Estimating the impacts of climate change on interactions between different lepidopteran stemborer species

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Thesis submitted for the degree Philosophiae Doctor in Environmental Sciences at the Potchefstroom Campus of the North-West University

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Co-supervisors: Dr. B. Le Ru
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April 2015
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April 2015

NORTH-WEST UNIVERSITY, SOUTH AFRICA
DEDICATION

This is dedicated to my parents Mr Harrison Ntiri and Mrs Constance Ntiri for all the support throughout the years
DECLARATION AND APPROVAL

Declaration by the candidate

I, Eric Siaw Ntiri, declare that this research project which I hereby submit for the degree of Philosophiae Doctor (Environmental Sciences) at the North-West University is entirely my original work and has not been submitted for a degree in any other university.

Signature

Date: 29/04/2015.

Approval by supervisors

The supervisors of this study give permission that the data generated during the study may be used for scientific publication by the student.

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Date: 25/04/2014
ACKNOWLEDGEMENTS

I acknowledge SIDA for the full financial support provided to carry out all research activities through the flagship programme-African Regional Postgraduate Research in Insect Science (ARPPIS) run by the Capacity Building and Institutional Development (CB & ID) office of the African insect for food and health-icipe.

I acknowledge all the staff at the CB &ID office who provided the administrative support needed to conduct this research; Dr Robert Skilton (current head), Mr Mario Margiotta (past head), Mrs Lillian Igweta-Tonnang (Training officer-your professionalism and great patience in dealing with any aspect to do with students affairs, was par exellence), Lisa Omondi and Margaret Ochanda.

I acknowledge Dr Bruno Le Ru, my supervisor at icipe for choosing me to do this PhD and also mentoring me in the development of my scientific career. I really value all your support, professional criticisms, and encouragement when I faced challenges with my work, the conducive environment you provided to hold frank discussions on the work have enabled me come through refined. I also acknowledge my co-supervisor Dr Paul-Andre-Calatayud, who assisted me with ideas on every aspect of the work. You gave me the opportunity to learn acquire extra skills through the valuable suggestions you make to work.

I acknowledge Professor Johnnie Van den Berg, my university professor for all the immense support given to facilitate this work. I really admired your patience and easy-going nature with all your students who worked under you. For your support also on all academic and administrative matters at the university

I acknowledge all the staff at the IRD-NSBB laboratory at icipe who provided all the technical support to my work: Messrs Gerphas Ogola, Julius Obonyo, Peter Ahuya, Anthony Kibe and Boaz Musyoka (special thanks to you for the great support in most of my work). I also acknowledge staff at the ARCU unit for the rearing and supply of the insects used in this work: Mr Peter Malusi, Faith Moses, Beritha Mutune and Frederick Ochieng.

I also duly acknowledge Dr George Onga’mo, Nancy Khadioli and Sizah Mwalusepoh for allowing me to use part of your field data in my work. I acknowledge Dr Salifu and Mr Benedict Orindi for all the statistical support and discussions on analysis concerning my work.

I acknowledge Ms Winnie Nunda who has stood with me all this period, providing the encouragement I needed to be able to carry out this work. Also to my siblings for their confidence in me.

Finally, I acknowledge all students I met and interacted with during my stay here. We got along to share lots of moments which helped me sail through. Mr Bayissa Wakuma, Valentina Migani George Asudi, Daniel Mutyambai, Eunice Awino, Yvonne, Ajamma Venansio Tuhumaise, Mwanasiti Bendera, Dr Fauster Akutse, Caroline Foba, Sheila Agha, Rosaline Macharia, Rosemary Twum.
ABSTRACT

The production of cereals, especially maize, which is a staple food in sub-Saharan Africa, is challenged by pests and diseases. In addition, climate change will exacerbate the magnitude of these challenges and agriculture in general. Lepidopteran stemborers are major pests of cereal crops in sub-Saharan Africa. Two indigenous noctuids, *Busseola fusca* and *Sesamia calamistis* and one exotic crambid, *Chilo partellus*, occur as single and mixed-species communities infesting cereal crops in East and southern Africa. The composition of these communities however varies with altitude and over seasons. Interactions between the species especially when in combination, can affect the level of damage to cereal crops. The objective of this study was to describe the intraspecific and interspecific interactions between the three stemborer species when they make use of the same resources. This study involved field surveys in maize fields in major agro-ecological zones and also different experiments under greenhouse and laboratory conditions to describe the interactions between the species as well as the effect of temperature, species density and duration of the period of competition on outcomes of these interactions. Results showed that stemborer communities are composed of single and mixed species of *B. fusca*, *S. calamistis* and *C. partellus*, which varied with the different agro-ecological zones and also along altitudinal gradients. Temperature was the most important abiotic factor that influenced the composition of stemborer communities. However, infestation patterns varied with season. This study also showed that female moths of the three species did not avoid oviposition on plants that were previously infested by stemborers. *Busseola fusca* showed a high preference for heterospecific-infested plants, while *C. partellus* preferred conspecific-infested plants. *Sesamia calamistis* did not show a significant preference for one plant over the other. This study further showed that both intra- and interspecific competition characterise communities of these stemborer species which utilise the same resources. Interspecific competition was stronger between the noctuids and the crambid than between the two noctuid species. Temperature had a significant influence on the competitive outcomes between the three species. Finally the study showed that density-dependent effects and the duration of the interactions are also important factors which influence the level of competitive outcomes between the species. Climate change is likely to influence the interactions and composition of stemborer communities.

**Key words:** Climate change, community, competition, oviposition responses, resource utilisation, species interactions, stemborer, temperature-dependence
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CHAPTER ONE: INTRODUCTION

1.0 Agriculture, food security and challenges in sub-Saharan Africa

The global estimate for people suffering from hunger was 842 million between 2011 and 2013 (Food and Agriculture Organisation, 2013). Although this figure is a reduction of previous estimates and thus shows progress especially in developing countries, sub-Saharan Africa (SSA) was the region with the highest incidence of undernourishment (FAO, 2013). An efficient and effective agricultural system is a major contributor to food security (World Economic Forum, 2013). In SSA, agriculture is characterised by small holdings and its development is faced with constraints such as political instability, poor governance, pests, drought and HIV.

1.1. Cereal crop production in SSA and its challenges

The bulk of the food supply in SSA consists of cereals, roots and tubers (FAO, 2005). The most important cereals are maize, rice, millet and sorghum (Polaszek & Khan, 1998). Maize production covers about 30% of the total area under cereal production in this region (Cairns et al., 2013) and makes up 6.5% of worldwide production (International Institute of Tropical Agriculture, 2009). Maize consumption in SSA is 21% of the total worldwide consumption of 116 million tons and it is mainly used as food (85% in Eastern and Southern Africa; 95% in West Africa) (IITA, 2009).

Maize production in SSA faces a myriad of challenges including pests, diseases, drought and nutrient deficiency (IITA, 2009). Lepidopteran insect species are the major pests of cereal crops in SSA. The larvae of these species feed on the leaves of cereal plants, after hatching from eggs oviposited by the adult moth on the plant. Larvae bore
into the stems of plants and cause physical damage that limits growth and causes economic loss (Kfir et al., 2002). Twenty-one species from three lepidopteran families (Noctuidae, Crambidae and Pyralidae) have been reported as cereal pests in Africa (Maes, 1998). In their SSA range, there are variations in their importance, with respect to their locations, season and the crops they attack (Ndemah et al., 2001; Kfir et al., 2002). The most important species that attack maize are the noctuids Busseola fusca (Fuller) and Sesamia calamistis Hampson, the pyralid Eldana saccharina Walker and the crambids Chilo partellus (Swinhoe) and C. orichalcociliellus Strand (Kfir et al., 2002). Other insect species which attack maize are ear borers, armyworms, cutworms, grain moths, beetles, weevils, grain borers, rootworms, and white grubs (IITA, 2009).

1.2. Interactions among insect pests and their effects on plants

Plants host diverse communities of insect species and other arthropods (Strong et al., 1984; Liss et al., 1986; Lewinsohn et al., 2005), which could be different taxonomic groups or functional guilds that have different spatial and temporal resource utilisation patterns (Imura, 2003; Lewinsohn et al., 2005; Rocca & Greco, 2011). Insects within the same guild utilise the same parts of the plant in the same way, irrespective of their taxonomic group (Hawkins & MacMahon, 1989; Simberloff & Dayan, 1991). Based on guilds, a plant’s arthropod community could be grouped into leaf chewers, sap suckers, leaf miners, borers, gall-makers and root feeders (Stiling et al., 1999; Imura, 2003; Truter et al., 2014; Stam et al., 2014).

Direct and indirect interactions, of which outcomes could be positive, negative or neutral, occur within and between different guilds, affecting the structure and functions of insect communities on plants (Hudson & Stiling, 1997; Kaplan & Eubanks, 2005; Wootton & Emmerson, 2005). Competitive interactions result in negative outcomes,
while facilitative interactions result in positive outcomes on the species involved (Denno et al., 1995; Bruno et al., 2003; Kaplan & Denno, 2007). Additionally, these interactions between species can affect the productivity of the plant on which they are found. For instance the damage caused by multiple species of pests on crop plants is usually higher than the individual damage caused by each species (Van den Berg et al., 1991; Dangles et al., 2009).

1.3. Temperature and climate change effects on species interactions

Temperature is the most important abiotic factor that influences insect species since it directly drives the rate of growth and development, fecundity and mortality, influences resource utilisation, interspecific and intraspecific interactions and also limits the geographic distribution of insect species (Howe, 1967; Hodkinson et al., 1999; Bale et al., 2002; Sporleder et al., 2004; Dangles et al., 2008; Speight et al., 2008; Damos & Savopoulou-Soultani, 2012). Temperature also indirectly influences insect species through the impacts it has on host plants, competitors and natural enemies (Bale et al., 2002; Estay et al., 2009). It is therefore the most limiting factor in insect biology and distribution of species (Damos & Savopoulou-Soultani, 2012).

The past decade has seen changes in the global climatic elements including a decrease in cold temperature extremes, an increase in warm temperature extremes, extreme high sea levels and changes in the number of heavy precipitation events in a number of regions. These changes have been influenced by natural and increasing anthropogenic substances and processes (Intergovernmental Panel on Climate Change, 2014). Of much importance is the increase in atmospheric and ocean temperatures, as it will have large effects on natural and human systems at a global level (Bale et al., 2002; IPCC,
2014). Current observed effects of climate change include changes in rainfall patterns and the dynamics of organisms (Woiwod, 1997; Bale et al., 2002; IPCC, 2014).

Climate change has been reported to change arthropod population dynamics such as species abundance, phenology and their distribution on the host plants which they utilise (Woiwod, 1997; Masters et al., 1998; Bale et al., 2002; Hagen et al., 2007). Furthermore, species interactions such as plant-insect, predator-prey and competitive interactions are also being affected by changes in climate (Cammell & Knight, 1992; Buse et al., 1999; Gordo & Sanz, 2005; Hegland et al., 2009).

1.4. Problem statement

Lepidopteran stem borers such as *B. fusca*, *S. calamistis* and *C. partellus* attack maize in East and southern Africa (Reddy, 1998; Kfir et al., 2002). Depending on altitude, they may occur as single species or communities of mixed species attacking cereals in the same field (Van den Berg et al., 1991; Tefera, 2004; Onga’amo et al., 2006a; 2006b; Krüger et al., 2008). In Kenya, the composition of these stem borer communities varies with altitudinal gradient. *Busseola fusca* is the predominant species in the highlands characterised by comparatively low temperatures, while *C. partellus* is the most abundant species in the hot lowlands. In contrast, *S. calamistis* is present in low numbers at all altitudes. In the mid-altitudes, the three species occur as a mixed community, but the predominance of a species may vary with respect to locality and season (Guofa et al., 2001; Ong’amo et al., 2006a, 2006b). Reports of competitive displacement of *B. fusca* by *C. partellus* due to overlap in resource use have been reported in South Africa (Kfir, 1997; Rebe et al., 2004) while *C. partellus* has been reported to have displaced *C. orichalcociliellus* in the coastal region of Kenya (Ofomata et al., 1999). However, the mechanisms behind these species displacements are still
not known. Furthermore, while the influence of temperature on the distribution of these stemborer communities is known, the influence of temperature and the likely impacts of climate change on their interactions have yet to be elucidated.

1.5. General objective

The general objective of this study was to describe the type of intra- and interspecific interactions within stemborer pest communities that utilise the same maize resource, and to assess the influence of temperature and the potential impacts of climate change on these interactions.

1.6. Specific objectives

The specific objectives of this study were:

1. to describe the structure of stemborer communities infesting maize plants under field conditions in different agro-ecological zones, their spatio-temporal dynamics in mixed communities and the important abiotic factors which influence them.

2. to describe the oviposition response of different stemborer species to intra- and interspecific infested maize plants.

3. to describe the type of intra- and interspecific interactions within stemborer communities and the effect of temperature on interactions.

4. to describe the effect of larval density and duration of interactions on the outcomes of intra- and interspecific interactions within different stemborer communities.
1.7. References


CHAPTER TWO: LITERATURE REVIEW

2.0. Biological communities and ecological interactions

The existence of species interactions has been given much attention in ecological studies. Species interactions generally characterise all life forms, as they are phylogenetically-conserved traits within clades, conferred from ancestors (Gómez et al., 2010). The ecological importance of species interactions is defined by their overall influence on the conservation of biodiversity or species loss (Loreau & Hector, 2001; Memmott et al., 2006) and provision of ecosystem services such as pest control, pollination and seed dispersal (Memmott et al., 2007). Another ecosystem service is the structuring of biological communities through regulation of abundance (Connell, 1980; Peacor & Werner, 2004; Agrawal, 2005; van Veen et al., 2006; Bulleri et al., 2008), which could greatly influence ecosystem functioning (Duffy et al., 2007). Additionally, some communities get modified through these species interactions in a process referred to as “ecosystem engineering” (Calderón-Cortés, 2011) and also through newly-initiated interactions created by invasive species (Duyck et al., 2006). Furthermore, the intensity of an interaction, e.g. the number of trophic linkages, affects the magnitude and frequency of cascading effects through the community (Halaj & Wise, 2001).

All life forms exhibit some type of interactions within themselves and also with other life forms. Plants compete for light with their neighbours and for soil resources such as water and nutrients (Casper & Jackson, 1997). For example, intra- and interspecific competition for nutrients at early growth stages was reported within the native perennial species, bluebunch wheatgrass (Pseudoroegneria spicata (Pursh) Á. Lôve (Poaceae)) and Sandberg bluegrass Poa secunda J. Presl (Poaceae) as well as the invasive annual species, cheatgrass Bromus tectorum L. (Poaceae) and medusa head Taeniatherum caput-medusae (L.) Nevski (Poaceae) (Mangla et al., 2011). On the other
hand, plants also protect other plants from herbivores, other competitors and extreme climatic conditions (Brooker et al., 2008). Plants generally interact positively with other plants to structure communities, support co-existence and to enhance diversity and productivity (Callaway, 1995). Furthermore, plants also interact with animals during processes such as pollination, seed dispersing and mutualistic interactions (Bascompte & Jordano, 2007). Microorganisms also exhibit competitive interactions (Hsu et al., 1981). Griffin et al. (2004) reported on the competition for siderophore (iron-scavenging agents) production by the pathogenic bacterium Pseudomonas aeruginosa (Schröter) Migula (Pseudomonadaceae). Microorganisms also compete with other life forms. For example, microorganisms were found to compete with the roots of sorghum and barley for iron in the root apoplasm (Von Wirén et al., 1995).

The type of interactions that occur in animal communities include trophic-based interactions such as herbivory, folivory, predation and parasitism as well as non-trophic based interactions, such as pollination, seed dispersal, competition, nitrogen fixation, decomposition and facilitation (Memmott et al., 2007; Gómez et al., 2010).

Different types of interactions can be differentiated based on certain characteristics they exhibit. For instance, based on effect type, species interactions are grouped into those which have negative impacts (negative interactions), e.g. competition, parasitism and predation, and those which have positive impacts on interacting species (positive interactions) such as pollination, nitrogen fixation and facilitation (Connell, 1980). Species can also interact directly with each other or interact indirectly through the influence of a shared environment (Pulliam, 2000; Ohgushi, 2008) e.g. through the mediation effect of host plants (Anderson et al., 2009) or through the influence of their natural enemies (van Veen et al., 2006). Ecological interactions also occur spatially and
temporally within communities. Spatial interactions are differentiated as vertically occurring across trophic levels, characterised by consumptive interactions, and horizontally within levels defined by competitive and facilitative interactions (Duffy et al., 2007). Vertical interactions such as predation and parasitism are also known as “top-down” interactions, because of the direction of their effect, in comparison with “bottom-up” effects which limit food resources (Debouzie et al., 2002; Moon & Stiling, 2002). Another distinction is made between generalised species interactions and specialised species interactions, both of which are conserved phylogenetically (Gómez et al., 2010).

2.1. Interactions between insects

Insect species dominate global biodiversity, in terms of numbers and distribution (Memmot et al., 2007; Speight et al., 2008). Over 50% of the animal biodiversity that has been identified and described are insects (Speight et al., 2008). Given this dominance, the ecological studies of insects, that is, their interactions with other organisms and abiotic factors, have provided thematic foundations for general ecological studies on topics such as herbivory and predation (Schowalter, 2011) as well as population dynamics and community diversity (Kaplan & Denno, 2007). Furthermore, insects play important ecological roles and provide essential ecosystem services such as pollination and seed dispersal, which are critical for the conservation of biodiversity (Schowalter, 2011).

All the types of ecological interactions described above are found within insect communities. Insects compete for resources (Karban, 1989; Denno et al., 1995; Inbar et al., 1995; Hudson & Stiling, 1997; Fischer et al., 2001; Bográn et al., 2002; Duyck et al., 2006), facilitate other important ecological processes such as modifying the habitats for other insects and biodiversity (Shea, 1989; Lill & Marquis, 2003; Kaplan & Eubanks,
2005; Hammons et al., 2009; Calderón-Cortés, 2011), pollinate flowers and disperse plant seeds (Memmott et al., 2007). Parasitism (Redman & Scriber, 2000; Sallam et al., 2002; Mucheru et al., 2009), invasion (Duyck et al., 2006; Ishii et al., 2008), predation (Crawley, 1975; Kindlmann & Dixon, 2003) and decomposition (Jonsson & Malmqvist, 2000) are the other types of interactions in which insect species are involved.

2.2. Types of interactions between phytophagous insects

Phytophagous insects make up over a quarter of all macro-organisms and over half of all insects species (Bernays & Chapman, 1994; Speight et al., 2008). They serve as the major link between plants and other animal species that occur at higher levels in the food chain hierarchy. In addition, they are also of economic interest as they are major pests, but also provide essential services such as pollination and weed control (Bernays & Chapman, 1994). Since phytophagous insects as largely specialised feeders on plants, this group is characterised by high diversity (Jaenike, 1990). The utilisation of plant resources by phytophagous insects is characterised by interactions between themselves and between plant resources (Speight et al., 2008). Interactions between phytophagous species are best viewed as interplay between competition and facilitation (Callaway & Walker, 1997) which take place within the same trophic level (Duffy et al., 2007).

2.2.1. Competition

Competition is an interaction type between two or more individuals of the same or different species, sharing the same resources, but which is limited in supply. This often leads to a negative impact on one of the species involved (Klomp, 1964; Agrawal, 2005), demonstrating that competitive interactions are often asymmetrical (Redman & Scriber, 2000). While competition for food is the dominant competition type amongst
arthropods (Klomp, 1964) competition for space, shelter and oviposition site is also common.

The importance of competition between species in communities has been a long debate in ecological literature (Connell, 1983; Karban, 1986; Gurevitch et al., 1992, Denno et al., 1995). The issue at play is whether competition is a regulator of communities, whether it structures communities and to a further extent if it even exists in communities (Klomp, 1964; Schoener, 1983; van Veen et al., 2006). Studies on the structuring role of competition in insect communities have been the dominant source of this debate. It was suggested that entomologists were strong sceptics of competition, because the characteristics of insects such as their small sizes, short life-span, high sensitivity to variations in environmental factors, as well as their lack of population equilibrium, dismissed them for competition (Rathcke, 1976). Furthermore, it was also suggested that insect herbivores, would not likely compete because they were predator-limited rather than resource-limited (Hairston et al., 1960). Even more, some insect communities are characterised by vacant niches, resource under-utilisation and unsaturation, which implies that competition should be absent (Lawton, 1982). Research showed that when resources were reduced for free-living grasshopper species in tall-grass prairie, no competition occurred (Evans, 1992).

Nonetheless, past and present evidence from laboratory and field studies show competition in phytophagous insect communities. The lack of such studies could have fuelled the scepticism regarding this subject (Lawton & Strong, 1981). Two critical reviews reported that competition did however exist and also played a structuring role in phytophagous insect communities (Denno et al., 1995; Kaplan & Denno, 2007). Denno et al. (1995) provided a strong evidence (76% of 193 studies on pair-wise interactions)
for the dominance of competition in phytophagous insects and indicated that it was higher within stem and wood borers, as well as the sap, fruit and seed feeding guilds. Competition was often asymmetric in phytophagous insect communities and the most influencing factor on competition was host plant (vegetation texture, changes in plant nutrition or allelochemistry and plant phenology), among other factors such as natural enemies, abiotic factors and intraspecific competition. Species sharing the same niche as well as closely-related species were highly competitive. Competition was also highly likely among insect populations that were introduced, fed internally, sessile and aggregative. In a meta-analysis, Kaplan and Denno (2007) reported of differences in some of the earlier patterns which characterised competition in phytophagous insects. Closely-related species were less competitive than distant species. Competition also had an equal effect within feeding guilds. Competition however remained frequent amongst phytophagous insects and also very asymmetric, but was greatly influenced indirectly by host plants (changes in plant quality and quantity) and natural enemies.

2.2.2. Ecological niches, resource partitioning and competition

The concept of an ecological niche is widely accepted as an important ecological factor which structures communities (Colwell & Fuentes, 1975; Leibold, 1995; Jackson et al., 2009; Soberón & Nakamura, 2009) and it is often reported to influence the geographical distribution of species (Pulliam, 2000; Hirzel & Le Lay, 2008; Soberón & Nakamura, 2009). However, since its proposition, the concept has been tainted with confusion (Leibold, 1995; Pulliam, 2000). Two schools of thought on the subject have been established. The first, the Grinnellian and Hutchinson’s niche (so named after Grinnell (1917) and Hutchinson (1957)), described a niche as the environmental requirements essential for the indefinite support of the survival of a species. The other school of thought, the Eltonian niche (Elton, (1927) and MacArthur & Levins (1967)), described
the niche as the role species play or the impacts they have on other species through
resource utilisation (Leibold, 1995; Hirzel & Le Lay, 2008; Jackson et al., 2009; Soberón
& Nakamura, 2009). According to the above, two types of niches can be differentiated
on the basis of niche variable (conditions or resources) involved (Soberón, 2007).
These two types are the “requirement niche” and “impact/role” niche (Leibold, 1995).
The integration of these two types of niches into the overarching term “total niche” has
been suggested, as this allows for “linking mechanistic community theory and
conventional niche theory” (Leibold, 1995).

Despite the challenge of a clear description of the niche concept, the existence of
different niches, also known as niche complementarities (Mason et al., 2011) has a
great impact on communities. Differences in niche characteristics allows for co-
existence of species in communities and result in a huge diversity of species (Levine &
HilleRisLambers, 2009). For instance, niche differences were reported to play a role in
enhancing the plant diversity of European grasslands, which positively impacted on their
primary production (Loreau & Hector, 2001).

