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

**E.S. Ntiri**

**24375292**

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

Supervisor: Prof. J. van den Berg

Co-supervisors: Dr. B. Le Ru

Dr. P.-A. Calatayud

April 2015

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

**ERIC SIAW NTIRI**

Thesis submitted in fulfilment of the requirements for the award of the degree Doctor of Environmental Sciences at the North-West University (Potchefstroom Campus)

Supervisor: Prof. J. van den Berg

Co-supervisors: Dr. B. Le Ru

Dr. P.-A. Calatayud

**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

**Supervisors:**

**Prof. Johnnie Van den Berg**

School of Environmental Sciences and Development, North-West University, Private Bag X6001, Potchefstroom, 2520, South Africa

Signature: J van den Berg Date: 18/08/2015

**Dr Bruno Le Ru**

-*icipe* – African Insect Science for Food and Health, P.O. Box 30772-00100, Nairobi, Kenya -UMR Laboratoire Evolution, Génomes, Comportement et Ecologie, groupe IRD, Diversité, Ecologie et Evolution des Insectes Tropicaux, UPR 9034, 22 CNRS, 91198 – Gif-sur-Yvette, France and Université de Paris-Sud, 91405 - Orsay, France.

Signature Date: 29/04/2015

**Dr Paul-André Calatayud**

-*icipe* – African Insect Science for Food and Health, P.O. Box 30772-00100, Nairobi, Kenya

-UMR Laboratoire Evolution, Génomes, Comportement et Ecologie, groupe IRD, Diversité, Ecologie et Evolution des Insectes Tropicaux, UPR 9034, 22 CNRS, 91198 – Gif-sur-Yvette, France and Université de Paris-Sud, 91405 - Orsay, France.

Signature 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 ultilise 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

# TABLE OF CONTENTS

## CHAPTER SIX: DENSITY- AND DURATION-DEPENDENT COMPETITIVE INTERACTIONS DURING THE UTILISATION OF RESOURCES BY A COMMUNITY OF LEPIDOPTERAN STEMBORER SPECIES ........................................................................................135

# LIST OF TABLES

## LIST OF FIGURES

# LIST OF PLATES

# 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 stemborers 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'mo *et al.*, 2006a; 2006b; Krüger *et al.*, 2008). 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. 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

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. & Whittaker, J.B. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1-16.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119-125.

Buse, A., Dury, S.J., Woodburn, R.J.W., Perrins, C.M. & Good, J.E.G. (1999). Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology* 13:74-82.

Cairns, J.E., Hellin, J., Sonder, K., Araus, J.L., MacRobert, J.F., Thierfelder, C. & Prasanna, B. (2013). Adapting maize production to climate change in sub-Saharan Africa. *Food Security* 5:345-360.

Cammell, M.E. & Knight, J.D. (1992). Effects of climatic-change on the population dynamics of crop pests. *Advances in Ecological Research* 22:117-162.

Damos, P. & Savopoulou-Soultani, M. (2012). Temperature-driven models for insect development and vital thermal requirements. *Psyche* 2012:13 pp.

Dangles, O., Carpio, C., Barragan, A.R., Zeddam, J.-L. & Silvain, J.-F. (2008). Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. *Ecological Applications* 18:1795–1809.

Dangles, O., Mesías, V., Crespo-Perez, V. & Silvain, J.-F. (2009). Crop damage increases with pest species diversity: evidence from potato tuber moths in the tropical Andes. *Journal of Applied Ecology* 46:1115-1121.

Denno, R.F., McClure, M.S. & Ott, J.R. (1995). Interspecific interactions in phytophagous insects: competition re-examined and resurrected. *Annual Review of Entomology* 40:297-331.

Estay, S.A., Lima, M. & Labra, F.A. (2009). Predicting insect pest status under climate change scenarios: combining experimental data and population dynamics modelling. *Journal of Applied Entomology* 133:491-499.

Food and Agriculture Organisation (2005). Food security and agricultural development in sub-Saharan Africa. Building a case for more public support. *Policy Brief No. 1.* http://www.oecd.org/tad/agricultural-policies/36784159.pdf. Accessed on 10th February, 2014.

Food and Agriculture Organisation, (2013). The state of food insecurity in the world 2013. The multiple dimensions of food security. Rome, FAO.

