larval instars. Consequently, the data were pooled into four age categories; small (first and second instars), medium (third instar), large (fourth and fifth instars) larvae and pupae.

### Life table analysis

The number of individuals entering a specific stage (lx) was determined using the graphical method of Southwood and Jepson (1962). The density of each life stage was plotted against sample occasion for successive census data. The area beneath the curve represented the total number of population estimates of the particular stage. Due to the variations in different life stages and also due to other

mortality factors, it was necessary to standardize population estimates that were obtained by dividing the estimated area under the curve by the developmental time of the *C. partellus* life stage obtained at 25°C under laboratory conditions (Ampofo, 1988).

Partial ecological life tables for each season and each treatment were constructed for the first generation of *C. partellus* according to the method described by Morris and Miller (1954), to determine the impact of natural enemies on the pest's populations. Each mortality factor was treated as a percent proportion of the population estimate of the stage at which it acted (apparent mortality) and percent proportion of the population estimate at the beginning of the generation/cohort (real mortality). In both cases, the total mortality for every *C. partellus* stage was obtained by adding the proportions contributed by each mortality factor at that stage. The population estimates for each developmental stage from the graphical method of Southwood and Jepson (1962), the apparent, real and total mortality proportions were then tabulated to give the life tables used in subsequent analysis.

Mortality factors ( $dx_F$ ) were partitioned into two causes; parasitism, where the parasitoids were identified, and disappearance, which covered all other undetermined losses to predators, dispersal, disease or abiotic factors (Bonhof, 2000). Mortality estimates ( $dx$ ) were obtained by dividing the population density estimates of the parasitoids (obtained as the pest life stage estimates described above), i.e. the area under the curve, by their developmental time in the host (Ngi-Song *et al.*, 1995; Mbapila and Overholt, 2001). For disappearance, the estimates were obtained by subtracting the population estimates of the succeeding life stage from the difference between population estimates of the life stage on which the mortality factor acted and the mortality due to parasitism. Mortality occurring in each age category (apparent mortality,  $100q_x$ ) was obtained by dividing  $l_x$  by the corresponding  $dx$ , while mortality in relation to the original population at the beginning of the generation (real mortality,  $100r_x$ ) was obtained by dividing  $l_x$  at the beginning of the generation by all the  $dx$  values.

#### *Key factor analysis and density relationships*

Key factor analysis was used to compare the relative importance of each stage-specific mortality factor to overall generation mortality. The intensity or 'killing power' of mortality during each stage was expressed as a k-value equal to the difference between the logarithms of the stage density ( $l_x$ ) before and after mortality. The sum of all successive

mortality factors ( $k_i$ ) equals total generation mortality ( $K$ ). Only mortality factors recovered in at least three generations of *C. partellus* were used in key factor analysis. The life table data were used to construct partial mortality budgets from which the various k-values were calculated for each cropping system.

The Podoler and Rogers (1975) regression method of key factor analysis was used to identify individual mortality factors (k-values) most closely associated with variations in generation mortality ( $K$ ). In order to detect possible density-dependence, individual k-values were regressed on the  $\log_{10}$  densities upon which they acted. The regression of  $k_x$  on  $\log$  density for each  $l_x$  interval was computed to determine the relationship between the stage-specific mortality and *C. partellus* density (test of density dependence).

## Results

### *Life table analysis*

Life tables were constructed for *C. partellus* populations during the long and short rains of 1999 and 2000 under the various cropping systems from which subsequent analyses were carried out. The real generation mortalities for each age category are summarized in Table 1. In all cases, lowest mean mortality occurred during the pupal stage with a range of 3.3% in unmulched maize monocrop to 8.9% in maize/leucaena/giricidia. Mortality of small and medium larvae was high in all the cropping systems (Table 1). There was little variation in the total inter-generation mortality expressed as total  $100r_x$  in all the cropping systems (Table 1). The mean mortality values varied only slightly from 90.9% in maize/leucaena to 97% in maize/giricidia systems with no evidence of support for the enemy hypothesis.

