IMPACT OF A HABITAT MANAGEMENT SYSTEM AND BT-MAIZE ON STEMBORER NATURAL ENEMIES AND BIODIVERSITY OF ARTHROPODS AND SOIL FAUNA IN KENYA AND SOUTH AFRICA

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This thesis is my original work and has not been presented for a degree in any other University

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DEDICATION

The work reported herein is dedicated to my loving family who gave me immeasurable moral support and always understood when I had to stay away during the study period.

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Diogenes Laertius, a Cicilian and famous biographer of ancient Greek philosophers, once said that a man should live with his superiors as he does with his fire: not too near, lest he burns; nor too far off, lest he freezes. The work reported herein arose from a very close association between me and my supervisors, Dr. C.K.P.O. Ogol, Dr. Z.R. Khan and Prof. J. van den Berg, whom I'm greatly indebted to for their invaluable guidance throughout the course of the work and therefore a direct disapproval of Laertius' view. Their approach to supervision has been the most significant input since it created for me an environment to think and research broadly while providing not only expert but moral assistance as well at every turn. I am forever grateful!

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Abstract

Lepidopteran stemborers are a major constraint to efficient production of cereals in Sub-saharan Africa. As part of continuing efforts to manage these pests, the International Centre of Insect Physiology and Ecology and its partners have developed a habitat management strategy by use of gramineous and leguminous fodder plants that provide a diversionary strategy whereby stemborers are repelled from the maize and subsequently attracted to a discard or trap crop around the field ('push-pull' strategy). The European corn borer, *Ostrinia nubilalis* (Hubner), is also a major pest of corn in North America. Bt corn hybrids, in which a gene from a bacterium, *Bacillus thuringiensis* subsp. *kurstaki* has been sliced into the DNA of corn plants, have been developed as a management option for European corn borer due to its insecticidal properties. This technology is also used for *Busseola fusca* in South Africa. Bt maize therefore represents a promising technology for reducing losses from stemborer infestations in Africa. The current studies were conducted to assess the impact of both technologies on stemborer natural enemy abundance and activity and arthropod abundance and diversity in western Kenya and South Africa. Treatments consisted of a maize monocrop and an intercrop of maize and desmodium with Napier grass as a perimeter crop around the plots ('push-pull') with varied number of replications in each site and study. Oviposition preference rates were significantly higher in the maize monocrop than in the 'push-pull' systems at all sites indicating that the stemborer moths preferred the maize monocrop to the 'push-pull' system for oviposition. Results showed that the incidence of the larvae and pupae was significantly higher in the maize monocrop than in the 'push-pull' systems. Similarly, plant damage in terms of number of entry/exit holes, foliar damage, broken stems and dead plants, were significantly higher in the maize monocrop than in the 'push-pull' systems. Maize yields in terms of average dry kernel weight per plant and average weight of kernels per plot were significantly higher in the 'push-pull' than in the maize monocrop plots in Kenya but were the same between the two cropping systems in South Africa. Maize stemborer egg parasitism rates were significantly higher in the 'push-pull' than in the maize monocrop plots in Kenya and insignificant in South Africa. Larval and pupal parasitism rates followed the same trend at all sites while larval and pupal mortality did not differ between treatments. Generalist predators were significantly more abundant in the 'push-pull' than in the maize monocrop systems at all sites while species diversity did not show a consistent trend between the two systems. Stemborer egg predator activity was significantly more enhanced in the 'push-pull' than in the maize monocrop systems at all sites. There were, however, no significant differences with regard to larval and pupal predation rates between the two cropping systems at all sites. Spiders were more abundant in the 'push-pull' than in the maize monocrop systems at all sites. Their overall species diversity and dominance were however not affected by either the cropping system or Bt-maize, except for the family Lycosidae which were more species diverse in the 'push-pull' than in the maize monocrop systems. Both individual families and total springtail numbers did not differ between the 'push-pull' and the maize monocrop plots. The same was observed for these treatments under the Bt and non-Bt maize. Bt-maize did not affect springtail diversity and abundance. These studies imply that 'push-pull' systems enhance maize stemborer natural enemy abundance and activity, arthropod abundance and has no deleterious effects on springtail populations. Similarly Bt-maize has no effect on spider and springtail abundance and diversity.

CHAPTER ONE

1. GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 General Introduction

Maize, *Zea mays* L., and sorghum, *Sorghum bicolor* Moench (Poacea), are the two most important cereal crops in sub-Saharan Africa (FAO, 1998). These crops are primarily grown by subsistence farmers and provide apart from food, also animal fodder and building material (Bonhof, 2000). Unfortunately, there is a widening gap between food supply and demand in Africa, with per capita production steadily declining (Byerlee and Heisey, 1997). According to FAO reports (1998), the grain yields in Africa are the lowest in the world.

Lepidopteran stemborers constitute one of the major constraints to efficient maize and sorghum production in the developing world. There is a complex of stemborer species in the region with about 12 species occurring in east Africa (Seshu Reddy, 1998) and about four main species in Southern Africa (Kfir, 1998). These include *Busseola fusca* (Fuller) (Noctuidae), *Sesamia calamistis* (Hampson) (Noctuidae), *Chilo orichalcocilliellus* Strand, *Chilo partellus* Swinhoe (Crambidae), and *Eldana saccharina* Walker (Pyralidae). While the other species are indigenous to Africa, *C. partellus* is not, having been introduced into Africa in the early 1930's (Tams, 1932) from Asia. It now occurs throughout the eastern, central and southern parts of the African continent (CIE, 1989; Harris, 1990) and is one of the major stemborer pests in Kenya (Overholt *et al.*, 1994). It is the most important stemborer at low and mid elevations in East Africa (Seshu Reddy, 1983), more injurious than the indigenous species (van den Berg *et al.*, 1991a; van den Berg *et al.*, 1991b; Kfir *et al.*, 2002) and is reported as partially displacing some of the indigenous stemborer species in the region (Kfir, 1997; Kfir *et al.*, 2002).

The species of stemborers infesting maize and sorghum are for the most part the same, and produce similar symptoms of damage. Newly hatched larvae congregate inside the leaf whorls and feed on folded central leaves, causing typical pinhole damage symptoms. Later on, they feed on the growing stem of the young plants, resulting in dead hearts. If the growing point has moved upwards, only stem tunneling takes place. The damaged plants become weak and stunted and bear very small ears/panicles. The stemborer larvae also bore into the maize ears and feed on the developing seeds.

Stemborers have a wide range of wild hosts including the numerous wild grasses that serve as reservoirs during non-cropping seasons (Khan *et al.*, 1997b; Polaszek and Khan, 1998; van den Berg *et al.*, 2001; Rebe *et al.*, 2004a, 2004b). It has been suggested by some authors that these wild grasses be destroyed to decrease the survival of stemborers between seasons (Ingram, 1958). This is however less practical as it is labor intensive. The wild hosts that maintain populations of stemborers between seasons could also indirectly maintain the populations of the natural enemies (Khan *et al.*, 1997b).

Biodiversity in agroecosystems has greatly been reduced in the last decades as a result of intensification of agricultural systems. Empirical data have shown that systems with an enhanced overall biodiversity have relatively fewer pest problems. As a result of this observation it has often been stated that enhancement of biodiversity within agroecosystems can greatly contribute to the development of sustainable crop protection systems, with a reduced reliance on pesticides. This would also ensure ecological balance, system health and stability and greater productivity of the agroecosystems.

In considering the strategies for the management of cereal stemborers, it is important and essential to develop Biologically Intensive Integrated Pest Management (BIPM) strategies that are environmentally safe, economically feasible and acceptable to resource-limited farmers.

1.2 Literature review

1.2.1 Pest status of stemborers and associated yield losses

Early stemborer instar larvae feed initially by scraping in leaf whorls of growing plants, producing characteristic "window-paning" and "pinholes" (Seshu Reddy, 1998). Later, the larvae tunnel into the stems and may kill the central leaves and growing points producing "dead-hearts". The larvae also bore into the maize ears and feed on the developing seeds/grains (Kfir, 1998; Seshu Reddy, 1998). This feeding and stem tunneling by borer larvae on plants result in crop losses as a consequence of destruction of the growing point, early leaf senescence, interference with translocation of metabolites, and nutrients that result in malformation of the grain, stem breakage, plant stunting, lodging and direct damage to ears (Kfir, 1998; Seshu Reddy, 1998; Kfir *et al.*, 2002).

Yield losses of 18% in maize due to damage caused by *C. partellus* and *C. orichalcocilliellus* have been recorded in Kenya (Warui and Kuria, 1983). Seshu

Reddy and Sum (1991) also reported maximum grain yield reduction and stalk damage in maize (cultivar Quatrain) due to *C. partellus* infestation at 20 days after plant emergence, while there was an insignificant larval effect on yield in plants infested at 60 days after emergence. In Uganda a 56% loss of grain yield resulted when sorghum was infested with *C. partellus* 20 days after plant emergence (Starks, 1969), whereas in Kenya losses have ranged between 2% and 88% (Seshu Reddy, 1988). In South Africa, estimated yield losses from *B. fusca* damage ranged between 10% and a total loss (Mally, 1920; Matthee, 1974; van Rensburg and Bate, 1987). Yield loss in maize by *B. fusca* was significantly correlated with leaf damage, but a higher correlation was observed with stem-boring damage, with yield reductions of up to 100% (Barrow, 1987). In Kenya, loss of about 12% maize grain for every 10% plants infested by *B. fusca* has been reported (Walker and Hodson, 1976). In general, in eastern and southern Africa, cereal stemborers cause yield loss ranging from 10% to total loss (van Rensburg and Bate, 1987; Seshu Reddy and Walker 1990; van den Berg and van Rensburg, 1991a, 1991b; van den Berg and Nur, 1998; Kfir *et al.*, 2002).

1.2.2 Management of stemborers

Methods currently used to manage stemborers include chemical, cultural and biological control (Litsinger and Moody, 1976; Minja, 1990; Kfir *et al.*, 2002). Several cultural practices have been implicated in the stemborer control, mainly in disrupting or slowing down the population build-up (Minja, 1990; Ebenebe *et al.*, 2000a). These include appropriate disposal of crop residues, time of planting, tillage and mulching, spacing, intercropping, removal and destruction of volunteer and alternative host plants, removal of borer-infested plants, fertilizer application and crop rotation (Minja, 1990; van den Berg *et al.*, 1998; Kfir *et al.*, 2002). Cultural methods such as intercropping with non-cereals and early planting have been used for quite a long time by farmers (Litsinger and Moody, 1976; Minja, 1990). However, studies have shown that their impact on stemborer populations is limited (Oloo, 1989; Skövgard and Päts, 1996; van den Berg *et al.*, 1998).

Several insecticides have been screened for the control of stemborers in different regions in Africa. These include carbofuran, carbaryl, deltamethrin, endosulfan, trichlorfon and synthetic pyrethroids (Seshu Reddy, 1985; Ajayi, 1989; Minja, 1990; Sithole, 1990; van Rensburg and van den Berg, 1992; van den Berg and Nur, 1998). Chemical control can effectively reduce stemborer numbers (Mathez, 1972; Warui and Kuria, 1983; van den Berg and Nur, 1998) but the relatively short time larvae are exposed before they enter the stems makes it necessary to apply pesticides on a regular basis. This is time consuming and expensive and may not be feasible for the small-scale farmer in Africa (van den Berg and Nur, 1998; Kfir *et al.*, 2002).

Botanical pesticide extracts have been used traditionally by resource limited small-scale farmers to protect crops from pest damage. In Tanzania, 4% leaf extracts of *Tephrosia vogelii*, Hook F. (Fabaceae: Papilionoideae) and *Cassia didymobotrya* (Caesalpionioideae) plants in water were compared with commercial insecticides (Mallya, 1985). The extracts from *T. vogelii* plants gave promising results (Mallya, 1985, 1986; Marandu *et al.*, 1987). In Zambia, *T. vogelii* leaf extracts prevented oviposition by *C. partellus* in maize in addition to being a phagodeterrent (Mugoya and Chinsembu, 1995). The percentage of plants damaged by stemborers in control plots (unsprayed) was almost three times higher than those sprayed with a 15% *T. vogelii* extract (Mugoya and Chinsembu, 1995). Other botanicals include the use of neem seed (*Azadirachta indica*) oil extract which is being promoted by the International Centre of Insect Physiology and Ecology (ICIPE). In both maize and sorghum, neem oil extracts reduced stemborer attack to the same magnitude as the insecticide control (Seshu Reddy, 1998).

The search for alternative control measures that would overcome the drawbacks of insecticides has included research into sex pheromones and how they might be used in the stemborer control. These pheromones could be used in population monitoring and control of the pest by mass trapping and mating disruption (Unnithan and Saxena, 1990). These pheromone-baited traps would be very useful for moth detection for monitoring their first emergence, particularly in areas where larval diapause is prevalent during the off-season and for monitoring the flight phenology (Unnithan and Saxena, 1990; Kfir and Bell, 1993; Ebenebe *et al.*, 2000b; Kfir, 2000). Campion and Nesbitt (1983) reviewed the progress in the identification and utilization of sex pheromones for stemborer monitoring and concluded that mass trapping is unlikely to provide satisfactory control but that mating disruption is more likely to be effective.

Host plant resistance is one of the most important and promising ways of reducing stemborer damage and subsequent yield losses in target crops, either by resistance to initial attack, antibiosis once attacked or tolerance to attack (van den Berg and Wenzel, 1994; Wenzel and van den Berg, 1996; van den Berg and van der Westhuizen, 1997; Seshu Reddy, 1998; Ebenebe *et al.*, 2000c; van den Berg, 2000). Resistant cultivars confer many advantages including provision of an inherent control that involves no environmental problems and are generally compatible with other insect control methods (Bosque-Pérez and Schulthess, 1998; Kfir *et al.*, 2002). Their cultivation is not subject to vagaries of weather as are chemical control measures, and in certain circumstances it is the only effective means of control. Resistant varieties control even a low pest density, whereas insecticide use is justifiable only when the density reaches the economic injury level (Kfir *et al.*, 2002) Research conducted in Kenya (Dabrowski and Kidiavai, 1983; Omolo, 1983; Ampofo *et al.*, 1986) and South Africa (van Rensburg and van den Berg, 1995; Wenzel and van den Berg, 1996; van den Berg, 1997; van den Berg and van der Westhuizen, 1997; van den Berg and van der Westhuizen, 1998; Wenzel *et al.*, 1998; van den Berg, 2000) on the evaluation of maize and sorghum lines has shown good levels of resistance/tolerance to stemborer attack. A wide range of mechanisms were involved in *C. partellus* resistance in maize and sorghum, including non-preference for oviposition, reduced feeding, reduced tunneling, tolerance of plants to leaf damage, deadheart and stem tunneling and antibiosis. In addition, morphological, physical, chemical and other plant characteristics and non-plant factors including photo- and geotactic stimuli, were involved (Dabrowski and Kidiavai, 1983; Saxena, 1985, 1990; Kumar and Saxena, 1992; van Rensburg and Malan, 1992; Kumar, 1993). Efforts are underway in Africa to identify further sources of stemborer resistance in cereal crops, but high levels of resistance have not been found (Kfir *et al.*, 2002).

1.2.3 Biological control

Several biocontrol agents such as parasitoids, predators and diseases targeting different growth stages of the stemborers have been reported as naturally occurring. A number of parasitoids have been recovered from cereal stemborers in Africa (Kfir, 1992; Overholt *et al.*, 1994; Omwega *et al.*, 1995; Bonhof *et al.*, 1997; Overholt, 1998; Bonhof, 2000; Kfir *et al.*, 2002; Zhou *et al.*, 2003).

Different parasitoid species attack different stages of development of the stemborer. Egg parasitism, caused by *Trichogramma* spp. and *Telonomus* spp., fluctuates greatly between seasons and geographical locations, presumably because of different climatic conditions. At the Kenya coast, up to 92% parasitism of *Chilo* sp. eggs by *Trichogramma* spp. has been recorded (Mathez, 1972; Ogol *et al.*, 1998; Midega, 2001). The larval stages of the stemborer are attacked by a great variety of parasitoids. *Cotesia sesamiae* Cameron (Hymenoptera: Braconidae) and *Sturmiopsis parasiticae* (Orvan) (Diptera: Tachinidae) are the most widespread and abundant indigenous larval parasitoids in Eastern Africa (Ingram, 1958; Milner, 1967; Mohyuddin and Greathead, 1970; Skövgard and Päts, 1996; Ogol *et al.*, 1998; Midega *et al.*, 2004; Midega *et al.*, 2005), with the former being the most abundant and important in South Africa (Kfir, 1992; Kfir *et al.*, 2002).

The exotic parasitoid *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) was introduced at the Kenyan coast in 1993 as part of a biological control program. Since then parasitism has been rising steadily and has become an important mortality factor in some areas (Skövgard and Päts, 1996; Ogol *et al.*, 1998; Overholt, 1998; Midega, 2001; Zhou *et al.*, 2001; Zhou *et al.*, 2003). Larval parasitism was less than 10% at the coast (Skövgard and Päts, 1996; Ogol *et al.*, 1998; Midega *et al.*, 2004) and less than 20% in western Kenya (Ogol *et al.*, 1998), with the parasitoid *C. sesamiae* being the most abundant species. In South Africa, up to 75% larval parasitism has been recorded (Kfir, 1992), with the same parasitoid being the most important.

Pupal parasitoids such as *Pediobius furvus* Gahan (Hymenoptera: Eulophidae), *Dentichasmias busseolae* Heinrich (Hymenoptera: Ichneumonidae) and *Psilochalsis soudanensis* Steffan (Hymenoptera: Chalcididae) are widespread in Africa, but are generally not able to keep the stemborer populations at low levels (Oloo and Ogeda, 1990). Parasitism of pupae, primarily by *P. furvus* and *D. busseolae,* was 0-10% at the Kenyan coast (Skovgard and Pats 1996; Ogol *et al.*, 1998; Midega *et al.*, 2004), up to 58% in western Kenya (Oloo and Ogeda, 1990) and up to 100% in South Africa (Kfir, 1992).

There seems to be a consensus that predators play an important role as mortality agents of cereal stemborers (Mohyuddin and Greathead, 1970; Oloo, 1989; Greathead, 1990; Oloo and Ogeda, 1990; Bonhof, 2000; Midega, 2001; Midega and Khan, 2003; Midega *et al.*, 2005). Eggs are among the most vulnerable life stages of the stemborers and their disappearance is usually attributed to predators. In western Kenya, disappearance of naturally occurring stemborer eggs was 93% (Oloo, 1989). Neonate larvae are vulnerable to predation, especially while migrating from the egg batch to the leaf whorl. Ants are frequently named as predators of all life stages of the stemborer. Spiders, ladybirds and earwigs are also frequently found on agricultural crops in Africa (Oloo, 1989; Bonholf *et al.*, 1997; Ogol *et al.*, 1998; Midega and Khan, 2003) but they appear to be less numerous and widespread than ants. Earwigs and cockroaches are also predators but occur less frequently (Bonhof, 2000; Midega and Khan, 2003).

1.2.4 Vegetation diversity and pest management

Agroecosystem diversification is a cultural practice generally thought to increase system stability and decrease the incidence of major insect pest outbreaks often prevalent in monocultures (Perrin, 1977, 1980; Altieri and Letourneau, 1982; Risch, 1983; Risch *et al.*, 1983; Andow, 1991; Finch and Collier, 2000; Banks and Stark, 2004). The ecological basis for reduced insect pest populations in diverse systems has been explained in part by two complementary hypotheses (Root, 1973; Sheehan, 1986; Russel, 1989). The resource concentration hypothesis predicts that monophagous and oligophagous herbivores will locate, remain and increase in concentrated patches of host plants such as monocultures, whereas polyphagous herbivores will tend to disperse out of low diversity patches and into the surrounding vegetational matrix (Root, 1973; Sheehan, 1986; Russel, 1989; Ogol *et al.*, 1999).

The enemies hypothesis predicts that populations of natural enemies will be greater, and insect pest populations lower, in more diverse habitats due in large part to the availability of alternate prey, suitable microhabitats, and nectar sources (Altieri *et al.*, 1981; Nordlund *et al.*, 1988; Midega and Khan, 2003). Thus, the decreased incidence of insect pests often seen in diverse agroecosystems may be caused by a combination of factors including altered patterns of colonization, reproduction, and mortality or dispersal (Perrin and Phillips, 1978; Banks and Stark, 2004). The performance of the natural enemies may also be enhanced by chemical cues from the associated plants (Altieri *et al.*, 1981; Nordland *et al.*, 1988; Khan *et al.*, 1997a, b; Khan *et al.*, 2000; Khan and Pickett, 2004).

Increasing the vegetational diversity of agroecosystems has been proposed as a means of augmenting entomophagous predators and parasitoids for the control of arthropod pests (Risch, 1983; Herzog and Funderback, 1986; Russel, 1989; Andow 1991). There are currently several other competing explanations which are probably best synthesized by Finch and Collier (2000). Their 'appropriate/inappropriate landings' hypothesis states that insect pests settle on plants only when various plant host factors such as visual stimuli, taste and smell are satisfied. This is more likely in monocultures than polycultures where the chance of encountering a 'wrong' stimulus is much increased.

1.2.5 Agroecosystems and Biodiversity

Biodiversity is the variety of all flora and fauna living and interacting in an ecosystem. It has an intricate role in the functioning of natural and agricultural ecosystems (Smeding and de Snoo, 2003). In natural ecosystems, plant diversity in the form of vegetative cover helps to protect top soil from wind and water erosion, while reducing flood hazards to the ecosystem by enhancing infiltration and reducing run-off (Johnson, 2000; Granger, 2000). One of the most important reasons for maintaining and/or encouraging natural biodiversity is that it performs a variety of ecological services (Altieri, 1991; Smeding and de Snoo, 2003). In agroecosystems, pollinators, natural enemies, earthworms and soil microorganisms are all key components of biodiversity that play important ecological roles thus mediating processes such as genetic introgression, natural control, nutrient cycling and decomposition (Altieri, 1983; Smeding and de Snoo, 2003).

The degree of biodiversity in agroecosystems depends on the diversity of vegetation within and around the agroecosystem, the permanence of the various crops within the agroecosystem and the intensity of management (Altieri, 1991). Ground dwelling arthropods such as the ground beetles have the potential of reducing the populations of both weeds and insect pests (Thiele, 1977; Hengeveld, 1980a, b; Cardina *et al.*, 1996; Horgan and Myers, 2004). Intensive management of agricultural systems can negatively affect the abundance, diversity and efficiency of ground beetles and spiders (Lys *et al.*, 1994). Frequent disturbances such as repeated cultivation, pesticide application and other management practices are known to be deleterious to ground dwelling arthropods (Booij and den Nijs, 1992; Castañé *et al.*, 2004).

Farming practices that conserve these ground fauna and other natural enemies may be a practical alternative to manage pests in agricultural systems (Carcamo and Spence, 1994; Horgan and Myers, 2004). Previous research has shown that use of crop rotation, cover crops, reduced tillage or no-tillage and agroecosystem diversification tend to promote greater overall arthropod diversity and abundance (Brust and House, 1988; Andow, 1991; Manley, 1996). Because they benefit from, or even require additional food sources, moisture or shelter, the abundance and diversity of these arthropods within fields is also closely related to the proximity of undisturbed habitats such as uncultivated field edges and trap plants/vegetation (Desender, 1982; Sotherton, 1985; Carmona and Landis, 1999). Non-crop habitats bordering agricultural fields have favourable effects on a number of beneficial arthropod groups including Aranae (Alderweireldt, 1986; Maelfait and de Keer, 1990), Carabidae (Desender, 1982), Coccinelidae (Perrin, 1975), Syrphidae (Pollard, 1971) and mixed taxa (Sotherton, 1985; Coombes and Sotherton, 1986; Kromp and Steinberger, 1992). In addition, spatial and structural complexity at the farm and landscape scale has been shown to favour certain beneficial arthropods (Baudry, 1988; Landis and Haas, 1992; Marino and Landis, 1996).

1.2.6 Springtails and their role in sustainable agriculture

Springtails (Hexapoda: Parainsecta: Collembola) as decomposers are important consumers of plant residues and soil fungi and help in humus creation. Like earthworms, they fragment and condition plant debris in their guts before microorganisms break down this residue further (Potter *et al.*, 1990). They also act as prey for beneficial stenophagous (Bauer, 1982, 1985) and polyphagous predatory arthropods (Hopkin, 1997). At certain times of the year, springtails may provide a large proportion of the diet of some beneficial species of Araneae and Coleoptera (Sunderland, 1975; Sunderland *et al.*, 1986; Alderweireldt, 1994) and therefore their occurrence in the field early in the season could be significant in sustaining such predator populations and enhancing subsequent control of pests (Sunderland *et al.*, 1997).

Springtails also contribute to the ability of the soil to suppress plant pathogens such as *Rhizoctonia solani*, *Fusarium oxysporum* f. sp. *vasinfectum*, and *Pythium* spp. (Wiggins and Curl, 1979; Curl *et al.*, 1985a, b; Rickerl *et al.*, 1989; Lartey *et al.*, 1994), because these organisms are, for the most part, mycophagous, modifying the community of fungi. The sensitivity of springtails to various crop management practices suggests their potential use as biological indicators of disturbance (Rebek *et al.*, 2002). Any technology that reduces abundance or diversity of springtails may thus be detrimental to soil health and thus to agricultural system sustainability (Bitzer *et al.*, 2002).

1.2.7 Habitat management and conservation biological control

Habitat management can be considered a subset of conservation biological control methods that alters habitats to improve availability of the resources required by natural enemies for optimal performance (Landis *et al.*, 2000). Habitat management may occur at the within-crop, within-farm, or landscape levels. Underlying these practices is the understanding that agricultural landscapes often do not provide resources for natural enemies at the optimal time or place (Landis *et al.*, 2000).

The need for habitat management is directly linked to the biology of specific pests and natural enemies, and the qualities of the environment in which they occur. As a result of frequent and intense disturbance regimes, many agricultural systems are recognised as particularly difficult environments for natural enemies (Powell, 1986; Letourneau, 1998; Landis and Marino, 1999). This is especially true for annual monocultural cropping systems where the rates of establishment of imported natural enemies and their success in controlling the target pest are lower than in more stable cropping systems (Hall *et al.*, 1980; Stiling, 1990). Many of the proximate factors identified as limiting the effectiveness of natural enemies in agricultural systems (pesticides, lack of adult food, lack of alternative hosts) (Powell, 1986; Rabb *et al.*, 1976; Dutcher, 1993) can be viewed as direct results of the disturbance regimes imposed on these systems (Landis and Menalled, 1998). Recently, increasing attention has been paid to conservation practices that seek to alter the quality of the natural enemies' habitat (Landis *et al.*, 2000). Identifying the key elements of the'right' diversity may be a difficult process, but the process can be guided by an understanding of the resources needed by natural enemies (Wratten and van Emden, 1995; Wratten *et al.*, 1998). Potential mechanisms include improving the availability of alternative foods such as nectar, pollen and honey dew; providing shelter or a moderated micro climate in which natural enemies may overwinter or seek refuge from factors such as environmental extremes or pesticides; and providing a habitat in which alternative hosts or prey are present (Landis *et al.*, 2000). In addition, the temporal availability of such resources may be manipulated to encourage early season activity of natural enemies. Finally, the spatial arrangement of such resources to enhance natural enemy activity within the crop must be considered (Landis *et al.*, 2000)

1.2.8 Genetically modified maize

Bacillus thuringiensis subsp. *kurstaki* (Bt), an aerobic soil bacterium, produces an insecticidal crystal protein during sporulation (Barton *et al.*, 1987; McGaughey and Whalon, 1992; Lambert *et al.*, 1996). These insecticidal crystal proteins have to be ingested by the insect where they bind to specific receptors in the mid gut of the target pest species and cause death (Gill *et al.*, 1992). These Bt crystal proteins are non-toxic to humans, birds and other beneficial insects and have been used as biological insecticides to control agricultural insect pests for over 30 years (Koziel *et al.*, 1993; Huang *et al.*, 2003). The genes (Cry genes) that encode Bt crystal proteins have been cloned, sequenced and transformed into various crops and are now available commercially (Barton and Miller, 1993; Jansens *et al.*, 1997; Binning and Rice, 2002).