The Eltonian niche (the role-resource utilisation niche) has been used to describe the
dynamics of competing species. The use of common resources predisposes species to
interact. The effect of such interaction is the dominance of a superior competitor or the
dominance of co-existing species in an equilibrium state (Duyck et al., 2004). This
ecological “rule” has become what is known as the “competitive exclusion principle”
which has also been described in the following two ways: “complete competitors cannot
co-exist” or “ecological differentiation is the necessary condition for co-existence”
(Hardin, 1960) on the same or shared limited resources. Therefore, co-existing species
should differentiate their resource utilisation to avoid being competitively forced out of
the community. This is further encapsulated in the niche overlap hypothesis (Pianka, 1974), which states that the strength of competition is inversely related to the level of tolerable niche overlap between the species involved.

Ecological studies into resource partitioning have been done to assess the effects of competition-induced limits on stable co-existence of species (Schoener, 1974). The extent of resource specialisation or generalisation by species influences the strength and character of interspecies and apparent competition, which in turn influences functional diversity, especially diversity of co-existing species and their role in ecosystem processes (Pianka, 1974; Duffy et al., 2007). Species partition resources along the food, habitat and time dimensions (Pianka, 1974; Schoener, 1974). Habitat dimensions are the most important of these followed by food and time dimensions (Schoener, 1974). The morphology of species, especially the size of feeding organs, influence resource utilisation and hence the extent of their resource partitioning (Schoener, 1974).

Resource partitioning is regularly reported in insect communities. In order to avoid competition, butterfly species on passion vine were shown to partition resources along the dimensions of plant species, plant habitat and plant part or growth conditions (Benson, 1978). Resource partitioning was suggested as an important factor influencing the co-occurrence of the peacock fly *Chaetorellia australis* Hering (Tephritidae) and hairy weevil *Eustenopus villosus* (Boheman) (Curculionidae) on yellow starthistle *Centaurea solstitialis* L. (Asteraceae) (Tonkel & Piper, 2009). Two invasive *Ceratitis* fruitfly species, *C. rosa* Karsch and *C. capitata* (Wiedemann) (Tephritidae) partitioned their niches along the climate dimension (Duyck, et al., 2006). This indicates that there is variation in resource partitioning among insect species.
2.2.3. Competition types

Different forms of competition have been identified to occur in biological communities (Holt, 1977; Schoener, 1983; Denno et al., 1995). These are described below.

2.2.3.1. Intra- and interspecific competition

Interspecific competition occurs between two or more species while intraspecific competition occurs between individuals of the same species (Lale & Vidal, 2001). Interspecific competition is the dominant interaction in phytophagous insects (Denno et al., 1995). Theoretically, the importance of one competition type is inversely dependent on the other. A stronger intraspecific competition should self-limit a superior competitor to co-exist with other species in an interspecific interaction. Furthermore an increased intraspecific competition should lead to an increase in the niche of a species, while interspecific competition decreases it (Connell, 1983). It was also reported that stronger intraspecific competition than interspecific competition induces stable co-existence between species in a community (Duyck et al., 2004). Intraspecific competition was identified as one of the factors influencing interspecific competition when the former has a greater effect than interspecific competition. However, this was reported to occur in situations in which interactions were symmetric. When interspecific competition was asymmetric, the reverse was the case (Denno et al., 1995).

The lepidopteran leafminer *Cameraria* sp. nov. Davis (Gracillariidae) was reported to exhibit intraspecific competition in the form of density-dependent larval mortalities on the branches of *Quercus emoryi* Torrey (Fagaceae) (Bultman & Faeth, 1986). Furthermore, the sawfly leaf miner *Profenusa japonica* Togashi (Tenthredinidae) exhibited intraspecific competition in the form of density-dependent larval mortality and avoidance of sites with prior oviposition (Sugiura et al., 2007). Intraspecific competition
was however reported to be of less importance as limiting factor within two bruchid species, *Callosobruchus subinnotatus* (Pic) and *C. maculatus* (F.). However, in terms of interspecific competition, *C. maculatus* exhibited a potential competitive advantage over *C. subinnotatus* since it caused more damage to stored Bambara groundnut and its presence also resulted in the reduction in the numbers of *C. subinnotatus* (Lale & Vidal, 2001).

### 2.2.3.2. Direct and indirect competition

Direct competition occurs when individuals of species come into physical contact during their use of shared but limited food resources, oviposition sites and territory (Petersen & Sandström, 2001; Reitz & Trumble, 2002). This often results in the killing of individuals of one species, through for example, biting from the superior competitor (Denno *et al.*, 1995). Individuals may also use other non-lethal tactics such as excretion of repellent chemicals to displace other competitors (Reitz & Trumble, 2002). Indirect competition on the other hand, is mediated by host plants or shared enemies (Faeth, 1986; Fisher *et al.*, 2000; Kaplan & Denno, 2007). Plant-mediated indirect competition between insects occurs when prior feeding by one species changes the nutrition or allelochemicals of the plant which negatively affects subsequent visiting insects (Denno & Kaplan, 2007). Changes in the quality of the shared plant, induced by insect herbivory, are likely to bring about competition between insect species utilising the resource (Harrison & Karban, 1986). Plant-mediated competition between insects is likely to be the most dominant mechanism in insect ecology (Denno & Kaplan, 2007). In the case of enemy-mediated indirect competition, two or more insect species are induced to compete through the influence of shared natural enemies (Holt & Lawton, 1993; Chaneton & Bonsall, 2000).
Evidence for some form of direct and indirect competition in the form of increased mortality was identified experimentally between insects within the folivorous guild and the birch leaf miner *Eriocrania* spp. (Eriocraiiidae) (Fisher *et al.*, 2000). Indirect competition between *Eriocrania* spp. and the other insects was mediated by the host plant. In another experiment, the pupal weight, fecundity and early stage larval growth rate of *Orgyia vetusta* Boisduval (Lymantriidae) were lower, compared to larvae feeding on branches of the bush lupine *Lupinus arbores* Sims (Fabaceae) which was experimentally damaged by *Platyprepia virginalis* Boisduval (Arctiidae) (Harrison & Karban, 1986).

2.2.3.3. Resource and apparent competition

Resources are environmental elements on which species depend for survival, but which has a potential limiting ability on these species (Leibold, 1995). With insects, these resources include food, space, shelter and oviposition sites (Klomp, 1964). Because of the limited supply of resources, species compete with each other or between themselves, to gain more access to these resources or partition their resource use to co-exist (Speight *et al.*, 2008). Competition for resources generates outcomes in communities which include non-random distribution of species along a resource gradient, competitive release of species, character displacement, non-overlapping species that do not co-exist, and convergence of community structures (van Veen *et al.*, 2006). Competition for resources between the potato leafhopper *Empoasca fabae* Harris (Cicadellidae) and the Colorado potato beetle *Leptinotarsa decemlineata* Say (Chrysomelidae) resulted in poorer performance of *Leptinotarsa decemlineata* Say. Prior feeding by the leafhopper on potato plants affected the oviposition preference (less egg deposition), larval performance and survival of the potato beetle (Lynch *et al.*, 2006). Resource competition was also reported between the co-occurring meadow spittlebug,
Philaenus spumarius L. (Cercopidae) and the calendula plume moth, Platyptilia williamsii Grinnell (Pterophoridae), on plants of the seaside daisy Erigeron glaucus Ker Gawler (Asteraceae) with survival of spittlebug being negatively affected by earlier resource utilisation by plume moths (Karban, 1986). Another example of resource competition was shown in an experiment involving three species of leaf miners and gall makers on the woody shrub, Baccharis halimifolia L. (Asteraceae). Defoliation of the host plant by the beetle larvae reduced the densities of the leaf miners and gall makers (Hudson & Stiling, 1997).

Apparent competition is an indirect interaction, which occurs between two species through the mediation of a shared natural enemy, which can be a predator, herbivore or parasite (Holt, 1977; Chaneton & Bonsall, 2000). This type of competition is considered to influence the structuring of communities in the same way as resource competition (Holt, 1977; Holt & Kotler, 1987; van Veen et al., 2006). Apparent competition is termed short-term, when the natural enemy, through changes in its foraging behaviour, causes an effect on prey. It is termed long-term when the effect is caused through a change in density of the natural enemy (Holt & Kotler, 1987; Morris et al., 2005; van Veen et al., 2006).

One difference between competition for resources and apparent competition is the level of influence of competitors on either the resource or enemy (van Veen et al., 2006). In resource competition, the dynamics of the competitors involved does not affect the level of resource input. On the other hand the natural enemy, which mediates apparent competition, is influenced by the dynamics of competing species (van Veen et al., 2006). Additionally, it has been suggested that where resource competition is not
important, apparent competition can effectively regulate insect numbers (Holt & Lawton, 1993).

2.2.3.4 Interference and exploitative competition

When one of two competing species behaviourally restricts the other to access resources which is limited in supply, interference competition is said to have occurred. This competition type is direct and is characterised by aggressive domination of a territory through fighting and killing which often causes harm or the release of chemicals to repel other species. On the other hand, two species are involved in exploitative competition when resource use by one species, reduces availability for the other (Schoener, 1983; Denno et al., 1995; Duyck et al., 2004). The difference between these two types of competition centres on behaviour mechanisms. Interference competition is a behaviour-induced interaction, while exploitative competition is not (Duyck et al., 2004). Different forms of each of the two competition types have been described. These include consumptive, pre-emptive, overgrowth, territorial, chemical and encounter competition (See Schoener, 1983 for descriptions). Consumptive competition is an example of exploitative competition, while chemical, encounter, overgrowth and territorial competition are forms of interference competition. Pre-emptive competition however exhibits both competition types (Schoener, 1983; Hudson & Stiling, 1997). Interference and exploitative competition is however reported to be weak among phytophagous insects (Kaplan & Denno, 2007).

Exploitative competition can be direct or indirectly mediated, for example by a host plant (Denno et al., 1995). Exploitative competition was exhibited by larvae of *Trirhabda bacharidis* Weber (Chrysomelidae), whose prior feeding on *Baccharis halimifolia* L. (Asteraceae) reduced the densities of leaf mining and gall forming insects that use the
same plant (Hudson & Stiling, 1997). Studies on interference and exploitative competition on biotic and abiotic resources showed that when interference competition was beneficial, it promoted co-occurrence between species, through a trade-off between interference and exploitative competition and vice versa (Amarasekare, 2002).

2.2.3.5 Competition for oviposition sites in phytophagous insects

The majority of phytophagous insects are specialised to feed on specific plant species, parts and even tissues. However, these specialisations are more pronounced in some species than others (Bernays & Chapman, 1994). The search for, and acceptance of host plants by phytophagous insects involve several biotic and abiotic factors, behavioural processes and presence of other species (Bernays & Chapman, 1994). Additionally, the genetic make-up and previous experience of the insect greatly influence host selection (Courtney et al., 1989; Jaenike, 1990).

Oviposition and feeding are the end-activities following host search and acceptance by female insects (Courtney et al., 1989). Generally, female insects make a final choice of a host plant that shows great potential for the survival and development of their larval fitness (Resetarits Jr & Wilbur, 1989; Cunningham & West, 2001). The factors which influence the final acceptance of hosts for oviposition include age and physiology of insects, egg load, searching time for oviposition site and learning. These vary within insects and together promote variability in insect host acceptance (Jaenike, 1990). In polyphagous insects, females select their various hosts for oviposition, by ranking them in order of preference (Cunningham & West, 2001). Thus more eggs are laid on the highly preferred hosts and fewer on the least preferred hosts (Thompson & Pellmyr, 1990).
Ovipositing females are known to release pheromones to mark oviposition sites on the host plant(s). Pheromones are usually released in or on the host plant or from the deposited egg or hatched larvae. In addition, host plants can also be induced to produce kairomones, when they interact with insects (Nufio & Papaj, 2001). These pheromone markings serve as deterrents to other conspecifics and other species, to ensure the survival of their offspring (Nufio & Papaj, 2001; Howlett & Clarke, 2005). They are also used to enable the maximisation of the use of a resource by a species, through the uniform dispersal of their offspring and the reduction of overcrowding on the resource from other species (Prokopy, 1981). The marking of a resource by means of a pheromone released by a female insect, is viewed as a mechanism to reduce resource competition especially for its offspring (Nufio & Papaj, 2001) or to dominate and specialise on a host plant (Bernays & Chapman, 1994).

Intraspecific competition in the form of exploitative competition was indicated as a selective pressure for oviposition sites within a population of the sawfly leaf miner, Profenusa japonica Togashi (Tenthredinidae) on leaflets of the shrub Rosa multiflora Thunberg (Rosaceae). Leaflets on which eggs were previously laid were avoided by other females. Furthermore, density-dependent larval mortality on the same leaflets resulted in avoidance of oviposition sites that were already utilised by females (Sugiura et al., 2007). However, in an experiment involving the goldenrod ball gallformer, Eurosta solidaginis Fitch (Tephritidae), on Solidago altissima L. (Asteraceae), little avoidance of previously used oviposition sites was observed and females largely oviposited on buds which had ovipunctures or contained eggs. Previous experience was the sole factor suggested to influence this behaviour, although chemical factors could be involved (Craig et al., 2000).
Signs of prior use of oviposition sites by insects have not always been deterrent to conspecifics. These signs have also facilitated the use of host plants by other insects. For instance, the presence of galls on shoots of arroyo willow, *Salix lasiolepis* Bentham (Salicaceae), formed by prior usage of the sawfly species *Euura lasiolepis* Smith (Tenthredinidae), induced further oviposition on the shoots by other conspecifics (Craig *et al.*, 1990).

### 2.2.4. Measuring competitive effects

Measurement of the outcome of competition on species is often determined through experiments conducted in the laboratory and in greenhouses. Other methods involve field observations and manipulative field experiments (Schoener, 1983; Gurevitch *et al.*, 1992; Denno *et al.*, 1995). The latter, however, has much potential to provide answers to questions about ecological competition (Connell, 1983; Gurevitch *et al.*, 1992).

The study of competition under field conditions often involves measuring changes in biomass, density and mortality of interacting species (Gurevitch *et al.*, 1992). Additionally, shifts in niches and competitive displacement of species are also measured as indicators of responses to competition (Connell, 1983). To study density-dependent competition one of the interacting species is removed from the study plot or site, or one or more species are added in addition to already established species to interact in the created habitat (Schoener, 1983).

Although field experiments have been touted as the better method to measure competition, it is not without practical problems. Connell (1983) identified four main problems with the study of competition under field conditions. These were 1) the nature of the control, which should have the same level of environmental variation as the
treatment, but which should not be influenced by the manipulation of the treatment, 2) the density of interacting species to be used, which should be lower than the natural densities, rather than higher because they serve as baseline, 3) relating experimental results to natural populations, and 4) interpretation of results.

2.2.5. Facilitation

Positive or facilitative interactions recently emerged as possible ecological processes that influence the regulation and structuring of communities. Positive interactions include all interaction types, which benefits at least one of the interacting species, without harming any of the species (Stachowicz, 2001; Bruno et al., 2003). A well-known example of positive interaction in biological communities is mutualism, in which each of the species involved in the interaction benefits (Stachowicz, 2001; Bruno et al., 2003). A classical example of this mutualistic interaction is between ants and honey-dew producing insects, especially aphids (Kaplan & Eubanks, 2005) and also between plants and their pollinators and seed dispersers (Bascompte & Jordano, 2007). Other facilitative interactions involve the amelioration of unfavourable habitat conditions by one organism or groups of organisms to the benefit of other organisms (Stachowicz, 2001). This has been called ecosystem engineering and the species involved as ecosystem engineers (Stachowicz, 2001; Lil & Marquis, 2003; Calderón-Cortés, 2011). Based on the use of a conceptual model to assess facilitation in species invasion, it was suggested that natives and already established exotic species facilitate exotic species (Bulleri et al., 2008).

Many examples of positive or facilitative interactions have been shown to exist in biological communities, including insects (Stachowicz, 2001). For example, injury caused by the invasive Japanese beetle *Popillia japonica* Newman (Rutelinae) to grapes, facilitated feeding of the native green June beetle *Cotinis nitida* L. (Cetoniinae),
allowing it to use its blunt mandibles. They further created conditions for yeasts associated with June beetles, which produced volatiles, to be used as aggregation kairomones by June beetles (Hammons et al., 2009).

Facilitative interactions have not received as much attention in ecological studies as other interaction types and a need exists to include positive or facilitative interactions into general ecological theories as important processes influencing the structure of communities (Stachowicz, 2001; Bruno et al., 2003; Lill & Marquis, 2003; Bullerii et al., 2008).

2.3. Temperature and climate change impacts on insect species interactions

Among the abiotic factors that influence insect species, temperature is the most important (Hodkinson et al., 1999; Bale et al., 2002; Sporleder et al., 2004; Damos & Savopoulou-Soultani, 2012). It has, however, also been suggested that precipitation is the most important factor for ectothermic species e.g. grasshoppers, since it was likely to reduce their temperatures and subsequent thermoregulation (Ovadia & Schmitz, 2004). Nevertheless, temperature directly drives the rate of growth and development, fecundity and mortality, resource utilisation, interspecific and intraspecific interactions and also limits the geographic distribution of insect species (Howe, 1967; Bale et al., 2002; Sporleder et al., 2004; Hodkinson, 2005; Dangles et al., 2008; Speight et al., 2008). It also indirectly influences insect species through the impacts it has on host plants, competitors and natural enemies (Bale et al., 2002; Estay et al., 2009).

The behaviour of insects is influenced along a continuum of temperatures. Along this gradient, three temperature points are of importance in insect behaviour. Usually, the rate of physiological processes and activity increase with increasing temperature from the minimum or basal point, up to an optimal point. A further increase beyond the
optimum results in slowing down of processes and activities until a maximum point is reached. Beyond the lower and maximum temperature limits, insects are negatively affected (Taylor, 1963; Speight et al., 2008; Damos & Savopoulou-Soltani, 2012).

Two important developmental parameters are used for modelling this temperature phenomenon. These are the base temperature for development and the thermal constant. The thermal constant is described simply as the accumulation of the total temperature needed to reach a certain developmental point, spread equally over given days and is measured in degree days. The thermal constant is linked to the base temperature as the product of degrees of temperature above base temperature and time (Damos & Savopoulou-Soltani, 2012). The use of degree-days, based on constant temperatures has been challenged. In a review of studies on temperature and insects, Beck (1983) pointed out the inherent errors in the application of the degree-day temperature threshold for forecasting phenological events and suggested the integration of the daily cycles of environmental temperatures, referred to as the thermoperiods (the photophase and scotophase temperatures are termed thermophase and cryophase respectively) and the degree-day temperature thresholds. However, the most important similarity of these views is the fact that changes in temperatures markedly affect insect development and behavior.

Temperature generally influences interaction types among insect species. For example, cooler temperatures confer a competitive advantage on smaller males of the seed beetle Stator limbatus Horn (Chrysomelidae), who out-competes larger males in reaching a potential mate (Moya-Laraño et al., 2007). However, differences in temperature were also shown not to affect competition in mosquitoes. Larvae of Aedes albopictus Skuse (Culicidae) and A. aegypti (L.), performed similarly at different
temperature regimes and no competition was observed between species (Lounibos et al., 2002).

Temperature also affects the distribution of insects. For instance, the distribution of three invasive potato tuber moths species (Gelechiidae) *Symmetrischema tangolias* Gyen, *Phthorimaea operculella* Zeller and *Tecia solanivora* Povolny in the tropical Andes in South America, were linked to the differences in their physiological responses to different temperatures. The cold-tolerant *S. tangolias* was dominant in elevations above 3000m, while *T. solanivora*, the warm-tolerant species dominated in elevations lower than 2700m. The less cold-tolerant *P. operculella* co-occurred with the other two species at mid-altitudes (Dangles et al., 2008).

Changes in earth’s climate and its potential effects on ecosystems have received a lot of attention from the 1990s onwards with sceptics and non-sceptics alike. Insects, especially the lepidopterans and coleopterans have become some of the most important indicators of climate change (Woiwod, 1997; Coope, 2004). Changes will likely occur in all climatic elements, but changes in temperature seem to be the most important, as it will have the largest effect on life in general and especially for insects (Bale et al., 2002). It has been indicated that climate change will largely affect the abundance, distribution and phenology of host plants, phytophagous insects, and natural enemies (Woiwod, 1997). For example climate-changed induced migrations of lepidopteran species have been reported (Sparks et al., 2007).

There is growing evidence of the direct and indirect impacts of climate change on insects. Climate change will not only influence population dynamics of insects through increases and decreases in population sizes among species but will also result in
changes in species distribution (Woiwod, 1997; Masters et al., 1998; Bale et al., 2002; Hagen et al., 2007).

The level of influence that climate change will have on species interactions depends on how those interactions are also influenced by climate (Hegland et al., 2009). Climate change is likely to affect plant-insect pollinator interactions by affecting changes in the phenology, abundance and distribution of both plants and insect pollinators, but also creating temporal mismatches between them (Hegland et al., 2009). Using climatic data from 1943 to 2003, it was shown that the synchronised appearance of two insect pollinators, *Apis mellifera* L. (Apidae) and *Pieris rapae* L. (Pieridae) and flowering plants in the Mediterranean regions have been increasingly disrupted due to temperature increases. In addition, temperature increase resulted in an earlier appearance time for females of *Bactrocera oleae* Rossi (Tephritidae), which misses oviposition site opportunities because the flowering of their associated olive trees did not correspond with their earlier appearances (Gordo & Sanz, 2005). Increased temperature will also affect predator-prey interactions. Buse et al. (1999) suggested that temperature increase significantly affected the interactions between the great tit *Parus major* L., blue tits *P. caeruleus* L. (Paridae) and their prey, the winter moth *Operophtera brumata* L. (Geometridae), but not between the oak *Quercus robur* L. (Fagaceae) and winter moth in the UK. Competitive interactions between insects, especially crop pests, will also be influenced by changes in climate, as competition types and intensity is affected by climatic factors (Cammell & Knight, 1992).

### 2.4. African lepidopteran cereal stem borers

In Africa, the most important cereal crops are maize, rice, millets and sorghum (Polaszek and Khan, 1998). They serve as the main staple food for households in Africa
and are mostly grown on small scale by resource-poor farmers (Kfir et al., 2002; Khan et al., 2010). Some lepidopteran species utilise these cereals crops as hosts.

Twenty-one species from three lepidopteran families (Noctuidae, Crambidae and Pyralidae) have been reported as cereal pests in Africa (Maes, 1998a). The most important species that attack maize are the noctuids *Busseola fusca* (Fuller), *Sesamia calamistis* Hampson, the pyralid *Eldana saccharina* Walker and the crambids *Chilo partellus* (Swinhoe) and *C. orichalcociliellus* Strand (Kfir et al., 2002). The three species of interest in this study are described below.

2.4.1. *Busseola fusca* (Fuller) – African maize stemborer

*Busseola fusca* is endemic to the sub-Saharan African region, but varies in its importance and distribution within the continent (Harris & Nwanze, 1992; Kfir et al., 2002). It has been recorded in countries in West, East and southern Africa, with varying altitudinal limits and habitat. *Busseola fusca* is found from sea level to altitudes above 2000m. While it occurs from sea level to over 2000m in West Africa, this species is limited to altitudes between 600m and 2700m in eastern and southern Africa (Harris & Nwanze, 1992). A recent phylogenetic analysis described three distinct mitochondrial clades of *B. fusca* with respect to geographic location within the African region. One clade was restricted to West Africa (W) and the other two clades were restricted to East Africa (Kenya I or KI) and central to east Africa (Kenya II or KII) respectively. The KI and KII clades overlap geographically (Sezonlin et al., 2006). Differentiation and restricted gene flow were suggested to have influenced inter-clade and local population differences.
The host plants of *B. fusca* include some indigenous African grasses for example *Sorghum verticilliflorum* (Steud.) Stapf, *Sorghum arundinaceum* (Desv.) Stapf, *Pennisetum purpureum* Schumacher and *Panicum maximum*, Jacquin, but it is largely found on maize and sorghum. Additionally, they can also be found on pearl and finger millet (Harris & Nwanze, 1992). However in Ethiopia, Sudan (*Sorghum vulgare* Pers. var. *sudanense*), and Columbus grasses (*Sorghum almum* Parodi) were reported to be the preferred hosts (Haile & Hofsvang, 2002).