### *Key factor analysis and density relationships*

$k_2$ , which represented mortality due to disappearance of small larvae (Table 2) had the greatest positive slopes under the maize/leucaena, maize/leucaena/giricidia/cowpea, maize/cowpea, maize/cowpea, mulched and unmulched maize monocrop systems.  $k_4$  which represented mortality due to disappearance of the medium larvae (Table 2) had the greatest positive slope in the maize/giricidia system.  $k_8$  which represented mortality due to disappearance of pupae (Table 2) had the greatest slope in maize/leucaena/giricidia system (Table 3).  $k_2$ ,  $k_4$  and  $k_8$  were thus the key mortality factors associated with population changes in the respective cropping

**Table 1.** Real generation mortality (100rx) of *Chilo partellus* under different cropping systems

Stage	Cropping system	Generations				Mean	SE
		1	2	3	4		
Small larvae	ML	45	29.6	25	31.8	32.8	4.3
	MG	37	10	47.8	13	26.9	9.2
	MCLG	28.5	58.3	41.6	22.2	37.6	7.9
	MLG	37.9	36.8	8.3	23.1	26.5	6.9
	MC	19.3	21.4	46.4	38.5	31.4	6.6
	MMu	15.4	20	26	44	26.3	6.3
	M	26	14.3	58.8	50	37.3	10.3
Medium larvae	ML	30	55.6	25	18.2	32.2	8.2
	MG	44.4	70	30.4	17.4	40.5	11.3
	MCLG	47.6	29.2	16.7	11.1	26.1	8.1
	MLG	37.9	36.8	33.3	23.1	32.8	3.4
	MC	61.3	47.1	28.6	23	40	8.8
	MMu	50	40	21.7	24	33.9	6.7
	M	34.8	71.4	11.8	31.2	37.3	12.4
Large larvae	ML	10	11.1	41.7	27.3	22.5	7.5
	MG	7.4	20	13	56.5	24.2	11.1
	MCLG	14.3	12.5	25	55.5	26.8	9.9
	MLG	17.2	26.3	33.3	30.8	26.9	3.5
	MC	12.9	21.4	14.3	30.8	19.8	4.1
	MMu	26.9	40	30.4	12	27.3	5.8
	M	21.7	14.3	17.6	12.5	16.5	2.0
Pupae	ML	0	0	0	13.6	3.4	3.4
	MG	0	0	8.7	13	5.4	3.3
	MCLG	0	0	8.3	5.5	3.4	2.1
	MLG	3.4	0	16.7	15.4	8.9	4.2
	MC	3.2	0	7.1	7.7	4.5	1.8
	MMu	3.8	0	8.7	8	5.1	2
	M	4.3	0	8.8	0	3.3	2.1
Total	ML	85	96.3	91.7	90.9	90.9	
	MG	88.8	100	99.9	99.9	97	
	MCLG	90.4	100	91.6	94.3	93.9	
	MLG	96.4	99.9	91.6	92.4	95.1	
	MC	96.7	89.9	96.4	100	95.7	
	MMu	96.1	100	86.8	88	92.6	
	M	86.8	100	97	93.7	94	

Key: ML, maize/leucaena; MG, maize/gliceridia; MCLG, maize/cowpea/leucaena/gliceridia; MLG, maize/leucaena/gliceridia; MC, maize/cowpea; MMu, maize/mulch; M, maize unmulched.

systems. Mortality due to parasitism at the medium larval stage by *C. sesamiae* and *C. flavipes* (k3a and k3b) ranged from 0.0 to 0.09 (Table 2) in all the systems, representing a minimal contribution to changes in *C. partellus* population density in all the cropping systems studied with no evidence of support for the enemy hypothesis.

The results on density-dependence tests showed that only k3a (mortality due to *C. sesamiae*) under maize/gliceridia was significant (Table 4). It acted in an inverse density dependent manner, meaning that the activity of the mortality of *C. partellus* by the natural enemy decreased with an increase in

*Ch. partellus* population density under maize/gliceridia system. All the other mortality factors acted in a density independent manner in all the cropping systems (Table 4).