Gordo, O. & Sanz, J.J. (2005). Phenology and climate change: a long-term study in a Mediterranean locality. *Oecologia* 146:484-495.

Guofa, Z., Overholt, W.A. & Mochiah, M.B. (2001). Changes in the distribution of lepidopteran maize stemborers in Kenya from the 1950s to 1990s. *International Journal of Tropical Insect Science* 21:395-402.

Hagen, S.B., Jepsen, J.U., Ims, R.A. & Yoccoz, N.G. (2007). Shifting altitudinal distribution of outbreak zones of winter moth *Operophtera brumata* in sub-arctic birch forest: a response to recent climate warming? *Ecography* 30:299-307.

Hawkins, C.P. & MacMahon, J.A. (1989). Guilds: the multiple meanings of a concept. *Annual Review of Entomology* 34:423-451.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12:184-195.

Hodkinson, I.D., Bird, J., Miles, J.E., Bale, J.S. & Lennon, J.J. (1999). Climatic signals in the life histories of insects: the distribution and abundance of heather psyllids (*Strophingia* spp.) in the UK. *Functional Ecology* 13:83-95.

Howe, R.W. (1967). Temperature effects on embryonic development in insects. *Annual Review of Entomology* 12:15-42.

Hudson, E.E. & Stiling, P. (1997). Exploitative competition strongly affects the herbivorous insect community on *Baccharis halimifolia*. *Oikos* 79:521-528.

Imura, O. (2003). Herbivorous arthropod community of an alien weed *Solanum carolinense* L. *Applied Entomology and Zoology* 38:293-300.

Intergovernmental Panel on Climate Change (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

International Institute of Tropical Agriculture (2009). Maize. http://www.iita.org/maize. Accessed on 10th April, 2015.

Kaplan, I. & Denno, R.F. (2007). Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory*. Ecology Letters* 10:977-994.

Kaplan, I. & Eubanks, M.D. (2005). Aphids alter the community-wide impact of fire ants. *Ecology* 86:1640-1649.

Kfir, R., Overholt, W.A., Khan, Z.R. & Polaszek, A. (2002). Biology and management of economically important Lepidopteran cereal stemborers in Africa. *Annual Review of Entomology* 47:701-731.

Krüger, W., Van den Berg, J. & Van Hamburg, H. (2008). The relative abundance of maize stemborers and their parasitoids at the Tshiombo irrigation scheme in Venda, South Africa. *South African Journal of Plant and Soil* 25:144-151.

Lewinsohn, T.M., Novotny, V. & Basset, Y. (2005). Insects on plants: diversity of herbivore assemblages revisited. *Annual Review of Ecology, Evolution and Systematics* 36:597-620.

Liss, W., Gut, L. & Westigard, P. (1986). Perspectives on arthropod community structure, organization, and development in agricultural crops. *Annual Review of Entomology* 31:455-478.

Maes, K.V.N. (1998). Lepidoptera: Introduction; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford, UK. pp 75-78.

Masters, G.J., Brown, V.K., Clarke, I.P., Whittaker, J.B. & Hollier, J.A. (1998). Direct and indirect effects of climate change on insect herbivores: Auchenorrhyncha (Homoptera). *Ecological Entomology* 23:45-52.

Ndemah, R., Schulthess, F., Korie, S., Borgemeister, C. & Cardwell, K.F. (2001). Distribution, relative importance and effect of lepidopterous borers on maize yields in the forest zone and mid-altitude of Cameroon. *Journal of Economic Entomology* 94:1434-1444.

Ofomata, V.C., Overholt, W.A., Van Huis, A., Egwuatu, R.I. & Ngi-Song, A.J. (1999). Niche overlap and interspecific association between *Chilo partellus* and *Chilo orichalcociliellus* on the Kenya coast. *Entomologia Experimentalis et Applicata* 93:141-148.

Ong’amo, G.O., Le Ru, B.P., Dupas, S., Moyal, P., Calatayud, P.-A. & Silvain, J.-F. (2006a). Distribution, pest status and agro-climatic preferences of Lepidopteran stemborers of maize in Kenya. *Annales de la Société Entomologique de France* (Nouvelle série) 42:171-177.

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 lepidopteran stemborers along altitudinal gradient in Kenya. *Annales de la Société Entomologique de France* (Nouvelle série) 42:1-9.