Recombinant DNA technology has allowed the insertion of the bacterial gene that codes toxin production into the maize genome resulting in plants that produce Bt toxins at high levels in most plant tissues (Marcon *et al.*, 1999; Mwangi and Elly, 2001; Cellini *et al.*, 2004). This unique form of insecticide delivery circumvents problems associated with poor spray coverage and degradation of foliar applications and provides season-long insect control without the use of conventional neurotoxic insecticides (Burkness *et al.*, 2001; Pierce *et al.*, 2001; Huang *et al.*, 2003). These transgenic maize plants therefore seem to represent a promising technology for reducing losses from stemborer infestation in Kenya (Mwangi and Elly, 2001). Because Bt-technology is a relatively new agricultural pest management tool, there are still lingering concerns among farmers and agricultural scientists over the long term effect on biodiversity, non-target pests and natural enemies, crop yields and economic performance (Catangui and Berg, 2002; Ervin *et al.*, 2003; Kuiper and Kleter, 2003; Levidow, 2003; Otsuka, 2003; Gray, 2004; Lumbierres *et al.*, 2004). Investigations into the direct and indirect effects of *B. thuringiensis* on natural enemies have revealed harmful effects (Sétamou *et al.*, 2002; Baur and Boethel, 2003; Prûtz and Dettner, 2004; Schuler *et al.*, 2004) ranging from mortality and reduced longevity and fecundity, with variations for different specialist natural enemies and host herbivores.

Additionally, the usefulness of the transgenic cultivars may be cut short should the target pests develop resistance to them, although pests have not yet developed resistance to Bt crops in the field (Tabashnik *et al.*, 2003). However, many have been selected for resistance in the laboratory, and diamondback moth (*Plutella xylostella*) has evolved resistance to Bt sprays in the field (Tabashnik, 1994; Ferré and van Rie, 2002; Tabashnik *et al.*, 2003).

Consumption of sub-lethal doses, especially from those parts of the plant with lower concentrations of the Bt-proteins such as silk and upper plant parts (van Rensburg, 2001) leads to increased survival of stemborer larvae. This enhances selection pressure which leads to evolution of resistance (Gould, 1998). Besides, adverse environmental conditions could interfere with production of the Bt proteins allowing for further survival of stemborer larvae (van Rensburg, 1999). Resistance management is therefore recognized as essential to the long-term success of Bt crops (Pierce *et al.*, 2001). To counter the threat of resistance, the ‘high-dose/structured refuge strategy’ has been instituted (Chilcutt and Tabashnik, 2004); requiring farmers to grow toxin-free crop refuges near Bt crops (Gould, 1998). This strategy assumes that resistance is recessive and is conferred by a single locus with two alleles in three insect genotypes (RR, SS and RS), and that resistance alleles are initially rare and that there will be random mating between these rare resistant and the relatively more abundant susceptible adults (Gould, 1998; Glaser and Matten, 2003). The purpose of the toxin-free crop is to promote survival of these susceptible adults. Ideally, the resultant heterozygous progeny will be killed by the high-dose of toxin from Bt plants. Models predict that resistance will be delayed substantially if these assumptions hold (Gould, 1998), but pollen-mediated gene flow from Bt crop plants to the non-Bt refuge could disrupt this strategy. Furthermore, Chilcutt and Tabashnik (2004) have demonstrated contamination of refuges by Bt genes from surrounding transgenic maize. This could become a problem in subsistence farming systems where farmers are known to retain seeds for subsequent plantings. This could accelerate pest resistance either by reducing the population of susceptible adults emerging from the refuge crop (due to the toxin in the non-Bt maize) thereby diminishing the mating chances between the two populations or allowing for the survival of heterozygote population from the non-Bt maize. This would increase the functional dominance of resistance leading to faster evolution of resistance (Gould, 1998; Horner *et al.*, 2003a, 2003b; Chilcutt and Tabashnik, 2004; Tabashnik *et al.*, 2004). There is therefore a need for further research into potential components of an integrated resistance management strategy.

1.2.9 Utilisation of wild graminaceous plants for the management of cereal stemborers

Most cereal stemborers are generally polyphagous and have several other graminaceous and/or non-cultivated host plants (Ingram, 1958; Seshu Reddy, 1983; Khan *et al.*, 1997b; Polaszek and Khan, 1998; Haile and Hofsvang, 2001; van den Berg *et al.*, 2001; Rebe *et al.*, 2004a, 2004b). The stemborer damage to cultivated crops, which is short-lived in comparison to wild hosts, is typically caused by populations that move into fields from outside (Usua, 1968; Joyce, 1976). The wild habitats often harbor food sources for many insect pest species, and they may encourage insect invasion and outbreaks in neighboring agroecosystems (van Emden, 1965).

In extension of this approach, Khan *et al.* (1997b) carried out field trials that demonstrated that the forage grass, *Sorghum vulgare sudanense* (Pers.) (Sudan grass) attracted greater oviposition by stemborers than cultivated maize, resulting in significant increase in maize yield. On the other hand, the non-host forage plant, *Melinis minutiflora* Beauv. (Poaceae) (Molasses grass), when intercropped with maize, repelled gravid stemborer females from ovipositing on maize, resulting in significant reduction in stemborer infestation (Khan *et al.*, 1997b) and higher larval parasitism by *C. sesamiae* (Khan *et al.*, 1997a). Similarly, use of Napier grass, *Pennisetum purpureum* (Schumach), as a trap crop and desmodium, *Desmodium uncinatum* Jacq., as an intercrop in a 'push-pull' system resulted in a significantly lower maize stemborer population and damage to the maize crop than a maize monocrop system in the same region (Khan *et al.*, 1997b; Khan *et al.*, 2000; Khan *et al.*, 2001).

Studies on semiochemicals of the 'push' and 'pull' plants in this system have revealed that the plants emit a host of volatiles (semiochemicals) that influence orientation of the ovipositing moths. The host plants have been shown to produce active compounds such as octanal, nonanal, naphthalene, 4-allylanisole, eugenol and linalool (Khan *et al.*, 2000; Khan and Pickett 2004) which are attractant to the moths. Similarly, desmodium was found to produce volatiles such as ocimene and nonatriene, semiochemicals associated with high levels of stemborer colonisation and plant damage, which are repellent to ovipositing moths (Khan *et al.*, 2000; Khan and Pickett 2004). Using these trap and repellent graminaceous plants, a novel pest management strategy based on a 'push-pull' or stimulo-detterent diversionary strategy has been developed where stemborers are repelled from the food crop and are simultaneously attracted to a discard or trap crop (Khan *et al.*, 1997b; Khan *et al.*, 2000; Khan *et al.*, 2001; Khan and Pickett 2004). This technology is currently being disseminated in Eastern and South Africa among subsistence cereal producers.

1.3 Rationale of the Study

Maize is one of the most important food crops/sources for much of the human population of Africa. One of the major constraints to its efficient production are the lepidopteran stemborers. They are however protected within the stems making their chemical control difficult. As part of continuing efforts to manage these pests, ICIPE and partners have developed a habitat management strategy by use of gramineous and leguminous fodder plants that provide a diversionary strategy whereby stemborers are repelled from the maize and subsequently attracted to a discard or trap crop around the field ('push-pull' strategy).

The European corn borer, *Ostrinia nubilalis* (Hubner), is also a major pest of maize in North America where it causes losses estimated at $8-10/ha. Despite these losses, most farmers have not treated the maize for the European corn borer because no effective, economically viable pest management tactic has been available. Bt maize hybrids, in which a gene from a bacterium, *Bacillus thuringiensis* subsp. *kurstaki* has been sliced into the DNA of maize plants, have the potential to be a viable management option for European corn borer due to its insecticidal properties. Bt-maize therefore represents a promising technology for reducing losses from stemborer infestation in Africa. Currently, Bt-maize hybrids are used to manage *B. fusca* in South Africa. There are however potential risks that need to be investigated. These include its impact on non-target arthropods, which include natural enemies of stemborers, and arthropod and soil faunal abundance and diversity and development of resistance within stemborer populations. To manage resistance, it is a requirement that a minimum of 20% of each Bt-maize field be planted with non-transformed maize as a 'refuge' where borer larvae are not exposed to plants with Bt toxin. This refuge area provides a pool of borer adults, with Bt-susceptible alleles, to mate with any resistant survivors emerging from the Bt-maize, thus prolonging the local population's susceptibility to Bt-toxin. This has a complication in that most small-scale farmers will not be able to create the required buffer zone or allocate land for a 'refugia'. Similarly, data have emerged showing contamination of refuges by Bt toxin genes from the surrounding Bt maize resulting from pollen transfer (Chilcutt and Tabashnik, 2004).

The ‘push-pull’ system is an ideal option as it does not require a separate field for refugia and is manageable by small-scale farmers. Additionally, this habitat management system and other strategies may be strategically combined with Bt-maize, both for added stemborer control and to provide the refuges necessary for insect resistance management. In employing these technologies for stemborer management, it was desirable to investigate how the pest’s natural enemy populations and activity levels and arthropod biodiversity are influenced by them individually and combined, by closely monitoring these populations in maize monocrop systems, ‘push-pull’ system and a combination of the "push-pull" and Bt technology. This would contribute to the understanding of the impact of ‘push-pull’, Bt-maize and ‘push-pull’-Bt-maize on target, non-target and arthropod and soil faunal abundance and diversity in the dominant maize cropping systems of Africa.

1.4 Hypotheses

1 The ‘push-pull’ system and Bt-maize have no impact on population and activity of maize stemborer natural enemies.

2 Excluding stemborer predators has no influence on stemborer population dynamics under ‘push-pull’ systems and Bt-maize.

3 There is no difference in ground-dwelling arthropod abundance and diversity between ‘push-pull’ and maize monocrop systems.

4 Bt-maize has no impact on abundance and diversity of ground dwelling arthropod and springtail species.

6 'Push-pull' and maize monocrop systems have similar pest management benefits.

1.5 Objectives

1.5.1 General objective

To establish the potential of the 'push-pull' system and Bt-maize in pest management and sustainable food production through their impact on stemborer natural enemy abundance and activity levels and faunal diversity in the dominant maize cropping systems of Africa.

1.5.2 Specific objectives

1 To assess the numerical and efficacy response levels of maize stemborer natural enemies to the 'push-pull' system and Bt-maize (test of enemies hypothesis).

2 To assess the response of stemborer predators and their importance in the stemborer population dynamics through exclusion studies under the 'push-pull' system and Bt-maize.

3 To determine the impact of the 'push-pull' system and Bt-maize on abundance and diversity of ground dwelling arthropods.

4 To assess the impact of the 'push-pull' system and Bt-maize on springtail abundance and diversity.

5 To assess stemborer management benefits of the 'push-pull' system and Bt-maize.

CHAPTER TWO

2. IMPACT OF THE 'PUSH-PULL' SYSTEM ON MAIZE STEMBORER NATURAL ENEMY ABUNDANCE, DIVERSITY AND ACTIVITY

2.1 Introduction

One of the major constraints to efficient cereal production in sub-Saharan Africa is insect pests (Ajayi, 1998; Kfir, 1998; Seshu Reddy, 1998), with Lepidopteran stemborers being the most damaging (Zhou *et al.,* 2001). Despite the large number of control strategies available, many small-scale farmers still do not actively control stemborers (Chitere and Omolo, 1993, Grisley, 1997; van den Berg *et al.,* 1998; Bonhof, 2000; Ebenebe *et al*., 2000a).

The polyphagous nature of stemborers enables them to exploit non-cultivated hosts when the cultivated ones are unavailable (Ngi-Song *et al*., 1996). It has been suggested that as a control strategy, these wild hosts be destroyed (Lawali, 1982; Seshu Reddy, 1983). It has however been shown in recent studies that the wild hosts, especially the graminaceous hosts, are important in the ecology of the stemborers (Khan *et al*., 1997a, b). Preference of stemborers for some of these hosts has been exploited in the 'push-pull' strategy (Chapter one) for use in managing these pests.

There are several factors that impact on stemborer populations at all their life stages (Midega *et al.,* 2005), with natural enemies as the main biotic factors responsible for stemborer population reduction in Africa (Bonhof, 2000). This 'push-pull' system has been shown to lower stemborer populations. However, the impact of this system on stemborer natural enemies has not been determined. Studies were therefore conducted to evaluate the occurrence levels of stemborers and their natural enemies under the 'push-pull' system in Kenya and South Africa.

2.2 Materials and methods

2.2.1 Study sites

Kenya: The studies were conducted in experimental fields at Homabay Farmers Training Centre (Homabay) in Homabay District (0°31′S, 34°27′E) and Lambwe School of the Deaf (Lambwe) (0°34′S, 34°22′E) in Suba District of western Kenya.

South Africa: The studies were conducted at the ARC-Grain Crops Institute (26°43′S, 27°06′E), Potchefstroom, North West Province, South Africa.

2.2.2 Plots layout

Kenya: 4 plots measuring 40 m by 40 m were established at Homabay. Napier grass was planted around two of the plots. Maize was planted in rows in all the plots at a spacing of 0.8m between the rows and an intra-row spacing of 0.3 m. Silverleaf desmodium was then planted between the rows of maize in the two Napier grass-surrounded plots ('push-pull'). The plots without Napier grass and desmodium formed the controls (maize monocrop). Each of these fields was subdivided into four subplots measuring 15m by 15m from where data were collected. Plots were laid out in the same manner at Lambwe where also four fields were established and subdivided as above.

South Africa: The layout above was repeated in four fields. Treatments consisted of Bt-maize (Phb 33A14) and its susceptible isoline (Phb 33 A13). Both had a monocrop and 'push-pull' set up. In each field, four plots were created measuring 15m by 15m. The current studies were conducted only in the non-Bt-maize plots.

2.2.3 Incidence of stemborer natural enemies

Monitoring commenced one to two weeks after crop emergence and was conducted by hand-collecting any potential predators that crawl and using yellow sticky traps for flying predators. Hand collection was carried out early in the morning in dry weather. Ten maize plants were randomly selected in each subplot and inspected for stemborer life stages and potential predators by:

1. briefly checking all plant parts for fast moving insects without touching it;
2. thoroughly checking all plant parts for other arthropods including stemborer egg batches;
3. dissecting the plants for the presence of stemborer larvae and pupae;
4. Hand-collecting arthropods on and around the plant within a radius of 15 cm.

The yellow sticky traps were held above maize plants just before hand collection of insects and inspected immediately after the hand collection was over. Specimens were preserved in 70% alcohol in the laboratory for identification. The stemborer life stages collected were used for subsequent studies (2.2.4-2.2.6). The procedure was repeated fortnightly until physiological maturity of the maize crop. The potential predators were identified at the ARC-Plant Protection Research Institute, Pretoria, South Africa and ICIPE-Thomas Odhiambo Campus, Mbita, Kenya (ICIPE-Mbita).

2.2.4 Stemborer egg parasitism

All stemborer egg batches recovered from the sampling procedure above (2.2.3) were cut out with a portion of the leaf and taken to the laboratory (under ambient temperature) individually in labeled glass vials (0.06 m * 0.026 m) and the eggs counted under a dissecting microscope. The healthy ones were observed in these vials (placed in large plastic containers on wooden shelves) until they hatched, parasitoids emerged, or failed to develop after two weeks. The vials were corked with cotton wool to prevent escape of emerging larvae and parasitoids. To prevent desiccation of the eggs, blotting paper was placed under the egg batches and a few drops of water applied to it every two days. Data obtained were expressed as percentage of eggs parasitized per plot.

2.2.5 Larval and pupal parasitism

Both dead and live larvae and pupae recovered from the sampling procedure above (2.2.3) were taken to the laboratory for observation. Live larvae were placed individually in vials with natural diet (pieces of maize stalks) until they pupated or died. Similarly, pupae were kept until they emerged as adults or died. These were checked daily for parasitoid emergence. The parasitoids were preserved in 70% alcohol and representative samples sent to ICIPE-Mbita for identification. Data were expressed as percentage larval and pupal parasitism per plot.

2.2.6 Larval and pupal mortality

Dead larvae and pupae obtained from the same sampling program (2.2.3) and those that died while being held in the laboratory (see larval and pupal parasitism) were counted (the parasitised ones were excluded from this category). These were used to test for the possibility that microbial mortality agents might be affected by the 'push-pull' strategy. No further attempts were made to identify the cause of death due to the complexity of the process in relation to the facilities available. The data were expressed as percentage larval and pupal mortality per plot.

2.3 Data analysis

Data were averaged for each plot and site. For stemborer predator species diversity studies, Shannon's, H', diversity index (Shannon and Weaver, 1949) was calculated for each plot and site thus;

$$H' = -\sum_{i=1}^{s} \frac{n_i}{n} \log \frac{n_i}{n},$$

where S is the number of species in a sample; n_i is the number of individuals belonging to species i; and n = the number of individuals in a sample from a population.

The data were then subjected to t-test analysis (SAS Institute, 2001) for comparing differences between the 'push-pull' and maize monocrop systems in terms of parasitism rates and mortality for stemborer life stages, overall predator populations and species diversity per plot for each site. Because very minimal and more often insignificant numbers of stemborer life stages were recovered during sampling, ratios of the natural enemies in relation to stemborer density could not be calculated. Results (means) are presented in figures.

2.4 Results

Lepidopteran pest species recovered from the study were *C. partellus*, *B. fusca* and *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) at all sites.

2.4.1 Stemborer egg parasitism

Mean percentage stemborer egg parasitism rates caused by *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) ranged between 16.7% and 21.6% in the maize monocrop and 27.3% and 30.2% in the 'push-pull' plots at both Lambwe and Homabay (Fig 1). These rates were significantly higher in the 'push-pull' than in the maize monocrop plots at both sites ($P<0.05$, t-test) (Fig 1). Stemborer egg parasitism rates were however negligible at ARC-GCI and are therefore not reported here.

2.4.2 Larval and pupal parasitism

The larval parasitoids recovered were *Cotesia sesamiae* Cameron (Hymenoptera: Braconidae) and *C. flavipes* Cameron (Hymenoptera: Braconidae) at both Lambwe and Homabay while *C. sesamiae*, and *Bracon* sp. (Hymenoptera: Braconidae) were recovered from ARC-GCI. The pupal parasitoid *Dentichasmias busseolae* Heinrich (Hymenoptera: Ichneumonidae) was recovered at all sites. Because of very minimal larval and pupal parasitism rates, the data were combined into larval-pupal parasitism. Mean stemborer larval and pupal parasitism rates ranged between 10.5% and 13.5% in the maize monocrop and 18% and 24.6% in the 'push-pull' plots at Lambwe, Homabay and ARC-GCI (Fig 2). These rates were significantly higher in the 'push-pull' than maize monocrop plots at all sites ($P<0.05$, t-test).

2.4.3 Larval and pupal mortality

Mean stemborer larval and pupal mortality rates ranged between 9.5% and 15% in the maize monocrop and 12.5% and 20.1% in the 'push-pull' plots at Lambwe, Homabay and ARC-GCI. These rates were however not different between the two cropping systems ($P>0.05$, t-test). The majority of the larvae and pupae in this category had a characteristic dark (black) coloration of the entire body suggesting a microbial mortality factor (Hoekstra and Kfir, 1997; Ogol *et al.*, 1998; Midega *et al.*, 2004). These results therefore suggest that the microbial mortality factors were not affected by the vegetation and cultural structure of the 'push-pull' cropping system.

2.4.4 Stemborer predator abundance and diversity

Several generalist predator taxa from the two major arthropod classes (Insecta and Arachnida) were recovered (Table 1). These predators were significantly more abundant in the 'push-pull' than maize monocrop systems ($P<0.05$) at all sites. Species diversity was however not significantly different between the two cropping systems.

2.5 Discussion

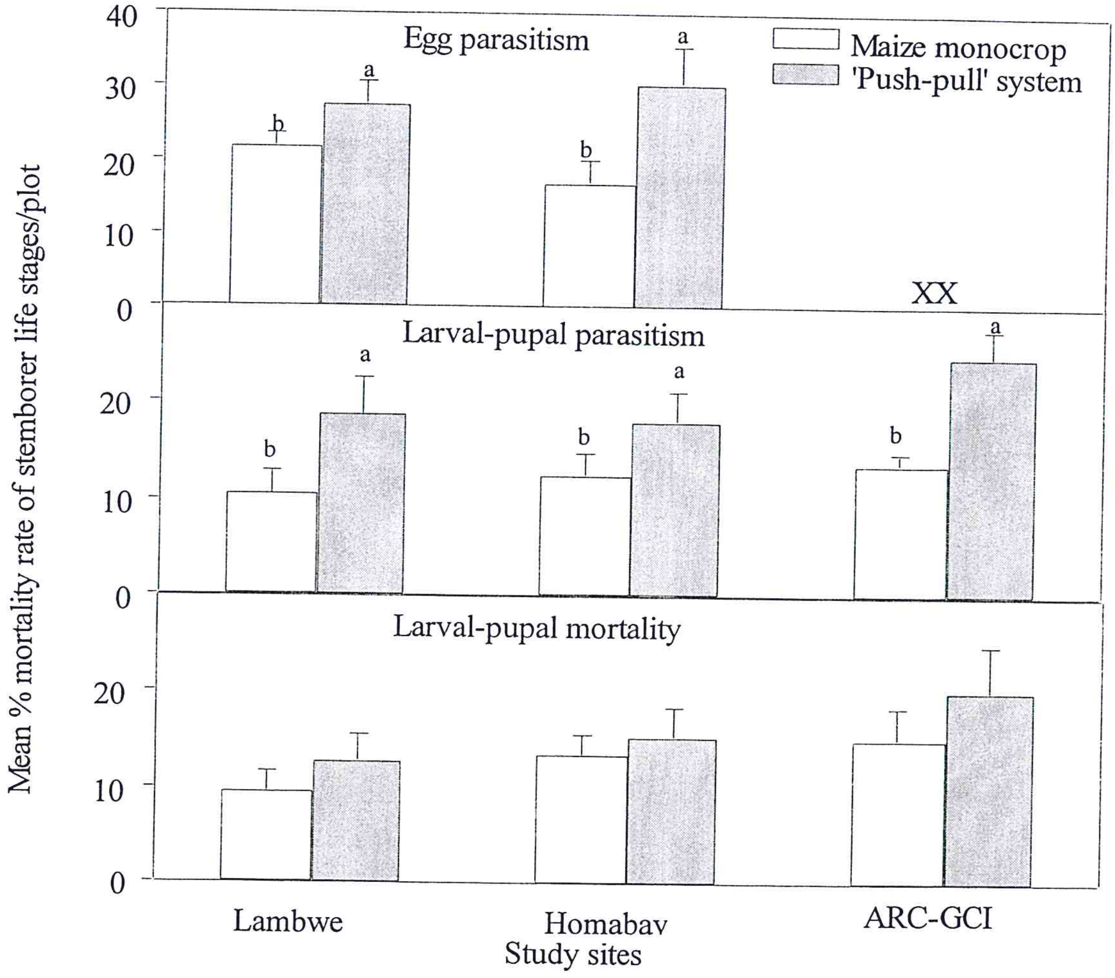
That plant odors play an important role in the foraging behavior of natural enemies of herbivores, particularly parasitic wasps, has been recognized for a long time (reviewed by Nordlund *et al.*, 1988; Turlings *et al.*, 1998). Parasitoids in search of stemborer larvae as hosts use volatiles emitted by herbivore-damaged plants to locate their prey (Mattiacci *et al.*, 1994; Turlings *et al.*, 1998).

Studies have revealed that the 'push-pull' system is associated with significantly reduced stemborer populations and plant damage (Khan *et al.*, 1997a, 2000, 2001; Khan and Pickett, 2004). Similarly, studies have shown that desmodium produces volatiles similar to those associated with high stemborer infestation, such as ocimene and nonatriene, which are repellent to ovipositing moths (Khan and Pickett, 2004) but attractant to stemborer parasitoids (Ngi-Song *et al.*, 2000). The results of the current study therefore imply that recruitment of the parasitoids is due largely to the effect of these volatiles as plant damage caused by stemborers was significantly lower in the 'push-pull' than in the maize monocrop (chapter six). These results are similar to those of Khan *et al.* (1997b) who found that intercropping maize with molasses grass, *Melinis minutiflora* Beauv, increased stemborer parasitism rates by *C. sesamiae*. Furthermore, diverse habitats offer more important requisites for adult parasitoids such as nectar at more times in a cropping season than monocultures (Vinson, 1981), consumption of which increases their longevity and fecundity (Russel, 1989). These data however need to be interpreted with care since the stemborer populations were significantly lower in the 'push-pull' than in the maize monocrop systems (chapter six).

In this study, mortality attributable to pathogens was not influenced by the cropping system. These results are consistent with those of Williams *et al.* (1995) who reported that the incidence of the entomopathogenic fungus, *Nomuraea riley* (Farlow) Sampson, was not significantly different between green cloverworms, *Hypena scabra* (Fabricius), in a monocropped soybean and those in soybean intercropped with sorghum. Ogol *et al.* (1998) also found that alley cropping leucaena, *Leucaena leucocephala* (Lam.) de Wit, and maize did not influence the activity of microbial agents against maize stemborers. Similarly, Midega *et al.* (2004) concluded that alley cropping leucaena and gliricidia, *Gliricidia sepium* Jacq. (Steud), in different intercropping combinations with cowpea, *Vigna unguiculata* L., did not have any effect on pathogens. Ogol *et al.* (1998) suggested that the microclimate in the crop canopy created by intercropping would have little influence on the climatic conditions inside the plant stems where older larvae and pupae reside and so the incidence of microbial agents are expected to remain fairly uniform in any cropping system, a plausible explanation for the trend in the current study.

Results indicate enhanced predator populations and support the findings of Midega and Khan (2003) who reported enhanced stemborer predator abundance in the 'push-pull' system. Natural enemy hypothesis (Root, 1973) predicts that natural enemies will be more abundant in vegetationally diverse agroecosystems due to greater diversity of additional prey which becomes available at different times in addition to suitable microhabitats, supported by the current study. Due to significantly lower stemborer populations in the 'push-pull' than in the maize monocrop systems, the observation in the current study imply that the numerical response of the predators were as a result of factors other than stemborer populations, such as lower soil temperature and higher relative humidity (Khan *et al*., 2002), herbivores associated with desmodium and Napier (as suggested by Midega and Khan, 2003) and other benefits associated with such polycultures (Andow, 1991).