## Discussion

No evidence of more activity/effectiveness of *C. partellus* natural mortality factors was observed in the agroforestry and intercropping systems as compared to the maize monocrop system. There was very little variation in total intergeneration and

**Table 2.** Summary of k-values obtained from the partial budgets of *Chilo partellus* under various cropping systems

Cropping systems	Life stage	Mortality factor	Generational mortality			
			1	2	3	4
Maize/leucaena	Small larvae	k2 disappearance	0.26	0.15	0.12	0.17
	Medium larvae	k4 disappearance	0.26	0.58	0.18	0.03
	Large larvae	k6 disappearance	0.22	0.6	0.78	0.34
	TOTAL (K)		0.74	1.33	1.08	0.54
Maize/gliciridia	Small larvae	k2 disappearance	0.2	0.05	0.22	0.06
	Medium larvae	k3a <i>Cotesia sesamiae</i>	0.03	0.05	0.03	0.02
		k4 disappearance	0.45	0.48	0.24	0.07
	Large larvae	k6 disappearance	0.22	0.03	0.24	0.73
TOTAL (K)		0.9	0.61	0.73	0.88	
Maize/leucaena/gliciridia/cowpea	Small larvae	k2 disappearance	0.15	0.38	0.23	0.11
	Medium larvae	k3a <i>Cotesia sesamiae</i>	0	0.09	0.07	0.03
		k3b <i>Co. flavipes</i>	0	0.05	0.07	0.03
	Large larvae	k6 disappearance	0.04	0.48	0.4	0.78
TOTAL (K)		0.19	1.0	0.77	0.95	
Maize/leucaena/gliciridia	Small larvae	k2 disappearance	0.21	0.2	0.04	0.11
	Medium larvae	k4 disappearance	0.35	0.38	0.2	0.05
	Large larvae	k6 disappearance	0.54	0.7	0.37	0.37
	Pupae	k8 disappearance	0.3	0	0.48	0.18
	TOTAL (K)		1.4	1.28	1.09	0.71
Maize/cowpea	Small larvae	k2 disappearance	0.09	0.1	0.33	0.21
	Medium larvae	k4 disappearance	0.62	0.52	0.27	0.09
	Large larvae	k6 disappearance	0.48	0.48	0.37	0.70
	TOTAL (K)		1.19	1.1	0.97	1.00
Mulched maize	Small larvae	k2 disappearance	0.07	0.09	0.13	0.25
	Medium larvae	k3a <i>Cotesia sesamiae</i>	0.02	0	0.03	0.07
		k4 disappearance	0.34	0.3	0.05	0.07
	Large larvae	k6 disappearance	0.65	0.78	0.38	0.2
	Pupae	k8 disappearance	0.3	0	0.22	0.22
TOTAL (K)		1.38	1.17	0.81	0.81	
Unmulched maize	Small larvae	k2 disappearance	0.13	0.07	0.38	0.3
	Medium larvae	k3a <i>Cotesia sesamiae</i>	0	0.04	0.1	0.06
		k4 disappearance	0.28	1.13	0	0.2
	Large larvae	k6 disappearance	0.35	0.3	0.4	0.48
TOTAL (K)		0.76	1.54	0.88	1.04	

mean real generation mortalities within and among the various cropping systems. Observations on mortality factors and their role in population regulation as presented in the analyses showed that the highest mortality occurred in the small (first and second instars) and medium (third instar) larval age categories in all the cropping systems studied. This mortality was attributable to 'disappearance', which represented mortality due to predation, disease, emigration and other unknown biotic and abiotic factors (Bonhof, 2000; Midega *et al.*, 2004). These early stages of *C. partellus* are exposed before the larvae enter the stem of the host plants. This exposure predisposes them to the natural enemies and other biotic and abiotic mortality factors, resulting in high mortality rates.