Polaszek, A. & Khan, Z.R. (1998). Host plants; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford. pp 3-10.

Rebe, M., Van den Berg, J. & McGeoch, M.A. (2004). Colonization of cultivated and indigenous graminaceous host plants by *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) and *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) under field conditions. *African Entomology* 12:1-13.

Reddy, K. (1998). Maize and Sorghum: East Africa; In African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control, Polaszek A. (ed), Wallingford, pp 25-28.

Rocca, M. & Greco, N. (2011). Diversity of herbivorous communities in blueberry crops of different regions of Argentina. *Environmental Entomology* 40:247-259.

Simberloff, D. & Dayan, T. (1991). The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22:115-143.

Speight, M.R., Hunter, M.D. & Watt, A.D. (2008). *Ecology of insects: concepts and applications.* Second edition. John Wiley & Sons Ltd, UK. 628pp.

Sporleder, M., Kroschel, J., Quispe, M.R.G. & Lagnaoui, A. (2004). A temperature-based simulation model for the potato tuberworm, *Phthorimaea operculella* Zeller (Lepidoptera; Gelechiidae). *Environmental Entomology* 33:477-486.

Stam, J.M., Kroes, A., Li, Y., Gols, R., van Loon, J.J., Poelman, E.H. & Dicke, M. (2014). Plant interactions with multiple insect herbivores: from community to genes. *Plant Biology* 65:689.

Stiling, P., Rossi, A. M., Cattell, M. & Bowdish, T. I. (1999). Weak competition between coastal insect herbivores. *Florida Entomologist* 82:599-608.

Strong, D.R., Lawton, J.H. & Southwood, S.R. (1984). *Insects on plants. Community patterns and mechanisms:* Blackwell Scientific Publicatons, 313 pp.

Tefera, T. (2004). Lepidopterous stemborers of sorghum and their natural enemies in eastern Ethiopia. *Tropical Science* 44:128-130.

Truter, J., Van Hamburg, H. & Van den Berg, J. (2014). Comparative diversity of arthropods on Bt maize and non-Bt maize in two different cropping systems in South Africa. *Environmental Entomology* 43:197-208.

Van Den Berg, J., Van Rensburg, J.B.J. & Van der Westhuizen, M.C. (1991). The effect of single and mixed populations of *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Pyralidae) on damage to grain sorghum. *Journal of the Entomological Society of Southern Africa* 54:231-242.

Woiwod, I.P. (1997). Detecting the effects of climate change on Lepidoptera. *Journal of Insect Conservation* 1:149-158.

Wootton, J.T. & Emmerson, M. (2005). Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution and Systematics* 36:419-444.

World Economic Forum (2013). Achieving the New Vision for Agriculture: New Models for Action. A report by the World Economic Forum's New Vision for Agriculture initiative. Prepared in collaboration with McKinsey & Company. http://www3.weforum.org/docs/IP/2013/NVA/WEF_IP_NVA_New_Models_for_Action_report.pdf. 32pp. Accessed on 10th February, 2014.

# 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. Löve (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). Microorgansims 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. (Eriocraniidae) (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 arboreus* 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 Colorado potato beetle. 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; Lill & 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-Soultani, 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-Soultani, 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 syncronised 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 stemborers

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 to100, 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 to14 days, after which moths emerge (Harris & Nwanze, 1992; Bosque-Pérez & Schulthess, 1998).