The life cycle is indicated in Figure 2.1. Adults emerge from pupae usually from late afternoon to evening. Female moths then release pheromones to attract males for mating. After 2 to 4 nights, females lay eggs in batches of 30 to 100, usually underneath the leaf sheath. Eggs hatch after a week after which larvae disperse and establish on host plants (Harris & Nwanze, 1992; Holloway, 1998). Between six and eight larval instars (each instar lasting between 5 to 7 days) characterises *B. fusca* during its life cycle of 30 to 45 days. During this period, larvae initially feed in plant whorls after which they migrate into stems where they complete their cycle. The most favourable temperature range for development is between 25°C and 30°C. Larvae then pupate for a period of 9 to 14 days, after which moths emerge (Harris & Nwanze, 1992; Bosque-Pérez & Schulthess, 1998).
Zalucki et al. (2002) reviewed the ecology and behaviour of first instar larvae of lepidopteran species and indicated challenges with host plant features as well as biotic and abiotic constraints that have to be overcome by neonates to establish themselves on host plants.

2.4.2. *Chilo partellus* (Swinhoe) – Spotted stemborer

*Chilo partellus* (Plate 2.1) is an invasive species from Asia and the Indian subcontinent, which was first recorded in Africa in the late 1920’s in Malawi (Kfir, 1997; Overholt et al., 2001). It is the most important stemborer species of cereal crops in the low to medium elevations in eastern and southern Africa and has the potential to invade West Africa (Maes, 1998b; Overholt et al., 2001). *Chilo partellus* attacks maize, sorghum, pearl and finger millets and is also hosted by grass species such as *P. maximum*, *P. purpuraeum*, *Arundo donax* (L.), *Echinochloa pyramidalis* (Lam.) Hitchc. and Chase, *Phragmites*
*mauritianus* Kunth, *Hyparrhenia rufa* (Nees) Stapf, *Sorghum halepense* (L.) Persoon, *S. verticilliflorum* and *S. arundinaceum* (Maes, 1998b; Le Ru *et al.*, 2006b; Otieno *et al.*, 2006). Eighty-nine percent of larvae of *C. partellus* were collected on *S. arundinaceum* during a survey by Le Ru *et al.* (2006b), on grasses in the eastern and part of southern Africa. *Chilo partellus* is estimated to cause yield loss of 24%, 20% and 10% in the dry transitional, lowland tropics the moist mid-altitude and dry mid-altitude areas respectively in Kenya (Ong’amo *et al.*, 2006a).

The life cycle of *C. partellus* takes between 25 and 50 days to complete. The favourable temperature range for its development is between 26°-30°C. Adults (Plate 2.1) emerge from pupae from late afternoons to early evenings. Mating immediately follow emergence and females oviposit on the upper and undersides of plant leaves, within two to three days after mating. Eggs hatch between 4 and 8 days after oviposition. Young larvae start to feed within leaf whorls, but later bore into stems where they feed for approximately 2 to 3 weeks after which they pupate in stems for 5 to12 days. Five or more generations can develop in a single cropping season. However, in unfavourable conditions, larvae may go into diapause in plant residues for a maximum of six months followed by pupation under favourable conditions (Singh, 1991; Maes, 1998b; Overholt *et al.*, 2001; Kfir *et al.*, 2002).

![Plate 2.1. (a) Adult, (b) larva and (c) pupae of *Chilo partellus*. Photo credits: Johnnie van den Berg](image)
2.4.3. *Sesamia calamistis* Hampson - (African pink stemborer)

*Sesamia calamistis* (Figure 3) is a widespread species in Africa and its importance as pest varies greatly between regions. It causes damage to cereal crops in West Africa, but is of moderate importance in the eastern and southern Africa (Overholt *et al.*, 2001). *Sesamia calamistis* is a polyphagous species and has been reported on two host plant families in East Africa (Le Ru *et al.*, 2006a; 2006b). Cereal crops and some of the wild grass species on which *S. calamistis* has been recorded include rice, maize, sorghum, finger millet, sugar cane, *S. versicolor*, *Tripsacum laxum* Scrib and Merr., *P. purpureum*, *S. arundinaceum*, *A. donax*, *Cynodon dactylon* (L.) Persoon, *Echinochloa colonum* (L.) Link, *E. pyramidalis*, *Eriochloa meyerana* (Nees) Pilger, and *P. maximum* (Le Ru *et al.*, 2006b).

![Plate 2.2](image1.png)  
(a) Larva and (b) adult of *Sesamia calamistis*. Photo credits: Johnnie van den Berg

*Sesamia calamistis* moths lay eggs between the leaf sheath and stem of plants, 3 to 5 days after mating. Approximately 350 eggs can be laid by one female. Hatched larvae spend between 30 to 60 days feeding inside the stems of host plants. Larvae moult up to six times and develop into pupae inside the stem or sometimes between stem and sheath. Pupae require a temperature of 25°C to complete pupation in 10 to 12 days and
up to six generations can be achieved without diapause within a year (Holloway, 1998; Overholt et al., 2001).

2.5. Host plant selection, resource utilisation and interactions in Lepidoptera

Host plant selection behaviour of insects, especially oviposition behaviour is better studied in the Lepidoptera than in other insect orders and provided the theoretical bases for ecological concepts such as host specificity, modes of co-evolution, host shifts, pattern of host plant attack and sympatric speciation (Thompson & Pellmyr, 1991). The oviposition preference of moths and food choice by larvae influence the host range of a species. Oviposition preference is however the most important step since it affects the fitness of her offspring (Honda, 1995). Chemical stimuli and sensory cues are factors that influence host plant search, acceptance and oviposition by lepidopterans (Renwick & Chew, 1994). Honda (1995) indicated that the genetic make-up, presence of conspecific eggs or larvae, learning or past experience and the age and motivation of female adult also influence oviposition response in lepidopteran females (Thompson & Pellmyr, 1991; Renwick & Chew, 1994; Cunningham et al., 1999). The behavioural sequence followed by a female lepidopteran for oviposition is divided into two phases: pre-alighting and post-alighting. The pre-alighting phase involves searching, orientation and encounter. Post-alighting involves landing, surface evaluation and acceptance (Thompson & Pellmyr, 1991; Renwick & Chew, 1994).

2.5.1. Host plant selection in African lepidopteran stemborers

Host plant selection and resource utilisation vary among African stemborer species. The majority of African stemborers are specialized phytophagous feeders and they have been recorded to feed on one host plant genus (monophagy) or one host plant family (oligophagy). A few are however polyphagous (feeding on many plants from different
families) (*sensu* Bernays & Chapman, 1994; Le Ru *et al.*, 2006a; 2006b). *Busseola fusca* and *C. partellus* are reported to be oligophagous, while *S. calamistis* is polyphagous (Le Ru *et al.*, 2006a; 2006b).

The mechanisms and the factors that influence host plant acceptance for oviposition have been described for *B. fusca* (Calatayud *et al.*, 2008a). The behaviour involved in host acceptance was divided in two successive steps: the pre-landing step which involved quiescence (period of inactivity), taking-off, oriented flight towards plants and landing on plants, and the post-landing steps which involves standing still, walking and antennating on the plant, ovipositor sweeping and oviposition. Physical and chemical plant contact cues have a greater influence on oviposition response than visual and volatile cues (Calatayud *et al.*, 2008a). Of the different plant physical cues, stem diameter, surface texture and rigidity of sheath leaf were the most important. *Busseola fusca* preferred stems with larger diameters, smooth surfaces and less rigid leaf sheaths for oviposition (Van Rensburg & Van den Berg, 1992; Calatayud *et al.*, 2008b).

Host plants preference of *C. partellus* when provided with choices between maize, sorghum, Napier grass and two varieties (local and improved) of signal grass *Brachiaria brizantha* (A. Rich.) Stapf is toward Napier grass. Females oviposited more eggs on Napier grass than other species, although the larvae preferred maize and sorghum to Napier grass (Midega *et al.*, 2011). Van den Berg (2006) and Glas *et al.* (2007) also reported that *C. partellus* showed a preference for Vetiver grass, *Vetiveria zizanioides* (L.) (Nash) (Poaceae) to maize for oviposition. Plant morphology and an old association between *C. partellus* and Vetiver grass were hypothesized for this preference. The detail behavioural steps prior to host acceptance and oviposition by *C. partellus* involve the antennae, ovipositor and tarsi (Chadha & Roome, 1980). The process involves the
female walking over leaf, touching the leaf with antennae tips, followed by touching the leaf with the ovipositor tip and the bending of the abdomen sharply to bring the ovipositor tip firmly down on the leaf. The female then lifts the antennae and extends the ovipositor further to probe the leaf surface. Eggs are laid by releasing them at a rate of one per 10 to 12 seconds, pressing them down flat with the ovipositor tip (Chadha & Roome, 1980).

There is no detailed study of the behavioural processes of host acceptance and selection by *S. calamistis*. However, genetic differentiation in resource utilisation, which was associated with host plant preference, has been reported for *S. calamistis* in Kenya (Ong’amo *et al.*, 2008). The majority of clade I individuals were recovered from cultivated crops, while clade II individuals were recovered from wild plants.

2.5.2. Resource utilisation by African lepidopteran stemborers on cultivated cereal crops

A review on stemborer pests in Africa showed the distribution of each species and the dominant crops they attacked (Kfir *et al.*, 2002). In West Africa, the most important species were *B. fusca*, *S. calamistis* and *E. saccharina*, which attacked maize and sorghum. *Busseola fusca*, *C. partellus*, *Chilo orichalcociliellus*, *S. calamistis* and *E. saccharina* were the dominant stem borer pests of maize and sorghum in East Africa. The southern part is dominated by *C. partellus* and *B. fusca* on maize and sorghum. *Coniesta ignefusalis* (Hampson) (Pyralidae) was the most important stem borer on pearl millet in the Sahel region (Kfir *et al.*, 2002).

A further variation in resource utilisation may exist within the same agro-ecological zones (AEZs) in a country and also between seasons. These variations are usually dependent on altitude and temperature. For instance in Kenya, it was found that *B.*
Busseola fusca dominated on maize farms in the highland tropics, the moist transitional zone and moist mid-altitude AEZs, which are characterised by cooler temperatures. *Chilo partellus* dominated in the dry mid-altitude, dry transitional and lowland tropical AEZs which are characterised by warmer temperatures. *Sesamia calamistis* is reported to occur in all AEZs. These three species existed together as single, 2- or 3-species communities of stemborers in the mid-altitude zones (Ong’amo et al., 2006a; 2006b). Similar variations in maize infestations by stemborers have been reported in Cameroon. *Busseola fusca* and *E. saccharina* were the dominant species in the forest regions which had an average annual temperature around 23.5°C. *Sesamia calamistis* was found in all zones while *B. fusca* alone dominated in the mid-altitude which had an average annual temperature of 20°C. Infestation levels on maize also varied largely. Stem and ear damage were the most important damage caused to maize in the forest regions, while stem tunnelling was the most important in the mid-altitudes (Ndemah et al., 2001).

Some level of overlap in resource use has been reported between *B. fusca* and *C. partellus* (Kfir, 1997) and *C. partellus* and *C. orichalcociliellus* in the coastal region of Kenya (Ofomata et al., 1999). The combined effect on the same host plant used by two or more species is usually higher than their single effects. Mixed populations of *B. fusca* and *C. partellus* on sorghum caused more damage and crop loss than when these species occurred in single populations (Van den Berg et al., 1991).

### 2.5.3. Interactions in use of resources for oviposition by female moths

Intra- and interspecific overlap in host plant use for oviposition influence interactions among species of Lepidoptera (Bernays & Chapman, 1994). For example in the phycitid moths, which overlap in their resource use on stored food, intra- and interspecific
competition for oviposition sites was an important factor regulating these species (Anderson & Löfqvist, 1996). It was suggested that female moths in mixed populations would likely distribute their eggs uniformly due to competition for oviposition sites (Thompson & Pellmyr, 1991).

The oviposition preferences of gravid females in a community utilising the same host plant can be influenced by the interactions among species (Craig et al., 2000; Shiojiri et al., 2002). Thus, competition for or facilitation in the use of the same resource can influence oviposition responses by female moths especially on host plants with signs of prior use. For example, Shiojiri et al. (2002) and Poelman et al. (2008) reported on the differential oviposition responses from three moth species *Mamestra brassicae* L. (Noctuidae), *Plutella xylostella* L. (Yponomeutidae) and *Pieris rapae* on uninfested and *P. rapae*-infested cabbage leaves. While *P. rapae* did not show preference for both infested and uninfested leaves, *P. xylostella* and *M. brassicae* showed a preference for infested over uninfested and uninfested over infested leaves respectively. Similar variation in oviposition responses by different moth species using the same resource was reported by Anderson and Löfqvist (1996). Several studies have reported on the oviposition preferences by female moths for prior infested plants (Karban & Courtney, 1987; Anderson & Alborn, 1999; Craig et al., 2000; Groot et al., 2003; Viswanathan et al., 2005; Facknath, 2012) and also on those which were deterred from ovipositing on prior infested plants (Sato et al., 1999; De Moraes et al., 2001; Wise & Weinberg, 2002; Fatouro et al., 2012).

No studies have been carried out to describe the oviposition responses from mixed communities of stemborer species which utilise the same resources especially those with signs of prior use from other species.
2.5.4. Interactions in resource use by stem boring larvae

Generally, insects in the stem boring guild have been noted to compete more severely for their resources than external feeders (Denno et al., 1995). The larvae of stemborers spend their lifetime feeding within the stems of plants. This favours a competitive interaction, as an aggregation of species feed on the same limited resource (Stiling & Strong, 1984). The dominant interaction identified within lepidopteran stemboring species has been interspecific (Rathcke, 1976; Stiling & Strong, 1983; Moon & Stiling, 2002) and intraspecific competition (Kfir, 1997; Ofomata et al., 1999; Teder & Tammaru, 2003; Dorhout & Rice, 2010). Indications of intraspecific competition in B. fusca in maize have been described by Van Rensburg et al. (1987).

Lepidopteran stemborers that occur on cereal crops and grasses in Africa are likely to exhibit intra- and interspecific interactions. Mixed communities of different stemborer species have been recorded from the same maize fields and plant. For example, B. fusca, C. partellus and S. calamistis were recorded in the same maize field and plant in the Limpopo province in South Africa (Krüger et al., 2008) and also the mid altitudes in Kenya (Ong’amo et al., 2006b). Similar mixed infestations were also observed in grain sorghum (Van Rensburg & Van den Berg, 1992).

Some form of competitive interaction has been reported in the African stemborers. It was reported that B. fusca was competitively displaced by C. partellus on some cereal crops, especially in ratoon sorghum, in the highlands of South Africa (Kfir, 1997). Chilo partellus was found to have life characteristics that provided it with a competitive advantage over B. fusca. These included the capacity to survive better at the lower temperatures in the region, by hibernating in available enclosures, shorter developmental time due to its facultative diapause, compared to B. fusca (obligative
diapause in South Africa) and also its ability to oviposit on plants already infested by *B. fusca*. *Busseola fusca* on the other hand, avoids plants that were infested by *C. partellus* (Kfir, 1997). A further example of competitive displacement was reported between *C. partellus* and *C. orichalcociliellus* in Kenya (Ofomata et al., 2000). It was found that *C. partellus* laid more eggs and survived better than *C. orichalcociliellus* at temperatures between 25°C and 28°C. *Chilo partellus* also had a shorter developmental time and consumed more maize compared to *C. orichalcociliellus*. Ofomata et al. (2000) also showed that some pupae of *C. orichalcociliellus* survived on Napier and Guinea grasses, which *C. partellus* could not. Thus the advantageous characteristics of *C. partellus* were suggested to confer a competitive advantage over *C. orichalcociliellus* and could partly be responsible for the displacement of *C. orichalcociliellus* by *C. partellus* in the coastal region of Kenya. Results from an earlier survey of these two species showed a high niche overlap between them on maize, wild sorghum, Napier and guinea grasses (Ofomata et al., 1999).

All the above examples mostly originate from field surveys. Only a few experiments have been conducted to detect the real mechanisms of these displacements and other interactions responsible for the tempo-spatial variations in resource use and existence in communities of stemborers. An experiment conducted by Ofomata et al. (2000) only provided information on the fecundity, larval food consumption, survival and developmental rates of *C. partellus* and *C. orichalcociliellus*. Experiments to detect and explain competitive interactions usually involve putting the species involved together on the same resource or manipulating the density of shared enemies, of those species involved in apparent competition. The parameters measured after a period of interactions include mortality, growth rate, developmental time, density and distribution of each species. In addition, differences in the individual impact of each species on the
resource and their combined rates are compared to detect competition. Little or no such work has been done with the cereal stemborers.

2.6. Climate change impacts on lepidopteran cereal stemborers

Assessment of the impacts of climate change on Lepidoptera has been undertaken (Woiwod, 1997). It was reported that their abundance, distribution and flight phenology will be the factors that will most likely to be impacted on. Changes in the phenology and expansion in the range of lepidopteran species in the UK for instance, has been reported (Woiwod, 1997).

Climate change will also impact on the dynamics of crop insect pests like the lepidopteran stemborers of cereals. Climate change will directly affect individuals and populations of insect pests, through the influence of increasing temperature on physiological processes such as the reproduction, growth and development, distribution and migration. Indirectly, climate change will impact on crop hosts by influencing plant growth, plant phenology and the geographical regions where different crops can be cultivated. Natural enemies of pests (pathogens, predators, parasitoids) and their competitive interactions on crop plants will also be affected (Cammell & Knight, 1992). Little or no information is available on the influence of temperature increases on the interactions that regulate communities of lepidopteran cereal stemborers and their impacts on crop damage.

2.7. References


Lale, N.E.S. & Vidal, S. (2001). Intraspecific and interspecific competition in *Callosobruchus maculatus* (F.) and *Callosobruchus subinnotatus* (Pic) on stored


CHAPTER THREE

COMMUNITY STRUCTURE AND THE SPATIO-TEMPORAL DYNAMICS WITHIN A COMMUNITY OF MAIZE STEMBORENS

Abstract

Multi-species of insects which utilise the same host plant are often involved in intraspecific and interspecific, competitive or facilitative interactions with one other. These interactions are influenced by temperature and rainfall. Lepidopteran stemborers are major pests of cereal crops in sub-Saharan Africa. Two indigenous noctuids, *Busseola fusca* and *Sesamia calamistis* and one exotic crambid *Chilo partellus* occur as single and mixed-species communities infesting cereal crops in East and southern Africa. The composition of these communities however varies with altitude and seasons. Surveys were conducted in maize fields in different localities along an altitudinal gradient in the major agro-ecological zones in Kenya and Tanzania. Another monitoring survey to study the spatio-temporal dynamics of infestation by the community of the three stemborer species was conducted over three seasons, in one locality in the mid-altitudinal ranges in Kenya. Destructive sampling of infested maize plants was done in the fields in all localities, to record the species and the number of larvae of each species inside maize stems. The results of this study confirmed that stemborer communities are composed of single and mixed species of *B. fusca*, *S. calamistis* and *C. partellus*. The composition of the stemborer species varied with the different agro-ecological zones and also along altitudinal gradients. Temperature was the most influencing factor on the composition of stemborer communities. Similarly, the stemborer community in the mid-altitude locality was composed of single- and multi-species of *B. fusca*, *S. calamistis* and *C. partellus* with single-species populations of *B. fusca* dominating the community in all the three seasons. However, infestation levels and larval density of *S. calamistis* were higher in one season than another. The pattern of infestations between the stemborer species followed a clustered distribution in all seasons. Temperature and rainfall had significant effects on these dynamics at the micro-level of stemborer community.
3.0. Introduction

Plants, including crops, host a diversity of insect species and other arthropods, forming communities that utilise the resources both spatially and temporally (Strong et al., 1984; Liss et al., 1986; Lewinsohn et al., 2005). The species in these communities can be grouped into different taxonomic groups or functional guilds such as stem borers, leaf chewers, sap suckers, leaf miners, borers, gall-makers and root feeders (Stiling et al., 1999; Imura, 2003; Rocca and Greco, 2011; Truter et al., 2014; Stam et al., 2014).

Interactions within and between different guilds can be direct or indirect, and have positive or negative outcomes which affect the structure and functions of the insect community on plants (Hudson & Stiling, 1997; Kaplan & Eubanks, 2005; Wootton & Emmerson, 2005; Soler et al., 2012; Sánchez-Galván et al., 2013). However, the role of species interactions, especially competition, in the organisation of insect communities, has been questioned (Connell, 1983; Karban, 1986; Gurevitch et al., 1992; Denno et al., 1995). Two critical reviews on the subject showed strong evidence for the dominance of competition and the structuring role it plays in phytophagous insect communities (Denno et al., 1995; Kaplan and Denno, 2007). Competition is regarded to be higher within stem and wood borer guilds, species sharing the same niche and those that are closely related, as well as insect populations that are invasive and those that are sessile and aggregative.

The structuring of insect communities is not influenced by species interactions alone, but also by abiotic factors such as temperature, humidity, rainfall, salinity, soil chemistry, and carbon dioxide concentrations (Dunson & Travis, 1991; Denno et al., 1995; Ovadia & Schmitz, 2004; Jiang & Morin, 2004; Sanders et al., 2004). Temperature is the most limiting abiotic factor regarding insects since it directly drives their rate of growth,
development, fecundity and mortality. It also influences resource utilisation, interspecific and intraspecific interactions and limits the geographic distribution of insect species (Howe, 1967; Bale et al., 2002; Sporleder et al., 2004; Hodkinson, 2005; Dangles et al., 2008; Speight et al., 2008; Damos & Savopoulou-Soultani, 2012). The importance of temperature in structuring biological communities has been highlighted by the possible effect that climate change could have on these communities (Woiwod, 1997; Bale et al., 2002; Tylianakis et al., 2008; Cornelissen, 2011).

Lepidopteran stemborers are major pests of cereal crops in sub-Saharan Africa (SSA). Three species have been identified to attack maize and sorghum, in East and southern Africa (Polaszek and Khan, 1998; Reddy, 1998; Kfir et al., 2002). These are the two indigenous noctuids Busseola fusca (Fuller) and Sesamia calamistis Hampson and one exotic crambid Chilo partellus (Swinhoe). In East and southern Africa, these species occur as communities of single and mixed species infesting not only crops (Kalule, 1997; Tefera, 2004; Ong’amo et al., 2006a; 2006b; Krüger et al., 2008), but also in wild graminaceous plants (Le Ru et al., 2006; Moolman et al., 2014). The community structure of stemborers varies with locality, altitude and season. In Kenya, for instance, B. fusca is the dominant species in the highlands, while C. partellus dominates in the lowlands. Sesamia calamistis is present at all altitudes in low numbers. In the mid-altitudes regions, stemborers occur as a mixed community of the three species, but with variation in species dominance with respect to locality and season (Guofa et al., 2001; Ong’amo et al., 2006a; 2006b; 2013). Despite frequent reports on these spatial and temporal variations in stemborer communities, there is inadequate information on the extent of single-species and multi-species infestations (at field and plant level) by these three species in the different maize agro-ecological zones as well as their utilisation of the same resources and the damage they cause to maize production. Chilo partellus
has been reported to competitively displace *B. fusca* on ratoon sorghum in the highlands of South Africa (Kfir, 1997), while in Kenya it has displaced *C. orichalcociliellus* in the coastal region (Ofomata *et al.*, 1999). Furthermore, the possible effects of changes in temperature on these interactions and on the structuring of stemborer communities are not understood. It is highly likely that changes in temperatures due to climate change may influence these interactions, leading to altered pest communities which will require changes in pest management strategies.