Mean total real generation mortality showed that from the initial cohort of first and second instar larvae, less than 10% *C. partellus* survived to the

adult stage under field conditions in all the cropping systems studied. These results coincide with those of Ogeda (1999) who found that on the average, less than 10% of the first and second *C. partellus* larvae survived to adult stage under natural conditions in western Kenya. Similarly, life table studies by Oloo (1989) and Oloo and Ogeda (1990) in western Kenya showed that only 5% of *C. partellus* eggs produced moths under natural conditions. The lowest mortality occurred at the pupal stage in all the cropping systems in the study. These findings corroborate those of Mathez (1972), Oloo (1989), Oloo and Ogeda (1990) and Ogeda (1999) who reported high egg and small larval mortality (>90%) and much lower pupal mortality (<10%) in natural populations of *C. partellus*. This suggests that the relative inactivity, immobility, pupal case covering and the fact that pupae are burrowed in the stems of host plants greatly

**Table 3.** Key factor analysis under the various cropping systems (Podoler and Rogers method, 1975). Submortalities ( $k_i$ ) with the greatest positive slope contribute most to total mortality (K)

Cropping systems	Stage	$k_i$	$R^2$	$P$	Slope
Maize/leucaena	Small larvae	k2	0.261	0.489	0.256
	Medium larvae	k4	0.707	0.159	-0.249
	Large larvae	k6	0.548	0.259	-0.006
Maize/gliricidia	Small larvae	k2	0.081	0.715	-0.014
	Medium larvae	k3a	0.730	0.145	0.094
	Large larvae	k4	0.171	0.585	0.766
Maize/leucaena/gliricidia/cowpea	Small larvae	k6	0.453	0.327	-0.845
	Medium larvae	k2	0.185	0.570	0.117
	Large larvae	k3a	0.578	0.239	-0.012
Maize/leucaena/gliricidia	Medium larvae	k3b	0.489	0.301	-0.003
	Large larvae	k6	0.780	0.116	0.101
	Small larvae	k2	0.374	0.388	-0.042
	Medium larvae	k4	0.925	0.038*	-0.298
Maize/cowpea	Large larvae	k6	0.490	0.299	0.083
	Pupae	k8	0.001	0.977	0.257
	Small larvae	k2	0.803	0.104	1.253
	Medium larvae	k4	0.790	0.111	-0.89
Mulched maize	Large larvae	k6	0.008	0.907	0.644
	Small larvae	k2	0.61	0.219	0.368
	Medium larvae	k3a	0.439	0.337	0.102
	Large larvae	k4	0.957	0.021*	-0.36
Unmulched maize	Large larvae	k6	0.692	0.168	-0.30
	Pupae	k8	0	0.99	0.189
	Small larvae	k2	0.257	0.493	0.445
	Medium larvae	k3a	0.001	0.977	0.047
	Large larvae	k4	0.81	0.099	-0.98
	Pupae	k8	0.196	0.557	0.487

\*Significant at  $P = 0.05$ .**Table 4.** Regression analysis and density relationships of *Chilo partellus* under various cropping systems

Cropping systems	Mortality factors						
	k2	K3a	k3b	k4	k6	k7	k8
Maize/leucaena	b = 0.13 P = 0.678	0.11 0.693	0.05 0.237	0.79 0.499	-0.35 0.739	-	-0.28 0.667
Maize/gliricidia	b = 0.3 P = 0.334	-0.08 0.024*	-	-0.86 0.326	0.45 0.302	0.08 0.775	0.5 0.438
Maize/cowpea/leucaena/gliricidia	b = 0.26 P = 0.715	-0.21 0.208	-0.18 0.064	0.79 0.473	0.58 0.198	-	0.67 0.423
Maize/leucaena/gliricidia	b = 0.4 P = 0.109	-0.04 0.822	-0.12 0.448	0.64 0.553	-1.82 0.137	0.19 0.514	0.68 0.239
Maize/cowpea	b = 0.28 P = 0.615	-0.02 0.936	0.13 -	0.32 0.808	0.29 0.548	0.39 0.467	0.39 0.467
Maize/mulch	b = 0.27 P = 0.636	0.01 0.979	-0.05 0.832	0.25 0.811	-1.04 0.58	-	0.24 0.366
Maize/no mulch	b = 0.76 P = 0.071	-0.22 0.658	0.13 0.708	-6.678 0.254	0.12 0.484	-	0.65 0.342

-Absence of mortality factor in the cropping system.