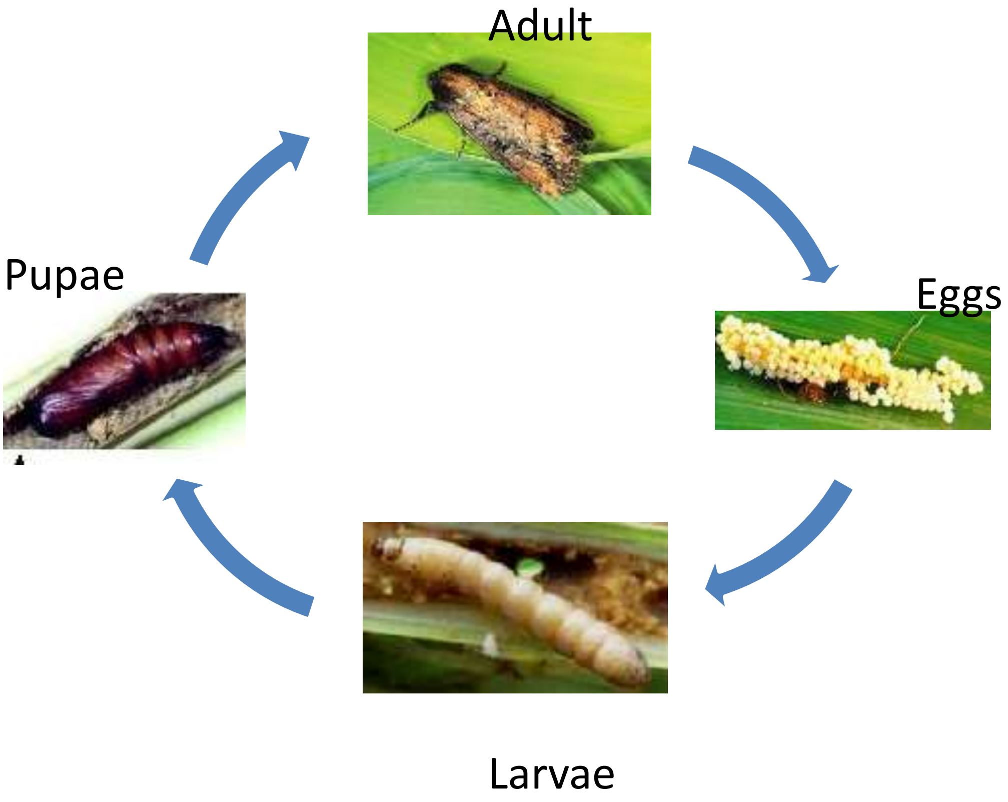


**Figure 2.1.** Life cycle of *Busseola fusca*

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 late1920'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. purpureum, 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).

(a) (b) (c)

**Plate 2.1**. (a) Adult, (b) larva and (c) pupae of *Chilo partellus*. Photo credits: Johnnie van den Berg

### 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).

(a) (b)

**Plate 2.2.** (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.*

*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

Agrawal, A.A. (2005). Future directions in the study of induced plant responses to herbivory. *Entomologia Experimentalis et Applicata* 115:97-105.

Amarasekare, P. (2002). Interference competition and species coexistence. *Proceedings of the Royal Society of London B* 269:2541-2550.

Anderson, K.E., Inouye, B.D. & Underwood, N. (2009). Modeling herbivore competition mediated by inducible changes in plant quality. *Oikos* 118:1633-1646.

Anderson, P. & Löfqvist, J. (1996). Asymmetric oviposition behaviour & the influence of larval competition in the two pyralid moths *Ephestia kuehniella* and *Plodia interpunctella. Oikos* 76:47-56.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. & Whittaker, J.B. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1-16.

Bascompte, J. & Jordano, P. (2007). Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 38:567-593.

Beck, S.D. (1983). Insect thermoperiodism. *Annual Review of Entomology* 28:91-108.

Benson, W.W. (1978). Resource partitioning in passion vine butterflies. *Evolution* 32:493-518.

Bernays, E.A. & Chapman, R.E. (1994). *Host-plant selection by phytophagous insects*. Chapman & Hall, New York, USA. 312pp.

Bográn, C.E., Heinz, K.M. & Ciomperlik, M.A. (2002). Interspecific competition among insect parasitoids field experiments with whiteflies as hosts in cotton. *Ecology* 83:653-668.

Bosque-Pérez, N.A. & Schulthess, F. (1998). Maize: West & Central Africa; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford, UK. pp 11-27.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B. & Michalet, R. (2008). Facilitation in plant communities: the past, the present and the future. *Journal of Ecology* 96:18-34.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119-125.

Bulleri, F., Bruno, J.F. & Benedetti-Cecchi, L. (2008). Beyond competition: incorporating positive interactions between species to predict ecosystem invisibility. *PLoS Biology* 6:1136-1140.

Bultman, T.L. & Faeth, S.H. (1986). Experimental evidence for intraspecific competition in a lepidopteran leafminer. *Ecology* 67:442-448.