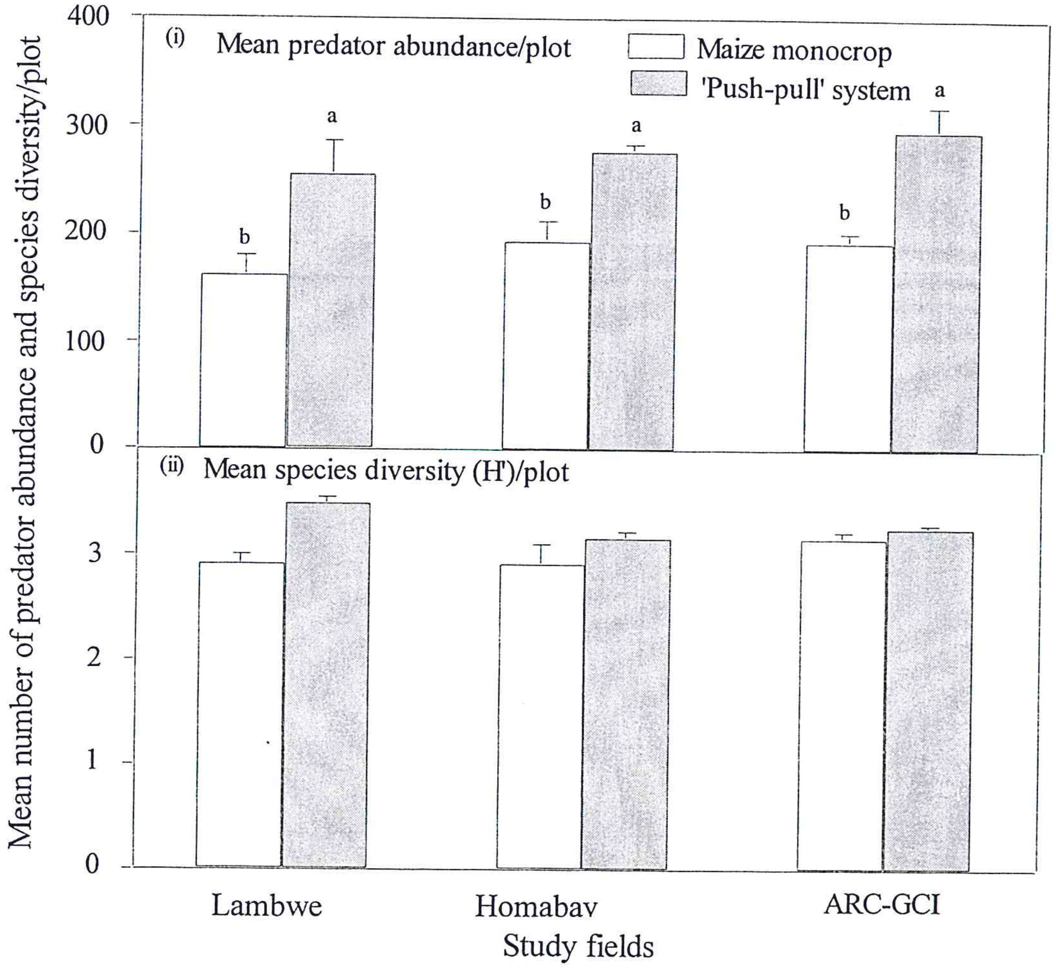
Leigh *et al*. (1974) showed both plant density/cover and moisture content to be positively correlated with the densities of *Orius tristicolor*, a generalist predator, in cotton fields. Thus, the altered microclimate caused by desmodium, a high-ground-cover, and Napier grass may have played a role in making the habitats more suitable for the predators. These results are similar to those of Shrewsburry (1996) who concluded that diverse and structurally complex plant communities support a higher diversity and abundance of natural enemies resulting in better regulation of phytophagous insects. Moreover, there are indications that generalist predators stay relatively longer in diverse ecosystems with ground cover than in simple ones (Russel, 1989). From the foregoing, it is evident that the 'push-pull' system described here has a potential in controlling stemborers through reduced recruitment of the moths and enhanced natural enemy abundance and activity.



XX- Insignificant stemborer egg parasitism at ARC-GCI

Key:
Lambwe- Lambwe School of the deaf
Homabay- Homabay Farmers Training Centre
ARC-GCI- ARC-Grain Crops Institute

Fig 1. Mean (±SE) stemborer egg parasitism, larval-pupal parasitism and mortality per plot at Lambwe, Homabay and ARC-GCI. Means represent data averages over two cropping seasons. Within a study site and mortality factor, bars marked with different letters are significantly different ($P<0.05$). The unmarked bars are not significantly different



Key: As in fig 1.

Fig 2. Mean stemborer (i) predator populations and (ii) species diversity at Lambwe, Homabay and ARC-GCI per plot. Means represent data averages of two cropping seasons in each site. Within each study site, bars marked with different letters are significantly different (P<0.05). The unmarked bars are not significantly different.

Table 1. Presence (+) and/or absence (-) in the 'push-pull' and maize monocrop plots of the various taxa observed in the study

Predator/predator group	Lambwe		Homabay		ARC-GCI	
	mm	pp	mm	pp	mm	pp
1. INSECTA						
Hymenoptera						
Formicidae						
Crematogaster sp1	+	+	+	+	-	-
Crematogaster sp2	+	+	+	+	-	-
Camponotus sp. 1	+	+	+	+	-	-
Camponotus sp. 2	+	+	+	+	-	-
Camponotus sp. 3	-	-	-	-	+	+
Dorylus sp. 1	+	+	+	+	-	-
Dorylus sp. 2	+	+	+	+	-	-
Dorylus sp. 3	-	-	-	-	+	+
Pheidole sp 1	+	+	+	+	-	-
Pheidole sp 2	+	+	+	+	-	-
Pheidole sp. 3	-	-	-	-	+	+
Unidentified sp. 1	-	-	-	-	+	+
Unidentified sp. 2	-	-	-	-	+	+
Unidentified sp. 3	-	-	-	-	+	+
Dermaptera						
Forficulidae						
Diaperasticus erythrocephala	+	+	+	+	-	-
Forficular auricularia	+	+	+	+	-	-
Unidentified sp.	+	+	+	+	-	-

Labiduridae						
Labidura riparia	-	-	-	-	+	+
Labidura sp.	-	-	-	-	+	+
Heteroptera						
Chrysopidae						
Chrysopa sp.	-	+	-	+	-	-
Coreidae						
Anoplocnemis sp.	+	+	-	+	+	+
Unidentified sp.	-	-	-	-	+	-
Coleoptera						
Carabidae						
Notonomus sp.	+	+	-	+	-	-
Pterostichus sp.	-	+	+	+	-	-
Lebia sp.	+	+	+	+	-	-
Stenocalida fasciata	-	+	+	-	-	-
M. latiusculum	-	-	-	-	+	+
Mecyclothorax insolitus	-	-	-	-	+	+
Amblytomus natalicus	-	-	-	-	+	+
Aulacoryssus sp.	-	-	-	-	+	+
Hyparpalus tomentosus	-	-	-	-	+	+
Cratognasus sp.	-	-	-	-	+	+
Panagaeus bipustulatus	-	-	-	-	+	+
Abacetus crenulatus	-	-	-	-	+	+
Unidentified sp. 1	+	+	-	+	-	-
Unidentified sp. 2	+	+	+	-	-	+
Unidentified sp. 3	-	-	-	-	+	+
Staphylinidae						
Phylonthus sp.	+	+	-	+	-	-
Unidentified sp. 1	+	+	+	-	-	-

Unidentified sp. 2	-	-	-	-	+	+
Unidentified sp. 3	-	-	-	-	+	-
Paederus sabaeus	+	+	+	+	-	-
Anthicidae						
Anthicus sp. 1	-	-	-	-	+	+
Anthicus sp. 2	-	-	-	-	+	+
Coccinellidae						
Cheilomenes lunata	-	+	-	+	+	+
Cheilomenes vicina	+	+	-	+	-	-
Cheilomenes sp. 1	-	+	-	+	-	-
Cheilomenes sp. 2	-	-	-	-	+	+
Chilocorus sp.	+	+	-	-	-	-
Unidentified sp. 1	+	+	+	+	-	-
Tenebrionidae						
Gonocephalum simplex	+	+	+	+	+	+
Gonocephalum sp.	+	+	+	+	-	-
Hemiptera						
Reduviidae						
Gardena sp.	-	+	+	-	-	-
Anthocoridae						
Unidenfied sp.	-	-	-	-	+	-
Nabiidae						
Nabis sp.	+	+	-	+	-	-
Unidentified 1	+	+	+	-	-	-

Unidentified 2	-	+	-	+	-	-
Orthoptera						
Gryllidae						
Trigonidium sp.	+	+	+	+	-	-
Gryllus sp.	-	-	-	-	+	+
Teleogrylus sp.	-	-	-	-	+	+
Unidentified sp. 1	-	+	-	-	+	+
Unidentified sp. 2	+	+	-	-	-	-
Dictyoptera						
Blattelidae						
Blatella sp. 1	+	+	+	+	-	-
Blatella sp. 2	-	-	-	-	+	+
Pseudoderopeltis sp.	-	-	-	-	+	+
2 ARACHNIDA						
ARANEAE						
Araneidae						
Araneus sp.	+	-	-	-	-	-
Kilima decens	-	-	+	-	-	-
Unidentified sp.	+	+	+	+	-	-
Corinnidae						
Castianeira sp.	+	+	+	+	-	-
Brachyphaea simoni?	-	+	-	+	-	-
Copa sp.	-	+	-	-	-	-
Philodromidae						
Thanatus sp.	-	+	+	+	-	-
Unidentified sp.	+	+	-	+	-	-
Gnaphosidae						
Zelotes oneili	-	-	-	-	-	+
Zelotes sp.	-	+	-	+	-	+
Setaphis subtilis	+	+	-	-		+

Lycosidae						
Pardosa crassipalpis	-	+	+	-	+	+
Pardosa clavipalpis	-	-	-	-	+	+
Lycosa sp.	-	-	-	-	+	+
Trabea sp.	-	-	-	-	+	+
Hippasa sp.	+	+	+	+	-	-
Pardosa sp.	+	+	+	+	+	+
Unidentified sp. 1	-	+	+	+	-	+
Unidentified sp. 2	-	-	+	+	-	+
Unidentified sp. 3	+	+	+	+	-	-
Clubionidae						
Clubiona annuligera	+	-	-	-	-	-
Unidentified sp.	+	+	-	+	-	-
Linyphiidae						
Ostearius melanopygius	-	+	-	-	-	+
Unidentified sp.	-	-	-	-	+	+
Salticidae						
Langona manicata	-	-	-	-	+	+
Pellenes sp.	-	-	-	-	+	+
Stenaelurillus sp.	+	+	+	-	-	-
Unidentified sp. 1	+	+	+	+	+	-
Unidentified sp. 2	+	-	+	+	-	-
Theridiidae						
Euryopis sp.	+	-	+	+	-	-
Theridion sp.	-	+	+	-	-	-

Key: mm Maize monocrop system
pp ‘push-pull’ system

CHAPTER THREE

3. MAIZE STEMBORER PREDATOR ACTIVITY UNDER THE 'PUSH-PULL' SYSTEM AND BT-MAIZE

3.1 Introduction

As described in chapter one, the usefulness of the transgenic cultivars (Bt-maize) may be cut short should the target pests develop resistance to them. The currently recommended resistance management strategy (high-dose/structured refuge strategy) and its assumptions and limitations have also been described in chapter one. Several studies have been conducted to assess the impact of these Bt-crops on the target pests' natural enemies. There has however been limited research on the impact of these natural enemies in resistance management. Any tactic that appreciably reduces the number of individuals of the target pest getting exposed to the Bt-toxin is desirable in an integrated resistance management strategy. Studies have indicated that the 'push-pull' strategy significantly reduces stemborer populations (Khan and Pickett, 2004) and could further play an important role in resistance management. Moreover, Midega and Khan (2003) have shown that this system enhances abundance and diversity of the potential maize stemborer predators.

The objective of the current study was therefore to assess the potential role of the 'push-pull' system in resistance management through its influence on stemborer oviposition and predator activity.

3.2 Materials and methods

3.2.1 Study site and plot layout

The studies were conducted at Lambwe School of the Deaf (Lambwe) in western Kenya and ARC-Grain Crops Institute (ARC-GCI) Potchefstroom, South Africa during the cropping seasons of 2002/2003 and 2003/2004. The fields were as described in chapter two with modifications. A method adapted from Smart *et al.* (1989) and Khan *et al.* (2001) was used to create plots within the established fields at ARC-GCI. Random paired plots of 5 m by 5 m along perpendicular transect lines bisecting both fields were demarcated with six replications in each field.

3.2.2 Oviposition preference and egg predation studies (natural infestation)

For these studies, conducted only at the ARC-GCI, methodologies adapted from Azerefegne and Gebre-Amlak (1994) and Ogol *et al.* (1998) were employed with modifications. Beginning at crop emergence, fortnightly inspection of the foliage of all maize plants in each plot was carried out. Because *B. fusca* prefers to oviposit under the plant's leaf sheath, the presence of its egg batches was felt by running finger tips over the leaf sheaths (Azerefegne and Gebre-Amlak, 1994). The egg batches were then removed by cutting this plant part around the egg batch by use of a scalpel. Newly laid stemborer egg batches were counted and recorded to provide data on oviposition preference. Because very minimal numbers of egg batches were recorded in the 'push-pull' plots, data on oviposition preference from any two plots were combined to obtain enough egg batches for subsequent studies. Five egg batches, each from a single plant, were selected, eggs counted and their locations marked with a permanent marker. On the third day, each egg batch was inspected and its condition recorded as healthy, partially eaten, or missing. Missing or partially eaten egg batches were presumed to have been predated upon (Midega *et al.*, 2004). These data were expressed as percentage of eggs predated upon per plot. All healthy and partially eaten eggs were cut out with a portion of the leaf, taken to the laboratory (under room temperature) in labelled vials and observed until they hatched, parasitoids emerged, or failed to develop after two weeks. Data obtained were expressed as percentage of parasitized eggs per plot.

3.2.3 Exclusion studies (Artificial infestation)

3.2.3.1 Cages

Single plant cages were used at Lambwe for experiments with stemborer eggs and early-instar larvae. Cages measuring 0.4 m by 0.4 m by 0.4 m covered by a mosquito netting mesh of 2 mm were sufficient to completely cover a single maize plant and exclude most predators in the exclusion plants. The nets were buried between 10 and 15 cm into the ground. As an additional precaution to exclude as much as possible the crawling predators, a band/ring of insect trap adhesive (tanglefoot) was applied around the base of the exclusion plants 5 cm above the ground. The control plants had the net removed making them completely exposed. At ARC-GCI, only crawling predators were excluded using insect trap adhesive.

3.2.3.2. Experimental insects

C. partellus was the stemborer species of study at Lambwe1 and Lambwe2 during both cropping seasons while at ARC-GCI, *B. fusca* and *C. partellus* were used during 2002/2003 and 2003/2004 cropping seasons respectively.

3.2.3.2.1. Eggs

Plants (non-transformed) were grown in pots in screen houses at ICIPE-Thomas Odhiambo Campus, Mbita and ARC-GCI with planting dates synchronised with that of plants in the experimental fields, ensuring that plants in the screen house and those in the field were of the same age at the time of the experiment. When two to three weeks old, they were introduced into large cages where stemborer adults from laboratory-reared pupae were allowed to oviposit on them overnight. The egg batches and individual eggs were counted and their location recorded and marked on the opposite leaf surface. These plants were then brought to the experimental fields where four of them were randomly assigned to a treatment (exclusion and control) in each plot for both maize monocrop and the ‘push-pull’ plots. The exclusion plants had trap adhesive applied around the base of the plant stems. After four days, the cages were removed and all plants checked for predators. They were then uprooted; egg batches recovered and their condition determined in the laboratory as either parasitised, partially eaten or non-viable after two weeks. Those that had disappeared and those partially eaten were presumed to have been preyed upon. Data were expressed as percentage disappearance, parasitism and non-viability.

3.2.3.2.2 Early instar larvae

Bonhof (2000) reported negligible recovery of stemborer first-instar larvae in an exclusion study conducted at the Kenyan coast and for that reason second-instar larvae (henceforth called small larvae) were used in this study. Experimental plants in the fields were each covered by a single plant cage (at Lambwe1 and Lambwe2) soon after germination to prevent natural infestation. Four WAE, each plant was randomly assigned to a treatment (exclusion or control), five for each treatment in each plot at Lambwe1 and Lambwe2. Each plant was infested with 10 to 15 small larvae. Five cages were then opened by removing the net (control) while the remaining five were left closed (exclusion) in each plot. Additionally, the exclusion plants had a band of insect trap adhesive around the base of the plant stem. At ARC-GCI, two plants were placed for each treatment per plot. The exclusion plants had an insect trap adhesive applied as above with no cages. Seven days after infestation, the experimental plants were uprooted and dissected to recover the larvae. The trap adhesive was inspected for any predators before dissection. Data were expressed as percentage larval recovery per plot.

3.2.3.2.3 Late instar larvae

Ten non-infested plants at Lambwe1 and Lambwe2 and four at ARC-GCI were randomly selected per plot and randomly assigned to a treatment (control or exclusion) six WAE. All naturally occurring insects were then hand-removed from them. Each plant was infested with three to five fourth-instar larvae (hence called large larvae) by boring holes through the stem and inserting one larva in each hole. The hole was then loosely plugged with soft material from the stem. Predators were kept from exclusion plants by a band of insect trap adhesive applied at the base of the plant stem and around the infestation holes. Six days after infestation, all the experimental plants and trap adhesive were inspected for predators, and following dissection of the stems, the number of recovered larvae was recorded.

3.2.3.2.4 Pupae

When plants were seven to eight weeks old, the above procedure was conducted with stemborer pupae with a little modification. Experimental plants were infested with three pupae (0-1 day old) as with large larvae. The holes were however left unplugged to resemble a natural situation where a mature larva makes an exit hole just before pupation for an emerging moth (Bonhof, 2000). Exclusion plants had an insect trap adhesive around the base of the plant to prevent crawling predators from reaching the plants. The dissection was conducted three days after infestation and the number of pupae recovered recorded.

3.2.3.2.5 Predators

Information on predator abundance was obtained by randomly selecting ten plants per plot and visually observing all parts for any predators. These were hand-collected and taken to the laboratory for observation. The data were expressed as mean number of each predator group per plot.

3.3 Data analysis

Data were averaged for each field and expressed as mean percentage recovery, disappearance, non-viability (eggs), parasitism and mortality. Data on predator abundance were expressed as average number of predator group per plot for each treatment. A t-test analysis was conducted to compare these averages between control and exclusion plants and maize monocrop and the 'push-pull' systems (SAS Institute, 2001) at Lambwe1 and Lambwe2 while one-way Analysis of Variance (ANOVA) using a generalized linear model (SAS Institute, 2001) was used to compare the treatments at ARC-GCI. Pre-planned orthogonal contrasts were then used to test for the effect of Bt-maize under monocrop, Bt-maize under 'push-pull', 'push-pull' under non-transformed maize and 'push-pull' under Bt-maize. These anayses were also used to compare Bt-maize and the 'push-pull' technologies. Results are presented in figures and table.

3.4 Results

3.4.1 Oviposition preference and egg predation studies (natural infestation)

Significantly higher numbers of *C. partellus* egg batches were recorded in the maize monocrop than in the 'push-pull' treatments at ARC-GCI ($P<0.05$) (Fig 3). There were however no significant differences in the number of egg batches between the non-Bt maize and Bt-maize monocrops for both stemborer species. Similarly, there were no significant differences between the Bt-maize under 'push-pull' and non-Bt maize under 'push-pull' system with regard to the number of stemborer egg batches for both species (Fig 3).

Predation of *B. fusca* eggs was negligible and therefore not reported here. Predation rates of *C. partellus* eggs were significantly higher in the 'push-pull' than in the monocrop treatments ($P<0.05$) (Fig 3). Parasitism and non-viability rates were negligible.

3.4.2 Exclusion studies (Artificial infestation)

3.4.2.1 Eggs

Disappearance of *C. partellus* eggs was significantly higher on the control plants (those exposed to predators) than on the exclusion plants in both cropping systems in both fields during both cropping seasons ($P<0.05$). Similarly, the disappearance of the eggs was significantly higher in the 'push-pull' than in the maize monocrop plots in both fields during the two cropping seasons ($P<0.05$) (Fig 4). The egg disappearance from the control plants in the 'push-pull' plots ranged from 12 to 65% at Lambwe1 and 39 to 51% at Lambwe2 in 2002 and 39.6% to 78.6% and 59.5 to 78.8% respectively in 2003 (Fig 4). In the maize monocrop plots, the range was from 11 to 49% at Lambwe1 and 25 and 41% at Lambwe2 in 2002 and 11.4% to 58.2 % and 27.6 to 52.3% respectively in 2003 (Fig 4).

At ARC-GCI, disappearance rates of *B. fusca* eggs were not significantly different between the control and the exclusion plants (P>0.05). They were also not significantly different among treatments. In the control plants the disappearance rates in the non-Bt maize under 'push pull', non-Bt maize monocrop, Bt-maize under 'push-pull' and the Bt-maize monocrop ranged from 12.5 to 33.3%, 11.1 to 21.3%, 14.5 to 24.5% and 6.5 to 18.5% respectively (P>0.05) (Fig 5). The disappearance rates of *C. partellus* eggs from the control plants were significantly higher in the 'push-pull' (Bt and non-Bt maize) than in the monocrop plots (Bt and no-Bt maize) (P<0.05) (Fig 6) and ranged from 38.5 to 80.3%, 13.5 to 50.6%, 45.9 to 79.8% and 15.3 to 56.5% respectively. These results were corroborated by the pre-planned contrasts, indicating that incorporation of the 'push-pull' technology in both Bt and non-Bt maize enhanced disappearance of *C. partellus* eggs (Table 2).

Egg parasitism of *C. partellus* caused by *Trichogramma* sp. in the control plants was significantly higher in the 'push-pull' than in the monocrop plot at Lambwe2 in 2002 (P<0.05, t-test) (Fig 4), while there were no differences between plants and plots in the remaining fields in the rest of the sites (Figs 4, 5, 6 and Table 2).

Non-viability of *C. partellus* eggs was significantly higher in the exclusion than the control plants at Lambwe1 in 2002 and Lambwe2 in 2003 in both the 'push-pull' and maize monocrop plots but the difference between these two cropping systems was not significant (Fig 4). The rest of the sites registered similar rates of non-viability between exclusion and control plants and cropping systems at Lambwe1 and Lambwe2 and among treatments at ARC-GCI (Figs 4, 5, 6 and Table 2).

3.4.2.2 Small-larvae

Significantly higher numbers of small larvae of *C. partellus* were recovered from the control plants in the maize monocrop than in the 'push-pull' plots at Lambwe1 during both cropping seasons (P<0.05). This recovery ranged from 20 to 75% at Lambwe1 and 39 to 89% at Lambwe2 in 2002 and 24.6 to 68.5% and 35 to 79.2% respectively in 2003 (Fig 7). In the 'push-pull' plots the recovery ranged from 31 to 45% at Lambwe1 and 38 to 57% at Lambwe2 in 2002 and 12.3 to 31.2% and 25.6 to 68.2% respectively in 2003 (Fig 7). At ARC-GCI, recovery of small larvae of *B. fusca* from the control plants ranged from 30 to 85%, 20 to 55%, 15 and 45% and 45 and 85% in non-Bt maize monocrop, non-Bt under 'push-pull', Bt-maize under 'push-pull' and Bt-maize monocrop respectively (Fig 8). There were significant differences between the monocrop plots and those under the 'push-pull' system (P<0.05) (Fig 7 and Table 2). The recovery of small larvae of *C. partellus* from the control plants ranged from 35 to 70%, 15 to 40%, 10 to 40% and 40 to 70% respectively with significant differences between monocrop and the 'push-pull' plots (P<0.05) (Fig 8 and Table 2). Recovery was however not significantly different between the control and exclusion plants (P>0.05) in all cases.

3.4.2.3 Large larvae

Recovery of large larvae of both *C. partellus* and *B. fusca* was not significantly different between the control and exclusion plants in all the fields under study. However, there were significantly more *C. partellus* larvae recovered from the control plants in the maize monocrop than in the 'push-pull' plots at Lambwe1 in 2002. Recovery from the control plants in the monocrop plots ranged from 76 and 85% at Lambwe1 and 58 to 95% at Lambwe2 while in the 'push pull' system it ranged between 35 and 65% at Lambwe1 and 23 and 87% at Lambwe2 (Fig 7) in 2002. In 2003, the recovery from the maize monocrop control plants ranged from 45.5 to 90.2% at Lambwe1 and 25.6 to 85.6% at Lambwe2. In the 'push-pull' system the range was from 45.6 to 89% at Lambwe1 and 32.5 to 90.8% at Lambwe2 (Fig 7). At ARC-GCI, recovery of *B. fusca* larvae from the control plants ranged from 20 to 70%, 20 to 60%, 20 to 80% and 20 to 80% in non-Bt maize monocrop, non-Bt maize under 'push-pull', Bt-maize monocrop and Bt-maize under 'push-pull' respectively (Fig 9). The recovery of *C. partellus* larvae ranged from 25 to 80%, 25 to 85%, 45 to 75% and 25 to 70% respectively (Fig 8), with no significant differences between treatments (P>0.05). Larval mortality due to parasitism and microbial pathogens were negligible.

3.4.2.4 Pupae

There were generally no significant differences in the numbers of pupae of both species recovered between the control and exclusion plants and treatments within and between cropping systems at Lambwe1 and Lambwe2 sites (Fig 7). Similarly, the recovery rates did not significantly differ among treatments at ARC-GCI (P>0.05), except for the Bt-maize and non-Bt maize monocrops (P<0.05) (Table 2).

The recovery of *C. partellus* pupae from the control plants in the maize monocrop plots ranged from 65 to 87% at Lambwe1 and 58 to 95% at Lambwe2 in 2002. In the same period, the recovery from the 'push-pull' plots ranged from 55 to 92% at Lambwe1 and 78 to 98% at Lambwe2 (Fig 7). In 2003, the recovery from the maize monocrop ranged from 35 to 89.6% at Lambwe1 and 24.6 to 95.5% at Lambwe2 while in the 'push-pull' plots, the ranges were from 25 to 90.5% at Lambwe1 and 35.8 to 78.2% at Lambwe2 (Fig 7). At ARC-GCI, the ranges were 55 to 85%, 65 to 90%, 30 to 80% and 25 to 85% in the non-Bt maize monocrop, non-Bt maize under 'push-pull', Bt-maize under 'push-pull' and the Bt-maize monocrop respectively (Fig 8). The recovery of *B. fusca* pupae however, ranged from 16.7 to 66.7%, 33.3 to 66.7% 16.7 to 66.7% and 16.7 to 66.7% respectively (Fig 9).