\*Significant at  $P = 0.05$ .

reduces their predisposition to natural enemies and other mortality factors. Additionally, pupae do not feed, and thus may not produce odours attractive to natural enemies (Ngi-Song *et al.*, 1996).

The Podoler and Rogers (1975) method of key factor analysis identified the various key mortality factors associated with *C. partellus* population changes in the various cropping systems studied.

It should be noted that the identification of a key factor does not necessarily point to the factor(s) that may regulate the population density (Southwood, 1967; De Bach *et al.*, 1976). Furthermore, it does not identify which factors were primarily responsible for maintaining the characteristic density of the population, or what the density would be if a particular factor were removed.  $k_{3a}$  and  $k_{3b}$ , which represented mortality at the medium larval stage by *C. sesamiae* and *C. flavipes*, respectively, were found to be very minimal, indicating that the parasitoids contributed little to the total generation mortality and thus were not important mortality factors of *C. partellus* in our trials at the Kenyan coast. However, the impact of natural enemies is not necessarily related to their status as key factors. Many natural enemies do not appear as key factors in life tables of their host populations (Bellows *et al.*, 1992). This observation agrees with the view of some authors (Knutson and Gilstrap, 1990; Ogeda, 1999; Midega, 2001) on the role of parasitoids in population regulation of insects. In a more extensive study, Zhou *et al.* (2001) found that parasitism by *C. flavipes* averaged nearly 13% at 66 sites in coastal Kenya in 1999, and showed a significant reduction in borer densities due to the parasitoid. Additionally, Zhou *et al.* (2003) have recovered a complex of 26 parasitoids from this pest at the Kenyan coast, suggesting that species composition of natural enemies and levels of parasitism may vary considerably in space and time.

From the current study, the effects of these parasitoids were not influenced by the cropping systems established (Midega *et al.*, 2004). Several studies (Skövgård and Päts, 1996; Ogol *et al.*, 1998; Midega *et al.*, 2004) have shown a neutral response to the enemies' hypothesis by maize stemborer parasitoids. Most of the studies that support the enemies' hypothesis have involved the generalist natural enemies (Sheehan, 1986; Russel, 1989; Andow, 1991; Midega and Khan, 2003). Furthermore, the provision of alternate food and microhabitats associated with diverse vegetation are more relevant to enemies with broad feeding ranges than to specialist enemies (Sheehan, 1986).

It was only *C. sesamiae* that acted in an inverse density dependent manner under maize/glicricidia cropping system, showing that mortality due to this parasitoid decreased with increasing population density of *C. partellus*, which has a destabilizing effect on the population. All the other mortality factors acted irrespective of population density of the pest. These results are consistent with other field studies (Knutson and Gilstrap 1989a,b, 1990) that showed that factors commonly responsible for density-dependent mortality (including predators, parasitoids, pathogens and competition) were

uncommon during the first generation. The observed inverse density-dependent relationship shows that the parasitoid did not keep up with increasing population densities of the borer. It was noted that the main mortality factor was disappearance, with specialist natural enemies (parasitoids) only providing minimal contribution to the total generation mortality. Their activity levels were not affected by the vegetation structure and cultural systems studied. This, however, does not mean absence of positive contribution of agroforestry and intercropping in enhancing the numerical and/or functional response of the *C. partellus* natural enemies. Thus, more detailed studies are desirable that would incorporate all the life stages in response to agroecosystem diversification by the natural enemies. The egg stage is known to be highly vulnerable to natural mortality factors as they are exposed and immobile. These and other reasons make them more vulnerable to both biotic and abiotic natural mortality factors. Moreover, Bonholf (2000) observed up to 78% mortality of stemborer eggs from natural causes at the Kenyan coast.