Buse, A., Dury, S.J., Woodburn, R.J. W., Perrins, C.M. & Good, J.E.G. (1999). Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology* 13:74-82.

Calatayud, P.-A., Guénégo, H., Ahuya, P., Wanjoya, A., Le Ru, B., Silvain, J.-F. & Frérot, B. (2008a). Flight and oviposition behaviour of the African stemborer, *Busseola fusca*, on various host plant species. *Entomologia Experimentalis et Applicata* 129:348-355.

Calatayud, P.-A., Ahuya, P.O., Wanjoya, A., Le Ru, B., Silvain, J.-F. & Frérot, B. (2008b). Importance of plant physical cues in host acceptance for oviposition by *Busseola fusca. Entomologia Experimentalis et Applicata* 126:233-243.

Calderón-Cortés, N., Quesada, M. & Escalera-Vázquez, L.H. (2011). Insects as stem engineers: interactions mediated by the twig-girdler *Oncideres albomarginata C*hamela enhance arthropod diversity. *PLoS ONE* 6:1-9.

Callaway, R.M. (1995). Positive interactions among plants. *Botanical Review* 61:306-349.

Callaway, R.M. & Walker, L.R. (1997). Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958-1965.

Cammell, M.E. & Knight, J.D. (1992). Effects of climatic-change on the population dynamics of crop pests. *Advances in Ecological Research* 22:117-162.

Casper, B.B. & Jackson, R.B. (1997). Plant competition underground. *Annual Review of Ecology and Systematics* 28:545-570.

Chadha, G.K. & Roome, R.E. (1980). Oviposition behaviour and the sensilla of the ovipositor of *Chilo partellus* and *Spodoptera littoralis* (Lepidoptera: Noctuidae). *Journal of Zoology* 192:169-178.

Chaneton, E.J. & Bonsall, M.B. (2000). Enemy-mediated apparent competition: empirical patterns and the evidence. *Oikos* 88:380-394.

Colwell, R.K. & Fuentes, E.R. (1975). Experimental studies of the niche. *Annual Review of Ecology, Evolution, and Systematics* 6:281-310.

Connell, J.H. (1980). Diversity and the coevolution of competitors, or the ghost of competition. *Oikos* 35:131-138.

Connell, J.H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122:661-696.

Coope, R. (2004). Quaternary climatic changes-what can we learn from history? *The ESS Bulletin* 2:57-75.

Courtney, S.P., Chen, G.K. & Gardner, A. (1989). A general model for individual host selection. *Oikos* 55:55-65.

Craig, T.P., Itami, J.K. & Price, P.W. (1990). Intraspecific competition and facilitation by a shoot-galling sawfly. *Journal of Animal Ecology* 59:147-159.

Craig, T.P., Itami, J.K., Shantz, C., Abrahamson, W.G., Horner, J.D. & Craig, J.V. (2000). The influence of host plant variation and intraspecific competition on oviposition preference and offspring performance in the host races of *Eurasta solidaginis*. *Ecological Entomology* 25:7-18.

Crawley, M.J. (1975). The numerical responses of insect predators to changes in prey density. *Journal of Animal Ecology* 44:877-892.

Cunningham, J.P. & West, S.A. (2001). Host selection in phytophagous insects: a new explanation for learning in adults. *Oikos* 95:537-543.

Cunningham, J.P., Zalucki, M.P. & West, S.A. (1999). Learning in *Helicoverpa armigera* (Lepidoptera: Noctuidae): a new look at the behaviour and control of a polyphagous pest. *Bulletin of Entomological Research* 89:201–207.

Damos, P. & Savopoulou-Soultani, M. (2012). Temperature-driven models for insect development and vital thermal requirements. *Psyche*: *A Journal of Entomology* 2012:13 pp.

Dangles, O., Carpio, C., Barragan, A.R., Zeddam, J.-L. & Silvain, J.-F. (2008). Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. *Ecological Applications* 18:1795-1809.

Dangles, O., Mesías, V., Crespo-Perez, V. & Silvain, J.-F. (2009). Crop damage increases with pest species diversity: evidence from potato tuber moths in the tropical Andes*. Journal of Applied Ecology* 46:1115-1121.

De Moraes, C.M., Mescher, M.C. & Tumlinson, J.H. (2001). Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* 410:577-580.