The aims of this study were to (i) describe the structure of stemborer communities in maize fields in different maize agro-ecological zones and important abiotic factors that influence these structures, and to (ii) describe the spatio-temporal dynamics of mixed stemborer communities that infest maize plants in the mid-altitude regions and how abiotic factors influence these.

### 3.1. Materials and methods

This study involved surveys conducted in maize farms selected in different localities found in all the agro-ecological zones of Kenya and part of Tanzania. The study also involved another season-long monitoring survey in one locality at the mid-altitudinal range in Kenya.

#### 3.1.1. Study areas

3.1.1.1. *Community structure of stemborers in different agro-ecological zones along altitudinal gradients*

Sampling was done in 28 localities situated in different agro-ecological zones (AEZs) in Kenya and Tanzania (Figure 3.1). These AEZs were described by Hassan *et al.* (1998) in Kenya and extrapolated for localities in Tanzania. Of these 28 localities, 11 were
distributed from the lowlands (sea level) to the highlands (2343 m) in Kenya. The others were situated along three mountainous gradients in Kenya (Taita hills-6 localities; Machakos hills - 5 localities) and in Tanzania (Kilimanjaro mountain-6 localities) (Table 3.1). Sampling was done between 2011 and 2014.

3.1.1.2. Spatio-temporal dynamics of multi-species stemborer communities at mid-altitudes

The monitoring survey on the spatio-temporal dynamics of a stemborer community was conducted in Makuyu (S 0°55.387, E 37°09.004) in Murang’a County in the central province of Kenya. This locality is situated in the mid-altitudinal range (1490-1500 m) (Figure 3.1) and the three stemborer species are known to occur together at this locality (Guofa et al., 2001; Ong’amo et al., 2006a; 2006b). The area has two rainy seasons, the long rain season from April to June and the short rain season from October to December.
Table 3.1. List of localities in the different agro-ecological zones in Kenya and Tanzania where stemborer communities were sampled in maize fields

<table>
<thead>
<tr>
<th>Country</th>
<th>Locality</th>
<th>Altitude (m)</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Agro-ecological Zones</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kenya</td>
<td>Kilifi Spatial gradient</td>
<td>23</td>
<td>-3.605</td>
<td>39.855</td>
<td>Lowland Tropical</td>
</tr>
<tr>
<td></td>
<td>Muhaka</td>
<td>50</td>
<td>-4.270</td>
<td>39.535</td>
<td>Lowland Tropical</td>
</tr>
<tr>
<td></td>
<td>Mariakani</td>
<td>197</td>
<td>-3.880</td>
<td>39.483</td>
<td>Lowland Tropical</td>
</tr>
<tr>
<td></td>
<td>Bungoma</td>
<td>1292</td>
<td>0.593</td>
<td>34.449</td>
<td>Moist Mid-altitude</td>
</tr>
<tr>
<td></td>
<td>Taita</td>
<td>1360</td>
<td>-3.426</td>
<td>38.361</td>
<td>Moist Mid-altitude</td>
</tr>
<tr>
<td></td>
<td>Kitale1</td>
<td>1729</td>
<td>0.790</td>
<td>34.824</td>
<td>Highland Tropical</td>
</tr>
<tr>
<td></td>
<td>Rift1</td>
<td>1864</td>
<td>-0.966</td>
<td>36.552</td>
<td>Moist Transitional</td>
</tr>
<tr>
<td></td>
<td>Rift4</td>
<td>1909</td>
<td>-0.333</td>
<td>36.155</td>
<td>Moist Transitional</td>
</tr>
<tr>
<td></td>
<td>Kitale2</td>
<td>1937</td>
<td>1.197</td>
<td>34.818</td>
<td>Highland Tropical</td>
</tr>
<tr>
<td></td>
<td>Kisii</td>
<td>2021</td>
<td>-0.772</td>
<td>34.975</td>
<td>Highland Tropical</td>
</tr>
<tr>
<td></td>
<td>Molo</td>
<td>2343</td>
<td>-0.173</td>
<td>35.623</td>
<td>Highland Tropical</td>
</tr>
<tr>
<td></td>
<td>Machakos gradient Mach.Loc1</td>
<td>1105</td>
<td>-1.276</td>
<td>37.420</td>
<td>Dry Transitional</td>
</tr>
<tr>
<td></td>
<td>Mach.Loc2</td>
<td>1317</td>
<td>-1.368</td>
<td>37.410</td>
<td>Dry Transitional</td>
</tr>
<tr>
<td></td>
<td>Mach.Loc3</td>
<td>1528</td>
<td>-1.251</td>
<td>37.387</td>
<td>Moist Transitional</td>
</tr>
<tr>
<td></td>
<td>Mach.Loc4</td>
<td>1729</td>
<td>-1.415</td>
<td>37.224</td>
<td>Moist Transitional</td>
</tr>
<tr>
<td></td>
<td>Mach.Loc5</td>
<td>1996</td>
<td>-1.493</td>
<td>37.274</td>
<td>Highland Tropical</td>
</tr>
<tr>
<td></td>
<td>Taita Hills gradient Kipusi</td>
<td>846</td>
<td>-3.478</td>
<td>38.380</td>
<td>Dry Mid-altitude</td>
</tr>
<tr>
<td></td>
<td>Dembwa</td>
<td>1094</td>
<td>-3.447</td>
<td>38.365</td>
<td>Dry Mid-altitude</td>
</tr>
<tr>
<td></td>
<td>Josa</td>
<td>1348</td>
<td>-3.432</td>
<td>38.356</td>
<td>Moist Mid-altitude</td>
</tr>
<tr>
<td></td>
<td>Mbengonyi</td>
<td>1478</td>
<td>-3.420</td>
<td>38.362</td>
<td>Moist Mid-altitude</td>
</tr>
<tr>
<td></td>
<td>Kighala</td>
<td>1688</td>
<td>-3.391</td>
<td>38.339</td>
<td>Highland Tropical</td>
</tr>
<tr>
<td></td>
<td>Vuria</td>
<td>1806</td>
<td>-3.404</td>
<td>38.296</td>
<td>Highland Tropical</td>
</tr>
<tr>
<td>Tanzania</td>
<td>Kilimanjaro gradient Miwaleni</td>
<td>752.3</td>
<td>-3.420</td>
<td>37.461</td>
<td>Dry Mid-altitude</td>
</tr>
<tr>
<td></td>
<td>Uparo-Iwaleni</td>
<td>952</td>
<td>-3.379</td>
<td>37.450</td>
<td>Dry Mid-altitude</td>
</tr>
<tr>
<td></td>
<td>Uparo</td>
<td>1168</td>
<td>-3.348</td>
<td>37.459</td>
<td>Dry Mid-altitude</td>
</tr>
<tr>
<td></td>
<td>Kopachi</td>
<td>1388</td>
<td>-3.332</td>
<td>37.472</td>
<td>Moist Transitional</td>
</tr>
<tr>
<td></td>
<td>Nduoni</td>
<td>1556.2</td>
<td>-3.310</td>
<td>37.464</td>
<td>Moist Transitional</td>
</tr>
<tr>
<td></td>
<td>Marua</td>
<td>1670.7</td>
<td>-3.286</td>
<td>37.457</td>
<td>Highland Tropical</td>
</tr>
</tbody>
</table>
3.1.2. Field sampling protocol

3.1.2.1. Community structure of stemborers in different agro-ecological zones along altitudinal gradients

In each of the 28 localities, ten maize farms were sampled three times during the growing season and infested maize plants recorded. Sampling followed the protocols described by Overholt et al. (1994). Ten infested maize plants were randomly selected from each maize field and dissected to record which stemborer species occurred inside these plants and to determine the numbers of larvae of each species.

3.1.2.2. Spatio-temporal dynamics of multi-species stemborer communities at mid-altitudes

Ten maize fields (each between 0.5 and 1.5 ha) and each not less than 100m apart from the other were selected in the Makuyu area of Kenya. Each field was divided into four quadrats to facilitate random sampling of infested maize plants. The sampling followed the protocols described by Overholt et al. (1994). In each quadrat, one person randomly sampled 15 maize plants, following a zig-zag pattern. Plant height, stem diameter and number of leaves of all 15 plants encountered were recorded. The geographic positions of infested plants among the 15 sampled plants were recorded with a GPS unit (Garmin etrex 20). Infested plants were then excised and dissected to record the species and the number of larvae (and pupae) per stem. Samplings were undertaken over three seasons in this locality. The three seasons were the (1) short rainfall season (November, 2012-January 2013)-SR1, (2) long rainfall season (April 2013-June-2013)-LR, and (3) short rainfall season (November, 2013-January 2014)-SR2.

Weekly sampling was conducted from three weeks after seedling emergence onwards, in all ten fields for 11 weeks in SR1 and LR. However, in SR2, sampling was carried out
for 7 weeks due to the short duration of rainfall and subsequent plant stress. Daily temperatures were recorded with a Hobo data logger (which recorded every hour) and rainfall with a rain gauge.

![Figure 3.1. Map of sampling localities in the different agro-ecological zones](image)

**Figure 3.1.** Map of sampling localities in the different agro-ecological zones

### 3.2. Data analysis

The number of single and multi-species infestation in each AEZ and along altitudinal gradients were determined and expressed as a percentage of total infestations within in each AEZs and localities. A canonical correspondence analysis (CCA) method (Zuur *et al.*, 2007) was used to determine which climatic factors had the strongest influence on the composition of stemborer communities in each AEZ and along the altitudinal
gradient. The average annual rainfall and temperatures for all the sampling localities were extracted from the WorldClim dataset (http://www.worldclim.org/download).

The incidence of infestation was analysed using the generalised linear model with binomial errors structure. Odd Ratios with a 95% confidence interval (O.R. [95%CI]) were calculated for each season from the GLM results obtained. Larval densities of the stemborer species were analysed using the generalised linear mixed model (glmm), with field set as a random effect. The spatial distribution of the stemborer community in Makuyu was analysed using the Ripley’s K function on the GPS positions of species infestations, assuming homogeneity (Bivand et al., 2008; Baddeley, 2008). The effect of temperature and rainfall on larval densities was analysed using glmm, with temperature and rainfall as fixed effects and field as a random effect. All analyses were carried out in R (R Development Team, 2014).

3.3. Results

3.3.1. Stemborer community structure in the different AEZs

The composition of stemborer communities varied between the different AEZs. At least two stemborer species were found in each AEZ. While *C. partellus* and *S. calamistis* were the only species found in the lowland tropical zone, *B. fusca* and *S. calamistis* were the only two species in the highland tropical zone. *Chilo partellus* was the dominant species in the lowland tropical-, dry transitional- and dry mid-altitude AEZs, while *B. fusca* was the dominant species in the moist mid-altitude, moist transitional- and highland tropical AEZs. *Sesamia calamistis* was present in all AEZs but in lower proportions. Multi-species infestations were recorded in all AEZs. The highest number of multi-species infestations was recorded in the moist mid-altitude zone (Figure 3.2).
3.3.2. Community structure along an altitudinal gradient

The community structure varied along altitudinal gradients. *Chilo partellus* was the dominant stemborer species at the lower altitudes (23m-200m) and in some localities at mid-altitudes. *Busseola fusca* was the dominant species in most localities at mid-altitudes and in the higher altitudes (>1680m). *Sesamia calamistis* was present in lower proportions at all altitudes, but dominated at two highland localities. In the mid-altitude areas (especially between 1290m-1550m), the stemborer communities were characterised by a higher number of multi-species infestations (Figure 3.3).
Figure 3.3. Percentage of maize plants with single- and multi-species infestations of *Busseola fusca* (Bf), *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) in different localities along altitudinal gradients

3.3.3. Effect of temperature and rainfall on the composition and distribution of stemborer communities

The multivariate analysis (Figure 3.4) showed that communities where *C. partellus* dominated were associated with higher temperatures, in the lower altitudes, while lower temperatures and higher rainfall characterised higher altitudes, which were dominated by *B. fusca*. *Sesamia calamistis* did not show a strong association with rainfall or temperature. In addition, multi-species communities of Cp+Sc were associated with increasing temperatures, while Bf+Cp communities were associated with increasing rainfall. Bf+Sc did not show a strong association with temperature or rainfall (Figure 3.4)
Figure 3.4. Biplot showing the relationship between average annual temperature and average annual rainfall and the occurrence of single- and multi-species communities consisting of *Busseola fusca* (Bf), *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc)

Average annual temperature and average annual rainfall together explained 56% of the variation in the composition data. This is termed as the constrained component of the model output. The unexplained variation or residuals of the model is termed the unconstrained component (Zuur *et al.*, 2007) (Table 3.2). The eigenvalues of each axis of the bi-plot and the proportions of variation explained by these are provided in Table 3.3.
Temperature was the most significant (p<0.05) environmental factor influencing the composition of stemborer communities along altitudinal gradients. Rainfall did not have a significant effect on the composition of stemborer communities (Table 3.4).

**Table 3.2.** The proportion of variation in the stemborer compositional data explained by the axes of the bi-plot (constrained) and the unexplained or residuals of regression (unconstrained)

<table>
<thead>
<tr>
<th></th>
<th>Inertia</th>
<th>Proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>0.877</td>
<td>1</td>
</tr>
<tr>
<td>Constrained</td>
<td>0.492</td>
<td>0.561</td>
</tr>
<tr>
<td>Unconstrained</td>
<td>0.385</td>
<td>0.439</td>
</tr>
</tbody>
</table>

**Table 3.3.** Eigenvalues of each axes of the bi-plot, showing their contributions to the explained variations in the compositional stemborer data

<table>
<thead>
<tr>
<th>Importance of components</th>
<th>CCA1</th>
<th>CCA2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>0.490</td>
<td>0.002</td>
</tr>
<tr>
<td>Proportion explained</td>
<td>0.558</td>
<td>0.003</td>
</tr>
<tr>
<td>Cumulative proportion</td>
<td>0.558</td>
<td>0.561</td>
</tr>
</tbody>
</table>

**Table 3.4.** Results from the forward selection method to test the significance of the influence of average annual temperature and average annual rainfall on the composition and distribution of the different stemborer communities

<table>
<thead>
<tr>
<th></th>
<th>F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average annual temperature</td>
<td>18.5</td>
<td>0.001</td>
</tr>
<tr>
<td>Average annual rainfall</td>
<td>2.4</td>
<td>0.29</td>
</tr>
</tbody>
</table>

Number of permutations=9999
3.3.4. Spatio-temporal dynamics of infestation of stemborer species at mid-altitudes

3.3.4.1. Incidence of infestation

The incidence of infested plants in fields increased over time in all three sampling periods (Figure 3.5). There was no significant difference in the incidence of infestation between seasons (Table 3.5).

![Figure 3.5. Percentage of stemborer infested plants over time in each season in Makuyu. SR=short rain season, LR=long rain season](image)

**Table 3.5.** Results from generalised linear model (binomial) analysis on the incidence of infestation between seasons in Makuyu

<table>
<thead>
<tr>
<th>Seasons</th>
<th>Odd Ratios (95%CI)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short Rain 1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Long Rain</td>
<td>1.25 (0.87-1.78)</td>
<td>0.24</td>
</tr>
<tr>
<td>Short Rain 2</td>
<td>0.85 (0.58-1.25)</td>
<td>0.42</td>
</tr>
</tbody>
</table>

O.R.=Odd Ratios

3.3.4.2. Proportion of single and multi-species infestation

Single-species infestations were recorded at higher frequency than multi-species infestations during the three seasons. *Busseola fusca* was the dominant species during
all three seasons. The occurrence of single-species infestation of *C. partellus*, *S. calamistis* and multi-species communities was higher during the long rain season than the short rain seasons (Figure 3.6).

![Graph showing percentage of plants infested with single-species and combinations of *Busseola fusca* (Bf), *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) over time in three growing seasons at Makuyu. SR=short rain season, LR=long rain season.]

**Figure 3.6.** The percentage of plants infested with single-species and combinations of *Busseola fusca* (Bf), *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) over time in three growing seasons at Makuyu. SR=short rain season, LR=long rain season

### 3.3.4.3. Larval number of each stemborer species

There was variation in the larval density of each species between seasons. *Busseola fusca* had a significantly lower larval density during the long rain season than the two short rain seasons. On the other hand, *C. partellus* and *S. calamistis* had significantly higher larval densities during the long rain season than in the two short rain seasons (Figure 3.7, Table 3.6). Between the three species, *B. fusca* had significantly higher larval densities than *C. partellus* and *S. calamistis* across all seasons. While the larval density of *S. calamistis* was significantly higher than that of *C. partellus* during the long
rain season, the opposite was observed during the two short rain seasons (Figure 3.7, Table 3.7).

![Figure 3.7](image)

**Figure 3.7.** Larval numbers of *Busseola fusca*, *Chilo partellus* and *Sesamia calamistis* per plant over time in three growing seasons. SR=short rain season, LR=long rain season

**Table 3.6.** GLMM results on the larval density of *Busseola fusca*, *Chilo partellus* and *Sesamia calamistis* between different seasons

<table>
<thead>
<tr>
<th>Seasons</th>
<th><em>Busseola fusca</em></th>
<th></th>
<th><em>Chilo partellus</em></th>
<th></th>
<th><em>Sesamia calamistis</em></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Z</td>
<td>P-value</td>
<td>Z</td>
<td>P-value</td>
<td>Z</td>
<td>P-value</td>
</tr>
<tr>
<td>Short Rain 1</td>
<td>47.7</td>
<td>&lt;0.001</td>
<td>3.7</td>
<td>&lt;0.001</td>
<td>3.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Long Rain</td>
<td>6.7</td>
<td>&lt;0.001</td>
<td>5.2</td>
<td>&lt;0.001</td>
<td>13.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Short Rain 2</td>
<td>0.9</td>
<td>0.38</td>
<td>1.9</td>
<td>0.05</td>
<td>1.8</td>
<td>0.07</td>
</tr>
</tbody>
</table>
Table 3.7. GLMM results on the larval density between *Busseola fusca*, *Chilo partellus* and *Sesamia calamistis* in each season

<table>
<thead>
<tr>
<th>Species</th>
<th>Seasons</th>
<th>Short rain 1</th>
<th>Long rain</th>
<th>Short rain 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Z</td>
<td>P-value</td>
<td>Z</td>
<td>P-value</td>
</tr>
<tr>
<td><em>Busseola fusca</em></td>
<td>35.13</td>
<td>&lt;0.001</td>
<td>28.12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><em>Chilo partellus</em></td>
<td>29.16</td>
<td>&lt;0.001</td>
<td>29.41</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><em>Sesamia calamistis</em></td>
<td>23.88</td>
<td>&lt;0.001</td>
<td>27.74</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

3.3.4.4. Spatial distribution of species among plants

The species distribution was similar in all 10 fields that were sampled. *Busseola fusca* was the dominant species and showed a clustered intraspecific and interspecific distribution with *C. partellus* and *S. calamistis* in almost all fields during both short rain seasons and long rain season (Figure 3.8a &b).
Figure 3.8. Clustered distribution pattern of *Busseola fusca* (Bf) intra-specifically and inter-specifically with *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) in each field in the (a) short rain season and (b) long rain season.
3.3.4.5. Effect of temperature and rainfall on larval density

The larval densities of all three species were significantly affected by temperature and rainfall (Table 3.8).

Table 3.8. GLMM results on the larval density between *Busseola fusca*, *Chilo partellus* and *Sesamia calamistis* in each sampling period

<table>
<thead>
<tr>
<th>Environmental factors</th>
<th>Species</th>
<th>Z</th>
<th>P-value</th>
<th>Z</th>
<th>P-value</th>
<th>Z</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Busseola fusca</em></td>
<td>7.4</td>
<td>&lt;0.001</td>
<td>5.9</td>
<td>&lt;0.001</td>
<td>7.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td><em>Chilo partellus</em></td>
<td>17.2</td>
<td>&lt;0.001</td>
<td>7.5</td>
<td>&lt;0.001</td>
<td>7.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td><em>Sesamia calamistis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

3.4. Discussion

This study showed that the composition of lepidopteran stem borers infesting maize in different agro-ecological zones in East Africa and also along altitudinal gradients, include single- and multi-species infestations of *B. fusca*, *C. partellus* and *S. calamistis*. This confirms earlier reports on community composition of stem borers in Kenya and Tanzania (Kalule, 1997; Guofa *et al.*, 2001; Tefera, 2004; Ong’a’mo *et al.*, 2006a; 2006b), Mozambique (Cugala & Omwega, 2001) and South Africa (Krüger *et al.*, 2008).

This study indicates the changes that occur in community structure of these three stem borers species, with simple communities of mixed populations of *B. fusca* and *C. partellus*, to complex communities consisting of mixed populations of single- and multi-species infestation of the three species. The result of this study is supported by observations of stem borers species composition from the lower to higher altitudes (Guofa *et al.*, 2001; Ong’a’mo *et al.*, 2006b; 2013). This study, however, also contradicts other studies which indicated that *C. partellus* dominates the stem borers community in the mid-altitudes. In this study, *B. fusca* dominated in most of the mid-altitude areas where the three species occur. One reason for this difference could be the difference in sites sampled along altitudinal gradients. In the case of Guofa *et al.* (2001), the number of
sites sampled was higher in the lower altitudes than higher altitudes. Since *C. partellus* dominates in these areas, their numbers could have inflated their density estimates.

This study showed that at some altitudes, *S. calamistis* dominated when it occurred in mixed populations with the other two species and also at higher altitudes, where it largely occurs alone. This is in contrast to earlier reports on the lower status of this species in the region (Wale, 1999; Guofa *et al*., 2001; Ong’amo *et al*., 2006a; 2006b). This study indicated that the most important environmental factor influencing the structuring of stemborer communities was temperature, with rainfall exerting a lesser influence. This confirms the temperature-dependence of the distribution and composition of communities involving these three species (Ong’amo *et al*., 2006a). While temperature was shown to be the most important factor determining community composition, rainfall seemingly has more impact on other aspects of the biology of these stem borer species. Jiang *et al*. (2006) reported that rainfall had a direct influence of the growth rates of *C. partellus* and *S. calamistis* in the south coast of Kenya. Similarly the flight activity and seasonal infestation levels of *B. fusca* was also influenced by rainfall in South Africa (Van Rensburg *et al*., 1987a).

This study showed that the incidence of infested plants in maize fields increased over time. This is attributed to infestation that takes place as the season progresses as well as to the movement of larvae from the plant on which they hatched, to other nearby plants, over time. Van den Berg *et al*. (1991) reported that *B. fusca* and *C. partellus* larvae from one primary infested plant has the potential to infest five other sorghum plants through migration over time. This movement to possibly avoid competition for resources explains the reduction in mean larval number per plant as plants develop. Krüger *et al*. (2008) reported a similar increase in the rate of infestation of *B. fusca* and
C. partellus in maize fields as time progressed. Migration of B. fusca larvae over time until they eventually occur at very low numbers per stem have been reported by Van Rensburg et al. (1987a; 1987b).

This study confirmed the single- and multi-species infestations of B. fusca, C. partellus and S. calamistis communities in mid-altitudinal areas. These infestations varied with season with B. fusca dominating in all seasons, while the infestation levels of S. calamistis was higher in the long rainfall season than short rainfall seasons. The dominance of single-species infestations of B. fusca and its high larval numbers per plant in mixed communities of stemborers, which was observed over three seasons, shows that it has an advantage in resource utilisation over the other two species. In most fields, it was the first species to colonise maize plants. The study also showed that temperature and rainfall influence the composition and dynamics of stemborer communities at this micro-scale level of community organisation.