Finally, it should be stressed that this study only examined mortality during the first generation. During a cropping season, there are typically two and sometimes three generations of *C. partellus* in the coastal area of Kenya (Overholt *et al.*, 1994a). It would seem likely that numerical responses may lead to higher densities of natural enemies, and perhaps greater impact, during the second and third borer generations (Zhou *et al.*, 2001).

#### Acknowledgements

The authors wish to acknowledge the Rockefeller Foundation Forum on Agricultural Resource Husbandry for funding the work, KARI Mtwapa for providing field facilities, ICIPE Biosystematics for identification of the parasitoids, the late John Ambajo and the many casual workers who contributed in one way or the other to the success of the study.

#### References

- Abate T., Van Huis A. and Ampofo J. K. O. (2000) Pest management strategies in traditional agriculture: An African perspective. *Annual Review of Entomology* 45, 631–659.
- Ampofo J. K. O. (1988) Some observations on *Chilo partellus* (Lepidoptera: Pyralidae) developmental biology under field and laboratory conditions. *Insect Science and Its Application* 9, 271–274.
- Andow D. A. (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36, 561–586.



- Bellows T. S. Jr., Van Driesche R. G. and Elkington J. S. (1992) Life table construction and analysis in the evaluation of natural enemies. *Annual Review of Entomology* 37, 587–614.
- Bonhof M. J. (2000) The impact of predators of maize stemborers in coastal Kenya. PhD dissertation, Wageningen Agricultural University, Netherlands, 181 pp.
- Chitere P. O. and Omolo B. A. (1993) Farmers' indigenous knowledge of crop pests and their damage in western Kenya. *International Journal of Pest Management* 39, 126–132.
- Cromartie W. J. Jr. (1981) The environmental control of insects using crop diversity, pp. 223–251. In *Handbook of Pest Management in Agriculture* (Edited by D. Pimentel). vol. III. CRC Press, Boca Raton, Florida.
- DeBach P., Huffacker C. B. and MacPhee A. W. (1976) Evaluation of the impact of natural enemies, pp. 225–285. In *Theory and Practice of Biological Control* (Edited by C. B. Huffacker and P. S. Messenger). 788 pp. Academic Press, New York.
- Ebenebe A. A., van den Berg J. and van der Linde T. C. (2001) Farm management practices and farmers' perceptions of stalk-borers of maize and sorghum in Lesotho. *International Journal of Pest Management* 47, 41–48.
- Grisley W. (1997) Crop pest yield loss: A diagnostic study in the Kenya highlands. *International Journal of Pest Management* 43, 137–142.
- Harcourt D. G. (1969) The development and use of life tables in the study of natural insect populations. *Annual Review of Entomology* 14, 175–196.
- Kfir R. (1997) Competitive displacement of *Busseola fusca* (Lepidoptera: Noctuidae) by *Chilo partellus* (Lepidoptera: Crambidae). *Annals of the Entomological Society of America* 90, 620–624.
- Kfir R., Overholt W. A., Khan Z. R. and Polaszek A. (2002) Biology and management of economically important lepidopteran cereal stemborers in Africa. *Annual Review of Entomology* 47, 701–731.