3.4.2.5 Predators

Ants, earwigs and spiders were recorded in significantly larger numbers than other predatory arthropods at Lambwe1 and Lambwe2 while earwigs and spiders seemed to be the most important at ARC-GCI (Fig 10 and 11). Their populations were significantly higher in the 'push-pull' than in the maize monocrop plots at all sites (P<0.05).

3.5 Discussion

Insect pests generally evolve in response to natural selection imposed by control efforts (Hawthorne, 1998). This evolution can limit the long term effectiveness of both traditional resistant and transgenic crop cultivars. However, there may be opportunities to slow or prevent the selection for resistance before the control technology is rendered ineffective (Hawthorne, 1998). Any strategy that reduces the size of the target population at the risk of developing resistance is therefore a useful component in an integrated resistance management. Because natural enemies play a crucial role in population dynamics of stemborers (Oloo, 1989), and because habitat management significantly reduces stemborer populations (Khan *et al.*, 1997a, b; 2000; 2001), it appeared likely that this system could play a role in resistance management through reduction of the stemborer population getting exposed to the Bt-toxin.

Results show that of the total number of stemborer egg batches recovered in the plots, each of the two the 'push-pull' treatments received less that 15% during both cropping seasons. Earlier workers have reported attractiveness of Napier grass for oviposition by stemborer moths (Khan *et al.*, 1997a; van den Berg *et al.*, 2001) and the role of desmodium in repelling the same (Khan *et al.*, 2000, 2001; Khan and Pickett, 2004). Semiochemistry studies of the 'push' and 'pull' plants in this system have revealed that the plants emit a host of volatiles (semiochemicals) that influence orientation of the ovipositing moths. The host plants have been shown to produce active compounds such as octanal, nonanal, naphthalene, 4-allylanisole, eugenol and linalool (Khan *et al.*, 2000; Khan and Pickett, 2004) which are attractant to the moths. Similarly, desmodium was found to produce volatiles such as ocimene and nonatriene, semiochemicals associated with high levels of stemborer colonisation and plant damage, which are repellent to ovipositing moths (Khan *et al.*, 2000; Khan and Pickett, 2004). The combined attractiveness of Napier grass and repugnant property of desmodium therefore ensured that lower numbers of moths settled and oviposited on the maize crop. Furthermore, previous studies have shown that under natural conditions only about 5% of stemborer eggs oviposited produce adults that survive to die of old age (Mathez, 1972; Oloo, 1989). Additional reduction in the number of oviposited eggs like in the current study therefore further reduces this proportion resulting into much lower populations of the surviving adults.

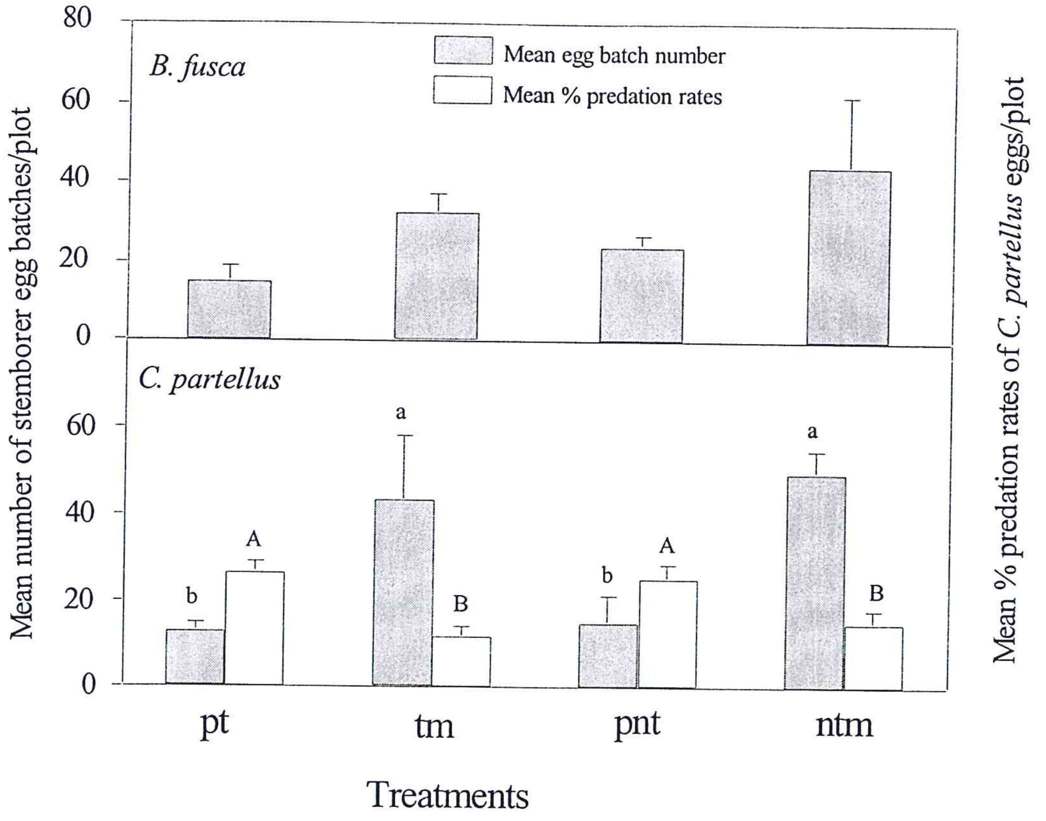
The underlying principle of exclusion studies is that the host population is observed in the presence and absence of natural enemies and any loss or reduction in host population from the plants exposed is attributed to the 'excluded' natural enemy (Luck *et al.*, 1988). These results therefore demonstrate enhancement of stemborer egg predator efficiency, especially on *C. partellus* eggs, since there were significantly higher egg disappearance levels in the 'exposed' than in the excluded plants in all cases. Similarly, the 'exposed' plants registered significantly higher disappearance of stemborer eggs in the 'push-pull' than in the maize monocrop treatments, with disappearance rates of >60% in the latter. These results are consistent with those of Phoofolo *et al.* (2001) who observed that egg masses of the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Crambidae), in the control cages were significantly more preyed upon than those in the exclusion cages. Predation rates were similarly higher in the 'push-pull' treatments than in the maize monocrops under natural infestation.

Numerically, ants, which are confirmed stemborer egg predators (Bonhof, 1998, 2000; Midega, 2001; Midega and Khan, 2003; Midega *et al.*, 2004), were significantly higher in the 'push-pull' than in the maize monocrop treatments, probably accounting for their higher efficacy. Ants have been observed to remove egg batches from the plant leaves and stems without leaving traces (Bonhof, 2000). *B. fusca* eggs are normally oviposited concealed behind leaf sheaths (Smith *et al.*, 1993; Azerefegne and Gebre-Amlak, 1994; Bonhof, 1998) and were therefore not easily predisposed to predation yielding the results. Bt-maize, however, did not seem to have any adverse effect on the populations of the predators encountered.

The enemies hypothesis (Root, 1973) which postulates that natural enemies of pests are more abundant and effective in complex systems than simple ones is supported by data on stemborer egg predators in the current study. The presence of desmodium and Napier grass seems to modify the agroecosystem in a number of ways making it attractive to the predators. The observation that the 'push-pull' system is positively associated with enhanced generalist predator numerical levels (Midega and Khan, 2003) is corroborated in the current study. Studies have also shown that stemborer populations are lower in the 'push-pull' than in the maize monocrop systems (Khan *et al.*, 1997a, b; Khan *et al.*, 2000, 2001). The presence of higher numerical levels of these generalists in the former therefore is not as a response to stemborer numbers but due to the benefits generated by the associated crops in the system (Midega and Khan, 2003). As explained in a number of studies (reviewed by Russell, 1989 and Andow, 1991), a greater diversity of prey/host species and microhabitats is available within complex environments. As a result, relatively stable populations of generalist predators can persist in these habitats because they can exploit the wide variety of herbivores, which become available at different times or in different microhabitats. Besides, these crops help modify the agroecosystem by lowering soil temperatures (Khan *et al.*, 2002).

Disappearance of small larvae in the study cannot be attributed entirely to predators since recovery was similar in the exposed and the excluded plants in both the 'push-pull' and and in the monocrop treatments. However, the number of small larvae recovered from the control plants was significantly lower in the 'push-pull' than in the maize monocrop treatments during both cropping seasons, with a disappearance rate of >70% in the latter. Harvey and Eubanks (2004) observed that predation of diamondback moth, *Plutella xylostella* (L.), was significantly higher in collard-white clover intercrops than in collard monocrops. Rainfall, starvation, desiccation and cannibalism are confirmed mortality factors operating on early instar larvae alongside predators (Bonhof, 2000) and might have played a significant part in their disappearance in this study. Onstad and Gould (1998) have estimated that of the hatching stemborer eggs there is up to 90% neonate dispersal rate through 'spinning' or 'ballooning' (Berger, 1989; Ogol *et al.*, 1999) to adjacent plants. Some of these larvae die during this dispersal (Berger, 1992) and chances of falling on non-hosts, like desmodium, become higher in such a polyculture. In a diverse system, chances of the fallen larvae finding the host are much reduced as compared to a monocrop. Some fallen larvae are also attacked by the predators present on the ground (Bonhof, 2000). Both the 'push-pull' and Bt-maize technologies however had no impact on the predation of late-instar larvae and pupae.

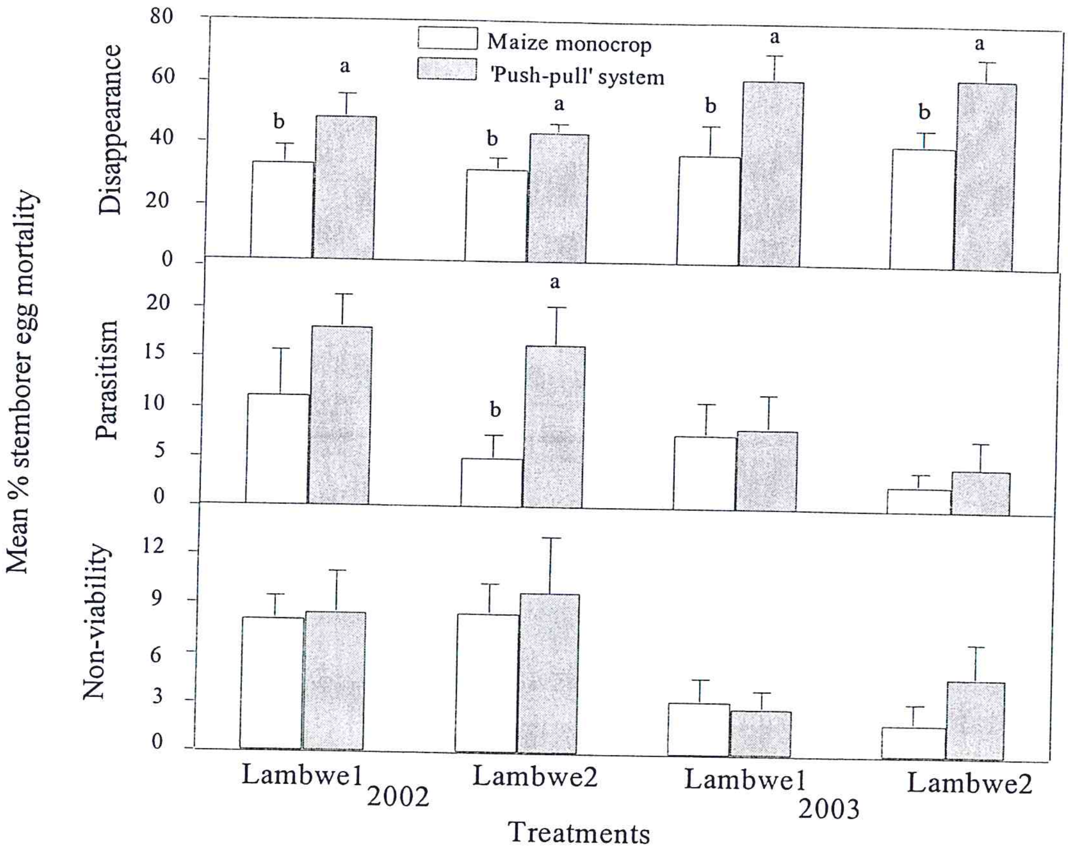
From the foregoing, it appears that incorporating habitat management into Bt-technology reduces oviposition on the maize crop. It also enhances both predator abundance and efficacy, with the latter being more pronounced at the earlier stages of stemborer development. Concern has been raised on a possible negative impact of Bt-toxin on natural enemies when they consume prey fed on the toxin (Dutton *et al.*, 2002). While this warrants further investigation, results of the current study indicate that the strategy is more effective on the adult moth, eggs, and, to an appreciable extent, early instar larvae (through predation and dispersal losses of neonates), stages not contaminated with the toxin. While other stemborer non-maize hosts are likely to act as 'nursery plants' which support partial but not complete stemborer development (Losey *et al.*, 2001), Napier grass in the 'push-pull' system has been shown to support minimal larval survival (van den Berg *et al.*, 2001). It produces a gummy substance which entangles and kills the stemborer larva when it punctures the stem in an attempt to bore into it (Khan and Pickett, 2004). This mechanism could further reduce the population of both resistant and susceptible larvae. These reductions in stemborer populations could be combined with other tactics in an integrated resistance management programme. Moreover, even in a Bt-maize monoculture system just a small proportion of the target pest survives (Catangui and Berg, 2002).



Key:

pt	Bt-maize under 'push-pull'
tm	Bt-maize monocrop
pnt	non-Bt under 'push-pull'
ntm	non-Bt maize monocrop

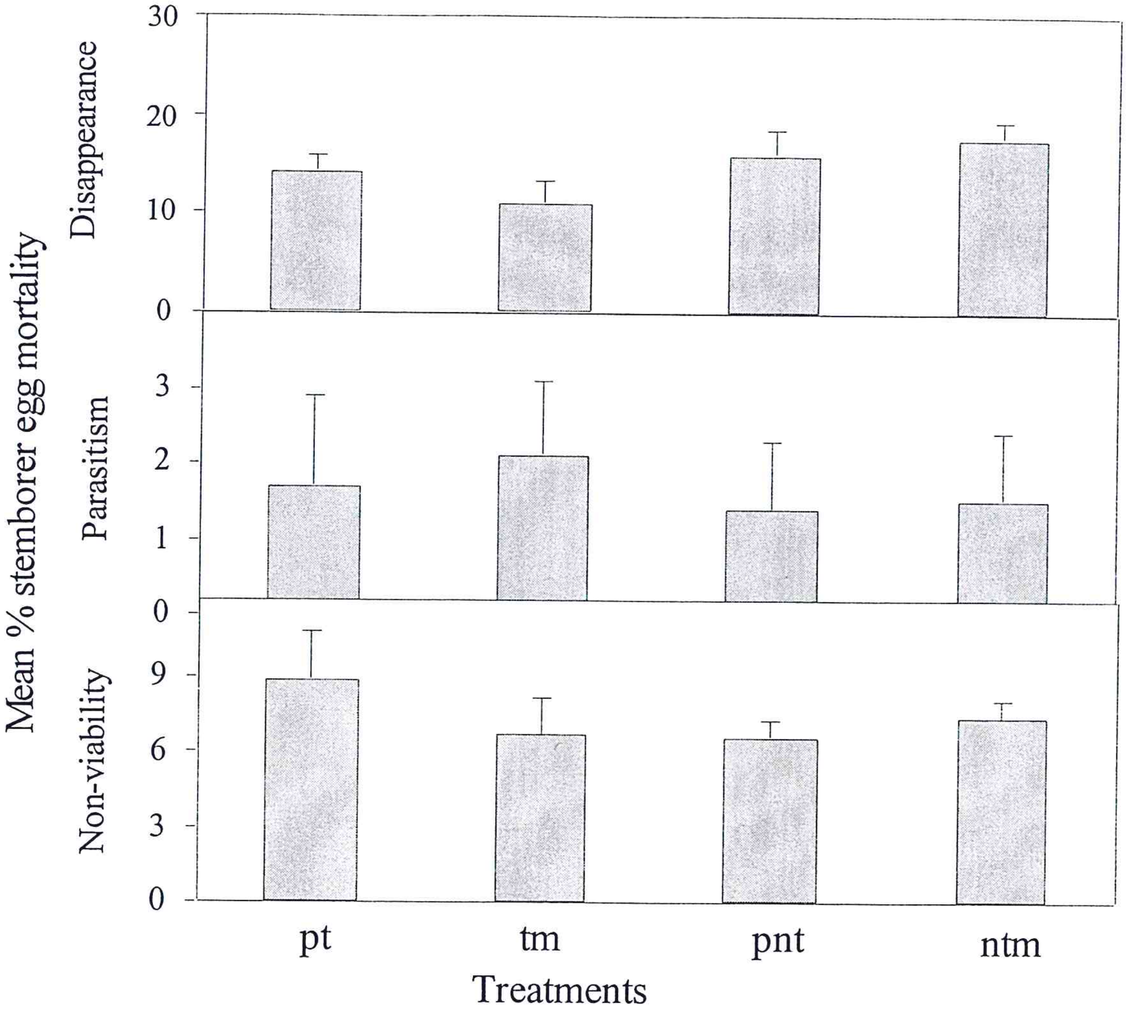
Fig 3. Mean number of stemborer egg batches and predation rates per plot at ARC-GCI. Means represent data averages of two cropping seasons. Bars marked with different letters (lower case for egg batch numbers and upper case for predation rates) are significantly different ($P<0.05$).



Key:

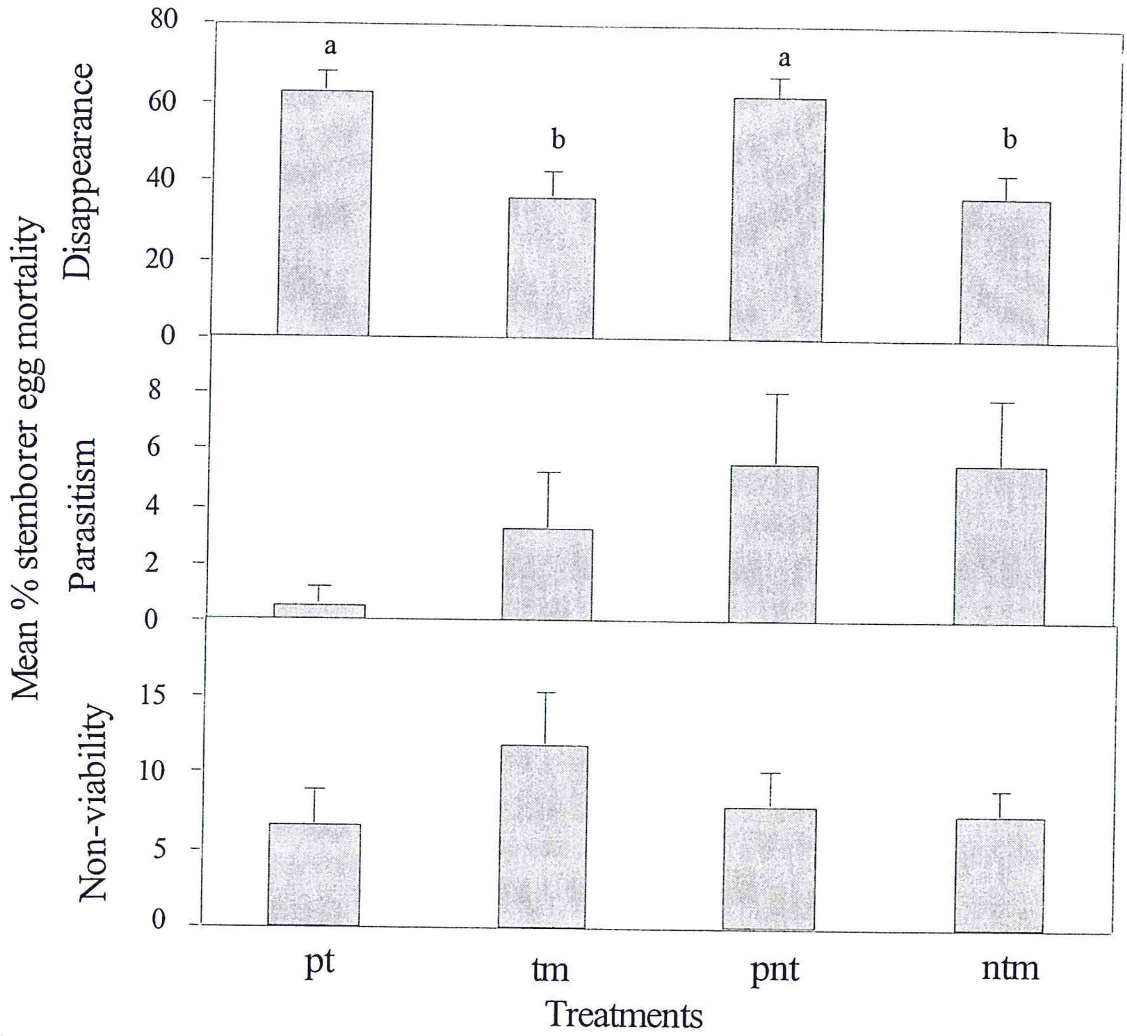
Lambwe1	Lambwe School of the Deaf Field One
Lambwe2	Lambwe School of the Deaf Field Two

Fig 4. Mean (± SE) disappearance, parasitism and non-viability of *C. partellus* eggs on plants exposed to natural enemies at Lambwe1 and Lambwe2 during 2002 and 2003 cropping seasons. Means represent data averages for 4 plots in each cropping system. Within a field, bars marked with different letters are significantly different ($P<0.05$). The unmarked bars are not significantly different.



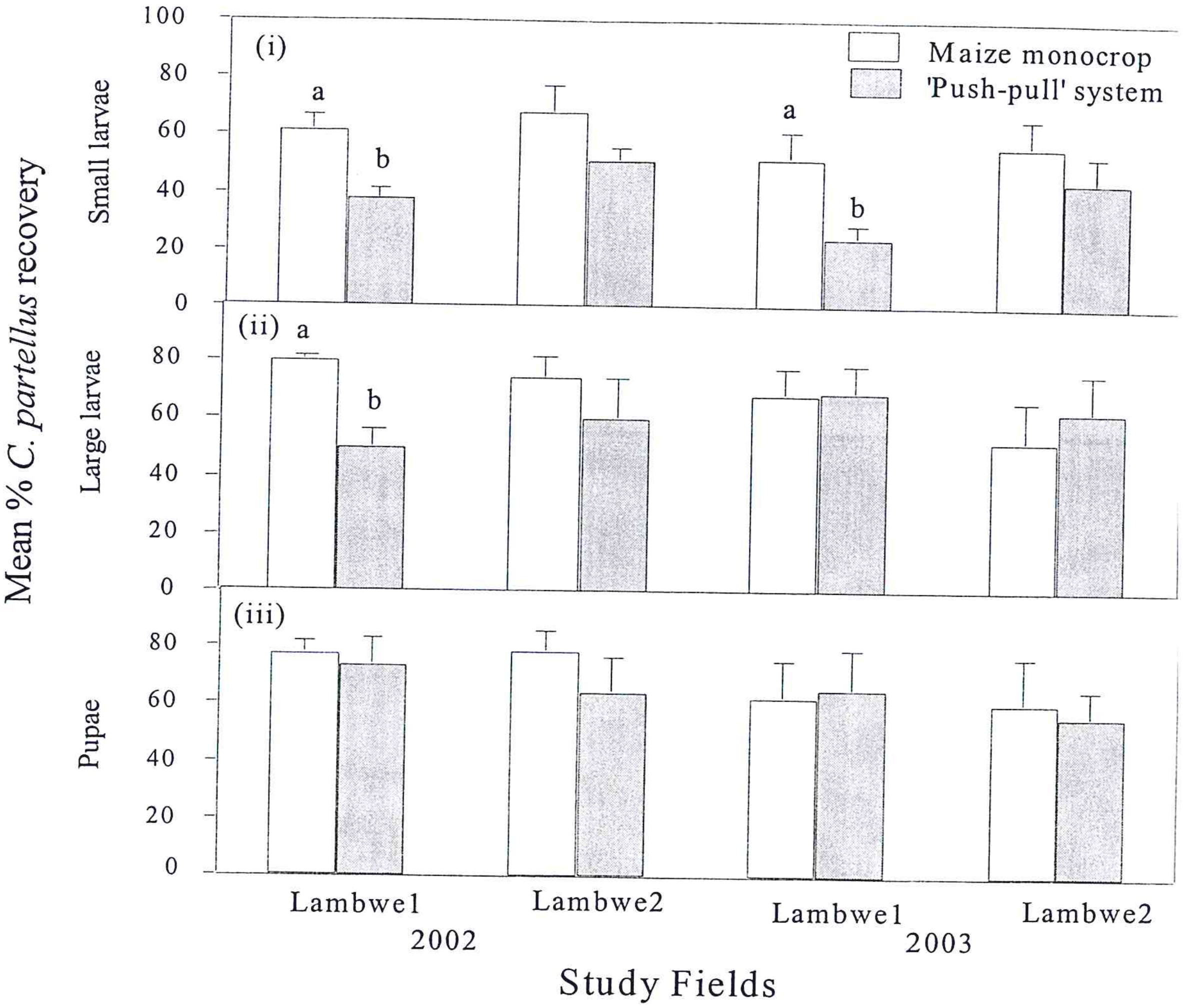
Key: As in fig 3.

Fig 5. Mean (± SE) disappearance, parasitism and non-viability of *B. fusca* eggs on plants exposed to natural enemies at ARC-GCI. Means represent data averages over two cropping seasons. Within a mortality factor, the bars are not significantly different.