This study further showed that the dominant species, B. fusca, colonises maize fields in a clustered distribution intra-specifically and inter-specifically with the other two species. This clustered distribution of stemborers has also been reported for C. partellus on the Kenya coast (Overholt et al., 1994) and B. fusca in the forest zones of Cameroon (Ndemah et al., 2001) and West Africa (Gounou & Schulthess, 2004). Although B. fusca dominated the stemborer community in the mid-altitude areas in this study, competition among the three species may not be responsible for this observed community structure. Competitive interactions among species are usually indicated by a regular distribution pattern of species in a resource (Bivand et al., 2008; Baddeley, 2010).
Future changes in temperatures, associated with climate change, could impact community structures of mixed stemborer communities in mid-altitude areas where crops are cultivated. *Chilo partellus* might displace *B. fusca* as the dominant species. As was indicated in this study, *C. partellus* is expanding its range into highlands. This phenomenon was also observed in South Africa where *C. partellus* competitively displaced *B. fusca* on the ratoon sorghum (Kfir, 1997) and in the coastal region of Kenya where it displaced *C. orichalcociliellus* (Ofomata *et al.*, 1999).

3.5. References


Ong’amo, G.O., Le Ru, B.P., Dupas, S., Moyal, P., Muchugu, E., Calatayud, P.-A. & Silvain, J.-F. (2006b). The role of wild host plants in the abundance of...


CHAPTER FOUR

OVIPOSITION RESPONSES OF DIFFERENT STEMBORETER SPECIES TO CONSPECIFIC AND HETEROSPECIFIC INFESTED MAIZE PLANTS

Abstract

Competitive or facilitative interactions characterise phytophagous insect communities that utilise the same resources. These interactions can be direct or indirect through the mediation of the host plant. Oviposition as a form of resource utilisation by insects is influenced by these interactions. For example, prior feeding of larvae on a plant induces oviposition in some females while this deters subsequent oviposition in other species. The oviposition responses between gravid females were studied in a choice-experiment involving Busseola fusca, Sesamia calamistis and Chilo partellus which attack cereal crops in East and southern Africa. Gravid females of each species were presented with a choice between uninfested and conspecific or heterospecific larvae-infested maize plants in cages. The number of eggs and egg batches were recorded as oviposition responses. The results showed that three stemborer species did not avoid oviposition on plants with prior infestation. However, B. fusca showed a high preference for S. calamistis-infested plants, while C. partellus preferred conspecific-infested plants. Sesamia calamistis did not show a significant preference for one plant over the other. This study provides insight into one possible mechanism by which cereal lepidopteran stemborer females interact in multi-species communities that utilise common resources.
4.0. Introduction

The structure and function of ecological communities are maintained by the direct and indirect interactions between the species which constitute the community (Wootton & Emmerson, 2005). Often, these interactions occur through the utilisation of the same resources and its outcome can be negative (e.g. competition), positive (e.g. facilitation) or neutral (Denno et al., 1995; Bruno et al., 2003; Denno & Kaplan, 2007). Such competitive or facilitative interactions characterise phytophagous insect communities that utilise the same resources (Denno et al., 1995; Kaplan & Denno, 2007; Speight et al., 2008, Schowalter, 2011). These interactions can be directly intraspecific or interspecific (Memmot et al., 2007) or can be indirect through the mediation of the same host plant (Faeth, 1986; Kaplan & Denno, 2007; Fisher et al., 2000). Plant-mediated interactions are common and also the dominant factor which influences interactions in phytophagous insects (Faeth, 1986; Denno et al., 1995; Ohgushi, 2005; Lynch et al., 2006; Denno & Kaplan, 2007).

Oviposition is a form of resource utilisation by insects on host plants (Klomp, 1964). This form of resource utilization also establishes the relationship between insect and host plant (Singer, 2004). Generally, the physical and chemical properties, as well as the physiological state of the host plant determine its final acceptability for the female. The final acceptance is however also influenced by the state of the gravid female, which includes egg load and learning through experience and the interplay between these factors (Courtney et al., 1989; Minkenberg et al., 1992; Cunningham et al., 1998; 1999 Bernays & Chapman, 1994; Awmack & Leather, 2002).

Two theories have been put forward to explain the oviposition behaviour of female insects. The dominating theory is termed the preference-performance hypothesis or
optimal oviposition theory, which states that a female will oviposit on host plants that provide the best conditions for survival of its offspring, thereby maximising her fitness (Jaenike, 1978; Thompson, 1988; Scheirs & De Bruyn, 2002; Gripenberg et al., 2010). However, other studies have reported on the non-correlation between adult preference and offspring performance (Thompson, 1988; Scheirs & De Bruyn, 2002). In fact, some female insects have been shown to oviposit on host plants which they also utilise for food for their own performance. This behaviour is known as optimal foraging and has been formulated into the other theory termed the optimal foraging theory (Scheirs & De Bruyn, 2002).

The oviposition preferences of gravid females utilising the same host plant in a community, can be influenced by the interactions among species (Craig et al., 2000; Shiojiri et al., 2002). Thus, competition for, or facilitation in the use of the same resource can influence the final choice by the female for oviposition. For example, prior feeding of larvae on a plant induces oviposition in some females (Anderson & Alborn, 1999; Craig et al., 2000; Groot et al., 2003; Viswanathan et al., 2005; Facknath, 2012), while on the other hand, this deters subsequent oviposition in other species (Sato et al., 1999; De Moraes et al., 2001; Wise & Weinberg, 2002; Fatouros et al., 2012).

Lepidopteran stemborers are major pests of cereals in sub-Saharan Africa and females utilise cultivated cereal crops for their oviposition. Several studies have been conducted on the different aspects of their host selection and preferences (Päts & Ekbom, 1994; Van den Berg, 2006; Van den Berg et al., 2006; Glas et al., 2007; Calatayud et al., 2008a). The indigenous noctuids Busseola fusca (Fuller) and Sesamia calamistis Hampson and the exotic crambid Chilo partellus (Swinhoe) attack cereals crops in East and southern Africa (Reddy, 1998; Kfir et al., 2002). In these regions, they occur as
communities of single or mixed species infesting the maize stems in cereal fields (Tefera, 2004; Ong’a’mo et al., 2006a; Krüger et al., 2008). In Kenya, the composition of these stemborer communities varies along an altitudinal gradient across the different agro-ecological zones. *Busseola fusca* is the dominant species in the wet highlands characterised by relatively low temperatures, while *C. partellus* dominates in the dry lowlands characterised by high temperatures. *Sesamia calamistis* is present at all altitudes in low numbers. However in the mid-altitudes, the three stemborer species occur as a mixed community, but with variation in species dominance with respect to location and season (Guofa et al., 2001; Ong’amo et al., 2006a; 2006b). Despite information on these spatial and temporal variations in stemborer communities, there is inadequate information on the kind of intraspecific and interspecific interactions that characterise resource utilisation in the form of oviposition by these stemborers on the same plant.

The objective of this study was to describe the oviposition response of each stemborer species. The questions to be answered were: (1) does prior resource use deter gravid females from ovipositing on the same plant to avoid competition? and (2) are females able to distinguish between plants infested by conspecific and heterospecific larvae?

4.1. Materials and methods

4.1.1. Plants and insects

Maize plants of hybrid H513 (Simlaw, Kenya Seed Company, Nairobi, Kenya) were grown in plastic pots (12 cm in height x 13 cm in diameter) in a greenhouse at the African Insect Science for Food And Health (*icipe*) campus, Nairobi, Kenya. Mean temperatures were approximately 31/17°C (day/night) with a L12:D12 photoperiod. Plants were used in experiments when they were between 4-6 weeks old.
Because wild insects are more responsive to plant odours compared to laboratory-reared insects as shown for *B. fusca* (Calatayud *et al.*, 2008b), only adult field-collected insects of *C. partellus* (Cp), *B. fusca* (Bf) and *S. calamistis* (Sc) were used in this experiment. For each species, fourth to fifth instar larvae were collected from maize fields. They were then reared on the artificial diet of Onyango and Ochieng’-Odero (1994) for *B. fusca* and *S. calamistis*, and of Ochieng *et al*. (1985) for *C. partellus*, until pupation. Pupae were sexed into males and females and kept separately in plastic containers (21 x 15 x 8 cm) until adult emergence. A cotton pad moistened with water was placed in the container, to maintain relative humidity at >80%. The insects were kept in a rearing room at a temperature of 25 ± 0.05°C, RH of 58.5 ± 0.4%, and photoperiod of L12:D12.

Emerged adult males and females of each species were then put together in a mating cage (40×40×63 cm), at onset of the scotophase. The mating status was checked at hourly intervals after releases into the mating cage until end of scotophase. Pairs of moths that were mating were collected in plastic jars (8 cm high × 5 cm in diameter). These gravid females were used in experiments on the following night.

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

4.1.2. Infestation of plants

Maize plants of 4-6 weeks old after emergence were manually infested with third and fourth instar larvae. These larval stages were chosen to ensure a high degree of feeding
damage within 24 hours before release of gravid females to lay eggs on these plants. A plant was infested with 12 larvae of either *B. fusca*, *C. partellus* or *S. calamistis*.

4.1.3. Oviposition experiment

For each experiment, a single infested maize plant was put together with a single uninfested maize plant in an oviposition cage measuring 70 x 50 x 50 cm. These cages were kept in a room with a temperature of 25 ± 0.05°C, RH of 58.5 ± 0.4%, and photoperiod of L12:D12. The gravid female collected the night before, was then released into the middle of the cage, between the two plants. The number of egg batches and the total number of eggs in each batch on each plant were determined after two nights. After each experiment, females were dissected to check for the presence of spermatophores in the bursa copulatrix, which in Lepidoptera indicates successful mating (Lum, 1979). Only females bearing spermatophores were considered in the results. For gravid females of each species, the following treatments, replicated 20 times were used:

1. uninfested maize vs Bf-infested maize plant
2. uninfested maize vs Cp-infested maize plant
3. uninfested maize vs Sc-infested maize plant.

4.2. Data analysis

The number of egg batches, total number of eggs and eggs per batch on uninfested and infested plants were analysed using the generalised linear model with Poisson errors. All analyses were carried out in R (R Development Team, 2014).

4.3. Results
4.3.1. Number of egg batches, eggs and number of eggs per batch oviposited by *B. fusca* females

*Busseola fusca* oviposited more egg batches on infested than on uninfested maize plants in all three treatments. However, this number was only significantly higher in the *S. calamistis*-infested treatment \((t=3.42, p=0.001)\) (Figure 4.1a, Table 4.1). *Busseola fusca* oviposited more eggs onto *C. partellus*-infested and *S. calamistis*-infested plants but fewer eggs on *B. fusca*-infested maize plants. However, this was only significant in *S. calamistis*-infested plants \((t=2.31, p=0.02)\) (Figure 4.1b, Table 4.1). The number of eggs per batch of *B. fusca* was significantly higher on uninfested than infested plants in the *B. fusca*-infested treatment. There were no significant differences between other infestation treatments (Figure 4.1c, Table 4.1).
Figure 4.1. (a) Mean number of egg batches per female, (b) Mean number of eggs per female and (c) Mean number of eggs per batch, ovposited on uninfested and infested maize plants by *Busseola fusca* (Bf), *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) moths. Bars indicate S.E.
4.3.2. Number of batches, number of eggs and number of eggs per batch oviposited by *S. calamistis* females

The mean number of batches oviposited by *S. calamistis* females was not significantly different between uninfested and infested plants either with conspecific or heterospecifics (Figure 4.2a, Table 4.1). The mean number of eggs oviposited by *S. calamistis* on uninfested and infested maize did not differ significantly between any of the treatment combinations (Figure 4.2b, Table 4.1). The number of eggs per batch of *S. calamistis* on uninfested and infested maize plants did not differ significantly between any of the treatments (Figure 4.2c, Table 4.1).
Figure 4.2. (a) Mean number of egg batches per female, (b) Mean number of eggs per female and (c) Mean number of eggs per batch ovposited on uninfested and infested maize plants by *Sesamia calamistis* (Sc), *Busseola fusca* (Bf) and *Chilo partellus* (Cp) moths. Bars indicate S.E.
4.3.3. Number of batches, number of eggs and eggs per batch oviposited by *C. partellus* females

The mean number of batches oviposited by *C. partellus* females was not significantly different between uninfested plants and plants infested either with conspecific or heterospecifics. Numbers did however show a tendency to be higher on infested plants in *C. partellus*-infested and *B. fusca*-infested plants, but vice versa in *S. calamistis*-infested plants (Figure 4.3a, Table 4.1). The mean number of eggs laid on plants by *C. partellus* was significantly higher on infested than on uninfested plants if plants were infested by *C. partellus* (t=2.14, p=0.03), but not in the other infested treatments. However, this species showed a preference towards infested plants when provided with a choice between Bf-infested and uninfested plants and uninfested plants if provided with a choice of uninfested and Sc-infested plants (Figure 4.3b, Table 4.1). The mean number of eggs per batch of *C. partellus* on uninfested and infested maize plants did not differ significantly between any treatments (Figure 4.3c, Table 4.1).
Figure 4.3. (a) Mean number of egg batches per female, (b) Mean number of eggs per female and (c) Mean number of eggs per batch ovposited on uninfested and infested maize plants *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) moths. Bars indicate S.E.
Table 4.1. Statistical values indicating significance of differences between mean numbers of egg batches, mean numbers of eggs and number of eggs per batch oviposited on uninfested and infested plants by *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus* in each treatment

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Mean number of egg batches</th>
<th>Mean number of eggs</th>
<th>Mean number of eggs / batch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>p-value</td>
<td>t</td>
</tr>
<tr>
<td>B. fusca-infested + B. fusca moth</td>
<td>0.67</td>
<td>0.51</td>
<td>2.14</td>
</tr>
<tr>
<td>S. calamistis-infested + B. fusca moth</td>
<td>3.42</td>
<td>0.001</td>
<td>2.31</td>
</tr>
<tr>
<td>C. partellus-infested + B. fusca moth</td>
<td>1.35</td>
<td>0.18</td>
<td>1.06</td>
</tr>
<tr>
<td>S. calamistis-infested + S. calamistis moth</td>
<td>0.38</td>
<td>0.71</td>
<td>0.19</td>
</tr>
<tr>
<td>B. fusca-infested + S. calamistis moth</td>
<td>0.95</td>
<td>0.35</td>
<td>1.30</td>
</tr>
<tr>
<td>C. partellus-infested + S. calamistis moth</td>
<td>0.16</td>
<td>0.87</td>
<td>0.50</td>
</tr>
<tr>
<td>C. partellus-infested + C. partellus moth</td>
<td>1.86</td>
<td>0.07</td>
<td>2.14</td>
</tr>
<tr>
<td>B. fusca-infested + C. partellus moth</td>
<td>1.37</td>
<td>0.18</td>
<td>0.64</td>
</tr>
<tr>
<td>S. calamistis-infested + C. partellus moth</td>
<td>0.91</td>
<td>0.37</td>
<td>0.67</td>
</tr>
</tbody>
</table>

4.4. Discussion

This study showed that generally gravid females of the three stemborer species did not avoid infested maize plants. There was however variations in their specific oviposition responses to infested and uninfested maize plants. Poelman *et al.* (2008) reported similar differential oviposition responses from three moth species *Mamestra brassicae* L. (Noctuidae), *Plutella xylostella* L. (Yponomeutidae) and *Pieris rapae* L. (Pieridae) on uninfested and *P. rapae*-infested cabbage leaves. While *P. rapae* did not show preference for either infested and uninfested leaves, *P. xylostella* and *M. brassicae* showed a preference for infested over uninfested and uninfested over infested leaves respectively. Shiojiri *et al.* (2002) earlier reported the same oviposition responses by *P. xylostella* and *P. rapae* on cabbage plants. Furthermore, Sigsgaard (2004) also showed a similar variation in the oviposition responses of a community of *Anthocoris nemorum* L. and *A. nemoralis* Fabricius (Heteroptera: Anthocoridae) on pear and apple leaves. While *A. nemorum* preferred damaged leaves, *A. nemoralis* showed a preference for undamaged leaves.
In addition, oviposition preferences for damaged to undamaged plants have been shown in the cabbage root flies, *Delia radicum* (L.) (Diptera: Anthomyiidae) on cauliflower and kale (Baur *et al.*, 1996), on cotton plants by *Spodoptera littoralis* Boisd. (Lepidoptera: Noctuidae) (Anderson & Alborn, 1999), on onions by *Delia antique* (Meigen) (Diptera: Anthomyiidae) (Hausmann & Miller, 1989) and also by the green capsid bug *Lygocoris pabulinus* (L.) (Heteroptera: Miridae) (Groot *et al.*, 2003). On the other hand, female oviposition preference for undamaged over damaged plant hosts was reported in the moth species *Heliothis virescens* F. (Lepidoptera: Noctuidae) on tobacco plants (De Moraes *et al.*, 2001), the leaf-feeding beetle *Leptinotarsa juncta* (Germar) (Coleoptera: Chrysomelidae) on *Solanum carolinense* (L.) (Solanaceae) (Wise & Weinberg, 2002) and also the moth species *P. rapae* on the crucifer plant *Rorippa indica* (L.) (Sato *et al.*, 1999).

This study also showed the variation in responses between the three stemborer species on conspecific and heterospecific infested maize plants. While *B. fusca* showed a stronger oviposition preference for Sc-infested maize than its conspecific infested maize plants, *C. partellus* showed a higher oviposition preference for conspecific infested maize plants than plants infested by heterospecifics. *Sesamia calamistis* did however not discriminate between infested maize plants. These results contrast with the observation made by Kfir (1997) that *B. fusca* avoided ovipositing on maize prior infested by *C. partellus*. Although it was not statistically significant, *B. fusca* a tendency for oviposition on Cp-infested than uninfested plants.

These varied oviposition preferences for conspecific and heterospecific infested plants have been reported from several studies. The leafminer species *Liriomyza trifolii*
Burgess) (Diptera: Agromyzidae) showed a strong oviposition preference for conspecific infested potato plants, but the opposite was observed with L. huidobrensis (Blanchard) (Facknath, 2012). Viswanathan et al. (2005) reported a similar oviposition preference on conspecific-damaged plants by the beetle Plagiometriona clavata (F.) (Coleoptera: Chrysomelidae) than on plants damaged by Psylliodes affinis Paykull (Coleoptera: Chrysomelidae). On the other hand, the ladybird species Harmonia axyridis Pallas (Coleoptera: Coccinellidae) was reported to show a stronger oviposition preference on broadbean plants contaminated with heterospecific than conspecific larval tracks (Yasuda et al., 2000). Similar results were reported for Narnia femorata Stål (Hemiptera: Coreidae) on cactus plants (Miller et al., 2013) and for the larch ladybird Aphidecta obliterata L. (Coleoptera: Coccinellidae) (Oliver et al., 2006).

This study showed that the preference-performance hypothesis underlying oviposition preference by female insects was not observed in the three stemborer species. Stemborer females oviposited, and in some cases significantly preferred, prior infested plants on which their offspring would face competition from larvae already present. Thompson (1988) attributed these variations in oviposition responses with regard to the preference-performance to genetics and also four other hypotheses on selection pressures on gravid females. These were the time, patch dynamics, parasite/grazer and enemy-free space hypotheses (see Thompson, 1988 for detailed discussions). Furthermore, different factors have been reported to be involved in final selection of a host plant for oviposition. They include the physical and chemical properties of the host plant, egg load of the female and learning through experience (Courtney et al., 1989; Minkenberg et al., 1992; Bernays & Chapman, 1994; Cunningham et al., 1998; 1999; Awmack & Leather, 2002).
The oviposition responses of the three stemborer species could have been influenced by some of the limitations of this study. Firstly, the choice of two plants was very limited, considering that female stemborers are presented with many plants in the field. Secondly, females were limited in the small enclosure available to them which could have forced them to oviposit anyway, considering that egg load can influence oviposition preference on less suitable hosts (Minkenberg et al., 1992). However, considering that multi-species larval infestations are common in the field, this study provides insight into one possible mechanism by which cereal lepidopteran stemborer females interact in their multi-utilisation of common resources.

4.5. References


CHAPTER FIVE

INFLUENCE OF TEMPERATURE ON INTRA- AND INTERSPECIFIC RESOURCE UTILISATION WITHIN A COMMUNITY OF LEPIDOPTERAN MAIZE STEMBORENS

Abstract

Competition or facilitation characterises intra- and interspecific interactions within communities of species that utilise the same resources. Temperature is an important factor influencing those interactions and eventual outcomes. The noctuid stemborers *Busseola fusca* and *Sesamia calamistis*, and the crambid *Chilo partellus* attack maize in sub-Saharan Africa. They often occur as a community of interacting species at nearly all altitudinal ranges, often in the same field and even the same plant. The influence of temperature on the intra- and interspecific interactions among larvae of these species was studied using potted maize plants exposed to fluctuating temperatures in a greenhouse and artificial surrogate stems kept at different constant temperatures (15°C, 20°C, 25°C and 30°C) in an incubator. The experiments involved single- and multi-species treatments. Survival and relative growth rate of each species were assessed. Both intra- and interspecific competitions were observed among all three species. Interspecific competition was stronger between the noctuids and the crambid than between the two noctuids. Temperature, intra- and interspecific interactions affected both survival and relative growth rates of the three species. Particularly at high temperatures, *Chilo partellus* was superior to the other two species in utilising resources in interspecific interactions as shown by higher larval survival and relative growth rates. In contrast, low temperatures favoured survival of *B. fusca* and *S. calamistis* but it affected the relative growth rates of all three species. Survival and relative growth rates of *B. fusca* and *S. calamistis* were similar across all temperatures irrespective of interspecific interactions. The implications of these findings are discussed with regard to utilization of resources (crops) by these pest species under future climate change scenarios.

Manuscript submitted to Plos One as

5.0. Introduction

The common use of a limited resource by several species for their survival predisposes them to interactions (Leibold, 1995). These interactions can be competitive (Agrawal, 2005; Denno et al., 1995) or facilitative (Denno et al., 1995; Stachowicz, 2001; Bruno et al., 2003). The outcome of competition is the dominance of a superior competitor or the co-existence of species that differentiate their niche or resource use in a given community (Duyck et al., 2004; Speight et al., 2008). However, the role of competition in the organisation of insect communities has been questioned by several authors (Connell, 1983; Karban, 1986; Gurevitch et al., 1992; Denno et al., 1995). Furthermore, positive or facilitative interactions have recently been rediscovered to influence the organisation of communities (Denno et al., 1995; Stachowicz, 2001; Cardinale et al., 2002; Bruno et al., 2003; Lill & Marquis, 2003; Kaplan & Eubanks, 2005; Calderón-Cortés, 2011). Despite these debates, two crucial reviews on the subject present strong evidence for the dominance of competition in phytophagous insect communities (Denno et al., 1995; Kaplan & Denno, 2007).

Temperature is the most crucial abiotic factor for insects, as it directly drives their life processes. It influences resource utilisation, intra- and inter-specific interactions and limits their geographic distribution (Howe, 1967; Bale et al., 2002; Sporleder et al., 2004; Hodkinson, 2005; Dangles et al., 2008; Speight et al., 2008; Damos & Savopoulou-Soultani, 2012). The effect of temperature on survival, fecundity and developmental rate has been studied for many insect species, all reporting that the growth and developmental rate of a species increase with temperature up to a certain optimum (Logan et al., 1976; Lactin et al., 1995; Bezemer et al., 1998; Dangles et al., 2008; Khadioli et al., 2014a; 2014b). The temperature also influences the interactions between insect species. For example, Wilson et al. (1984) found that competitive interactions
between the burying beetles *Nicrophorus arbicollis* and *N. defodiens* (Coleoptera: Silphidae), when feeding on the same carcass, were temperature dependent. In an experiment involving the seed beetle *Stator limbatus* (Horn) (Coleoptera: Chrysomelidae), cooler temperatures conferred a competitive advantage on smaller males, which out-competed larger ones in reaching a potential mate (Moya-Laraño *et al.*, 2007). In another experiment with larvae of *Aedes albopictus* Skuse and *A. aegypti* (L.) (Diptera: Culicidae), increased temperatures had the same effect on both species and thus negated its influence on the outcome of competition between larvae (Lounibos *et al.*, 2002). Future temperature increases (Intergovernmental Panel on Climate Change, 2014) is predicted to affect the type and intensity of species interactions (Cammell & Knight, 1992; Buse *et al.*, 1999; Bale *et al.*, 2002; Tylianakis *et al.*, 2008). Laws and Belovsky (2010) reported that changes in temperature influenced the intensity of intraspecific competition by the grasshopper *Camnula pellucida* (Scudder) (Orthoptera: Acrididae). Surprisingly, few studies have been carried out to assess the effect of possible future temperature increases on the competitive and facilitative interactions within communities of insects utilising the same resource (Tylianakis *et al.*, 2008; Gilman *et al.*, 2010).