Debouzie, D., Desouhant, E., Oberli, F. & Menu, F. (2002). Resource limitation in natural populations of phytophagous insects. A long-term study case with the chestnut weevil. *Acta Oecologica* 23:31-39.

Denno, R.F. & Kaplan, I. (2007). Plant-mediated interactions in herbivorous insects: mechanisms, symmetry, and challenging the paradigms of competition past; In *Ecological Communities: Plant Mediation in Indirect Interaction Webs,* Ohgushi, T., Craig, T.P. & Price, P.W. (eds) Cambridge University Press, UK. pp 19-50.

Denno, R.F., McClure, M.S. & Ott, J.R. (1995). Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology* 40:297-331.

Dorhout, D.L. & Rice, M.E. (2010). Intraguild competition and enhanced survival of western bean cutworm (Lepidoptera: Noctuidae) on transgenic cry1ab (mon810) *Bacillus thuringiensis* corn. *Journal of Economic Entomology* 103:54-62.

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E. & Loreau, M. (2007). The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522-538.

Duyck, P.-F., David, P. & Quilici, S. (2004). A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). *Ecological Entomology* 29:511-520.

Duyck, P.-F., David, P. & Quilici, S. (2006). Climatic niche partitioning following successive invasions by fruit flies in La Réunion. *Journal of Animal Ecology* 75:518-526.

Estay, S.A., Lima, M. & Labra, F.A. (2009). Predicting insect pest status under climate change scenarios: combining experimental data and population dynamics modelling. *Journal of Applied Entomology* 133: 491-499.

Evans, E.W. (1992). Absence of interspecific competition among tallgrass prairie grasshoppers during a drought. *Ecology* 73:1038-1044.

Facknath, S. (2012). Study of herbivore response to the presence of conspecifics and heterospecifics in an insect-host plant relationship. *University of Mauritius Research Journal* 18:250-274.

Faeth, S.H. (1986). Indirect interactions between temporally separated herbivores mediated by the host plant. *Ecology* 67:479-494.

Fatouros, N.E., Lucas-Barbosa, D., Weldegergis, B.T., Pashalidou, F.G., van Loon, J.J., Dicke, M., Harvey, J.A., Gols, R. & Huigens, M.E. (2012). Plant volatiles induced by herbivore egg deposition affect insects of different trophic levels. *PLoS ONE* 7:e43607.

Fischer, M.K., Hoffmann, K.H. & Völkl, W. (2001). Competition for mutualists in an ant-homopteran interaction mediated by hierarchies of ant attendance. *Oikos* 92:531-541.

Fisher, A.E.I., Hartley, S.E. & Young, M. (2000). Direct and indirect competitive effects of foliage feeding guilds on the performance of the birch leaf-miner *Eriocrania*. *Journal of Animal Ecology* 69:165-176.

Hardin, G. (1960). The competitive exclusion principle. *Science* 131:1292-1297.

Glas, J., Van den Berg, J. & Potting, R. (2007). Effect of learning on the oviposition preference of field-collected and laboratory-reared *Chilo partellus* (Lepidoptera: Crambidae) populations. *Bulletin of Entomological Research* 97:415-420.

Gómez, J.M., Verdú, M. & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature* 465:918-921.

Gordo, O. & Sanz, J.J. (2005). Phenology and climate change: a long-term study in a Mediterranean locality. *Oecologia* 146:484-495.

Griffin, A.S., West, S.A. & Buckling, A. (2004). Cooperation and competition in pathogenic bacteria. *Nature* 430:1024-1027.

Groot, A., Heijboer, A., Visser, J. & Dicke, M. (2003). Oviposition preference of *Lygocoris pabulinus* (Het.; Miridae) in relation to plants and conspecifics. *Journal of Applied Entomology* 127:65-71.

Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992). A meta-analysis of competition in field experiments. *The American Naturalist* 140:539-572.

Hagen, S.B., Jepsen, J.U., Ims, R.A. & Yoccoz, N.G. (2007). Shifting altitudinal distribution of outbreak zones of winter moth *Operophtera brumata* in sub-arctic birch forest: a response to recent climate warming? *Ecography* 30:299-307.

Haile, A. & Hofsvang, T. (2002). Host plant preference of the stem borer *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). *Crop Protection* 21:227-233.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control and competition*. The American Naturalist* 94:421-425.