- Khan Z. R., Ampong-Nyarko K., Chilishwa 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. and Pickett J. A. (2004) The 'push-pull' strategy for stemborer management: A case study in exploiting biodiversity and chemical ecology, pp. 155–164. In *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods* (Edited by G. M. Gurr, S. D. Wratten and M. A. Altieri). CABI Publishing, Wallingford, Oxon.
- Khan Z. R., Pickett J. A., van den Berg J., Wadhams L. J. and Woodcock C. M. (2000) Exploiting chemical ecology and species diversity: Stemborer and striga control for maize and sorghum in Africa. *Pest Management Science* 56, 957–962.
- Khan Z. R., Pickett J. A., Wadhams L. J. and Muyekho F. (2001) Habitat management strategies for the control of cereal stemborers and striga in maize in Kenya. *Insect Science and Its Application* 21, 375–380.
- Knutson A. E. and Gilstrap F. E. (1989a) Direct evaluation of natural enemies of the southwestern corn borer (Lepidoptera: Pyralidae) in Texas corn. *Environmental Entomology* 18, 732–739.
- Knutson A. E. and Gilstrap F. E. (1989b) Predators and parasites of the southwestern corn borer (Lepidoptera: Pyralidae) in Texas corn. *Journal of the Kansas Entomological Society* 62, 511–520.
- Knutson A. E. and Gilstrap F. E. (1990) Life tables and population dynamics of the southwestern corn borer (Lepidoptera: Pyralidae) in Texas corn. *Environmental Entomology* 19, 684–696.
- Kogan M. (1998) Integrated pest management: Historical perspectives and contemporary developments. *Annual Review of Entomology* 43, 243–270.
- Mathez F. C. (1972) *Chilo partellus* Swinh. (Lep. Pyralidae), *C. orichalcocilliellus* Strand (Lep. Crambidae) and *Sesamia calamistis* Hmps. (Lep. Noctuidae) on maize in the coast province, Kenya. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 45, 267–289.
- Mbapila J. C. and Overholt W. A. (2001) Comparative development, longevity and population growth of exotic and native parasitoids of lepidopteran cereal stemborers in Kenya. *Bulletin of Entomological Research* 91, 347–353.
- Midega A. C. O. (2001) Assessment of the impact of agroforestry and intercropping on maize stemborer, leucaena psyllid and their natural enemies at the Kenyan coast. Master of Science dissertation Kenyatta University, Kenya. 118 pp.
- Midega A. C. O. and Khan Z. R. (2003) Impact of a habitat management system on diversity and abundance of maize stemborer predators in western Kenya. *Insect Science and Its Application* 23, 301–308.
- Midega A. C. O., Ogol C. K. P. O. and Overholt W. A. (2004) Effect of agroecosystem diversity on natural enemies of maize stemborers in coastal Kenya. *International Journal of Tropical Insect Science* 24, 280–286.
- Minja E. M. (1990) Management of *Chilo* spp. infesting cereals in eastern Africa. *Insect Science and Its Application* 11, 489–499.
- Morris R. F. and Miller C. A. (1954) The development of life tables for the spruce budworm. *Canadian Journal of Zoology* 32, 283–301.
- Ngi-Song A. J., Overholt W. A. and Ayertey J. N. (1995) Suitability of African gramineous stemborers for the development of *Cotesia flavipes* and *Cotesia sesamiae* (Hymenoptera: Braconidae). *Environmental Entomology* 24, 978–984.
- Ngi-Song A. J., Overholt W. A., Njagi P. G. N., Dicke M., Ayertey J. N. and Lwande W. (1996) Volatile infochemicals in host and host habitat location by *Cotesia flavipes* Cameron and *C. sesamiae* (Cameron) (Hymenoptera: Braconidae), two larval parasitoids of gramineous stemborers. *Journal of Chemical Ecology* 22, 307–323.