Lepidopteran stemborers such as the indigenous noctuids *Busseola fusca* (Fuller) and *Sesamia calamistis* (Hampson) and the exotic crambid *Chilo partellus* (Swinhoe) attack maize crops in East and southern Africa (Reddy, 1998; Kfir *et al.*, 2002). Depending on the altitude they may occur as single species or communities of mixed species attacking cereal stems in the same field (Van den Berg *et al.*, 1991; Tefera, 2004; Ong’a’mo *et al.*, 2006a; Krüger *et al.*, 2008), although differences exist in the ranges of their wild host plants (Rebe *et al.*, 2000; Ong’a’mo *et al.*, 2006b). While *B. fusca* and *C. partellus* were identified as oligophagous, *S. calamistis* was found to be polyphagous (Le Ru *et al.*, 2000).
In Kenya, the composition of these stemborer communities varies with altitudinal gradient. *Busseola fusca* is the predominant species in the highlands characterised by comparatively low temperatures, while *C. partellus* is the most abundant species in the hot lowlands. By contrast, *S. calamistis* is present in low numbers at all altitudes. Only in the mid-altitudes do the three species occur as a mixed community, but the predominance of a species may vary with location and season (Guofa et al., 2001; Ong’amo et al., 2006a; 2006b). Reports of competitive displacement of *B. fusca* and *Chilo orichalcociliellus* by *C. partellus* from overlap in resource use have been reported in South Africa (Kfir, 1997; Rebe et al., 2004) and in the coastal region of Kenya (Ofomata et al., 1999), respectively, but the mechanisms behind the species displacements are not known. The temperature requirements of these stemborers have been well studied, but the influence of temperature and the likely impacts of climate change on their interactions have yet to be elucidated. This paper describes the effect of temperature on the intra- and interspecific interactions that characterise resource utilisation by the three stemborer species.

5.1. Materials and methods

5.1.1. Plants and insects

Seeds of the H513 hybrid maize variety (Simlaw, Kenya Seed Company, Nairobi, Kenya) were planted in plastic pots (12 cm in height x 13 cm in diameter), in a greenhouse at the campus of the African Insect Science for Food and Health (*icipe*), Nairobi, Kenya. Mean temperatures were approximately 31/17°C (day/night) with a 12:12 h (L:D) photoperiod. Four to six week old plants were used in the experiments.
Second instar larvae (L2) of *B. fusca* (Bf), *C. partellus* (Cp) and *S. calamistis* (Sc) were obtained from colonies reared at the Animal Rearing and Containment Unit (ARCU) at icipe, Nairobi, Kenya. Colonies were rejuvenated twice a year with field collected larvae.

5.1.2. *Surrogate stems*

In a preliminary trial, larvae-infested plants kept in an incubator deteriorated after only 5-7 days. Thus, a method using surrogate stems filled with artificial diet was used (Plate 5.1). These surrogate stems consisted of a 30cm piece of PVC pipe with a diameter of 5cm. Each piece was cut into equal halves to allow opening of the stem for observation of the larvae. The halves were held together with masking tape. One end of the pipe was covered with parafilm® and reinforced with masking tape. The pipe was wrapped in aluminium foil fastened with a rubber band leaving one end uncovered. The pipes were then filled with artificial diet developed by Onyango and Ochieng-Odero (1994). After the diet had solidified, part of the masking tape and aluminium foil were removed leaving only one quarter of the pipe covered.

![Plate 5.1. PVC surrogate stem for rearing stemborer larvae on artificial diet](image)

5.1.3. *Protocol for maize plant and surrogate stem infestation*

Maize and surrogate stems were infested with 2nd instar larvae using a small camel hair brush. The treatments involved 12 larvae of the same species for the single-species treatments (Bf, Cp, and Sc), six larvae of each species for the Cp+Bf, Cp+Sc, Bf+Sc pairings, and four larvae of each species for the three-species treatment Cp+Bf+Sc. A
density of 12 larvae per surrogate stem is representative of that found on maize in the field at the beginning of the infestation (Le Ru, unpublished data). The infested plants were covered with a netted metal frame tied with rubber bands at the base of the pots to prevent larvae from escaping. For the surrogate stems, the free ends were plugged with cotton wool after infestation with larvae. For both maize and surrogate stems, each treatment was replicated twenty times. The surrogate stems were placed in pots to keep them upright. For experiments under fluctuating temperatures, the treatments were set up in a greenhouse during the hot season from December to March (min. temp., 13°C, max. temp., 27°C, mean of 20°C) corresponding to the growing season of maize in most parts of Kenya. The temperature was recorded with a HOBO® Temp/RH data logger (Onset). For experiments under constant temperature, surrogate stems were set up in incubators at different constant temperatures of 15°, 20°, 25°, and 30°C, air humidity of 70±10% and LD 12:12. After 30 days, all maize stems were dissected and surrogate stems opened to record the number and the mass of live larvae of each species.

The three following experiments were conducted:

5.1.4. Experiment 1. The influence of maize and surrogate stems on the development of stemborer larvae

This experiment was conducted with potted plants and surrogate stems. Both substrates involved single-species infestation treatments (Bf, Sc and Cp). The experiments were undertaken under fluctuating temperatures in a greenhouse (Plate 5.2).
Plate 5.2. Maize plants and artificial stems infested with larvae of stemborer species in the greenhouse

5.1.5. Experiment 2. Influence of larval density on intra-specific interactions

This experiment was conducted to investigate intraspecific interactions at two different densities. Surrogate stems kept in an incubator at 25°C, the optimum temperature for all three species (Khadioli et al., 2014a; 2014b), were used. For each species, surrogate stems were infested with either six (6L) or twelve (12L) 2nd instar larvae.

5.1.6. Experiment 3. Influence of different constant temperatures on intra- and interspecific interactions

This experiment was conducted in incubators at four constant temperatures of 15, 20, 25, and 30°C. Surrogate stems were infested with larvae of one, two or three species.
5.2. Data analysis

Survival rates (i.e., the number of larvae alive after 30 days) and relative growth rates (RGR) were used as the response variables. The RGR for each species was calculated as follows derived from the equation of Ojeda-Avila et al. (2003): \[ \text{RGR} = \frac{\text{Total mass of surviving larvae-initial mass of larvae}}{30 \text{ days}}. \] RGR for communities was the sum of the RGR of each species in that community. Survival rates for each treatment were analysed using the generalized linear model with binomial error structure. Odd Ratios with a 95% confidence interval (O.R. [95%CI]) were calculated for each treatment from the GLM results obtained. RGR was analysed by analysis of variance (ANOVA). Means were separated with the Student-Newman-Keuls (SNK) test. The RGR data were first tested for normality of their distribution by a Kolmogorov-Smirnov test and for homoscedasticity by the Bartlett’s test. All analyses were carried out in R (R Development Team, 2014).

5.3. Results

5.3.1. Experiment 1. Influence of maize and surrogate stems on the development of stem borer larvae

For each species, survival rates were significantly higher on surrogate stems than maize plants (Figure 5.1a). RGRs were significantly higher on surrogate stems than on maize plants for *C. partellus* and *S calamistis* but not for *B. fusca* (Figure 5.1b).
Figure 5.1. Survival (a) and relative growth rates (b) of Chilo partellus (Cp), Busseola fusca (Bf) and Sesamia calamistis (Sc) larvae on maize and surrogate stems under fluctuating temperatures. Means (± SE) with different letters are significantly different at 5% level according to the GLM for survival and the Student-Newman-Keuls test for relative growth rates

5.3.2. Experiment 2. Influence of larval density on intra-specific interactions between stemborer larvae

The survival rates were significantly lower for 12L than for 6L for B. fusca [O.R.=1.8 (1.06-3.21), p=0.03], C. partellus [O.R.=1.9 (1.1-3.47), p=0.02] and S. calamistis [O.R.=2.0 (1.1-3.9), p=0.03] (Figure 5.2a). RGRs were significantly higher for 12L than for 6L for C. partellus (F=4.9, p=0.03) and S. calamistis (F=6.9, p=0.01), whereas for B. fusca (F=19.3, p<0.001), it was higher for 6L than for 12L (Figure 5.2b).

Figure 5.2. Survival (a) and relative growth rates (b) of Chilo partellus (Cp), Busseola fusca (Bf) and Sesamia calamistis (Sc) at densities of 6 (6L) and 12 (12L) larvae per stem at 25°C. Means (± SE) with different letters are significantly different at 5% level according to the GLM for survival and the Student-Newman-Keuls test for relative growth rates
5.3.3. Experiment 3. Influence of different constant temperatures on intra- and interspecific interactions.

5.3.3.1 The effect of temperature on survival and RGR of B. fusca, C. partellus and S. calamistis in single-species treatments

For each species, larval survival in the single-species treatments varied significantly between temperatures (Figure 5.3a). For B. fusca, it was highest at 20°C and lowest at 25°C. For C. partellus, it was highest at 20°C and similar among the other temperatures, while for S. calamistis it was higher at 15°C and 20°C than at 25°C and 30°C (Table 5.1). RGR of each species was lowest at 15°C (Figure 5.4a). For S. calamistis, it was similar at 20°C and 30°C and highest at 25°C, while for B. fusca, it was highest at 30°C. For C. partellus, the highest RGR was recorded at 20°C, whereafter it decreased with increasing temperature (Figure 5.4a, Table 5.2).

5.3.3.2. Comparison of survival and RGR of C. partellus, B. fusca and S. calamistis in multi-species communities under different constant temperatures

Survival was higher for C. partellus than its companion species at all temperatures (Figure 5.3b, Table 5.1). In pairings with B. fusca and S. calamistis, survival was similar between the two species regardless of the temperature.

In pairings with C. partellus, the crambid had higher RGRs than B. fusca and S. calamistis in two thirds of the treatments. In pairings involving both noctuids, RGRs did not vary significantly between the two species regardless of the temperature, except for the 3-species pairing at 25°C where S. calamistis had a higher RGR than B. fusca (Figure 5.4b, Table 5.2).
Figure 5.3. Comparison of survival of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae between (a) different constant temperatures in single-species communities, and between (b) borer species in multi-species communities at different constant temperatures.
Figure 5.4. Comparison of the relative growth rates (RGR) of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae between (a) different constant temperatures in single-species communities, and between (b) borer species in multi-species communities at different constant temperatures. Means (± SE) with different letters are significantly different at 5% level according to the Student-Newman-Keuls test.
5.3.3.3. Comparison of survival and relative growth rates between single- and multi-species communities of *B. fusca, C. partellus and S. calamistis* at different constant temperatures

Generally, survival and RGR of single species communities were higher than those of multi-species communities. Between 20-30°C, survival of mono-species of *B. fusca*, and *C. partellus* tended to be higher than total survival of the corresponding multi-species communities, while for *S. calamistis*, it was higher than that of multi-species communities at 15° and 20°C, and to a lesser extent at 25° and 30°C (Figure 5.5a, Table 5.3).

Likewise between 20° and 30°C, RGRs of single-species communities of *C. partellus*, *B. fusca*, and to a lesser extent of *S. calamistis* tended to be higher than total RGRs of the corresponding multi-species communities (Figure 5.5b, Table 5.4).

![Figure 5.5](image_url)

**Figure 5.5.** Comparative survival and RGR between single-species and multi-species communities under different constant temperatures. *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc). Statistical comparisons were only made between single- and the corresponding multi-species pairings (see Tables 5.3 and 5.4).
Table 5.1. Results of GLM analysis comparing larval survival between different constant temperatures in single-species communities and between borer species in multi-species communities at different constant temperatures. *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc).

### Single-species

<table>
<thead>
<tr>
<th>Temperature</th>
<th><strong>Chilo partellus</strong></th>
<th></th>
<th><strong>Busseola fusca</strong></th>
<th></th>
<th><strong>Sesamia calamistis</strong></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>O.R. (95% CI)</td>
<td>P-value</td>
<td>O.R. (95% CI)</td>
<td>P-value</td>
<td>O.R. (95% CI)</td>
<td>P-value</td>
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<td></td>
<td>1</td>
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<td>1</td>
<td></td>
</tr>
<tr>
<td>20°C</td>
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<td>2.7 (1.5-5.0)</td>
<td>0.002</td>
<td>0.8 (0.4-1.6)</td>
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<td>0.8 (0.5-1.4)</td>
<td>0.49</td>
<td>0.3 (0.1-0.5)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>30°C</td>
<td>1 (0.7-1.4)</td>
<td>0.93</td>
<td>1.6 (0.9-2.8)</td>
<td>0.1</td>
<td>0.1 (0.1-0.3)</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

### Multi-species communities

| Temperature | **Cp+Bf** |  | **Cp+Sc** |  | **Bf+Sc** |  | **Cp+Bf+Sc (Cp vs Bf)** |  | **Cp+Bf+Sc (Bf vs Sc)** |  |
|-------------|-----------|----------------|-----------|----------------|-----------|------------------------|----------------|------------------------|-----------|
|             | O.R. (95% CI) | P-value | O.R. (95% CI) | P-value | O.R. (95% CI) | P-value | O.R. (95% CI) | P-value | O.R. (95% CI) | P-value |
| 15°C        | 3.2 (1.6-6.6)   | 0.002   | 0.5 (0.2-0.8)   | 0.02   | 0.5 (0.3-0.9)   | 0.03   | 1.7 (0.9-3.6)       | 0.13   | 0.7 (0.3-1.3)       | 0.3      |
| 20°C        | 16.4 (7.7-37.2)  | <0.001  | 0.2 (0.1-0.4)   | <0.001 | 0.9 (0.4-1.9)   | 0.71   | 10.1 (4.2-26)       | <0.001 | 0.9 (0.4-2)         | 0.78     |
| 25°C        | 26.5 (11.8-65.9) | <0.001  | 0.2 (0.1-0.5)   | <0.001 | 0.6 (0.3-1.3)   | 0.21   | 14.9 (6-43.1)       | <0.001 | 2.8 (1.1-8.5)       | 0.05     |
| 30°C        | 7.7 (4.1-14.8)   | <0.001  | 0.1 (0.1-0.2)   | <0.001 | 1.4 (0.7-2.9)   | 0.35   | 13 (5.8-31.7)       | <0.001 | 1.2 (0.5-3.2)       | 0.66     |

O.R.=Odd Ratios
Table 5.2. Results of ANOVA: Comparison of relative growth rates between (a) different constant temperatures in single-species communities and between (b) borer species in multi-species communities at different constant temperatures. *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc).

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<tr>
<td>Bf</td>
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</tr>
<tr>
<td>Sc</td>
<td>15.0</td>
<td>&lt;0.001</td>
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<th>Cp+Sc</th>
<th>Bf+Sc</th>
<th>Cp+Bf+Sc</th>
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<td>P-value</td>
<td>F</td>
<td>P-value</td>
</tr>
<tr>
<td>15°C</td>
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<td>30°C</td>
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Table 5.3. Results of GLM: Comparison of percent survival between single-species and multi-species communities under different constant temperatures. *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc).

<table>
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<th>O.R. (95% CI)</th>
<th>P-value</th>
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<th>P-value</th>
<th>O.R. (95% CI)</th>
<th>P-value</th>
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<tr>
<td>Cp vs Cp+Bf</td>
<td>1.4 (1.0-2.1)</td>
<td>0.08</td>
<td></td>
<td>5.4 (3.6-8.2)</td>
<td>&lt;0.001</td>
<td>3.5 (2.4-5.2)</td>
<td>&lt;0.001</td>
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<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp vs Cp+Sc</td>
<td>0.7 (0.5-1.1)</td>
<td>0.17</td>
<td></td>
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<td>0.3 (0.2-0.5)</td>
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<tr>
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<td>&lt;0.001</td>
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<td>6.1 (3.9-9.6)</td>
<td>&lt;0.001</td>
<td>2.4 (1.6-3.5)</td>
<td>&lt;0.001</td>
<td>4.5 (2.9-7.3)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bf vs Bf+Sc</td>
<td>0.8 (0.4-1.3)</td>
<td>0.37</td>
<td></td>
<td>0.3 (0.2-0.6)</td>
<td>&lt;0.001</td>
<td>0.6 (0.4-1.0)</td>
<td>0.06</td>
<td>0.2 (0.1-0.3)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bf vs Cp+Bf+Sc</td>
<td>2.2 (1.3-3.7)</td>
<td>0.007</td>
<td></td>
<td>6.2 (3.8-10.2)</td>
<td>&lt;0.001</td>
<td>3.9 (2.7-5.7)</td>
<td>&lt;0.001</td>
<td>7.0 (4.4-11.3)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sc vs Bf+Sc</td>
<td>2.2 (1.1-4.1)</td>
<td>0.02</td>
<td></td>
<td>1.6 (0.8-3.2)</td>
<td>0.17</td>
<td>0.8 (0.5-1.4)</td>
<td>0.4</td>
<td>0.8 (0.4-1.4)</td>
<td>0.4</td>
</tr>
<tr>
<td>Sc vs Cp+Sc</td>
<td>2.7 (1.5-5.3)</td>
<td>0.003</td>
<td></td>
<td>2.4 (1.4-4.2)</td>
<td>0.002</td>
<td>1.1 (0.7-1.7)</td>
<td>0.71</td>
<td>0.6 (0.4-1.0)</td>
<td>0.05</td>
</tr>
<tr>
<td>Sc vs Cp+Bf+Sc</td>
<td>3.6 (1.9-6.9)</td>
<td>&lt;0.001</td>
<td></td>
<td>3.0 (1.7-5.3)</td>
<td>&lt;0.001</td>
<td>2.0 (1.3-3.2)</td>
<td>0.005</td>
<td>1.0 (0.6-1.6)</td>
<td>0.9</td>
</tr>
</tbody>
</table>

O.R.=Odd Ratios
Table 5.4. Results of ANOVA: Comparison of the relative growth rates between single-species and multi-species communities under different constant temperatures. *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc).

<table>
<thead>
<tr>
<th>Treatments comparisons</th>
<th>15°C F</th>
<th>P-value</th>
<th>20°C F</th>
<th>P-value</th>
<th>25°C F</th>
<th>P-value</th>
<th>30°C F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cp vs Cp+Bf</td>
<td>3.9</td>
<td>0.05</td>
<td>35.2</td>
<td>&lt;0.001</td>
<td>10.8</td>
<td>0.002</td>
<td>0.6</td>
<td>0.43</td>
</tr>
<tr>
<td>Cp vs Cp+Sc</td>
<td>2.7</td>
<td>0.11</td>
<td>8.0</td>
<td>0.007</td>
<td>3.9</td>
<td>0.05</td>
<td>0.8</td>
<td>0.37</td>
</tr>
<tr>
<td>Cp vs Cp+Bf+Sc</td>
<td>0.8</td>
<td>0.39</td>
<td>35.3</td>
<td>&lt;0.001</td>
<td>14.9</td>
<td>&lt;0.001</td>
<td>20.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bf vs Cp+Bf</td>
<td>0.1</td>
<td>0.74</td>
<td>30.1</td>
<td>&lt;0.001</td>
<td>7.3</td>
<td>0.01</td>
<td>39.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bf vs Bf+Sc</td>
<td>0.1</td>
<td>0.81</td>
<td>11.1</td>
<td>0.001</td>
<td>0.2</td>
<td>0.69</td>
<td>29.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bf vs Cp+Bf+Sc</td>
<td>0.8</td>
<td>0.39</td>
<td>30.6</td>
<td>&lt;0.001</td>
<td>10.9</td>
<td>0.002</td>
<td>59.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sc vs Bf+Sc</td>
<td>0.0</td>
<td>0.94</td>
<td>1.0</td>
<td>0.31</td>
<td>4.3</td>
<td>0.04</td>
<td>0.1</td>
<td>0.80</td>
</tr>
<tr>
<td>Sc vs Cp+Sc</td>
<td>2.3</td>
<td>0.14</td>
<td>7.9</td>
<td>0.007</td>
<td>11.5</td>
<td>0.001</td>
<td>0.4</td>
<td>0.54</td>
</tr>
<tr>
<td>Sc vs Cp+Bf+Sc</td>
<td>3.6</td>
<td>0.06</td>
<td>0.3</td>
<td>0.60</td>
<td>19.6</td>
<td>&lt;0.001</td>
<td>6.9</td>
<td>0.01</td>
</tr>
</tbody>
</table>
5.4. Discussion

As shown by higher survival and RGRs, surrogate stems were a good alternative to maize stems or whole plants. Similarly, Shanower et al. (1993) reported higher survival of *S. calamistis* reared on artificial diet than on maize stem cuttings. In general, insects tend to perform better on artificial than natural diets since diets possess optimum levels of nutrients and vitamins (Schoonhoven et al., 2005). However, in nature, early instars of *C. partellus* and *B. fusca* migrate by `ballooning off` of the plant (Kaufmann, 1983; Berger, 1989), which is not possible when surrogate stems are used. Thus, whether the higher survival on surrogate stems were due to lower mortality or reduced migration could not be determined with the present experimental set-up. Still, surrogate stems are more stable than maize stems or potted plants because they don´t deteriorate that easily and are thus ideal for such studies.

For each species, survival was reduced in the high-density treatment. Also, when reared together with one or several species, survival and RGR of each species tended to decrease compared to the single-species treatments. Thus, the intra- and interspecific interactions between the stemborer species tested in this study indicated competitive resource utilisation. An inverse effect of density on species fitness and their interactions is an established ecological fact (Applebaum & Heifetz, 1999; Agnew et al., 2002; Pascual & Callejas, 2004) and a typical characteristic of spatially restricted insects such as Lepidoptera living inside a stem and exploiting the same resource (Stiling & Strong, 1983; Gurevitch et al., 1992; Denno et al., 1995; Kaplan & Denno, 2007). Cereal stem borers in East Africa constitute an extreme case of interactions for resource utilisation. Their larvae have developed a close association with their host plants (Zilli et al., 2005) as they co-exist with a “restricted” resource, available over a short period of time (2-3 months) with the most nutritious stage between 2-8 weeks and
with unreliable availability of suitable hosts because drought spells commonly occur in the region. All these characteritics make cereal stem borers a good model for testing the competition theory (Denno et al., 1995; Kaplan & Denno, 2007; Stokes & Stiling, 2015).

Interspecific competition was more pronounced than intraspecific competition, especially when *C. partellus* was involved, with the outcomes skewed asymmetrically towards the crambid. This indicates a higher fitness of the crambid compared to the two noctuids. Interspecific competition outcomes in phytophagous insects are mostly asymmetric (Denno et al., 1995; Inbar et al., 1995; Kaplan & Denno, 2007).