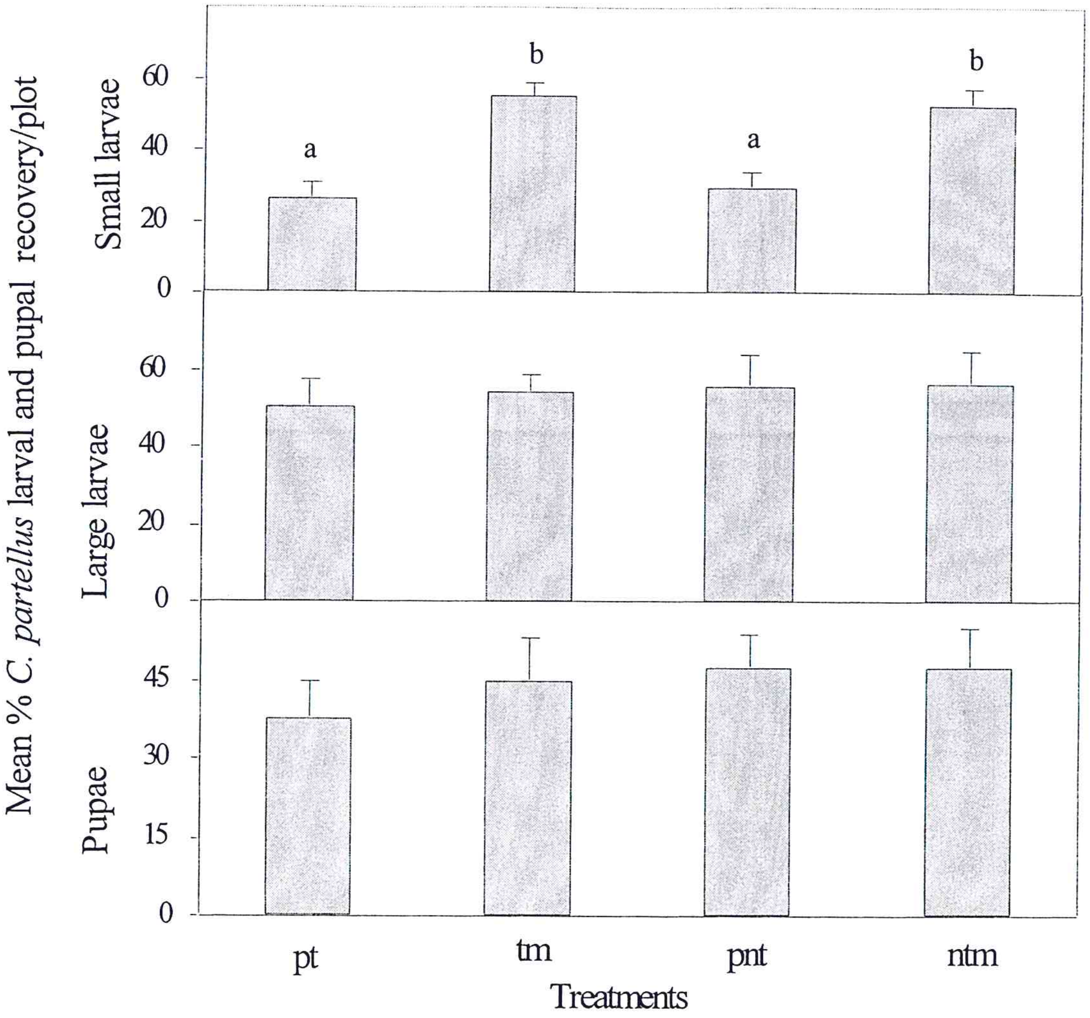
Key: As in fig 3.

Fig 6. Mean (± SE) disappearance, parasitism and non-viability of *C. partellus* eggs on plants exposed to natural enemies at ARC-GCI. Means represent data averages over two cropping seasons. Within a mortality factor, the bars marked with different letters are significantly different ($P<0.05$). The unmarked bars are not significantly different.



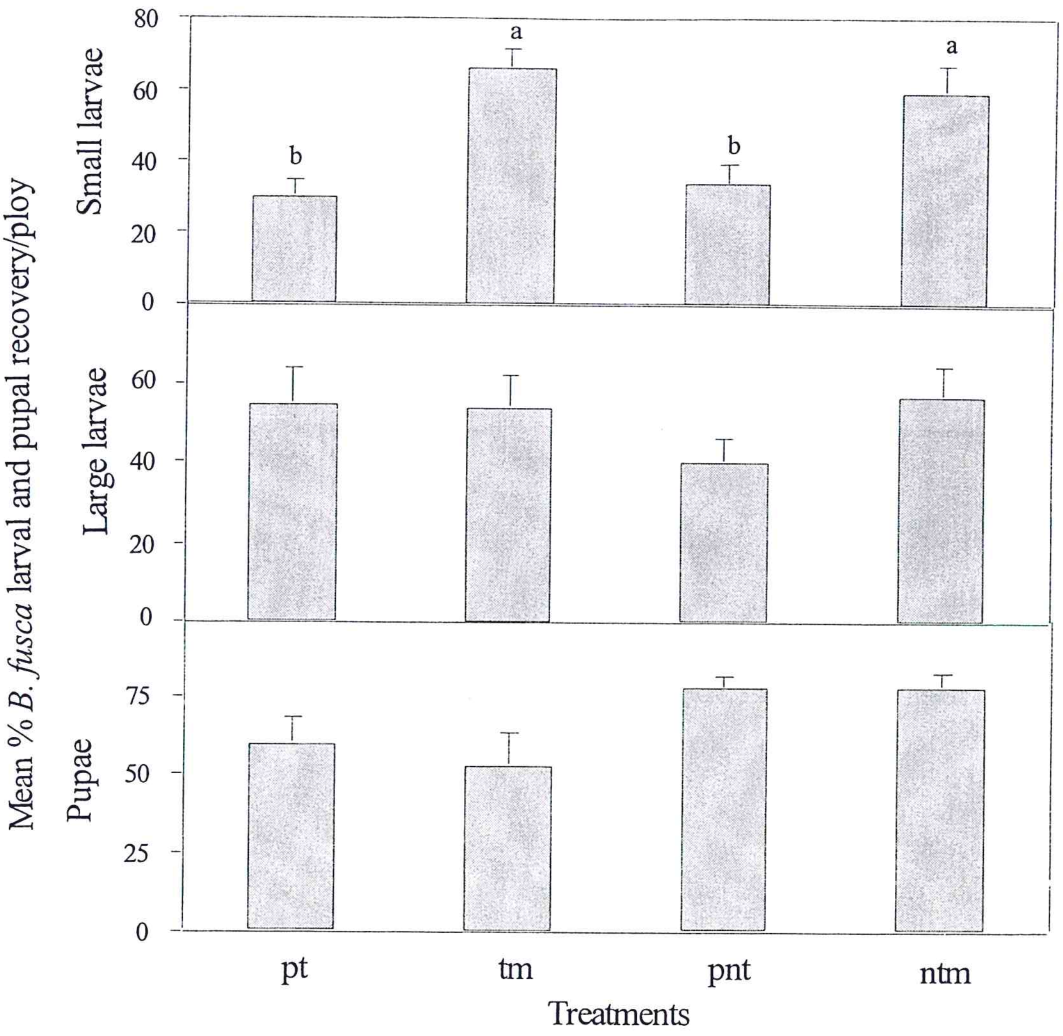
Key: As in fig 4.

Fig 7. Mean (± SE) recovery of (i) small (early instar) larvae, (ii) large (late-instar) larvae and (iii) pupae of *C. partellus* from plants exposed to predators at Lambwe1 and Lambwe2 during 2002 and 2003 cropping seasons. Means represent data averages for 4 plots in each cropping system. Within a field, bars marked with different letters are significantly different (P<0.05), the unmarked bars are not different.



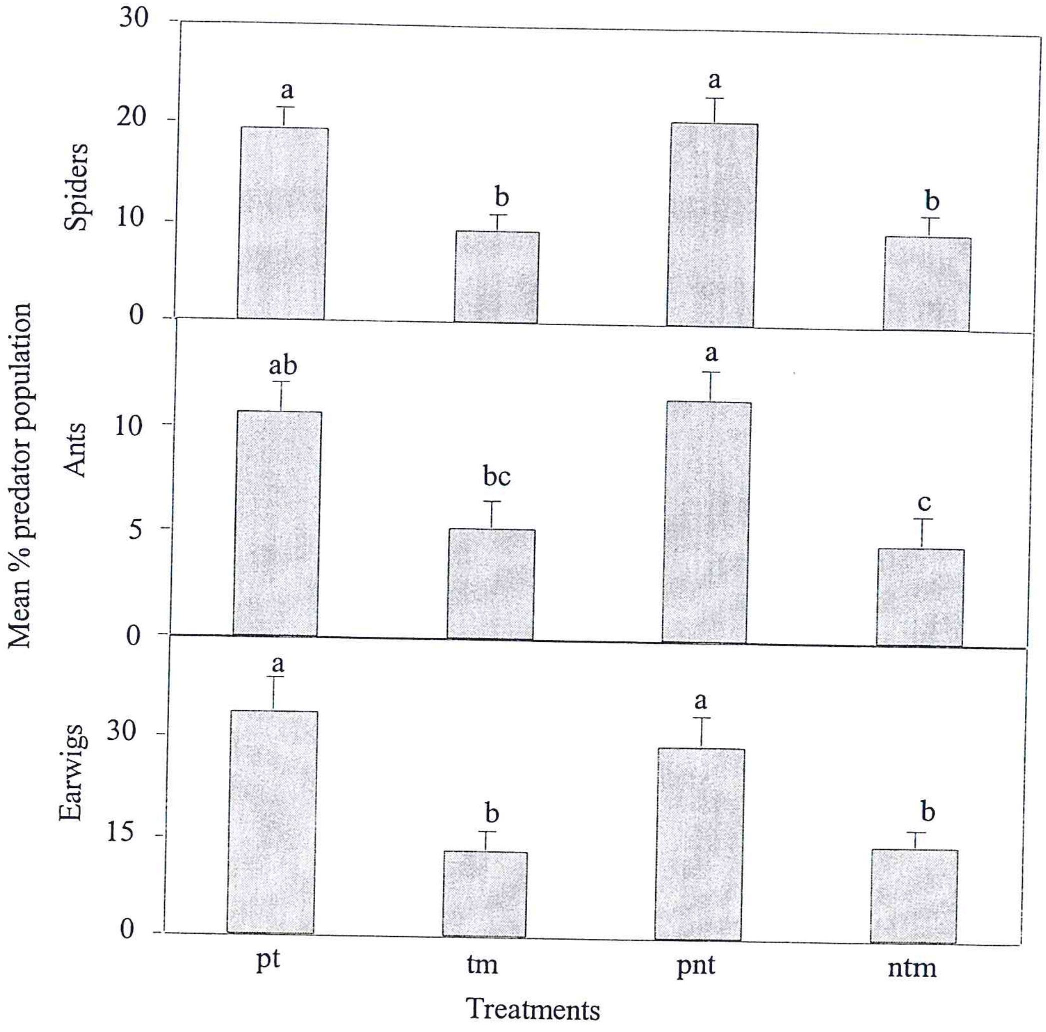
Key:As in fig 3.

Fig 8. Mean (± SE) recovery of small (early instar) larvae, large (late-instar) larvae and pupae of *C. partellus* from plants exposed to predators at ARC-GCI. Within a given stemborer species and life stage, bars marked with different letters are significantly different (P<0.05). The unmarked bars are not significantly different.



Key: As in fig 3.

Fig 9. Mean (± SE) recovery of small (early instar) larvae, large (late-instar) larvae and pupae of *B. fusca* from plants exposed to predators at ARC-GCI. Within a given stemborer species and life stage, bars marked with different letters are significantly different (P<0.05). The unmarked bars are not significantly different.



Key: As in fig 3.

Fig 10. Mean (± SE) stemborer predators recovered at ARC-GCI. Means represent data averages of two cropping seasons. Within a predator group, bars marked with different letters are significantly different ($P<0.05$).

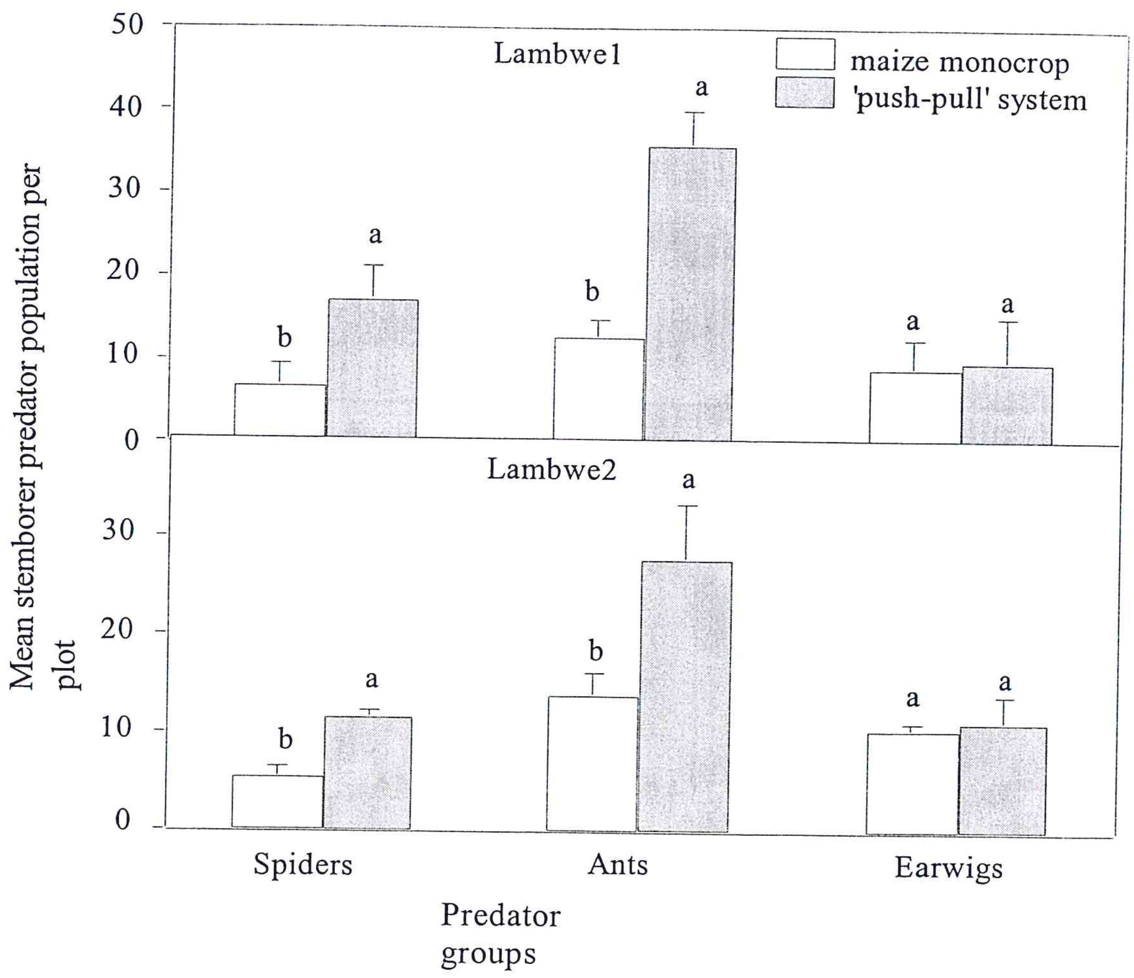


Fig 11. Mean (± SE) stemborer predators recovered at Lambwe1 and Lambwe2. Means represent data averages of four plots during two cropping seasons. Within a predator group, bars marked with different letters are significantly different (P<0.05).

Table 2. Probabilities of orthogonal contrasts for data on maize stemborer mortality and larval and pupal recovery from control plants for each plot during the 2002/2003 and 2003/2004 cropping seasons

		Probability levels				
Stemborer sp.	Study	pt / tm	pt / pnt	pnt / ntm	tm / ntm	pnt / tm
B. fusca	Egg disappearance	0.155	0.497	0.719	0.086	0.072
	Egg parasitism	0.936	0.881	0.809	0.637	0.818
	Non-viability	0.666	0.437	0.253	0.957	0.232
	Small-larval recovery	0.006	0.060	0.0003	0.080	0.616
	Large-larval recovery	0.154	0.826	0.942	0.249	0.222
	Pupal recovery	1.000	0.113	0.535	0.033	0.113
C. partellus	Egg disappearance	0.009	0.088	0.006	0.077	0.014
	Egg parasitism	0.991	0.09	0.352	0.424	0.09
	Non-viability	0.857	0.824	0.134	0.268	0.687
	Small-larval recovery	0.002	0.470	0.0003	0.890	0.702
	Large-larval recovery	0.935	0.569	0.744	0.87	0.625
	Pupal recovery	0.999	0.376	0.525	0.799	0.376

Key: As in fig 3.

CHAPTER FOUR

4. RESPONSE OF GROUND DWELLING ARTHROPODS TO THE 'PUSH-PULL' SYSTEM AND BT-MAIZE USING SPIDERS (ARANEAE) AS AN INDICATOR GROUP

4.1 Introduction

Ground dwelling arthropods are important in agroecosystems with some species having the potential to reduce populations of both weeds and insect pests (Thiele 1977; Cardina *et al.*, 1996). These organisms also play an integral part in the above- and below-ground food webs and can impact on litter decomposition (Witkamp and Crossley, 1966; Dindal, 1990) and nutrient dynamics within the soil/litter interface (Witkamp and Crossley, 1966; Lattin, 1993; Wardle, 1999). In both natural and managed ecosystems, arthropod species diversity is often positively correlated with the diversity of plant species and with plant density (Risch, 1981; Dean and Milton, 1995).

Spiders are a major component of the predatory arthropod trophic level in many ecosystems (Jackson and Pollard, 1996; Brown *et al.*, 2003) and they may often be one of the most diverse and numerically abundant groups in those systems (Weeks and Holtzer, 2000; Nyffeler and Sunderland, 2003). Being one of the major groups of generalist predators, spiders are needed in the development of efficient, sustainable, low-input agricultural systems (Dippenaar-Schoeman and Jocqué, 1997; Ekschmitt *et al.*, 1997). Intensive management of agricultural systems can negatively affect their abundance, diversity and efficiency (Lys *et al.*, 1994). Comparisons of the effect of insecticides on spider communities in cropping systems (e.g. Epstein *et* *al.*, 2000) and the effects of other levels of management [e.g. differing intensities of integrated pest management (Miliczky *et al.*, 2000) and the use of flowering plants (Samu *et al.*, 1997)] have showed that the spider communities were negatively affected by increased levels of management and positively affected by increased habitat diversity (Brown *et al.*, 2003).

Due to the unreliability, questionable efficacy and unsustainability of the previously available stemborer management options, the International Centre of Insect Physiology and Ecology (ICIPE) and its partners have developed the 'push-pull' system described in chapter two. Similarly, Bt-maize (described in chapter three) has also become available for the management of maize stemborers. Because of the ubiquitous distribution and functional diversity of the ground- and litter-dwelling arthropods, site conditions and habitat perturbations could have profound impacts on their abundance and diversity (Rieske and Buss, 2001). And since diversity of organisms in an ecosystem may be considered indicative of the stability, productivity and complexity of that ecosystem (Tilman *et al.*, 1996), it was important to quantify the abundance and diversity of these arthropods under the 'push-pull' system and Bt-maize.

Here, the objective was to evaluate species richness, diversity, evenness and abundance of ground-dwelling spiders as an indicator group of the impact of the 'push-pull' system and Bt-maize on ground dwelling arthropod abundance and diversity.

4.2 Materials and Methods

These studies were carried out in the fields described in chapter two with modifications. In addition to the two pairs of fields at Lambwe School of the Deaf, two farmers' fields, each with a 40 m by 40 m 'push-pull' and maize monocrop plots were incorporated giving four replications. The site is referred to as Lambwe. The rest of the sites (Homabay and ARC-GCI) were as described in chapter two.

4.2.1 Spider sampling

A combination of pitfall traps and soil monoliths was used to assess the abundance and diversity of ground-dwelling spiders under the 'push-pull' system and Bt-maize. Limitations of the individual techniques were minimized by using a combination of both procedures. Trap captures have an inherent insect-activity component that is highly influenced by prevailing weather conditions (Southwood, 1978). However, changes caused by daily weather conditions are averaged by the constant exposure of the traps (Tollefson and Calvin, 1994). Numbers generated from pitfall trap catches alone do not provide estimates of absolute density. They instead estimate active density, which is a function of a species population size, activity and ease of capture (Greenslade, 1964; French *et al.*, 2001). Sampling continuously for a period of weeks or months with pitfall traps effectively estimates relative abundance of species within a habitat and permits comparison of abundance across years or months or seasons in that habitat (Baars, 1979).

In each plot five traps were placed. The traps were 12-cm diameter by 16-cm high plastic cups set in the ground so that the rim was 2 cm below the soil surface. Formaldehyde (4%) was used in the traps to preserve the captured arthropods. Plastic plates were fastened over the traps at Lambwe and Homabay as a precaution against raindrops diluting the contents and litter/foliage dropping over the traps thereby blocking them.

To monitor the activity-density of the spiders, the traps were set throughout the seasons and emptied weekly. The captured specimens were sorted and spiders sent to the ARC-Plant Protection Institute, Pretoria, South Africa, for identification.

Soil monoliths of 20 by 20 by 20 cm were dug in all the plots. A random and systematic sampling was adapted. This ensured that samples were as representative of the plot as possible. Sampling was conducted fortnightly and five samples were taken from each plot between 0800hrs and 1200hrs. Litter enclosed by the monoliths and the dug out soils were placed on white plastic trays and spiders hand sorted from it. Samples were preserved and identified as above.

4.3 Data analysis

Relative abundance

The data were averaged for each plot and relative abundance measured as the overall number of spiders captured per plot and the number of individuals of the most abundant and diverse families, represented by at least five species (Midega and Khan, 2003) and 10 individual members per plot.

Species richness (H′)

Species richness is commonly used in entomological work and provides a relatively direct expression of diversity (Magurran, 1988; Weeks and Holtzer, 2000). This was determined as the average number of species captured per plot and the most abundant and diverse families as above. Shannon's diversity index, H′, (Shannon and Weaver, 1949) was calculated for spider species in each plot as follows:

$$H^{'} = -\sum_{i=1}^{s} \frac{n_i}{n} \log \frac{n_i}{n}$$

where s is the number of species in a sample, n_i is the number of individuals belonging to species I, and n = the number of individuals in a sample from a population.

Community evenness was measured by use of Shannon's equitability ($E_{H'}$) as follows:

$$H'/H'_{\max};$$

where $H'_{\max}$ is the total number of species.

Species dominance (d)

This estimation was conducted by use of the Berger-Parker Dominance equation for the most abundant species among the overall captured spider groups thus:

$$d=N_{\max}/N_{Tot,};$$

where $N_{\max}$ is the number of spiders of the abundant species and N_{Tot} is the number of spiders for all the species measured in the sample (Magurran, 1988). This index measures the proportional abundance of the most abundant species, is independent of the number of species and has low sensitivity to sample size (Southwood, 1978).

Differences between the maize monocrop and the 'push-pull' plots were compared by use of t-tests (SAS Institute, 2001) and one-way analysis of variance (ANOVA) was used to test for any differences between treatments at ARC-GCI (SAS Institute, 2001). Thereafter, pre-planned orthogonal contrasts were used to assess any impact of Bt-maize and the 'push-pull', in the various combinations, on total spider abundance, species diversity and community distributions.

4.4 Results

A total of 2175 individual spiders, representing 70 species in 18 families, were recovered in Kenya and a total of 658 spiders, representing 49 species in 12 families, were recovered at ARC-GCI. The vast majority (>90%) of spiders were hunting species, with only <10% being web-building species (Table 3). The community structure of the spiders encountered in this study comprised of Lycosidae as the most dominant and diverse family, accounting for 76.6% of all the spiders captured by numbers (Table 3) and 27.6% by species richness (Table 9). Salticidae (9.6%) and Oxyopidae (3.6%) were among the other abundant families (Table 3).

Together with the overall spider populations, lycosids were significantly more abundant in the 'push-pull' than in the maize monocrop plots at all sites ($P<0.05$) (Tables 4 and 5). Bt-maize on the other had no significant effect on spider abundance (Table 10).

Despite spider populations being larger in the 'push-pull' system, overall species diversity and dominance were not significantly different between the two cropping systems ($P>0.05$) (Tables 6 and 7) at all sites. Similarly, Bt-maize had no significant effect on spider species diversity and dominance ($P>0.05$) (Table 10). Lycosids on the other hand, were significantly more species diverse in the 'push-pull' than in the maize monocrop systems at Lambwe and Homabay, but not significantly different at ARC-GCI (Table 7). The overall spider community distribution was generally more even under the maize monocrop than in the 'push-pull' systems at Lambwe and ARC-GCI but not significantly different at Homabay (Table 5).

4.5 Discussion

Lycosids are known to have microhabitat preference in agroecosystems (Marshal and Rypstra, 1999), with available moisture, leaf litter and herbaceous vegetation being the cues with which they may select microhabitats (Richman, 1995). Other reports have shown that lycosids are abundant in the savanna habitats and are frequently encountered in agroecosystems (Russell-Smith, 1981; Van den Berg and Dippenaar-Schoeman, 1991). They have emerged as the numerically dominant spider group in agroecosystems in Botswana (Russell-Smith, 1981). They have also been shown to have an important potential role in integrated management of crop pests (Dippenaar-Schoeman, 1976). These findings show that lycosids were the main family determining the total spider abundance and diversity levels in the study plots. The results on relative abundance of spiders between the two cropping systems corroborate the findings of Midega and Khan (2003), showing that the 'push-pull' system enhances generalist predator populations and support the natural enemy hypothesis (Root, 1973) that natural enemies of pests are more abundant in vegetationally diverse ecosystems than in simple ones.

Several studies (reviewed in Cromartie, 1981 and Andow, 1991) have indicated that diverse vegetation may provide natural enemies with shelter, food and alternative prey. The 'push-pull' system described herein is associated with significantly lower maize stemborer populations (Khan *et al.*, 1997, 2000, 2001; Khan and Pickett, 2004). The numerical response of the spiders in the current study, therefore, must have been as a result of factors other than the maize stemborers as prey. Their populations may have been enhanced by other benefits accompanying vegetational diversification of these agroecosystems (Andow, 1991), including provision of alternative prey in the form of herbivores associated with desmodium and Napier grass (Midega and Khan, 2003).

Colonization of this system might have been a consequence of greater attractiveness of the polyculture provided by desmodium and Napier grass, in addition to maize, at least at the host habitat-location phase. Alternatively, because colonization represents not only immigration but also emigration, the greater abundance of the spiders in the 'push-pull' systems may have been caused by a more suitable combination of microhabitats in the polyculture, once the habitat was found by these generalist predators (Midega and Khan, 2003). Moreover, this system is associated with reduced soil temperatures and increased relative humidity (Khan *et al.*, 2002).

Bt-maize had no significant effect on spider abundance. As the Bt-maize used in the current study is designed to target Lepidoptera, the toxin is expressed in the foliage rather than the root system (Al-Deeb and Wilde, 2003). It is, therefore, unlikely to be directly toxic to ground-dwelling arthropods such as lycosids, although tritrophic interactions might be an indirect pathway to toxicity (Hilbeck and Andow, 2004).

H' is defined by both the number of species (species richness) and their evenness in abundance (Price, 1975). Because the differences in the number of lycosid species were negligible between the maize monocrop and the 'push-pull' systems at all sites, the higher lycosid species diversity observed in the latter indicates that the system supported a more even distribution of these spiders at the sites. Lycosids may be selective of microhabitats, and these findings suggest that they found more suitable microhabitats in the 'push-pull' than in the maize monocrop systems at the two sites.

When assessing the impact of any agricultural technology on the arthropod diversity, monitoring individual families, rather than whole communities, appears to be important, as individual families respond differently to different biotic and abiotic changes in the environment (Mrzljak and Wiegleb, 2000). It was, however, noteworthy that the overall spider community distribution was generally more even under the maize monocrop than in the 'push-pull' systems at Lambwe and ARC-GCI but not significantly different at Homabay. This implies clustering of spiders in the latter. Factors that could influence spider distribution in an ecosystem include distribution of prey and abiotic factors (temperature, soil type, moisture, litter etc). In a monoculture as opposed to a polyculture, these are expected to be uniform (Andow, 1991) and warrant further investigations in this system.