- Ogeda K. (1999) Evaluation of the impact of *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) and indigenous parasitoids on stemborer populations in southwestern Kenya. Master of Science dissertation, University of Nairobi, Kenya. 89 pp.
- Ogol C. K. P. O., Spence J. R. and Keddie A. (1998) Natural enemy abundance and activity in a maize-leucaena agroforestry system in Kenya. *Environmental Entomology* 27, 1444–1451.
- Oloo G. W. (1989) The role of local natural enemies in population dynamics of *Chilo partellus* (Swinh.) (Crambidae) under subsistence farming systems in Kenya. *Insect Science and Its Application* 10, 243–251.
- Oloo G. W. and Ogeda K. (1990) The incidence of *Chilo partellus* (Swinh.) (Crambidae) and the contribution of natural enemies to its mortality under intercropping systems in Kenya. *Tropical Pest Management* 36, 244–248.
- Omwega C. O., Kimani S. W., Overholt W. A. and Ogol C. K. P. O. (1995) Evidence of the establishment of *Cotesia flavipes* (Hymenoptera: Braconidae) in continental Africa. *Bulletin of Entomological Research* 85, 525–530.
- Overholt W. A. (1998) Biological control, pp. 349–362. In *African Cereal Stem-borers: Economic Importance, Taxonomy, Natural Enemies and Control* (Edited by A. Polaszek). CAB International, Wallingford, Oxon.
- Overholt W. A., Ogeda K. and Lammers P. M. (1994a) Distribution and sampling of *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) in maize and sorghum at the Kenya coast. *Bulletin of Entomological Research* 84, 367–378.
- Overholt W. A., Ngi-Song A. J., Kimani S. W., Mbatia J., Lammers P. M. and Kioko E. (1994b) Environmental considerations of the introduction of *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) for biological control of *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in Africa. *Biocontrol News and Information* 15, 19N–24N.
- Päts P., Ekbom B. and Skövgård H. (1997) Influence of intercropping on the abundance, distribution and parasitism of *Chilo* spp. (Lepidoptera: Pyralidae) eggs. *Bulletin of Entomological Research* 87, 507–513.
- Podoler H. and Rogers D. (1975) A new method for the identification of key factors from life table data. *Journal of Animal Ecology* 48, 85–115.
- Potting R. P. J., Perry J. N. and Powell W. (2005) Insect behavioural ecology and other factors affecting the control efficacy of agroecosystem diversification strategies. *Ecological Modelling* 182, 199–216.
- Root R. B. (1973) Organisation of plant–arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleraceae*). *Ecological Monographs* 43, 95–124.
- Russel E. P. (1989) Enemies hypothesis: A review of the effect of vegetational diversity on predatory insects and parasitoids. *Environmental Entomology* 18, 590–599.
- Seshu Reddy K. V. and Walker P. T. (1990) A review of the yield losses in graminaceous crops caused by *Chilo* spp. *Insect Science and Its Application* 11, 563–569.
- Sheehan W. (1986) Response by specialist and generalist natural enemies to agroecosystem diversification: A selective review. *Environmental Entomology* 15, 456–461.
- Skövgård H. and Päts P. (1996) Effects of intercropping on maize stem-borers and their natural enemies. *Bulletin of Entomological Research* 86, 599–607.
- Skövgård H. and Päts P. (1997) Reduction of stem-borer damage by intercropping maize with cowpea. *Agriculture, Ecosystems and Environment* 62, 13–19.
- Southwood T. R. E. (1967) The interpretation of population change. *Journal of Animal Ecology* 36, 519–529.
- Southwood T. R. E. (1978) *Ecological Methods*. John Wiley and Sons, New York. 419 pp.
- Southwood T. R. E. and Jepson W. F. (1962) Studies on the populations of *Oscinella frit* L. (Diptera: Chloropidae) in the oat crop. *Journal of Animal Ecology* 31, 481–495.
- Tams W. H. T. (1932) New species of African Heterocera. *Entomologist* 65, 1241–1249.
- van den Berg J., Nur A. F. and Polaszek A. (1998) Cultural control, pp. 333–349. In *African Cereal Stem-borers. Economic Importance, Taxonomy, Natural Enemies and Control* (Edited by A. Polaszek). CAB International, Wallingford, Oxon.
- Warui C. M. and Kuria J. N. (1983) Population incidence and the control of maize stalk-borers *Chilo partellus* Strand and *Chilo orichalcocilliellus* Strand and *Sesamiae calamistis* Hmps in Coast province, Kenya. *Insect Science and Its Application* 4, 11–18.
- Zhou G., Baumgärtner J. and Overholt W. A. (2001) Impact assessment of an exotic parasitoid on stem-borer population dynamics in Kenya. *Ecological Applications* 11, 1554–1562.
- Zhou G., Overholt W. A. and Kimani-Njogu S. W. (2003) Species richness and parasitism in an assemblage of parasitoids attacking maize stem-borers in coastal Kenya. *Ecological Entomology* 28, 109–118.