The competition theory states that strong intraspecific interactions in a species would limit it to be interspecifically competitive (Connell, 1983). This could not be verified by our studies, as *S. calamistis* competed better with *C. partellus* than with *B. fusca*, although it had the strongest intraspecific competition as indicated by the lowest survival rate. The superior competitive abilities of *C. partellus* over other species have been reported from other field and laboratory studies. In South Africa, Kfir (1997) showed that *C. partellus* was superior to *B. fusca* in colonizing ratoon sorghum and population build-up occurred faster. Ofomata et al. (2000), comparing life traits using five grasses showed that the invasive *C. partellus* laid more viable eggs, that the larvae consumed more food and had a higher survival and shorter developmental rate than the native *C. orichalcociliellus*. Various studies have described the superior competitive abilities of invasive over native species. For instance, Sakai et al. (2001) identified superior competitive abilities of several invasive species as a key factor for their successful establishment. Holway (1999) demonstrated that proficiency in both interference and exploitative competition confered a superior ability on the invasive Argentine ant, *Linepithema humile* Mayr (Hymenoptera: Formicidae) over native species.
The competition-relatedness hypothesis states that closely related species will compete stronger than distantly related species (Denno et al., 1995; Violle et al., 2011). In contrast, in the present study competition was stronger between distant-related species (noctuids and crambid) than between the two noctuids belonging to the same sub-tribe. Similarly, Kaplan and Denno (2007), applying a meta-analysis concluded that distant-relatedness rather than phylogenetic similarity determined the strength of competition in insects. The present study thus confirms others that dispute the competition-relatedness hypothesis (Best et al., 2013; Venail et al., 2014; Alexandrou et al., 2015).

The present results demonstrated that temperature is an important factor influencing the interactions between the noctuids and the crambid. Thereby, the competitive abilities of each of the species depended on its temperature tolerance limits for development. While high temperatures favoured C. partellus, the two noctuids had highest survival rates under lower temperatures. Likewise, as shown by Khadioli et al. (2014a; 2014b) the development rate of the three species increased with temperature but this was more pronounced for C. partellus and S. calamistis than for B. fusca. Also, the similar development of both noctuids in their utilisation of the same resource could be explained by their temperature ranges for development of 8.2-31.2°C for B. fusca and 9.3-35.8°C for S. calamistis with a common optimum between 25°C and 28°C. In the field, while C. partellus and B. fusca dominate within a limited thermal tolerance at the high and low temperature extremes, respectively, S. calamistis has a wider thermal tolerance by co-occurring with the two species along these temperature gradients (Guofa et al., 2001; Ong’amo et al., 2006a; 2006b).
The role of temperature in influencing varied competitive abilities of interacting species has been reported from three *Drosophila* species (Davis et al., 1998), between small and large seed beetles *Stator limbatus* (Moya-Laraño et al., 2007), the invasive fruit fly *Bactrocera invadens* over the indigenous fruit fly, *Ceratitis cosyra* (Diptera: Tephritidae) (Rwomushana et al., 2009) and two invasive leaf miner flies *Liriomyza sativae* and *L. trifolii* (Diptera: Agromyzidae) (Wang et al., 2014). In these studies, the competitive abilities of one of the competing species was enhanced by either low or high temperatures. Similar trends of temperature influence have been reported from competition studies involving plants (Breeuwer et al., 2008), fish (Taniguchi et al., 1998; Taniguchi & Nakano, 2000; Carmona-Catot et al., 2013) and bacterivorous ciliates (Jiang & Morin, 2004).

Several studies have been conducted to assess the impact of climate change on various life history parameters of insects. However, few studies exist on the effects of temperature increase on the interactions of species using the same resources (Laws & Belovsky, 2010). Results of the present study suggest that a future increase in temperature would confer a greater competitive ability on *C. partellus* than the two noctuid species. Similarly, Khadioli et al. (2014a), using temperature-dependent models predicted that *C. partellus* will expand into the highlands where *B. fusca* presently dominates. With its better competitive abilities, *C. partellus* is likely to outcompete the two noctuids in the highlands and become the dominant species. In fact, *C. partellus* has already been recorded from highlands in Kenya and cooler regions of South Africa, and in some cases it has become the dominant species (Kfir, 1997, Guofa et al., 2001; Kfir et al., 2002; Rebe et al., 2004; Ong’amo et al., 2006a; 2006b).
This study highlights the knowledge gap in our understanding of temperature effects on biodiversity, especially interactions between species utilizing the same resources. Besides temperature, rainfall is another abiotic factor which could influence interactions within stemborer communities (Van Rensburg et al., 1987, Matama-Kauma et al., 2001, Ndemah et al., 2003, Gounou & Schulthess, 2004, Jiang et al., 2006). In addition, biotic factors such as density dependence (Agnew et al., 2002), level of multi-species infestations in field and oviposition-site selection of the female adults (Craig et al., 2000; De Moraes et al., 2001; Shiojiri et al., 2002) could also influence stemborer species interactions. Further studies which elucidate the influences of these factors will enable a better understanding of the impact of stemborer interactions on cereal crop damage, especially under future climate scenarios and will contribute to the development of possible mitigation and adaption strategies.

5.5. References


CHAPTER SIX

DENSITY- AND DURATION-DEPENDENT COMPETITIVE INTERACTIONS DURING THE UTILISATION OF RESOURCES BY A COMMUNITY OF LEPIDOPTERAN STEMBORER SPECIES

Abstract
Intra- and interspecific interactions between species sharing the same resources is characterised by competition or facilitation and can be influenced by factors such as larval numbers and duration of the interactions. Competitive interactions characterise communities that use the same resource, e.g. the noctuid stemborers Busseola fusca and Sesamia calamistis and the crambid, Chilo partellus, which attack maize crops in sub-Saharan Africa. The effect of larval density and duration of competition was studied in these three species using artificial surrogate stems. Experiments were conducted in an incubator maintained at the optimum temperature (25°C) for stemborer development. The effect of larval density on competition was studied at low (6) and high (12) levels of larval infestation, while the effect of duration of competition was evaluated at 7, 14, 21 or 28 days after infestation. The two experiments involved single- and multi-species infestation treatments. The larval numbers and mass in each artificial stem were recorded in each experiment. The survival rates of the three species in single-species infestations were significantly lower at the high infestation level. However, the relative growth rates of C. partellus and S. calamistis at the low infestation level were significantly lower than at the high infestation level while the opposite was observed for B. fusca. The survival rates of the noctuids, although higher at low infestation levels, were significantly lower than that of C. partellus at both infestation levels. The survival rate of single and multi-species communities generally decreased as the duration of the competition period increased. While C. partellus survived better than the two noctuids, the survival rate between B. fusca and S. calamistis did not differ significantly after any of the different competition periods. The RGR of C. partellus was significantly higher than that of B. fusca and S. calamistis at all durations. However, the RGR between B. fusca and S. calamistis was not significantly different in any of the different competition periods. The survival and RGR of single-species communities differed significantly from that of multi-species communities at the different times after infestation.
6.0. Introduction

Resource utilisation among species is mostly influenced by the availability of resources (Manly et al., 1993) but also by other factors such as genetic variation (Futuyma & Peterson, 1985) and density of the species involved (Middendorf III, 1984). The common use of limited resources by several species predisposes species to interact competitively or facilitatively (Denno et al., 1995; Stachowicz, 2001; Bruno et al., 2003) and this can be influenced by variations in the density of the species involved (Thompson, 1988). The outcome of competitive interactions results in niche partitioning for co-existence or the dominance of one of the competing species (Schoener, 1974).

The effect of density on the life traits of organisms is well established. Density affects metabolic rates of organisms (DeLong et al., 2014), their survival, developmental time and size of adults. For example, higher larval density resulted in lower survival rate, prolonged developmental time and reduced adult sizes in Anopheles gambiae Giles, Aedes albopictus Skuse and Aedes triseriatus Say (Diptera: Culicidae) (Teng & Apperson, 2000; Muriu et al., 2013). Density-dependence also affects the functional responses of species to their environment (Tardy et al., 2014). Species interactions while utilising the same resource are the mechanisms through which density-dependence is expressed. Generally, competitive interactions within a highly-dense population of species often result in reduced survival and fecundity rate, increased development time and reduced adult sizes (Agnew et al., 2002). This phenomenon has been described in several studies. Density-dependent competition reduces the survival (Van Hamburg, 1980; Van Hamburg & Hassel, 1984) and dispersal of early instar larvae of Chilo partellus (Swinhoe) (Lepidoptera: Crambidae) (Berger, 1992). Density-dependence has also been reported to reduce development time and the choice of oviposition sites of the mosquito species A. albopictus (Yoshioka et al., 2012). In
addition, competition among larvae of *A. aegyptii*, when this species occur at high densities, leads to increased pupation time and reduced size of emerged adults (Agnew et al., 2002). Similar results were reported for the monarch butterfly (*Danaus plexippus* Kluk) (Lepidoptera: Nymphalidae) (Flockhart et al., 2012) and *Sesamia nonagrioides* Lefebvre (Lepidoptera: Noctuidae) on artificial rearing media (Fantinou et al., 2008).

Variation of competitive interactions with time is an important factor which influences the structure of communities (Connell, 1983; Schoener, 1983; Miner et al., 2005; Fordyce, 2006) and the temporality of this variability can be immediate or longer (Fordyce, 2006). It can determine the period when competition is likely to be intense and when its effect is likely to be exerted (Hemphill, 1991; Kirkland, 1993; Tamado et al., 2002). For example, in an experiment between the stream insects, *Simulium virgatum* (Simuliidae) and *Hydropsyche oslari* (Hydropsychidae), competition reduced the density of *S. virgatum* and this was highly variable with time (five seasons; fall, winter, late winter, spring and summer) (Hemphill, 1991). Furthermore, competition between larvae of the dragonfly species *Plathemis lydia* Drury and *Libellula luctuosa* Burmeister (Odonata) was suggested to be more intense in spring than in fall (Wissinger, 1989). Also a stronger superior competitiveness of *A. albopictus* over *A. aegypti* in the wet season was responsible for a higher increase in *A. albopictus* over *A. aegypti* in the early wet season than late wet season (Leisnham & Juliano, 2009).

Lepidopteran stemborers such as the indigenous noctuids, *Busseola fusca* (Fuller) and *Sesamia calamistis* (Hampson) and the exotic crambid *C. partellus* attack cereals crops in East and southern Africa (Reddy, 1998; Kfir et al., 2002). In these regions, depending on altitude, they occur as communities of single or mixed species, infesting maize and sorghum plants (Tefera, 2004; Onga’mo et al., 2006a; Krüger et al., 2008). In Kenya,
the composition of these stemborer communities varies along an altitudinal gradient. *Busseola fusca* is the dominant species in the highlands characterised by comparatively low temperatures, while *C. partellus* dominates in the lowlands characterised by comparatively high temperatures. *Sesamia calamistis* is present in low numbers at all altitudes. However in the mid-altitudes, the three stemborer species occur as a mixed community, but with variation in species dominance with respect to locality and season (Guofa *et al.*, 2001; Ong’amo *et al.*, 2006a, 2006b). Ntiri *et al.* (2015 unpublished, Chapter 5) observed that intra- and interspecific competition within communities of the three stemborer species, occur when they utilise similar food resources. While *C. partellus* was always the dominant competitor in interspecific competition with the two noctuids, the effect of interaction between the two noctuids was not significant (Chapter 5). Also, temperature significantly influenced these interaction outcomes (Chapter 5). The effect of density on the survival and dispersal of early instar larvae of *C. partellus* have also been reported (Van Hamburg, 1980; Van Hamburg & Hassel, 1984; Berger, 1992).

Since other factors could also influence the outcomes of these interactions between *S. calamistis, C. partellus* and *B. fusca*, this study was conducted to determine the effect that larval density and duration of the competitive interactions could have on these species when they share the same resource.

### 6.1. Materials and methods

Two experiments were conducted. One of the experiments involved infesting surrogate stems with either a low (6) or high number (12) of larvae per stem, while the other experiment involved different durations of competitive interactions between larvae of these species.
6.1.1. *Insects*

Second instar larvae (L2) of *B. fusca* (Bf), *C. partellus* (Cp) and *S. calamistis* (Sc) were obtained from rearing colonies maintained at the Animal Rearing and Containment Unit (ARCU) at the African insect science for food and health (*icipe*) Nairobi, Kenya. Colonies were infused twice a year with larvae from the field.

6.1.2. *Surrogate stems*

Surrogate stems were used in all experiments in this study. Stems were constructed following the methods described in Ntiri et al. (2015 unpublished, Chapter 5). Surrogate stems were wrapped in aluminium foil fastened with a rubber band leaving one end open. The pipes were then filled with artificial diet developed by Onyango and Ochieng-Odero (1994). After the diet had solidified, part of the masking tape and aluminium foil were removed leaving only one quarter of the pipe covered.

6.1.3. *Protocol used for surrogate stem infestation at different larval densities*

The effect of different larval densities on larval survival was evaluated in an experiment in which larvae were inoculated onto surrogate stems at low (6) and high (12) number of larvae per stem. Surrogate stems were filled with diet and infested with 2\textsuperscript{nd} instar larvae using a small camel brush. The high infestation level treatments involved 12 larvae of the same species for the single-species treatment (Cp, Bf and Sc), six larvae of each species for the Cp+Bf, Cp+Sc, Bf+Sc pairings and four larvae of each species for the three-species (Cp+Bf+Sc) treatment. The low infestation levels were as follows: six larvae of the same species for the single-species treatment (Cp, Bf and Sc), three larvae of each species for the Cp+Bf, Cp+Sc, Bf+Sc pairings and two larvae of each species for the three-species (Cp+Bf+Sc) treatment.
The uncovered ends of the surrogate stems were plugged with cotton wool after infestation with larvae. The surrogate stems were then placed in plastic containers to keep them upright. Each treatment was replicated twenty times. The experiment was set up in incubators in which a constant temperature of 25°C, 70±10% RH and LD 12:12 were maintained. This temperature is the optimum for development of these three species (Khadioli et al., 2014a; 2014b). After 30 days, all surrogate stems were opened to record the number and the mass of live larvae of each species.

6.1.4. Differences in duration of competition period

This experiment was done to determine the effect of duration of the competition period on competitive outcomes between the species. Treatments involved infestation with 12 larvae of the same species for the single-species treatments (Cp, Bf and Sc), six larvae of each species for the Cp+Bf, Cp+Sc and Bf+Sc pairings, and four larvae of each species for the three-species (Cp+Bf+Sc) treatment. Each treatment had 20 replicates. The experiment was set up in incubators in which a constant temperature of 25°C, 70±10% RH and LD 12:12 was maintained. Larval numbers and mass in each artificial stem were recorded 7, 14, 21 or 28 days after infestation. This was done by opening the surrogate stem and carefully inspecting the contents for larvae.

6.2. Data analysis

Survival rate and Relative Growth Rate (RGR) were calculated as the response variables. The survival rate was calculated as the number of live larvae at the end of the experiment in the density experiment, while in the duration experiment it was calculated at weekly intervals and expressed as percentage of the initial number introduced into the artificial stem. Data were analysed using the generalized linear model with a
binomial error structure. Odd Ratios with a 95% confidence interval (O.R. (95% CI)) were calculated for each treatment from the GLM results obtained.

The RGR for each species was calculated as follows derived from the equation of Ojeda-Avila et al. (2003): 

\[ RGR = \frac{\text{Total mass of surviving larvae} - \text{Initial mass of surviving larvae}}{\text{number of days of experiment}}. \]

The RGR for communities was calculated as the sum of the RGR of each species in that community. The RGR was analysed by means of analysis of variance (ANOVA) and means separated with the Student-Newman-Keuls (SNK) test. The RGR data were first tested for normality by a Kolmogorov-Smirnov test and for homoscedasticity by means of the Bartlett test. All analyses were carried out in R (R Development Team, 2014).

6.3. Results

6.3.1. Intraspecific competition at different densities

The survival of *C. partellus*, *B. fusca* and *S. calamistis* at low infestation levels was significantly higher than at high infestation levels (Figure 6.1a, Table 6.1). While RGRs at the low infestation level were significantly lower than at high levels for *C. partellus* (F=4.9, p=0.03) and *S. calamistis* (F=6.9, p=0.01), the opposite was observed for *B. fusca* (F=19.3, p<0.001) (Figure 6.1b).
6.3.2. Interspecific competition at different densities

6.3.2.1. Two-species combinations

In two-species infestations of Cp+Bf and Cp+Sc, the survival rate of *C. partellus* was higher than that of *B. fusca* and *S. calamistis* at both the lower and higher infestation levels. In species combinations of Bf+Sc, the survival rate of species did not differ significantly at either low or high infestation levels (Figure 6.2a, Table 6.1). RGR of *C. partellus* was significantly higher than of *B. fusca* at the high infestation level, but not at the low infestation level. The RGR of the two species in the Bf+Sc and Cp+Sc treatments did not differ significantly at low and high infestation levels (Figure 6.2b, Table 6.2).

6.3.2.2. Three-species combination

In mixed species treatments with all three species (Cp+Bf+Sc), the survival rate of *C. partellus* was significantly higher than that of *B. fusca* at both the low and high infestation levels. The survival rate of *B. fusca* was significantly lower than that of *S. calamistis* at high infestation levels only (Figure 6.2a, Table 6.1). RGRs of the three

Figure 6.1. Survival (a) and relative growth rate (b) of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae at low (6) and high (12) single species infestations. Bars indicate S.E.
species in combination (Cp+Bf+Sc) differed significantly from each other at high infestation levels (Figure 6.2b, Table 6.2).

**Figure 6.2.** Survival (a) and relative growth rate (b) of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae in different species combinations at low (6) and high (12) infestation levels. Bars indicate S.E.
6.3.3. Comparison between single and multi-species communities

The survival rate of single-species infestations of *B. fusca* was significantly higher than in the mixed species infestations at both low and high infestation levels, except for the treatment where *B. fusca* was in combination with *S. calamistis* at the high infestation level. The survival rate of *C. partellus* as a single species was significantly higher than in the multi-species communities at both low and high infestation levels. In the single-species treatments, *S. calamistis* survived at significantly higher levels than the multi-species treatments at 12 larvae per stem (Figure 6.3a, Table 6.3). The RGR of *B. fusca* in single-species treatments was significantly higher than in all multi-species communities at low and high infestation levels, except in combination with *C. partellus* (Cp+Bf) at the high infestation level. RGR of *C. partellus* single-species was significantly higher than multi-species combinations at the high infestation level. RGR of *S. calamistis* in single species-treatments was not significantly different from the multi-species combinations at the low and high infestation levels (Figure 6.3b, Table 6.4).

![Figure 6.3](image_url)

*Figure 6.3.* Survival (a) and relative growth rate (b) of larvae in single- and multi-species communities of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) at low (6) and high (12) infestation levels. Bars indicate S.E.
6.3.4. Duration of competition period in single-species treatments

The survival of *C. partellus* 7 days after infestation was not significantly different from that at 14 days after infestation (Figure 6.4a, Table 6.5). Survival rate at 21 and 28 days after infestation were significantly lower than at 7 days. The survival rate of *B. fusca* was significantly lower at 28 days after infestation than at other days after infestation. The survival rate in *S. calamistis* was significantly lower at 21 and 28 days after infestation.

The RGR of *C. partellus* was significantly higher 14 and 21 days after infestation. In *B. fusca* and *S. calamistis* the RGR was significantly higher at 21 days than during the other periods (Figure 6.4b, Table 6.6).

![Figure 6.4. Survival (a) and relative growth rate (RGR) (b) of single-species infestations of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae on different days after infestation. Bars indicate S.E.](image-url)
6.3.5. Duration of competition period in multi-species community

The survival rate of *C. partellus* was significantly higher than that of *B. fusca* and *S. calamistis* throughout the experiment. The survival rate did not differ between *B. fusca* and *S. calamistis* at any time during the experiment. In the 3-species community, the survival rate of *B. fusca* was significantly lower than that of *C. partellus*, but was significantly lower than *S. calamistis* at 7 days after infestation. (Figure 6.5a, Table 6.5).

The RGR of *C. partellus* was significantly higher than that of *B. fusca* throughout the experiment, but was significantly higher than *S. calamistis* at 14 days after infestation. The RGR did not differ between *B. fusca* and *S. calamistis* at any time during the experiment. In the 3-species community, the RGR between species differed only at the 7 and 28 day periods with *C. partellus* and *B. fusca* having the highest and lowest growth rates respectively (Figure 6.5b, Table 6.6).
Figure 6.5. Survival (a) and relative growth rate (RGR) (b) of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae in multi-species communities on different days after infestation. Bars indicate S.E.
6.3.6 Comparison between single and multi-species communities

*Busseola fusca* larvae survived higher in single-species treatments and in the 2-species treatment with *S. calamistis* (Figure 6.6a, Table 6.7). The survival rate of *S. calamistis* in the single-species treatment was significantly higher than in other treatments and it had its highest survival in the combination with *B. fusca* (Figure 6.6a, Table 6.7). Survival rate of *C. partellus* in the single-species treatment was significantly higher than in multi-species communities, and it had the highest survival of any species in the multi-species communities.