In general, the results showed that the 'push-pull' system enhances the overall abundance and species diversity of some spider families. The system also appears to influence spider community distribution through a variety of ways yet to be determined. The hunting spiders that dominate the 'push-pull' system have been shown to prefer lepidopteran and homopteran food sources (Bogya and Mols, 1996), but many spiders are known to accept almost any prey that are slightly smaller than the spider (Nyffeler *et al.*, 1994). With spiders being one of the most important predatory groups in cropping systems (Weeks and Holtzer, 2000), these findings suggest that the abundance and diversity of spiders in the 'push-pull' system should, therefore, be expected to correspond to a high potential for controlling many pest species in the system (Brown *et al.*, 2003). The 'push-pull' system, therefore, has considerable potential in further pest control in the maize agroecosystems. The results also suggest that family-specific responses to the 'push-pull' system are important in structuring the overall spider community, and that this sort of family level knowledge is necessary for predicting the habitat and seasonal distribution of the ground-dwelling spiders in these cropping systems.

Table 3. Percentage of the total spiders collected by family, including only families with more than 20 individuals, per site.

Family (Number of individuals)	Lambwe		Homabay		ARC			
					Bt-maize		Non Bt-maize	
	mm	pp	mm	pp	mm	pp	mm	pp
Lycosidae (2056)	27.9	40.1	3.5	6.3	4.4	10.0	2.4	5.4
Salticidae (272)	38.2	23.2	5.2	9.6	2.9	4.4	7.7	8.8
Gnaphosidae (84)	22.6	23.8	3.6	5.9	3.6	5.9	4.8	29.8
Corinnidae (41)	31.7	31.7	7.3	29.3	0.0	0.0	0.0	0.0
Oxyopidae (102)	25.5	51.9	7.8	13.7	0.0	0.0	0.0	1.1
Theridiidae (22)	31.8	22.8	9.1	9.1	4.5	9.1	4.5	9.1
Linyphiidae (33)	3.0	18.3	0.0	0.0	21.2	33.3	3.0	21.2
Ctenidae (53)	18.9	67.9	1.9	11.3	0.0	0.0	0.0	0.0
Miturgidae (23)	43.5	30.4	8.7	0.0	0.0	0.0	0.0	17.4
Philodromidae (85)	8.2	12.9	2.3	5.9	9.4	29.4	9.4	22.3
All others (62)	27.3	47.3	7.3	10.9	0.0	5.4	0.0	1.8
Total (2833)	27.7	37.6	3.9	7.3	3.2	10.3	2.8	7.1

Table 4. Mean number (±SE) of overall spiders captured per plot at each site. Means represent data averages over two cropping seasons. Within a site, means marked with different letters are significantly different at P=0.05.

	Sites			
Treatment	Lambwe	Homabay	ARC	
			Bt-maize	Non Bt-maize
Maize monocrop	196.5(47)^{b}	55.5(3.5)^{b}	22.7(4.8)^{b}	19.7(2.4)^{b}
‘Push-pull’ system	266.2(30.9)^{a}	103(6)^{a}	73.2(10.9)^{a}	48.7(5.4)^{a}

Table 5. Mean number (±SE) of Lycosid spiders captured per plot at each site. Means represent data averages over two cropping seasons. Within a site, means marked with different letters are significantly different at P=0.05.

	Sites			
Treatment	Lambwe	Homabay	ARC	
			Bt-maize	Non Bt-maize
Maize monocrop	143.5(30.9)^b	36(1.0)^b	16.0(2.7)^b	11.0(2.5)^b
Push-pull system	205.0(21.0)^a	65(4.0)^a	58.7(10.1)^a	29.5(6.8)^a

Table 6. Total number of species with associated average (±SE) diversity index (H′) of spiders captured per plot at each site. Means represent data averages over two cropping seasons.

Treatment	Sites							
	Lambwe		Homabay		ARC			
					Bt-maize		Non Bt-maize	
	spp.	H′	spp.	H′	spp.	H′	spp.	H′
Maize monocrop	55	2.6(0.2)	34	2.6(0.1)	19	1.7(0.1)	17	1.7(0.1)
Push-pull system	57	2.7(0.1)	32	2.7(0.1)	31	1.8(0.2)	35	2(0.1)

Table 7. Number of lycosid spider species with associated mean (±SE) diversity index (H′) per plot at each site. Means represent data averages over two cropping seasons. Within a site, means marked with different letters are significantly different at P=0.05.

	Sites							
Treatment	Lambwe		Homabay		ARC			
					Bt-maize		Non Bt-maize	
	spp.	H′	spp.	H′	spp.	H′	spp.	H′
Maize monocrop	19	2.0(0.1)^b	13	1.8(0.03)^b	10	1.1(0.1)^a	6	0.8(0.1)^a
'Push-pull' system	18	2.2(0.05)^a	12	2.0(0.02)^a	16	1.3(0.1)^a	12	1.1(0.1)^a

Table 8. Mean (±SE) spider community distribution (Evenness $E_{H'}$) per plot. Means represent data averages of two cropping seasons. Within a site, means marked with different letters are significantly different at P=0.05.

Treatment	Sites			
	Lambwe	Homabay	ARC	
			Bt-maize	Non Bt-maize
Maize monocrop	0.107(0.017)^{a}	0.115 (0.005)^{a}	0.205(0.016)^{a}	0.212(0.009)^{a}
Push-pull system	0.085(0.009)^{b}	0.115 (0.005)^{a}	0.135(0.005)^{b}	0.147(0.008)^{b}

Table 9. Mean (±SE) spider species dominance (d) per plot. Means represent data averages of two cropping seasons.

Treatment	Sites			
	Lambwe	Homabay	ARC	
			Bt-maize	Non Bt-maize
Maize monocrop	0.178(0.023)	0.234(0.024)	0.396(0.079)	0.42(0.03)
'Push-pull' system	0.158(0.012)	0.165(0.009)	0.436(0.058)	0.366(0.028)

Table 10. Pre-planned contrast results on the effect of Bt-maize and the ‘push-pull’ system on overall spider abundance, diversity and distribution at ARC-GCI.

			Probability levels		
	pt / tm	pt / pnt	pnt / ntm	tm / ntm	pnt / tm
Total spider abundance	0.0001	0.019	0.007	0.746	0.014
Total spider diversity	0.414	0.246	0.066	0.963	0.612
Total spider distribution	0.0006	0.427	0.001	0.631	0.003

Table 11. Spider species presence (+) and absence (-) in each site over two cropping seasons.

Site		Lambwe		Homabay		ARC-GCI			
						Bt-maize		Non Bt-maize	
Family	Species	mm	pp	mm	pp	mm	pp	mm	pp
Corinnidae	*Cambalida coriacea*	+	+	-	-	-	-	-	-
Corinnidae	*Castianeira sp.*	+	+	+	+	-	-	-	-
Corinnidae	*Graptartia mutillica*	+	+	+	+	-	-	-	-
Corinnidae	*Camillina* Sp. 1	-	-	-	-	-	-	-	+
Corinnidae	*Camillina* Sp. 2	-	-	-	-	-	-	-	+
Corinnidae	*Copa Sp. 1*	-	+	-	-	-	-	-	-
Corinnidae	*Brachyphaea simoni?*	-	+	-	-	-	-	-	-
Lycosidae	*Hippasa affinis*	+	+	+	+	-	-	-	-
Lycosidae	*Hippasa* sp. 9	+	+	+	+	-	-	-	-

Lycosidae	*Camillina aldabrae*	-	-	-	-	-	-	-	+
Lycosidae	*Pterartoria* sp. 1	-	-	-	-	+	+	-	-
Lycosidae	*Pterartoria* sp. 2	-	-	-	-	+	+	+	-
Lycosidae	*Trabea* sp. 1	-	-	-	-	+	+	+	+
Lycosidae	*Trabea* sp. 2	-	-	-	-	-	+	-	-
Lycosidae	*Lycosa* sp. 1	-	-	-	-	+	+	+	+
Lycosidae	*Lycosa* sp. 2	-	-	-	-	-	+	-	-
Lycosidae	*Pardosa crassipalpis*	+	+	-	+	+	+	+	+
Lycosidae	*Pardosa clavipalpis*	-	-	-	-	+	+	+	+
Lycosidae	*Pardosa* sp. 1	+	-	-	-	+	+	+	+
Lycosidae	*Pardosa* sp. 2	+	+	+	+	-	+	-	-
Lycosidae	*Pardosa* sp. 10	+	+	+	+	+	+	-	+
Lycosidae	Unidentified sp. 1	+	+	+	+	+	+	-	-
Lycosidae	Unidentified sp. 2	+	-	-	-	-	-	-	+
Lycosidae	Unidentified sp. 3	+	+	+	+	-	+	-	+

Lycosidae	Unidentified sp. 4	+	+	+	+	-	-	-	-
Lycosidae	Unidentified sp. 5	+	+	+	+	-	-	-	-
Lycosidae	Unidentified sp. 6	+	+	+	+	-	+	-	-
Lycosidae	Unidentified sp. 7	+	+	+	-	-	+	-	-
Lycosidae	Unidentified sp. 8	+	+	-	-	-	-	-	+
Lycosidae	Unidentified sp. 9	-	+	-	-	-	-	-	-
Lycosidae	Unidentified sp. 10	+	+	-	-	-	-	-	-
Lycosidae	Unidentified sp. 11	+	+	+	-	-	-	-	-
Lycosidae	Unidentified sp. 12	+	+	-	-	+	-	-	-
Lycosidae	Unidentified sp. 13	+	+	+	-	-	+	-	+
Lycosidae	Unidentified sp. 14	+	+	-	+	-	-	-	-
Lycosidae	Unidentified sp. 15	+	+	+	+	-	-	-	-
Salticidae	*Langelurillus* sp. 1	+	-	-	-	-	-	-	-
Salticidae	*Stenaelurillus* sp. 1	+	+	+	-	-	-	-	-
Salticidae	*Stenaelurillus* sp. 2	+	-	-	-	-	-	-	-

Salticidae	*Langona manicata*	-	-	-	-	+	+	+	+
Salticidae	*Pellenes* sp.	-	-	-	-	+	+	+	+
Salticidae	*Baryphas* sp.	-	-	-	-	+	+	+	+
Salticidae	*Evarcha* sp. 1	-	-	-	-	-	-	+	+
Salticidae	Unidentified sp. 1	+	+	+	+	-	-	-	-
Salticidae	Unidentified sp. 2	-	-	-	+	-	-	-	-
Salticidae	Unidentified sp. 3	+	+	+	+	-	-	-	+
Salticidae	Unidentified sp. 4	+	+	+	+	-	-	-	-
Salticidae	Unidentified sp. 5	+	+	+	+	-	+	-	-
Salticidae	Unidentified sp. 6	+	+	+	-	-	-	-	+
Salticidae	Unidentified sp. 7	+	+	-	+	-	-	-	-
Salticidae	Unidentified sp. 8	+	+	-	-	-	-	-	-
Salticidae	Unidentified sp. 9	-	+	-	-	-	-	-	-
Salticidae	Unidentified sp. 10	+	+	+	-	-	-	-	-
Salticidae	Unidentified sp. 11	+	-	-	-	-	-	-	-

Salticidae	Unidentified sp. 12	+	-	+	-	-	-	-	-
Araneidae	*Araneus* sp.	+	-	-	-	-	-	-	-
Araneidae	*Pararaneus perforatus*	-	-	-	-	-	+	-	-
Araneidae	*Lipocrea longissima*	+	-	-	-	-	-	-	-
Araneidae	*Kilima decens*	-	-	+	-	-	-	-	-
Gnaphosidae	*Setaphis subtilis*	+	+	-	-	-	-	+	+
Gnaphosidae	*Setaphis arcus*	-	-	-	-	-	+	-	+
Gnaphosidae	*Zelotes* sp. 1	+	+	+	+	-	-	-	+
Gnaphosidae	*Zelotes* sp. 2	+	-	+	+	-	-	-	+
Gnaphosidae	*Pterotricha* sp.	-	-	-	-	-	-	-	+
Gnaphosidae	*Camillina cordifera*	-	+	-	-	+	+	+	+
Gnaphosidae	*Zelotes oneili*	-	-	-	-	-	+	+	+
Gnaphosidae	*Camillina* sp. 1	-	-	-	-	-	-	-	+
Gnaphosidae	*Camillina* sp. 2	+	+	-	-	-	-	-	-
Gnaphosidae	Unidentified sp. 5.	-	+	-	-	-	-	-	-

Miturgidae	*Cheiracanthuim furculatum*	+	+	+	-	-	-	-	-
Miturgidae	*Cheiracanthium imbelle*	+	+	-	-	-	-	-	-
Linyphiidae	*Ostearius melanopygius*	+	+	-	-	+	+	-	+
Linyphiidae	Unidentified sp. 1	-	+	-	-	+	+	+	+
Oxyopidae	*Oxyopes pallidecoloratus*	+	+	+	+	-	-	-	-
Oxyopidae	*Oxyopes jacksoni*	+	-	-	-	-	-	-	-
Oxyopidae	*Oxyopes* sp.	-	-	-	-	-	-	-	+
Ctenidae	*Ctenus* sp. 1	+	+	+	+	-	-	-	-
Theridiidae	*Steatoda* sp. 1	+	+	-	+	+	+	+	+
Theridiidae	*Euryopis* sp. 1	+	-	+	+	-	-	-	-
Theridiidae	*Theridion* sp. 1	-	+	+	-	-	-	-	-
Liocranidae	Unidentified sp.	+	+	-	+	-	-	-	-
Thomisidae	*Thomisus blandus*	+	-	-	-	-	-	-	-
Thomisidae	*Sylligma hirsute*	-	-	+	-	-	-	-	-
Thomisidae	*Ozyptila lutulenta*	-	+	-	-	-	-	-	-

Thomisidae	*Parasmodix (n. Sp.?)*	-	-	-	+	-	-	-	-
Pisauridae	*Chiasmopes lineatus*	-	-	-	+	-	-	-	-
Pisauridae	*Charminus* sp. 1	-	-	-	-	-	-	+	+
Pisauridae	*Maypacius curiosus*	-	+	+	-	-	-	-	-
Pisauridae	*Perenethis symmetrica*	-	+	-	-	-	-	-	-
Pisauridae	*Euprosthenopsis Sp.*	-	+	-	-	-	-	-	-
Pisauridae	*Charminus* sp. 1	-	-	-	+	-	-	-	-
Philodromidae	*Thanatus* sp. 1	+	+	+	+	-	-	-	-
Philodromidae	*Thanatus* sp. 2	-	-	-	-	+	+	-	-
Philodromidae	*Thanatus vulgaris*	-	-	-	-	+	+	+	+
Philodromidae	*Tibellus minor*	-	-	-	-	-	-	-	+
Clubionidae	*Clubiona annuligera*	+	-	-	-	-	-	-	-
Zodariidae	*Diores* sp.	-	-	-	+	-	-	-	-
Zodariidae	*Cydrela* sp. 1	-	-	-	-	-	+	-	-
Zodariidae	*Diores strandi*	-	+	-	-	-	-	-	-

Tetragnathidae	*Tetragnatha jaculator*	+	+	-	-	-	-	-	-
Tetragnathidae	*Leucauge decorata*	-	+	-	-	-	-	-	-
Tetragnathidae	*Tetragnatha subsquamata*	-	+	-	-	-	-	-	-
Nesticidae	*Nesticella* sp.	-	-	-	-	-	+	-	-
Hahniidae	*Hahnia lobata*	-	-	-	-	-	-	-	+
Pholcidae	Unidentified sp. 1	-	+	-	-	-	-	-	-

CHAPTER FIVE

5.0 IMPACT OF THE 'PUSH-PULL' SYSTEM AND BT-MAIZE ON ABUNDANCE AND DIVERSITY OF SPRINGTAILS (COLLEMBOLA)

5.1 Introduction

Among the most important non-target inhabitants of cereal fields are arthropods (Bitzer *et al.*, 2002). The arthropod complex consists of hundreds of species, most beneficial (Zeiss and Klubertanz, 1994). Altering this ecosystem by use of habitat management and Bt-technology could disrupt populations and communities of beneficial predators, parasitoids, fungal grazers and organic residue decomposers (Bitzer *et al.*, 2002). Decomposers such as springtails are important consumers of plant residues and soil fungi and also help create humus. The sensitivity of springtails to various crop management practices suggests their potential use as biological indicators of disturbance (Rebek *et al.*, 2002; Earton *et al.*, 2004).

Desmodium, used as an intercrop in the 'push-pull' system (chapter one), also, through allelopathic mechanisms, effectively suppresses striga weed leading to improved crop yields (Khan *et al.*, 2000, 2001, 2002). Studies have revealed that the root exudates from this plant contain four main isoflavanones; 5,7,2',4'-tetrahydroxy-6-(3-methylbut-2-enyl)-isoflavanone, 4",5"-dihydro-5,2',4'- trihyddroxy-5"- isopropenylfurano- (2",3";7,6)-isoflavanone, 4",5' '-dihydro-2'-methoxy-5,4' -dihydroxy-5"- isopropenylfurano-(2",3";7,6)- isoflavanone and 5,7,4'-trihydroxyisoflavone (genistein) involved in striga weed suppression through induced/suicidal germination and inhibition of radical growth

(Tsanuo *et al.*, 2003). Additionally, Bt-maize, currently in use in South Africa against the maize stemborers, might soon be allowed in Kenya and other African countries. Understanding how the two technologies affect non-target species is important to understanding how the overall agricultural ecosystem may be affected. Studies were therefore conducted to assess the impact of the 'push-pull' system and Bt-maize on springtail diversity and abundance.

5.2 Materials and Methods

5.2.1 Study sites

Kenya: Study plots were as described in chapter two. The plots at Lambwe were separated into two 'sites', each with two plots, henceforth referred to as Lambwe1 and Lambwe2. Those at Homabay were treated the same way and are henceforth referred to as Homabay1 and Homabay2.

South Africa: The study fields were as described in chapter three.

5.2.2 Soil sampling, springtail extraction and identification

Soil samples were taken monthly from April to September for the two years in Kenya and November 2002 to March 2003 in South Africa, using a soil corer of 10 cm diameter. A method adapted from Badejo *et al.* (1998) was employed with modifications to sample soil for springtails in these subplots. Without removing the litter, the corer was pushed down into the soil to collect topsoil to a depth of 15 cm. Sample units were pushed from the corer into labeled polyethylene bags tied at the mouth to prevent desiccation and escape of springtails before reaching the laboratory (Badejo *et al.*, 1998). Springtails were extracted from the top 10 cm of each soil core using a simple Berlese funnel extraction apparatus. During this process, the soil cores were inverted in such a way that the topmost soil was at the lower end of the funnel. This enabled the surface-dwelling springtails to travel a shorter distance than the deep-living ones during extraction (Badejo *et al.*, 1998). Each collecting tube was to one-third of its volume filled with 70% alcohol, placed under the funnel and removed after 7 days (Lasebikan, 1974; Badejo *et al.*, 1998). The specimens were then preserved in freshly prepared 70% ethanol followed by identification. Identification keys adapted from Scott (1961) and Christiansen and Bellinger (1980) were used to separate the specimens into the various families.

5.3 Data analysis

Because of the limited springtail taxonomic resources in the Afro-tropical region, the family level was the lowest taxon possible in the current study. One-way Analysis of Variance (ANOVA) using the generalized linear model (SAS Institute, 2001) was used to determine whether treatments significantly affected both the abundance and diversity of springtails at ARC-GCI while t-test (SAS Institute, 2001) analysis was used for any differences between the 'push-pull' and the maize monocrop at Lambwe1, Lambwe2, Homabay1 and Homabay2. Springtail diversity (at the family taxon) was measured using Shannon's, H', diversity index (Shannon and Weaver, 1949) as follows:

$$H' = -\sum_{i=1}^{s} \frac{n_i}{n} \log \frac{n_i}{n},$$

where s is the number of families in a sample; n_i is the number of individuals belonging to family i; and n = the number of individuals in a sample from a population.

Because of the high variability observed for the actual counts both within and among treatments, $\log_{10}[n+1]$ transformations of the original data were performed which stabilized the variance for the analyses (Rebek *et al.*, 2002).

Graphs of monthly springtail population levels were constructed to identify any changes in population between treatments (population dynamics). Dominance of families was calculated for each family as a percentage of the total springtails captures per plot and averaged for the cropping seasons studied in each site.

5.4 Results

A total of seven springtail families were recovered in this study; Hypogastruridae, Tomoceridae, Entomobryidae, Neelidae, Onychiuridae, Sminthuridae and Isotomidae. The Neelidae, which were only recovered in the Kenyan sites in negligible numbers were excluded from analysis. All the other families were recovered at all sites.

Both individual families and the total springtail numbers did not differ between the ‘push-pull’ and the maize monocrop plots ($P>0.05$) (Fig 12). The same was observed for these treatments under the Bt and non-Bt maize ($P>0.05$) (Fig 13). These results imply that the Bt-maize and the ‘push-pull’ system had no deleterious impact on these springtail populations.

The 'push-pull' system had no impact on sprigtail diversity ($P>0.05$) (Fig 14). Similarly, the Bt-maize did not affect springtail diversity and abundance since no differences were observed between Bt-maize and the non-Bt isoline (Figs 13 and 15).

The population dynamics indicated no distinct (sharp) changes in populations in both the 'push-pull' and the maize monocrop (Fig 16) and Bt- and non-Bt maize treatments (Fig 17). Additionally, the treatments did not seem to influence dominance of springtail families (Figs 18 and 19).

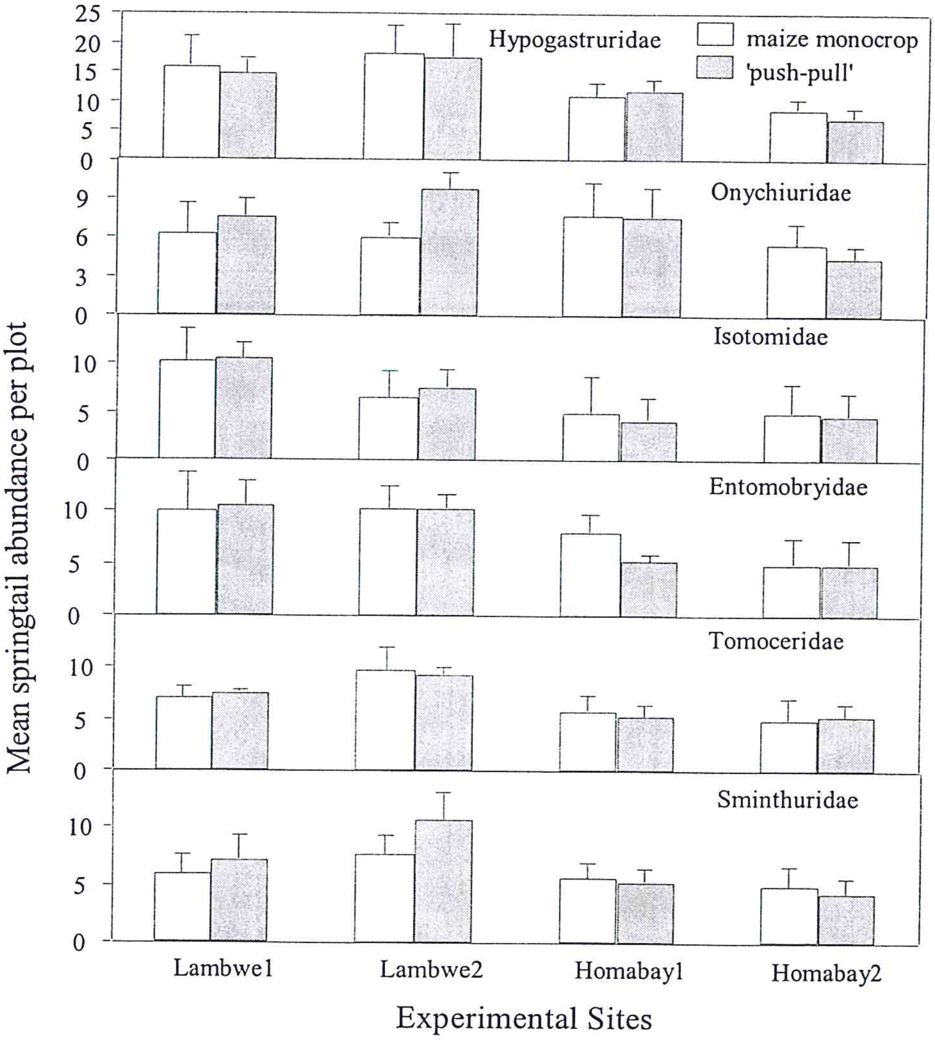
5.5 Discussion

Both technologies seemed to have no deleterious effect on relative abundance of springtails. According to Andrewartha and Birch (1954), the size of a population is determined by the four components of the environment; weather, food, other animals and pathogens, and a place to live. While these studies were conducted in recently established 'push-pull' plots, any marked deleterious effects of the system could have been established, resulting from modification/alteration of the factors above. Different springtail species respond differently to changes of the above environmental factors. Since the overall family abundance is the sum total of individual species, failure to detect any marked population fluctuations implies that the system did not affect the overall populations of these arthropods. The main climatic factor affecting population levels of soil animals (e.g. springtails) is moisture, either singly or in conjunction with temperature (Verhoef, 1977). While Desmodium has been shown to lower soil temperature and relative humidity by 0.6°C and 6.7% respectively (Khan *et al*., 2002), these changes did not seem to have any significant effect on the springtail microhabitat. Any changes in soil temperature and humidity will not necessarily result in enhancement or reduction in springtail numbers (Bellinger, 1954), unless the change is abrupt and to levels outside the conducive range. Desmodium and its allelopathic mechanism in the suppression of striga weed (Khan *et al.*, 2000, 2002) also seem to have no negative impact on the total springtail numbers. More work is however needed to identify individual contribution of both aspects to populations of specific springtails.

The ‘push-pull’ system had no impact on sprigtail diversity. Similarly, the Bt-maize did not affect springtail diversity and abundance since no differences were observed between Bt-maize and the non-Bt isoline. There are several possible explanations for these results. It is likely that the Bt-toxins from the plants in this study are not toxic to springtails or that the Bt-toxin is not released into the soil or is not present in lethal concentrations (Al-Deeb *et al.*, 2003). Head *et al.* (2002) detected no accumulation of Cry1Ac protein in the soil after multiple years (3-6 years) of transgenic Bt-cotton use. Results of the current study are in agreement with those of Al-Deeb *et al.* (2003) who reported no significant impact of Cry3Bb1 toxin on soil microarthropods including springtails. Similarly, Yu *et al.* (1997) found that the Bt toxins Cry1Ab and Cry1Ac had no effects on *Folsomia candida* Willem (Collembola: Isotomidae) and *Oppia nitens* Kock (Acari: Orbatidae). Sims and Martin (1997) also found no toxicological risk from Cry1Ab, Cry 1Ac, Cry 2A and Cry3A to two species of Collembola (*F. candida* and *Xenylla grisea* Axelson).

The results on population dynamics showed multiple peaks, an indication that springtails are multivoltine (Badejo and Olaifa, 1997). They also show absence of forces acting to either appreciably enhance or reduce the total springtail numbers. Additionally, the treatments did not seem to influence dominance of springtail families. Results showed that the Hypogastruridae was the most dominant family, with Sminthuridae as the consistently less dominant family in all the Kenyan sites while no single family consistently dominated at the South African site. While it is realized that family taxon may not be sensitive enough to indicate the impact of human activities such as the ones in the current study, an indication herein is that whichever the mechanism(s), the total springtail numbers are not adversely affected by these technologies.

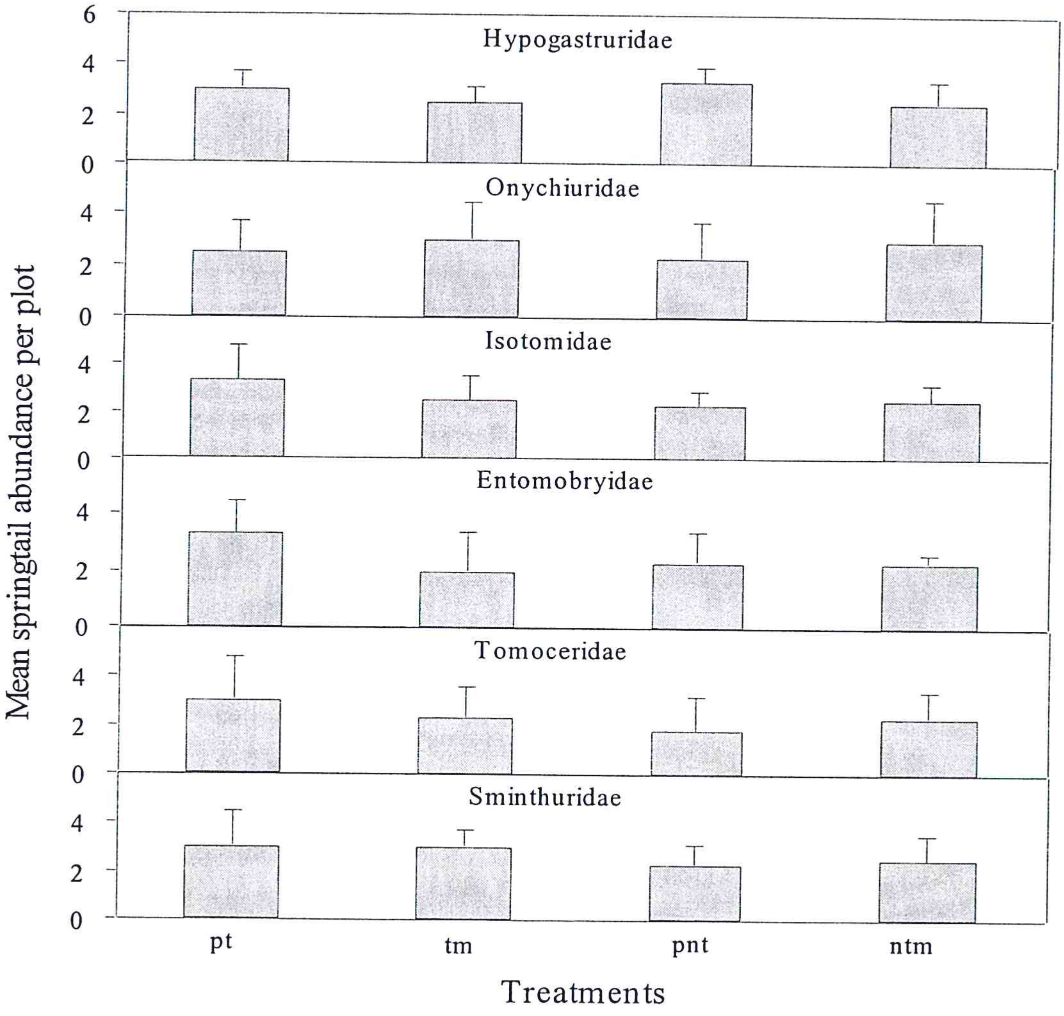
This study offers a perspective on the influence of both technologies on soil springtails. Although the factors that might possibly exhibit the greatest effect on springtails like temperature and moisture (Bandyopadhyaya *et al.*, 2002) were not isolated, and that species rather than family would have been a better taxon, it is hoped that this approach and the results might be more pertinent to addressing the potential impact of the strategies on non-target arthropods.



Key:

Lambwe1	Lambwe School of the Deaf field one
Lambwe2	Lambwe School of the Deaf field two
Homabay1	Homabay Farmers' Training Centre field one
Homabay2	Homabay Farmers' Training Centre field two

Fig 12. Mean number of springtails per plot at Lambwe School of the Deaf and Homabay Farmers' Training Centre fields one and two. Means (±SE) represent data averages of four subplots during two cropping seasons. Within a springtail family, the maize monocrop and the 'push-pull' bars are not significantly different (P>0.05).



Key: As in fig 3.

Fig 13. Average number of springtails per plot during the 2002/2003 cropping season at ARC-GCI. Means (±SE) represent data averages of four subplots. Within a springtail family, there are no differences between treatments (P>0.05).

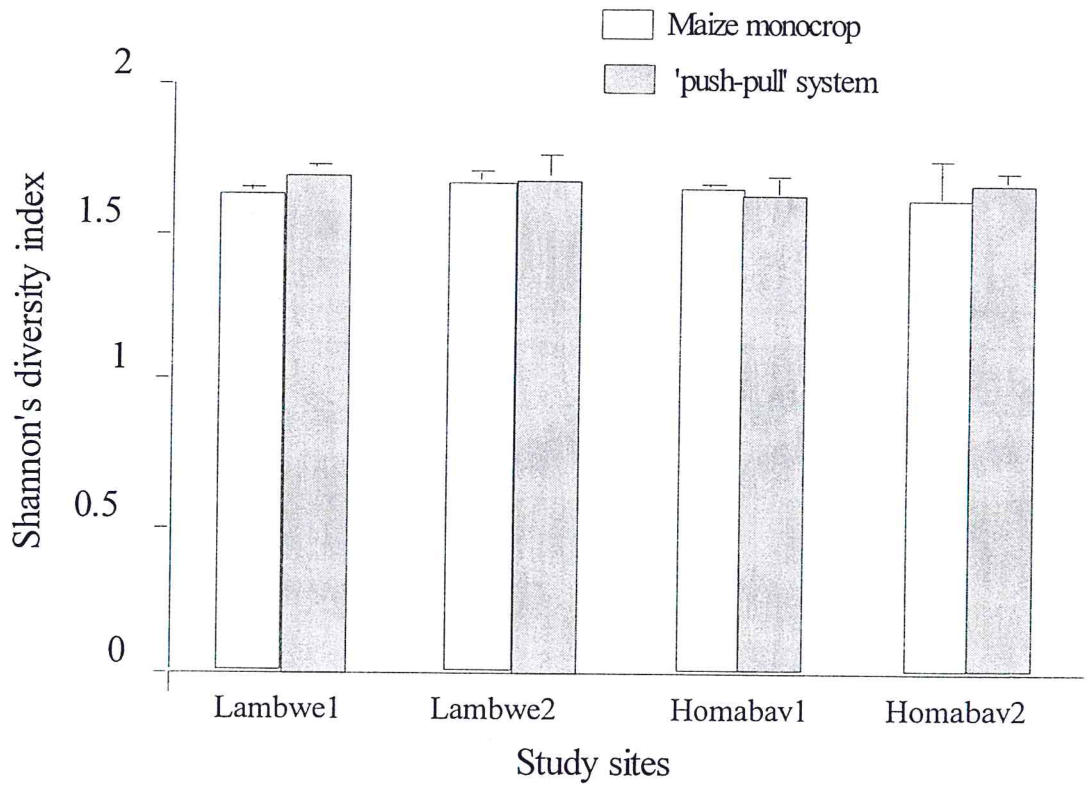
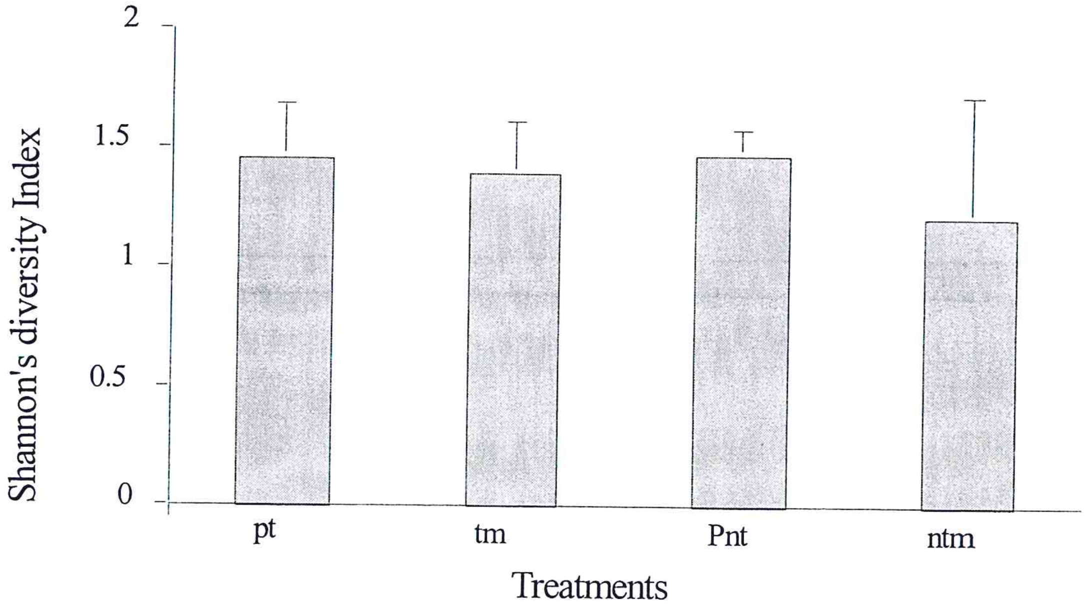


Fig 14. Diversity of the springtail families in maize fields at Lambwe School of the Deaf and Homabay Farmers' Training Centre fields one and two. Means represent data averages of four subplots during two cropping seasons. Within a springtail family, the maize monocrop and 'push-pull' bars are not significantly different (P>0.05).



Key; As in fig. 3.

Fig 15. Diversity of springtail families in maize fields during the 2002/2003 cropping season at ARC-GCI. Means (±SE) represent data averages of four subplots. Within a springtail family, there are no differences between treatments (P>0.05).

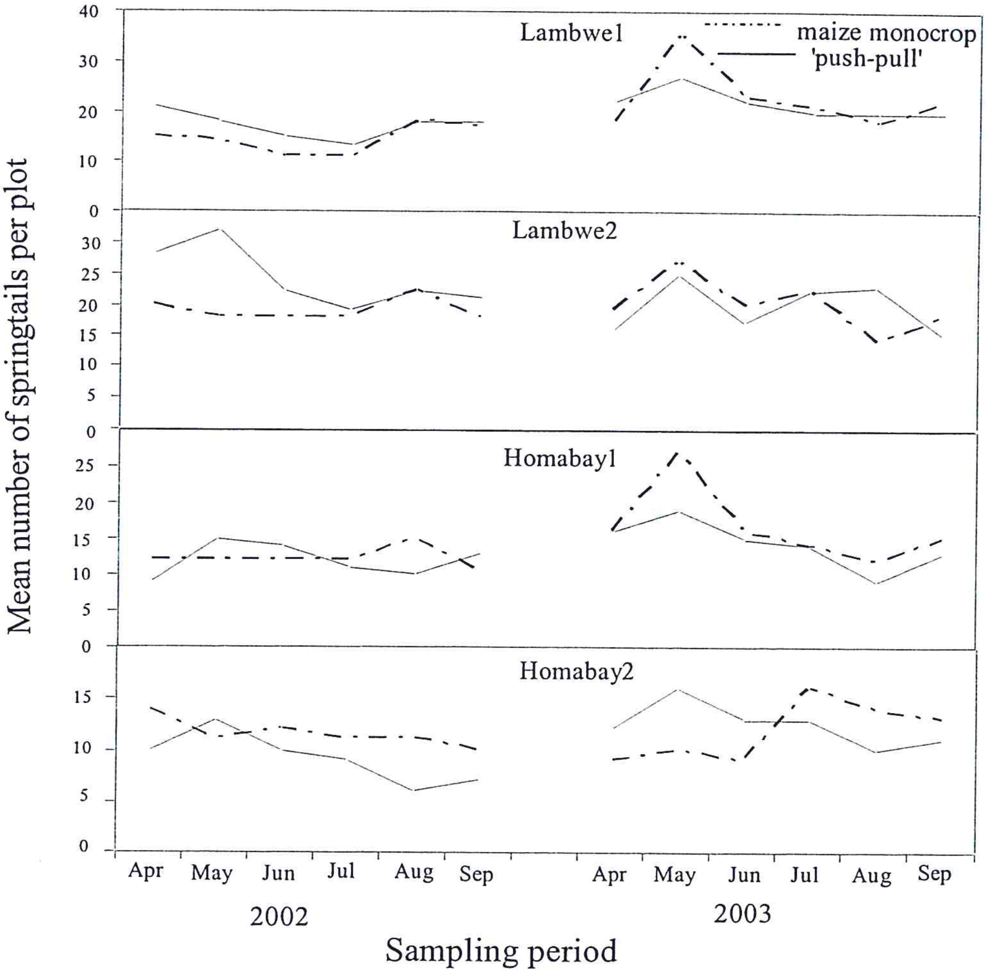


Fig 16. Population dynamics of springtails in maize fields during the long cropping seasons of 2002 and 2003 in Kenya. Means (±SE) represent data averages of four subplots. The breakages in graphs indicate periods between seasons.

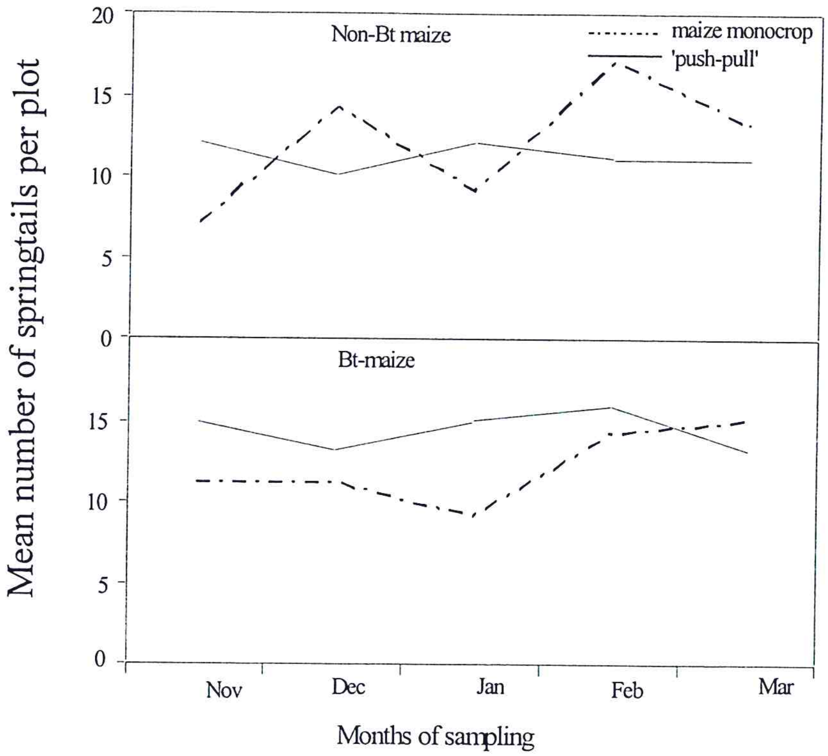


Fig 17. Population dynamics of springtails in maize fields during the 2002-2003 cropping season at ARC-GCI. Means (±SE) represent data averages of four subplots.

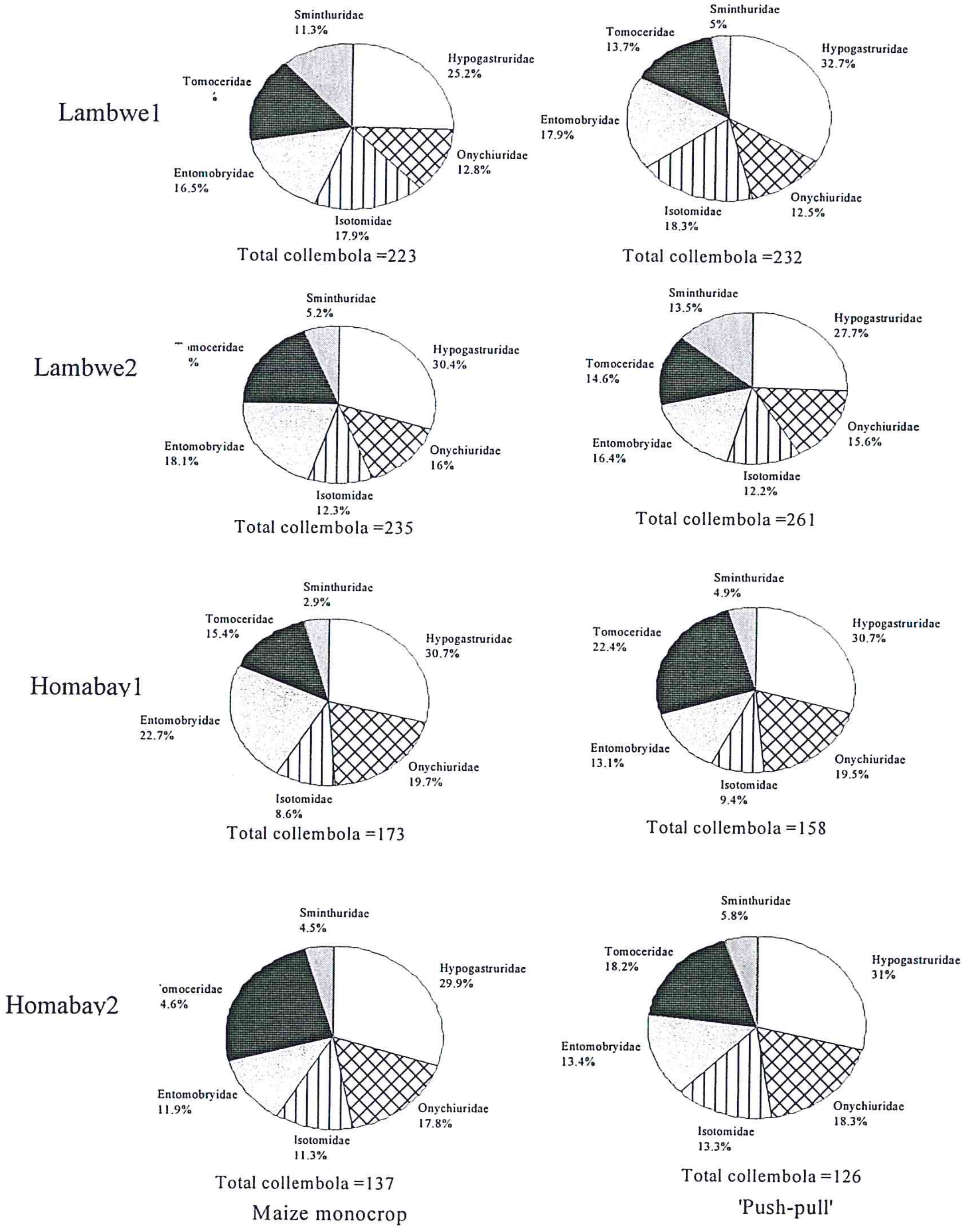


Fig 18. Mean percentage dominance and relative distribution of the springtail families at the Kenyan sites. Means represent data averages of four subplots during two cropping seasons.

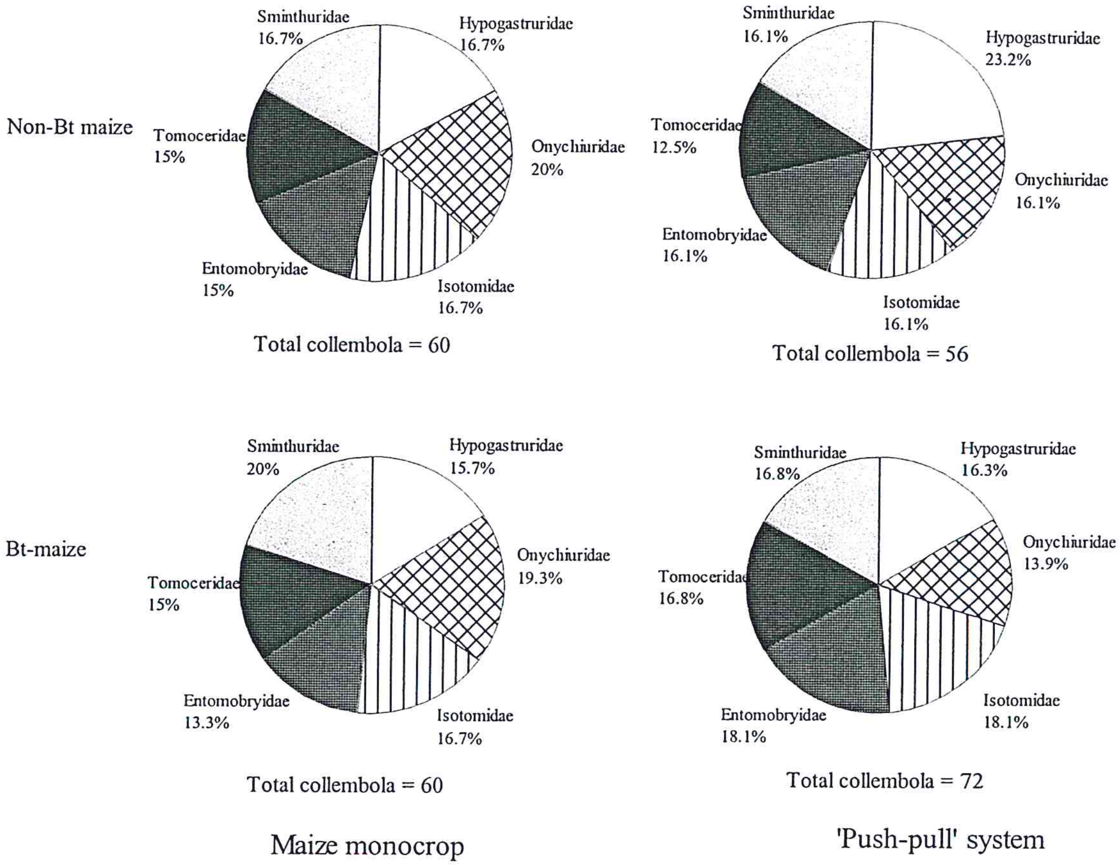


Fig 19. Mean percentage dominance and relative distribution of the springtail families in maize at ARC-GCI. Means represent data averages of four subplots.

CHAPTER SIX

6.0 IMPACT OF THE 'PUSH-PULL' SYSTEM ON MAIZE STEMBORER COLONISATION AND CROP DAMAGE LEVELS

6.1 Introduction

Vegetative diversification in some crop systems can lead to lower pest populations and crop damage, thereby enhancing yields (Andow, 1991). Vandermeer (1989) proposed the 'disruptive crop' hypothesis to explain how vegetative diversity can affect herbivore populations, similar to Root's (1973) 'resource concentration' hypothesis. It stipulates that a second plant species disrupts the ability of an insect to effectively attack its preferred host either by some sort of confusion (physical or chemical) or due to frequent encounters with non-host plant species. Under this hypothesis, stimuli that either elicit or inhibit reactions can be used to disrupt behaviour of the insect pest. In practice, stimulant and deterrent chemicals have been used for this purpose (Foster and Harris, 1997), either singly or in combination, with the latter yielding a complementary hypothesis, 'stimulo-deterrent' ('push-pull') hypothesis (Miller and Cowles, 1990; Khan *et al.*, 1997; Khan *et al.*, 2000; Khan *et al.*, 2001).

In an attempt to exploit the 'stimulo-deterrent' hypothesis, the International Centre of Insect Physiology and Ecology (ICIPE) (Kenya) and its partners have developed the 'push-pull' system (chapters one and two). This 'push-pull' system is expanding in Eastern Africa and trials are also on-going in South Africa following an extensive survey of wild hosts of stemborers in the region by van den Berg *et al.* (2001) and studies on colonisation, growth and survival of stemborers in indigenous grasses (Rebe *et al.*, 2004a, 2004 b).

The objective of this study was therefore to provide a step-wise assessment of the impact of this habitat management system on maize stemborer colonisation, crop damage and yield in the dominant maize production systems of Kenya and South Africa.

6.2 Materials and Methods

6.2.1 Study sites

Study fields were as described in chapter two. To facilitate sampling, each field was subdivided into plots of 15 m by 15 m each, with four replications. Plot data were collected and averaged for individual fields.

6.2.2 Oviposition preference

For these studies, methodologies adapted from Azerefegne and Gebre-Amlak (1994), Ogol *et al.* (1999) and Midega (2001) were employed with modifications. Commencing eight days after crop emergence, weekly inspection of all foliage in each plot was carefully conducted for stemborer egg batches. This focused mainly on eggs of *Chilo* spp., since they are often the ones prevalent during the early stages of crop colonization (Ogol *et al.*, 1999). This was done for a period of three weeks during the main period of crop colonization and when the plants are most attractive to moths for oviposition (van Rensburg *et al.*, 1987; van Rensburg and Pringle 1989). Thereafter, biweekly observation was conducted until physiological maturity (up to 16 weeks after crop emergence) of the maize crop. Because *B. fusca* prefers to oviposit under the plant's leaf sheath, the presence of its egg batches was felt by running finger tips over the leaf sheaths (Azerefegne and Gebre-Amlak, 1994). The egg batches were then counted and data expressed as number of stemborer egg batches per plot. Average (mean) values of the data were calculated over two seasons.

6.2.3 Larval numbers and plant damage

At four weeks after emergence, all maize seedlings in each plot were inspected for any characteristic foliar damage caused by stemborer larval feeding. Data were expressed as percentage plants with foliar damage per plot.

Ten maize plants were then randomly sampled from each plot and stalks inspected for stemborer entry or exit holes. This was repeated every two weeks and at harvest and data expressed as mean number of entry/exit holes per plot. The stalks were then split open and the number of stemborer larvae and pupae determined. Larval and pupal numbers were combined and expressed as mean number of borers per plot.

At flowering, the total number of maize plants that had died due to stemborer damage was counted in each plot. Such plants were identified by their characteristic symptoms of severe foliar and stem damage, deformation and retarded growth (Ogol *et al.*, 1999). These data were expressed as mean number of dead plants per plot. Additionally, the plants with broken stems due to stemborer damage were also counted and data expressed as percentage of plants with broken stems per plot.

6.2.4 Yield assessment

Yield data were obtained from the designated plots at Lambwe and Homabay fields while a modification was employed at ARC-GCI, where 5 m by 5 m plots were randomly created in each field from where the data were collected. Yield was assessed in two ways; (1) dry weight of kernels per plant for each plot, and (2) weight of kernels per plot. The number of maize plants with ears and number of ears per plant was determined on 20 randomly selected plants at Lambwe and Homabay and 10 at ARC-GCI (Ogol *et al.*, 1999). Ears from these plants were stored, sun-dried and individually weighed. They were then individually shelled and the kernels weighed to provide data on weight of seeds per plant for plants with ears (Ogol *et al.*, 1999).