The RGR of all three species was the highest when they occurred as single-species. The RGR of *C. partellus* larvae in the single-species community was significantly higher than in the multi-species communities throughout the experiment except when it co-occurred with *S. calamistis* in the 2-species treatment 7 and 21 days after infestation (Figure 6.6b, Table 6.8).
Figure 6.6. Survival (a) and relative growth rate (RGR) (b) of larvae in single- and multi-species communities of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) on different days after infestation.
**Table 6.1.** Results of GLM (binomial) analysis of the survival rate of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* larvae at low (6) and high (12) infestation levels in single-species and multi-species communities

<table>
<thead>
<tr>
<th>Treatments</th>
<th>O.R. (95%CI)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cp (6) &amp; Cp (12)</td>
<td>1.9 (1.1-3.5)</td>
<td>0.02</td>
</tr>
<tr>
<td>Bf (6) &amp; Bf (12)</td>
<td>1.8 (1.1-3.2)</td>
<td>0.03</td>
</tr>
<tr>
<td>Sc (6) &amp; Sc (12)</td>
<td>2.0 (1.1-3.9)</td>
<td>0.03</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Treatments</th>
<th>O.R. (95%CI)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cp+Bf</td>
<td>7.9 (2.9-24.7)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp+Sc</td>
<td>0.14 (0.05-0.35)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bf+Sc</td>
<td>1.18 (0.46-3)</td>
<td>0.73</td>
</tr>
<tr>
<td>Cp+Bf+Sc (Bf vs Cp)</td>
<td>9 (2.9-34.3)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp+Bf+Sc (Bf vs Sc)</td>
<td>1.1 (0.5-2.7)</td>
<td>0.82</td>
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</table>

<table>
<thead>
<tr>
<th>Treatments</th>
<th>O.R. (95% CI)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low infestation level</td>
<td>26.5 (11.8-65.9)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>High infestation level</td>
<td>0.2 (0.1-0.5)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp+Bf</td>
<td>0.6 (0.3-1.3)</td>
<td>0.21</td>
</tr>
<tr>
<td>Cp+Sc</td>
<td>14.9 (6-43.1)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bf+Sc</td>
<td>2.8 (1.1-8.5)</td>
<td>0.05</td>
</tr>
</tbody>
</table>

O.R.=Odd Ratios
Table 6.2. Results of the ANOVA on the relative growth rate of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae at low (6) and high (12) infestation levels in single-species and multi-species communities

<table>
<thead>
<tr>
<th>Treatments</th>
<th>F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cp (6) &amp; Cp (12)</td>
<td>4.9</td>
<td>0.03</td>
</tr>
<tr>
<td>Bf (6) &amp; Bf (12)</td>
<td>19.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sc (6) &amp; Sc (12)</td>
<td>6.9</td>
<td>0.01</td>
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</table>

<table>
<thead>
<tr>
<th>Treatment density</th>
<th>Cp+Bf</th>
<th>F</th>
<th>P-value</th>
<th>Cp+Sc</th>
<th>F</th>
<th>P-value</th>
<th>Bf+Sc</th>
<th>F</th>
<th>P-value</th>
<th>Cp+Bf+Sc</th>
<th>F</th>
<th>P-value</th>
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</thead>
<tbody>
<tr>
<td>Low larval density (6)</td>
<td>0.01</td>
<td>0.94</td>
<td>0.47</td>
<td>0.5</td>
<td>0.09</td>
<td>0.76</td>
<td>0.19</td>
<td>0.6</td>
<td>0.004</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High larval density (12)</td>
<td>32</td>
<td>&lt;0.001</td>
<td>0.1</td>
<td>0.74</td>
<td>0.01</td>
<td>0.94</td>
<td>6</td>
<td>0.004</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 6.3. Results of the GLM (binomial) analysis and comparison of survival rate between single- and multi-species communities of larvae of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) at low (6) and high (12) infestation levels.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Low larval numbers (6)</th>
<th></th>
<th>High larval numbers (12)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>O.R. (95%CI)</td>
<td>P-value</td>
<td>O.R. (95%CI)</td>
<td>P-value</td>
</tr>
<tr>
<td>Bf vs Cp+Bf</td>
<td>0.6 (0.3-1.1)</td>
<td>&lt;0.001</td>
<td>2.4 (1.6-3.5)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bf vs Bf+Sc</td>
<td>0.7 (0.4-1.4)</td>
<td>&lt;0.001</td>
<td>0.6 (0.4-1.0)</td>
<td>0.06</td>
</tr>
<tr>
<td>Bf vs Cp+Bf+Sc</td>
<td>0.6 (0.3-1.0)</td>
<td>&lt;0.001</td>
<td>3.9 (2.7-5.7)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp vs Cp+Bf</td>
<td>0.4 (0.2-0.7)</td>
<td>0.006</td>
<td>3.5 (2.4-5.2)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp vs Cp+Sc</td>
<td>0.4 (0.2-0.6)</td>
<td>0.001</td>
<td>0.3 (0.2-0.5)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp vs Cp+Bf+Sc</td>
<td>0.4 (0.2-0.7)</td>
<td>0.002</td>
<td>5.8 (3.9-8.6)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sc vs Bf+Sc</td>
<td>0.8 (0.4-1.6)</td>
<td>0.52</td>
<td>0.8 (0.5-1.4)</td>
<td>0.4</td>
</tr>
<tr>
<td>Sc vs Cp+Sc</td>
<td>1.0 (0.6-1.9)</td>
<td>0.91</td>
<td>1.1 (0.7-1.7)</td>
<td>0.71</td>
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<tr>
<td>Sc vs Cp+Bf+Sc</td>
<td>1.0 (0.5-1.7)</td>
<td>0.90</td>
<td>2.0 (1.3-3.2)</td>
<td>0.005</td>
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O.R.=Odd Ratios
Table 6.4. Results of the ANOVA on the relative growth rate between single- and multi-species communities of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae at low (6) and high (12) infestation levels

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Low larval numbers (6)</th>
<th>High larval numbers (12)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P-value</td>
</tr>
<tr>
<td>Bf vs Cp+Bf</td>
<td>36.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bf vs Bf+Sc</td>
<td>9.6</td>
<td>0.003</td>
</tr>
<tr>
<td>Bf vs Cp+Bf+Sc</td>
<td>32.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp vs Cp+Bf</td>
<td>1.3</td>
<td>0.26</td>
</tr>
<tr>
<td>Cp vs Cp+Sc</td>
<td>3.6</td>
<td>0.07</td>
</tr>
<tr>
<td>Cp vs Cp+Bf+Sc</td>
<td>0.1</td>
<td>0.75</td>
</tr>
<tr>
<td>Sc vs Bf+Sc</td>
<td>0.0</td>
<td>0.86</td>
</tr>
<tr>
<td>Sc vs Cp+Sc</td>
<td>2.3</td>
<td>0.14</td>
</tr>
<tr>
<td>Sc vs Cp+Bf+Sc</td>
<td>0.5</td>
<td>0.50</td>
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</table>
Table 6.5. Results of GLM (binomial) analysis on the survival rate of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae in single- and multi-species communities on different days after infestation (DAI)

<table>
<thead>
<tr>
<th>Duration (DAI)</th>
<th><em>Chilo partellus</em></th>
<th><em>Busseola fusca</em></th>
<th><em>Sesamia calamistis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>O.R. (95% CI)</td>
<td>P-value</td>
<td>O.R. (95% CI)</td>
</tr>
<tr>
<td>7</td>
<td>1</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>14</td>
<td>0.6 (0.4-1.0)</td>
<td>0.08</td>
<td>0.9 (0.5-1.5)</td>
</tr>
<tr>
<td>21</td>
<td>0.6 (0.3-1.0)</td>
<td>0.04</td>
<td>0.8 (0.5-1.4)</td>
</tr>
<tr>
<td>28</td>
<td>0.4 (0.3-0.7)</td>
<td>0.001</td>
<td>0.4 (0.3-0.7)</td>
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</table>

**Multi-species treatments**

<table>
<thead>
<tr>
<th>Duration (DAI)</th>
<th>Cp+Bf</th>
<th>Cp+Sc</th>
<th>Bf+Sc</th>
<th>Cp+Bf+Sc (Bf vs Cp)</th>
<th>Cp+Bf+Sc (Bf vs Sc)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>O.R. (95% CI)</td>
<td>P-value</td>
<td>O.R. (95% CI)</td>
<td>P-value</td>
<td>O.R. (95% CI)</td>
</tr>
<tr>
<td>7</td>
<td>3.7 (2.0-6.8)</td>
<td>&lt;0.001</td>
<td>0.2 (0.1-0.4)</td>
<td>&lt;0.001</td>
<td>0.7 (0.4-1.3)</td>
</tr>
<tr>
<td>14</td>
<td>7.6 (3.6-16.7)</td>
<td>&lt;0.001</td>
<td>0.5 (0.2-0.3)</td>
<td>0.03</td>
<td>1.0 (0.5-1.7)</td>
</tr>
<tr>
<td>21</td>
<td>14.5 (7.4-29.8)</td>
<td>&lt;0.001</td>
<td>0.3 (0.1-0.6)</td>
<td>0.001</td>
<td>1.0 (0.5-2.0)</td>
</tr>
<tr>
<td>28</td>
<td>26.5 (11.8-65.9)</td>
<td>&lt;0.001</td>
<td>0.2 (0.1-0.5)</td>
<td>&lt;0.001</td>
<td>0.6 (0.3-1.3)</td>
</tr>
</tbody>
</table>

O.R.=Odd Ratios
Table 6.6. Results of the ANOVA on the RGR of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae in single- and multi-species communities on different days after infestation (DAI)

<table>
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<td>Single species</td>
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<td>P-value</td>
</tr>
<tr>
<td><em>Chilo partellus</em></td>
<td>57.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><em>Busseola fusca</em></td>
<td>25.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><em>Sesamia calamistis</em></td>
<td>16.9</td>
<td>&lt;0.001</td>
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</table>

<table>
<thead>
<tr>
<th>Multi-species treatments</th>
<th>Cp+Bf</th>
<th>Cp+Sc</th>
<th>Bf+Sc</th>
<th>Cp+Bf+Sc</th>
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<tbody>
<tr>
<td>Duration (DAI)</td>
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<td>P-value</td>
<td>F</td>
<td>P-value</td>
</tr>
<tr>
<td>7</td>
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<td>&lt;0.001</td>
<td>0.6</td>
<td>0.43</td>
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<tr>
<td>14</td>
<td>26.6</td>
<td>&lt;0.001</td>
<td>14.0</td>
<td>&lt;0.001</td>
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<td>41.2</td>
<td>&lt;0.001</td>
<td>0.03</td>
<td>0.87</td>
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<td>31.6</td>
<td>&lt;0.001</td>
<td>0.1</td>
<td>0.74</td>
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</table>
Table 6.7. Results of GLM (binomial) analysis and comparison of the survival rate between single- and multi-species communities of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) on different days after infestation (DAI)

<table>
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<th>14DAI</th>
<th>P-value</th>
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<th>P-value</th>
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<th>P-value</th>
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<td></td>
<td>O.R. (95% Cl)</td>
<td></td>
<td>O.R. (95% Cl)</td>
<td></td>
<td>O.R. (95% Cl)</td>
<td></td>
</tr>
<tr>
<td>Bf vs Cp+Bf</td>
<td>0.3 (0.2-0.5)</td>
<td>&lt;0.001</td>
<td>0.3 (0.2-0.5)</td>
<td>&lt;0.001</td>
<td>0.3 (0.2-0.4)</td>
<td>&lt;0.001</td>
<td>2.4 (1.6-3.5)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bf vs Bf+Sc</td>
<td>0.7 (0.4-1.2)</td>
<td>0.25</td>
<td>0.7 (0.4-1.2)</td>
<td>0.25</td>
<td>0.7 (0.4-1.1)</td>
<td>0.16</td>
<td>0.6 (0.4-1.0)</td>
<td>0.06</td>
</tr>
<tr>
<td>Bf vs Cp+Bf+Sc</td>
<td>0.4 (0.2-0.6)</td>
<td>&lt;0.001</td>
<td>0.4 (0.3-0.7)</td>
<td>0.001</td>
<td>0.3 (0.2-0.4)</td>
<td>&lt;0.001</td>
<td>3.9 (2.7-5.7)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp vs Cp+Bf</td>
<td>0.2 (0.1-0.3)</td>
<td>&lt;0.001</td>
<td>0.3 (0.2-0.4)</td>
<td>&lt;0.001</td>
<td>0.3 (0.2-0.4)</td>
<td>&lt;0.001</td>
<td>3.5 (2.4-5.2)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp vs Cp+Sc</td>
<td>0.2 (0.1-0.4)</td>
<td>&lt;0.001</td>
<td>0.3 (0.2-0.5)</td>
<td>&lt;0.001</td>
<td>0.5 (0.3-0.7)</td>
<td>&lt;0.001</td>
<td>0.3 (0.2-0.5)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp vs Cp+Bf+Sc</td>
<td>0.2 (0.1-0.4)</td>
<td>&lt;0.001</td>
<td>0.4 (0.2-0.6)</td>
<td>&lt;0.001</td>
<td>0.3 (0.2-0.4)</td>
<td>&lt;0.001</td>
<td>5.8 (3.9-8.6)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sc vs Bf+Sc</td>
<td>2.0 (1.1-3.7)</td>
<td>0.02</td>
<td>1.8 (1.0-3.3)</td>
<td>0.05</td>
<td>1.2 (0.7-2.1)</td>
<td>0.47</td>
<td>0.8 (0.5-1.4)</td>
<td>0.4</td>
</tr>
<tr>
<td>Sc vs Cp+Sc</td>
<td>4.0 (2.2-7.4)</td>
<td>&lt;0.001</td>
<td>3.3 (1.9-5.8)</td>
<td>&lt;0.001</td>
<td>1.8 (1.1-2.8)</td>
<td>0.01</td>
<td>1.1 (0.7-1.7)</td>
<td>0.71</td>
</tr>
<tr>
<td>Sc vs Cp+Bf+Sc</td>
<td>4.0 (2.4-6.7)</td>
<td>&lt;0.001</td>
<td>3.1 (1.8-5.3)</td>
<td>&lt;0.001</td>
<td>3.0 (1.8-5.0)</td>
<td>&lt;0.001</td>
<td>2.0 (1.3-3.2)</td>
<td>0.005</td>
</tr>
</tbody>
</table>

O.R.=Odd Ratios
Table 6.8. Results of ANOVA on the RGR between single- and multi-species communities of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae on different days after infestation (DAI)

<table>
<thead>
<tr>
<th></th>
<th>7</th>
<th>14</th>
<th>21</th>
<th>28</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>F</strong></td>
<td>P-value</td>
<td>F</td>
<td>P-value</td>
<td>F</td>
</tr>
<tr>
<td>Bf vs Cp+Bf</td>
<td>0.14</td>
<td>0.71</td>
<td>10.7</td>
<td>0.002</td>
</tr>
<tr>
<td>Bf vs Bf+Sc</td>
<td>4.9</td>
<td>0.03</td>
<td>0.98</td>
<td>0.33</td>
</tr>
<tr>
<td>Bf vs Cp+Bf+Sc</td>
<td>2.19</td>
<td>0.15</td>
<td>15.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Cp vs Cp+Bf</td>
<td>13.8</td>
<td>&lt;0.001</td>
<td>5.5</td>
<td>0.02</td>
</tr>
<tr>
<td>Cp vs Cp+Sc</td>
<td>0.01</td>
<td>0.91</td>
<td>8.9</td>
<td>0.004</td>
</tr>
<tr>
<td>Cp vs Cp+Bf+Sc</td>
<td>4.80</td>
<td>0.03</td>
<td>18.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sc vs Bf+Sc</td>
<td>2.5</td>
<td>0.12</td>
<td>2.5</td>
<td>0.13</td>
</tr>
<tr>
<td>Sc vs Cp+Sc</td>
<td>0.4</td>
<td>0.53</td>
<td>0.26</td>
<td>0.61</td>
</tr>
<tr>
<td>Sc vs Cp+Bf+Sc</td>
<td>3.4</td>
<td>0.07</td>
<td>3.4</td>
<td>0.07</td>
</tr>
</tbody>
</table>
6.4 Discussion

Results showed that intra- and interspecific competition between the three stemborer species is density-dependent. Density-dependence reduces the survival (Van Hamburg, 1980; Van Hamburg & Hassel, 1984) and influences the dispersal (Berger, 1992) of early instar larvae of *C. partellus*. Generally, variations in species density can either have a positive or negative outcome in terms of the interactions between the species involved (Thompson, 1988). Density affects the basic processes which directly or indirectly affect interactions between species. DeLong *et al.* (2014) showed that there was an inverse relationship between metabolic rate of species in general, and population density. This relationship could be influenced by variation in foraging rates or lowering of activity, in response to population density. Density-dependent interactions was also shown to have a negative effect on immune responses of animals (Svensson *et al.*, 2001) and to influence resource utilisation patterns (Middendorf, 1984).

This study showed that the trend in the survival rate of the three stemborer species in intraspecific competition was similar in both low and high density populations. Competition was lowest in single-species populations of *C. partellus*, moderate in *B. fusca* and highest in *S. calamistis*. However, the intensity of intraspecific competition within the three stemborer species was density-dependent, as the fitness level, especially the survival rate was higher in treatments in which density was lower. Similar density-dependent outcomes have been reported from several studies. Gibbs *et al.* (2004) reported that intraspecific competition within the speckled wood butterfly *Pararge aegeria* L. (Nymphalidae) was affected by density. Higher density resulted in lower survival, longer developmental time and smaller-sized adults. Increased intraspecific competition was also observed in the mosquito species *A. albopictus* in which increased larval developmental time was observed when larval density was increased (Yoshioka *et al.*, 2012). Furthermore, similar effects of intraspecific competition in highly dense
populations of species have been reported on survival, developmental time, mass and adult size in the monarch butterfly *D. plexippus* (Flockhart *et al.*, 2012), cereal stemborer, *S. nonagrioides* (Fantinou *et al.*, 2008), the beet armyworm *Spodoptera exigua* Hübner (Noctuidae) (Underwood, 2010) and the emerald ash borer *Agrilus planipennis* Fairmaire (Buprestidae) (Duan *et al.*, 2013).

The observed trends of interspecific competition outcomes were similar in the lower and higher density treatments. *Chilo partellus* was the dominant competitor with its higher survival rate in all interspecific interactions with the noctuids, while interspecific interactions between the noctuids resulted in similar survival rates. This shows that *C. partellus* probably possesses an inherent competitive advantage over the two noctuids in their utilisation of similar resources. However, the intensity of competition was stronger in the high density than low density populations in all multi-species combinations between noctuids and crambid. The two noctuids had higher survival rates when they occurred in mixed populations with *C. partellus* at lower densities than higher densities. The effect of density-dependence on interspecific competition has been reported from several studies. Breden and Chippendale (1989) reported that varying densities influenced the interactions outcomes expressed in growth and developmental time between southwestern corn borer, *Diatraea grandiosella* Dyar (Crambidae), and the European cornborer *Ostrinia nubilalis* Hübner (Crambidae). Schneider *et al.* (2000) reported that the survival rate of the mosquito species *Anopheles arabiensis* Patton (Culicidae) was significantly reduced when interacting with *An. gambiae* Giles sensu stricto at varying densities. The effect of varying densities on interspecific competition outcomes have also been reported between two helminth species *Syncuaria squamata* and *Southwellina hispida* (Dezfuli *et al.*, 2002). Also, the survival rates of the two noctuids, *B. fusca* and *S. calamistis* were higher at the lower
density than higher density interactions. Smallegange and Tregenza (2008) reported that species relatedness in the bruchid beetle *Callosobruchus maculatus* F. (Coleoptera: Bruchidae) did not affect their survival rate in interactions with other bruchids. However density-dependence influenced the intensity of competition within the species.

This study showed that the intensity of intra- and interspecific competition between the three stemborer species was variable over time. The need for food for larval development increases with time as larvae moult into different instars and develop to adulthood. At early developmental stages, the small sizes of larvae enabled high survival and probably less contact between species in this study. However, as body size increased, the requirement and consumption of food become higher and increases the intensity of competition. This could be one underlying influence of duration of interactions on competition outcomes. Similar variability in duration of competitive interactions have been reported from studies involving the stream insects, *Simulium virgatum* and *Hydropsyche oslari* (Hemphill, 1991), dragonfly species *Plathemis lydia* and *Libellula luctuosa* (Odonata) (Wissinger, 1989), the mosquitio species *A. albopictus* and *A. aegypti* (Leisnham & Juliano, 2009). This trend was also reported in plants species. For instance, between the weed *Parthenium hysterophorus* L. with grain sorghum (Tamado *et al.*, 2002). Similarly, the yield of rice was reduced by 18% from its competition with *Echinochloa* weeds for 30 days (Gibson *et al.*, 2002). Furthermore, Kirkland (1993) reported that yield loss from competition between wild oats with spring wheat was higher when the duration of competition was longer (3 months vs 1 month).
This study showed that larval density and duration of the interaction between larvae of *B. fusca, C. partellus* and *S. calamistis* that utilise the same resource have a significant influence on the intra-and interspecific interaction outcomes between the species.

### 6.5. References


CHAPTER SEVEN

GENERAL DISCUSSION, CONCLUSION AND RECOMMENDATIONS

7.0. General discussion

The ecological importance of species interactions is defined by their overall influence on the conservation of biodiversity or species loss (Loreau & Hector, 2001; Memmott et al., 2006). Species interactions provide important ecosystem services such as pest control, pollination and seed dispersal, and they influence ecosystem functioning through the structuring of biological communities through regulation of abundance (van Veen et al., 2006; Duffy et al., 2007; Memmott et al., 2007).

This study showed that stemborer communities consisting of *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus*, when utilising the same resources, are characterised by competition and facilitative interactions, similar to interactions observed by Strong et al. (1984), Denno et al. (1995) and Bruno et al. (2003). The composition of stemborer communities in maize fields was shown to consist of both single and mixed species of *B. fusca*, *S. calamistis* and *C. partellus*, and the composition varied with the different agro-ecological zones and also along altitudinal gradients (Chapter three). The results also showed that the incidence of multi-species infestations were higher in agro-ecological zones and localities where the three stemborer species co-occur. The moist mid-altitude zone had the highest number of multi-species infestations. The implication of this is that the economic importance of stemborers could be higher in this zone than in other zones since the combined damage caused by multi-species communities on crops is higher than that caused by the individual species (Van den Berg et al., 1991a; Dangles et al., 2009).
This study also elucidated the spatio-temporal dynamics of infestations by *B. fusca*, *S. calamistis* and *C. partellus*, especially in the mid-altitudinal ranges where they occurred together. *Busseola fusca* was the dominant species across this zone. However, the structure also changed with different seasons, with infestation levels and larval density of *S. calamistis* being higher during the long rain season than short rain season. The spatial distributions of the three stemborer species followed a clustered distribution in all seasons. This indicated another phenomenon at play in mutli-species infestations, rather than competition between the three species.

The mixed composition of stemborers could be a result of the oviposition responses and choices by female moths of each species or movement of larvae from nearby infested plants. The mechanism of oviposition was demonstrated during the oviposition experiment involving the three species (Chapter four). Results showed that the three stemborer species did not avoid oviposition on plants with prior use or infestation. It has been hypothesised that female moths which avoid host plants with signs of prior use, do so to avoid their offspring from competing with other species (Jaenike, 1990; De Moraes *et al.*, 2001). Female moths of *B. fusca*, *S. calamistis* and *C. partellus* therefore do not compete intra- and interspecifically over their same utilisation of a host plant. They are rather induced to oviposit more on prior-infested plants than uninfested plants, especially in the case of *B. fusca*. This mechanism can be hypothesized as a facilitative interaction as supported by the preference-performance hypothesis or optimal oviposition theory, which states that a female will oviposit on host plants that provide the best conditions for survival of its offspring, thereby maximising her fitness (Jaenike, 1978; Thompson, 1988; Scheirs & De Bruyn, 2002).
The next level of interaction between *B. fusca*, *S. calamistis* and *C. partellus* was at the larval stage. This study showed that intra- and interspecific competitive interactions characterise the three species in their utilisation of the same resources (chapter five). While the magnitude of intraspecific competition varied with the three species, the outcomes from interspecific competition were established. Interspecific competition was stronger between the noctuids and the crambid than between the two noctuid species. *Chilo partellus* was superior to the other two species in utilising resources. This study and results from other studies (Kfir, 1997; Ofomata et al., 1999; 2000; Rebe et al., 2004) showed that *C. partellus* had advantageous characteristics which influenced their competitive abilities.

This study further showed that temperature is an important factor in the structuring of stemborer communities under field conditions. The variations in temperature influenced the establishment of different types of stemborer community structures in different localities across the agro-ecological zones. Temperature was also an important factor influencing the intra- and interspecific interactions between larvae of the three stemborer species when they used the same resource. It affected both survival and relative growth rates of the three species. For instance, high temperatures, favoured the fitness of *C. partellus*, while relatively low temperatures favoured the survival of *B. fusca* and *S. calamistis*. This study also showed that other factors such as larval density and duration of the interactions influenced the magnitude of competition within the three species.

This study showed that climate change would have an impact on the biology and the interactions between the three stemborer species. Temperature increase is likely to increase the rate of pest development and thus also increase the rate of resource
utilisation between the three species. This means that current damage levels inflicted by stemborers on cereal crops is likely to increase, especially as multi-species infestations of cereal plants may also increase. Reports of *C. partellus* advancing its range to higher altitudes where *B. fusca* currently dominates are on the rise (Kfir, 1997, Guofa *et al.*, 2001; Kfir *et al.*, 2002; Rebe *et al.*, 2004; Ong’amo *et al.*, 2006a; 2006b; Khadioli *et al.*, 2014). In the near future, areas where single-species of *B. fusca* dominate will see frequent multi-species infestations of both *B. fusca* and *C. partellus*. This is likely to increase the level of damage to cereal crops in these high altitude regions, given that *C. partellus* causes more injury than *B. fusca* on maize (Van den Berg, *et al.*, 1991b: Ong’amo *et al.*, 2006a).

7.1. Conclusion

This study showed the types of interactions that characterise the multi-species communities of cereal stemborers that infest maize crops. These interactions occur at two stages in the life cycle of the species. Firstly, female moths that oviposit on host plants and, secondly, competition interactions between larvae using the same restricted stem. Temperature had a significant influence on the structuring of stemborer communities and the interactions between larvae of the three species. In terms of damage, an increase in multi-species infestations, especially multi-infestations with *C. partellus*, would increase the damage levels of maize crops. Climate change will likely increase the extent of damage caused by infestations of these stemborer species.
7.2. Recommendations

It is recommended that:

1. further studies be conducted to determine the economic injury levels of single
   and mixed species stemborer communities, and the effect that interactions and
   changes in climate may have on these.

2. further studies using modelling techniques should capture the interactions
   between these species and their resource use, and how temperature affects
   these interactions, to enable prediction of changes that may result from climate
   change.

3. maize varieties which can withstand multiple-species infestations, especially
   under drought conditions and high temperatures, should be developed to mitigate
   future negative impacts from climate change.

7.3. References


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