Data on mean kernel weight per plant were then used to determine the yield potential of each plot. This was done by multiplying the mean kernel weight per plant with the potential plant stand per plot, after subtracting the additive effect of plant loss from plant mortality, stem breakage and plants without ears, calculated thus [(potential maximum number of maize plants in each row) (number of rows in each plot)].

All data were averaged for individual plots in each field and subjected to t-test analysis (SAS Institute, 2001) for any differences between the 'push-pull' and maize monocrop treatments with regard to the mentioned parameters.

6.3 Results

Chilo partellus and *B. fusca* were the main stemborer species encountered at all sites, with the former being relatively more abundant at Lambwe and Homabay while the latter was relatively more abundant at ARC-Grain Crops Institute. The number of egg batches for both species were significantly higher in the maize monocrop that in the 'push-pull' systems in all cases ($P<0.05$) (Fig 20).

The number of stemborer larvae and pupae, not separated into species, were combined to provide data on their numerical incidence per plot. Results show that the incidence of the larvae and pupae was significantly higher in the maize monocrop than in the 'push-pull' systems ($P<0.05$) at all sites (Fig 21). The numbers of these borer larvae and pupae ranged between 33 and 73 per plot in the maize monocrop and 9 and 29 per plot in the 'push-pull' plots at Lambwe; 19 and 62 in the maize monocrop and 10 and 37 in the 'push-pull' plots at Homabay. At the ARC-GCI, the number of larvae and pupae per plot was between 21 and 45 in the maize monocrop and 14 and 20 in the 'push-pull' plots (Fig 21).

Mean number of entry/exit holes per plot and the percentage number of plants with leaf damage were significantly higher in the maize monocrop than in the 'push-pull' plots in all the fields ($P<0.05$) (Figs 21 and 22 respectively) and support the principle that the lower the pest population the lower the plant damage (Abate *et al.*, 2000). Similarly, mean percentages of plants with broken stems and dead plants per plot were significantly higher in the maize monocrop than in the 'push-pull' plots at Lambwe and Homabay ($P<0.05$) but not different at ARC-GCI ($P>0.05$) (Fig 22).

Maize yields in terms of average dry kernel weight per plant and average weight of kernels per plot were significantly higher in the 'push-pull' than in the maize monocrop plots at Lambwe and Homabay ($P<0.05$) but were the same between the two cropping systems at ARC-GCI ($P>0.05$) (Fig 23).

6.4 Discussion

The results on oviposition preference indicate that the *C. partellus* and *B. fusca* moths preferred the maize monocrop to the 'push-pull' system for oviposition. The results are similar to those reported by Ogol *et al.* (1999) who observed significantly greater oviposition by maize stemborers in the maize monocrop systems than in the maize-leucaena (*Leucaena leucocephala* L.) intercrops. Khan *et al.* (1997b) also observed that a significantly higher number of egg batches were oviposited on maize in a monoculture situation than on maize intercropped with molasses grass.

Studies on semiochemicals of the 'push' and 'pull' plants in this system have revealed that the plants emit a host of volatiles (semiochemicals) that influence orientation of the ovipositing moths. The host plants have been shown to produce active compounds such as octanal, nonanal, naphthalene, 4-allylanisole, eugenol and linalool (Khan *et al.*, 2000; Khan and Pickett, 2004) which are attractant to the moths. Similarly, desmodium was found to produce volatiles such as ocimene and nonatriene, semiochemicals associated with high levels of stemborer colonisation and plant damage, which are repellent to ovipositing moths (Khan *et al.*, 2000; Khan and Pickett 2004). The combined attractiveness of Napier grass and repugnant property of desmodium therefore ensured that lower numbers of moths settled and oviposited on the maize crop in the 'push-pull' plots. As has been explained by Äsman *et al.* (2001), if intercropping can influence the oviposition behavior of a herbivore so that fewer eggs are laid on the crop, then, already at the preliminary stage, there will be an advantage compared with a monoculture. In the current study, the main crop (maize) was made less attractive to the stemborer moths by the chemical cues from a more attractive Napier grass in conjunction with the repugnant volatiles from the intercrop (desmodium), thereby providing a significant level of protection to the maize crop. Because the attraction of phytophagous insects to their hosts involves both olfactory and visual cues (Cardoza *et al.*, 2003), the position of the trap/perimeter crop in the 'push-pull' set up also seems to lead some of the adult moths to it, being the first host to be encountered as a component of a trap cropping system (Hokkanen, 1991).

These results are consistent with those of Khan *et al.* (1997b, 2001) who found significantly higher number of stemborer larvae in the maize monocrop than maize intercropped with desmodium or molasses grass and with Napier grass as a perimeter crop ('push-pull' system) in western Kenya. Ogol *et al.* (1999) also reported significantly lower stemborer larvae in the maize monocrop than in maize-leucaena intercrops at the Kenyan coast.

The 'push-pull' system described here is associated with up to 80% egg mortality and up to 89% early instar larval mortality (Chapter 3), levels significantly higher than in the maize monocrop systems. Besides, a study by Midega and Khan (2003) has revealed that the 'push-pull' system is associated with enhanced stemborer predator abundance and diversity. The lower number of larvae and pupae observed in this system could therefore be as a result of a combination of both reduced oviposition, and egg and larval mortality resulting from the activity of these natural enemies, alongside other mortality factors (Reviewed by Zalucki *et al.*, 2002).

Stem tunneling by stemborer larvae on plants results in destruction of the growing point, early leaf senescence, weakened stems, among other damage to the plant (Kfir *et al.*, 2002). Infestations by stemborers also increase the incidence and severity of stalk rots (Bosque-Perez and Mareck, 1991). These damages predispose the plants to stem breakage and lodging (Kfir *et al.*, 2002). Lower stemborer populations and crop damage could explain the lower incidence of broken stems in the 'push-pull' plots in this study. At ARC-GCI, the maize monocrop was sandwiched between the fields of maize on two sides, a 'push-pull' field on one side and wild vegetation comprising of trees and shrubs on the other. These may have influenced the results by their impact on the movements of wind, including its speed (Bottenberg and Irwig, 1992).

Increased yields result from measures that effectively reduce the adversity or severity of the factors that influence crop yield (Maddoni and Otegui, 2004). Under small-scale cropping systems of Africa, the major yield-reducing factors include pests, soil nutrient deficiencies, moisture and temperature (Abate *et al.*, 2000). Besides stemborers, the other serious pest of maize in the region is striga weed, *Striga hermonthica* (L.) Benth., which, when occurs together with the former, could cause yield losses of up to 100% (Oswald and Ransom 2001, 2004). The ‘push-pull’ system is associated with reduced oviposition by the stemborer moths, lower larval populations, enhanced stemborer predator abundance and diversity (Midega and Khan, 2003), reduced crop damage and death, higher moisture and humidity, enhanced nitrogen levels and reduced striga infestation (Khan *et al.*, 2002), and higher levels of organic matter resulting from decaying leaves of desmodium. These translated into the higher yields of maize observed in the current study and corroborate the findings of Khan *et al.* (1997, 2001), who reported enhanced maize yields in the maize intercropped with desmodium or molasses grass with Napier or Sudan grass as a perimeter crop around the field. The plants at Lambwe and Homabay were rain fed while irrigation was used at ARC-GCI which was often limiting. Yields at the latter site were therefore most likely influenced by competition for moisture between maize and desmodium plants. Results of the current study therefore demonstrate further that this ‘push-pull’ strategy reduces damage to maize by the stemborers thereby enhancing maize yields.

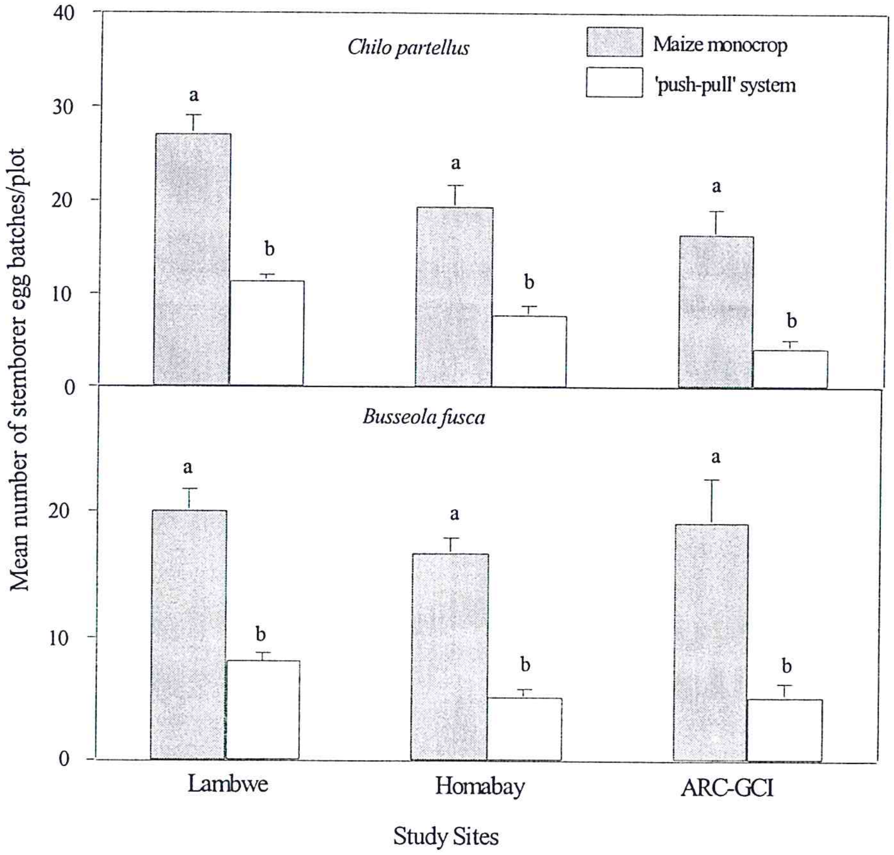


Fig 20. Incidence of stemborer egg batches at Lambwe School of the Deaf (Lambwe), Homabay Farmers' Training Centre (Homabay) and ARC-Grain Crops Institute (ARC-GCI). Means (± SE) represent treatment averages over two cropping seasons. For each locality, bars marked by different letters are significantly different ($P<0.05$).

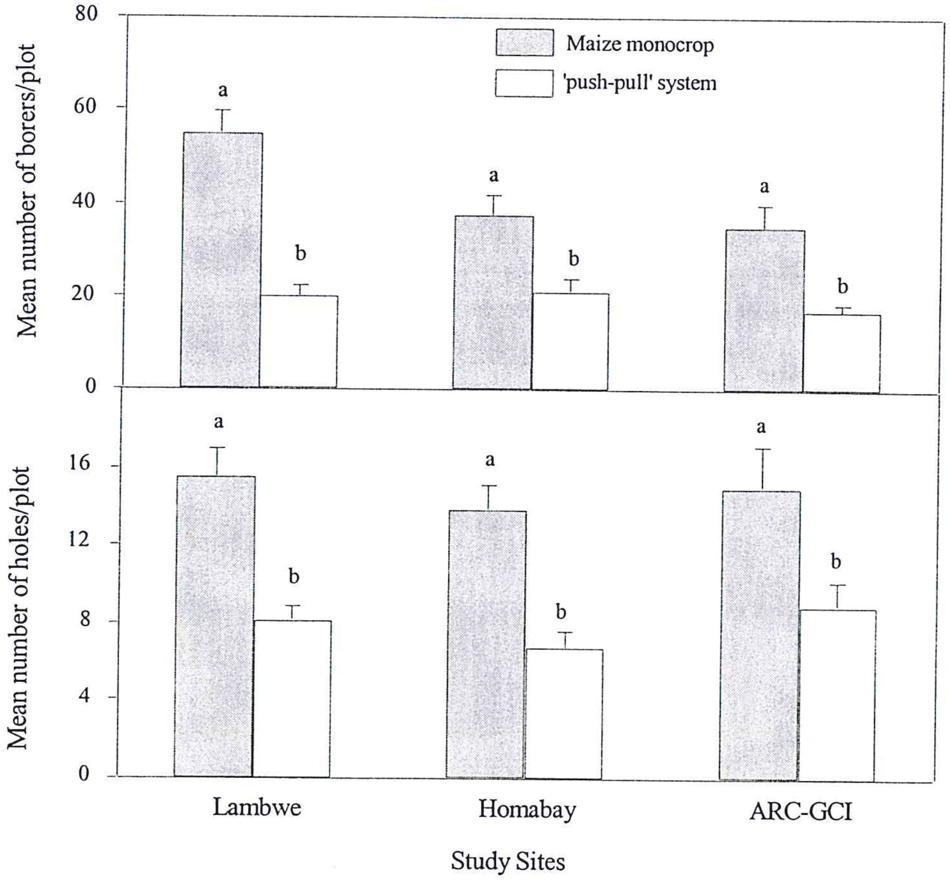


Fig 21. Mean (± SE) number of stemborer larvae and pupae and stemborer entry/exit holes per plot at Lambwe School of the Deaf (Lambwe), Homabay Farmers' Training Centre (Homabay) and ARC-Grain Crops Institute (ARC-GCI). Means represent treatment averages over two cropping seasons. For each locality, bars marked by different letters are significantly different (P<0.05).

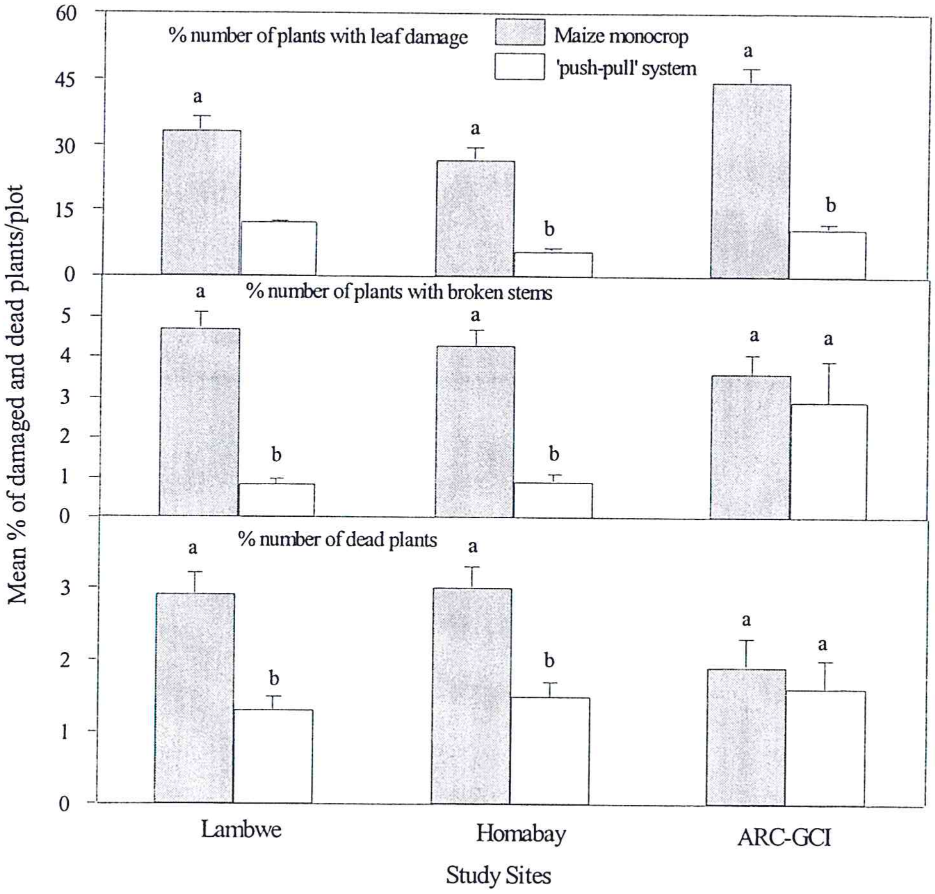


Fig 22. Mean (± SE) percentage of maize plants per plot with broken stems, leaf damage and dead at Lambwe School of the Deaf (Lambwe), Homabay Farmers' Training Centre (Homabay) and ARC-Grain Crops Institute (ARC-GCI). Means represent treatment averages over two cropping seasons. For each locality, bars marked by different letters are significantly different (P<0.05).

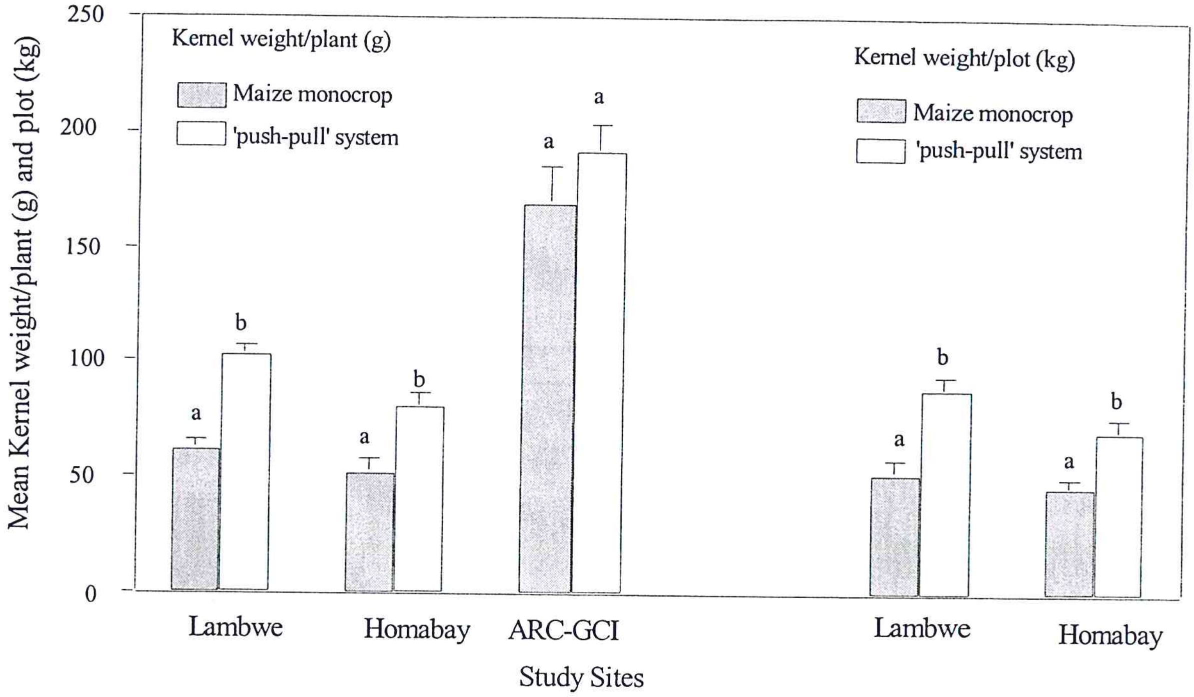


Fig 23. Average (± SE) yield of maize per yielding plant and plot at Lambwe School of the Deaf (Lambwe), Homabay Farmers' Training Centre (Homabay) and ARC-Grain Crops Institute (ARC-GCI). For each locality, bars marked by different letters are significantly different (P<0.05).

CHAPTER SEVEN

7. GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

7.1 General discussion, conclusions

7.1.1 The 'push-pull' system and maize stemborer colonization, crop damage and yield

'The 'push-pull' system in the current study was observed to reduce both oviposition and crop damage leading to enhanced crop yield (Chapter six). The reduced stemborer infestation in the 'push-pull' system was attributed to the combined repellence of the desmodium plants and attraction property of Napier grass to the stemborer moths. These results therefore confirmed those of previous studies by Khan *et al.* (1997b, 2000, 2001) and Khan and Pickett (2004). However, the observed increase in maize yield in the 'push-pull' systems in the current study cannot be attributed to the reduced stemborer infestation and crop damage levels alone but as a function of these reductions and the suppression by desmodium of the parasitic striga weed, *Striga hermonthica* (L.) Benth. (Khan *et al.*, 2002).

7.1.2 The 'push-pull' system and natural enemy abundance, diversity and activity

The study showed that both predator abundance and activity were enhanced under the 'push-pull' system. Similarly, parasitoid activity was equally enhanced. As has been suggested, the latter needs to be interpreted with caution due to significantly lower stemborer populations in the 'push-pull' system. The system has been shown to significantly reduce stemborer infestation (Chapter six). The enhanced population of the predators must have been therefore due to other benefits accompanying vegetational diversity of these systems such as alternative prey in the form of desmodium and Napier grass pests (Midega and Khan, 2003) and suitable microhabitats provided by the accompanied plants such as a reduction in soil temperature and increase in relative humidity (Khan *et al.*, 2002). This is more relevant to the generalist predators but not to the specialist parasitoids (Midega *et al.*, 2004). The observed response of the parasitoids therefore must have been due to the semiochemicals from desmodium similar to those produced by herbivore-damaged maize plants (Khan and Pickett, 2004) (Chapter 2).

7.1.3 The 'push-pull' system and Bt-maize: impacts on arthropod abundance and diversity

Arthropod abundance and diversity has been reduced immensely over the last century due to oversimplification of the agricultural system. In an agroecosystem, arthropods perform a variety of functions including regulation of pest populations, nutrient recycling, improvement of soil texture through feeding and burrowing, modification of the ecosystem food chains thereby determining ecosystem stability (Altieri, 1999). Because they occupy a middle tropic level in the food chain, spiders are one of the most important arthropod groups in many ecosystems whose abundance and diversity levels have been used as an indicator of the ecological integrity of the system (Mrzljak and Wiegleb, 2000). The 'push-pull' system and Bt-maize are relatively new stemborer management techniques whose impact on arthropod abundance and diversity levels had not been comprehensively assessed. Results of the current study have demonstrated that both technologies have no effect on the overall spider species diversity. The former however has an impact on species diversity of some spider families exemplified by the family

Lycosidae. The system was also observed to enhance spider abundance under both Bt- and non Bt-maize, indicative of a positive influence on populations of ground-dwelling arthropods. This was probably due to the factors described in 7.1.2 above.

7.1.4 The 'push-pull' system and Bt-maize: impacts on soil fauna

Soil arthropods such as springtails have a potential of being used as an integrative measure of soil quality due to their importance in regulating soil processes which are vital to the continued formation of soil in agroecosystems. They are important consumers of plant residues and soil fungi and help in the creation of humus besides being prey to many arthropod groups (Earton *et al.*, 2004). Because of their sensitivity to various environmental changes, springtails are able to provide a database of numerous species thereby offering an abundant tool to assess the ecological health of the agroecosystems (Al-Deeb *et al.*, 2003). They were therefore selected for the current study to assess the impact of Bt-maize and the 'push-pull' system on soil fauna. Results indicated that the two technologies had no effect on both abundance and diversity response levels of springtails (Chapter five). It is probable then that Bt-toxins from the plants in the current study are not toxic to springtails or that the Bt-toxin is not released into the soil or is not present in lethal concentrations (Al-Deeb *et al.*, 2003). Similarly, it implies that the volatiles from the root exudates of desmodium (Tsanuo *et al.*, 2003) are not toxic to springtails, at least at family level. Because species would have been the most appropriate level for this assessment, these results likewise need to be interpreted with care.

7.1.5 The 'push-pull' system: Role in stemborer resistance management to Bt-maize

The usefulness of the transgenic cultivars may be cut short should the target pests develop resistance to them. Factors that could lead to development of resistance and recommended management strategy, including their shortcomings have been discussed in Chapter 3. A potential strategy that has been hitherto neglected is the role of natural enemies and moth diversionary tactics including trap cropping. Reducing the population of the borer population getting exposed to the Bt-toxin would be an important component in an integrated resistance management strategy. The 'push-pull' system has been shown to be associated with reduced stemborer infestation of enhanced predator abundance and was thought to have a potential role in resistance management to Bt-maize. Results (Chapter 3) confirmed this and demonstrated that incorporating habitat management into Bt-technology reduces oviposition on the maize crop. It also enhances both predator abundance and efficacy, with the latter being more pronounced at the earlier stages of stemborer development reducing chances of any harmful effects on the natural enemies (Dutton *et al.*, 2002). Other benefits of this system include the sticky sap of Napier grass which entangles and kills the stemborer larva when it punctures the stem in an attempt to bore into it (Khan and Pickett, 2004). These reductions in stemborer populations could be combined with other tactics in an integrated resistance management programme. Moreover, even under a Bt-maize monoculture system just a small proportion of the target pest survives (Catangui and Berg, 2002). The results of this study therefore offer opportunities for insight investigation of the main stemborer predator species, their population dynamics in these cropping systems and impact of consumption of prey exposed to the Bt-toxin with a view to coming up with a 'push-pull' system compatible with the other management options in an attempt to develop an ecologically sound, economically feasible and user friendly integrated resistance management strategy.

7.2 Recommendations for future work

1. The 'natural enemy hypothesis' predicts that populations of natural enemies will be greater in diverse agroecosystems because of an increased availability and diversity of alternate host/prey and food sources and suitable microhabitats (influenced by temperature and relative humidity). Results of the current study alongside those of Midega and Khan (2003) have revealed enhanced generalist predator populations and diversity with significantly lower stemborer populations. The response of these predators has therefore not been accounted for. It is therefore desirable to assess the numerical response of the non-target pests in these systems. Pests of Desmodium, Napier and maize (other than stemborers) should be assessed in terms of abundance and diversity and tested against the encountered predator populations for a relationship. These data should be related to temperature and humidity levels during each sampling occasion to assess the role played by these environmental conditions on the recruitment of the predators.

2. Life tables are a means of systematically and numerically describing mortality according to specific age groups or times within a population and allow the ecological role natural enemies and other mortality factors play in a particular system to be quantified and to determine whether they are a source of regulation contributing to stability (Midega, 2001). In key factor analysis, the 'key factor' has been described as the mortality factor having the largest and most important effect in producing

seasonal/annual pest population fluctuations (Podoler and Rogers, 1975). A series of life tables and key factor analyses are desirable to establish the mortality factors operating to lower stemborer populations in the 'push-pull' systems and determine their interactions and identify any relationships between mortality and pest density.

3. The mechanisms associated with the natural enemy hypothesis have not been examined exhaustively in 'push-pull' systems and the little done so far has been without consideration of the plant-natural enemy interaction, but natural enemies and herbivores have evolved and function within multitrophic context. Besides, studies have revealed that desmodium produces volatiles similar to those of the stemborer infested maize plants (used by female parasitoids to locate prey). Studies therefore need to be conducted to determine the role on the 'push-pull' plants in mediating specialist natural enemy responses. A Y-tube olfactometer and malaise trap methods are proposed for the assessment of the response of these parasitoids to the volatiles of the 'push-pull' plants.

4. Insects have been used as indicators of a range of environmental attributes since the turn of the 20th century. In terrestrial environments, ants and carabid beetles have been the most preferred groups. Because they are fairly sensitive to environmental changes and easier to handle taxonomically, their response to the 'push-pull' systems need assessment as an indication of the impact of the system on arthropod abundance and diversity. They are also important stemborer predators and therefore their response to the system will be an additional indication of efficacy levels of the pests' predation. Pitfall traps are proposed for these studies. Directional pitfall traps should be used to assess their

recruitment into the system and provide an indication of arthropod conservation abilities of the same. More in depth studies are also desirable to assess the direct impact of Bt-maize and desmodium root exudates on specific springtail species and assess the potential use of the same as biological indicators of the environmental effect of both Bt-maize and the ‘push-pull’ system.

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