Halaj, J. & Wise, D.H. (2001). Terrestrial trophic cascades: how much do they trickle? *American Naturalist* 157:262-281.

Hammons, D.L., Kurtural, S.K., Newman, M.C. & Potter, D.A. (2009). Invasive Japanese beetles facilitate aggregation and injury by a native scarab pest of ripening fruits. *PNAS* 106:3686-3691.

Harris, K.M. & Nwanze, K.F. (1992). *Busseola fusca* (Fuller), the African maize stalk borer: a handbook of information. *Information Bulletin*, No. 33. ICRISAT, Patancheru, India, 92 pp.

Harrison, S. & Karban, R. (1986). Effects of an early-season folivorous moth on the success of a later-season species, mediated by a change in the quality of the shared host, *Lupinus arboreus* Sims. *Oecologia* 69:354-359.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12:184-195.

Hirzel, A.H. & Le Lay, G. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45:1372-1381.

Hodkinson, I.D. (2005). Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80:489-513.

Hodkinson, I.D., Bird, J., Miles, J.E., Bale, J.S. & Lennon, J.J. (1999). Climatic signals in the life histories of insects: the distribution and abundance of heather psyllids (*Strophingia spp*.) in the UK. *Functional Ecology* 13:83-95.

Holloway, J.D. (1998). Noctuidae; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford, UK. pp 79-86.

Holt, R.D. (1977). Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology* 12:197-229.

Holt, R.D. & Kotler, B.P. (1987). Short-term apparent competition. *American Naturalist* 130:412-430.

Holt, R.D. & Lawton, J.H. (1993). Apparent competition and enemy-free space in insect host-parasitoid communities. *American Naturalist* 142:623-645.

Honda, K. (1995). Chemical basis of differential oviposition by lepidopterous insects. *Archives of Insect Biochemistry and Physiology* 30:1-23.

Howe, R.W. (1967). Temperature effects on embryonic development in insects. *Annual Review of Entomology* 12:15-42.

Howlett, B.G. & Clarke, A.R. (2005). Oviposition deterrence is likely an effect, not a mechanism, in the leaf-bettle *Chrysophtharta Bimaculata* (Olivier) (Coleoptera: Chrysomelidae). *Journal of Insect Behavior* 18:609-618.

Hsu, S.-B., Cheng, K.-S. & Hubbell, S.P. (1981). Exploitative competition of microorganisms for two complementary nutrients in continuous cultures. *SIAM Journal on Applied Mathematics* 41:422-444.

Hudson, E.E. & Stiling, P. (1997). Exploitative competition strongly affects the herbivorous insect community on *Baccharis halimifolia. Oikos* 79:521-528.

Inbar, M., Eshel, A. & Wool, D. (1995). Interspecific competition among phloem-feeding insects mediated by induced host-plant sinks. *Ecology* 76:1506-1515.

Ishii, H.S., Kadoya, T., Kikuchi, R., Suda, S. & Washitani, I. (2008). Habitat and flower resource partitioning by an exotic and three native bumble bees in central Hokkaido, Japan. *Biological Conservation* 141:2597-2607.

Jackson, S.T., Betancourt, J.L., Booth, R.K. & Gray, S.T. (2009). Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *PNAS* 106:19685-19692.

Jaenike, J. (1990). Host specialization in phytophagous insects. *Annual Review of Ecology and Systematics* 21:243-273.

Jonsson, M. & Malmqvist, B. (2000). Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. *Oikos* 89:519-523.

Kaplan, I. & Denno, R.F. (2007). Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecology Letters* 10:977-994.

Kaplan, I. & Eubanks, M.D. (2005). Aphids alter the community-wide impact of fire ants. *Ecology* 86:1640-1649.

Karban, R. (1986). Interspecific competition between folivorous insects on *Erigeron glaucus. Ecology* 67:1063-1072.

Karban, R. (1989). Community organization of *Erigeron glaucus* folivores: effects of competition, predation and host plant. *Ecology* 70:1028-1039.

Karban, R. & Courtney, S. (1987). Intraspecific host plant choice: lack of consequences for *Streptanthus tortuosus* (Cruciferae) and *Euchloe hyantis* (Lepidoptera: Pieridae). *Oikos* 48:243-248.

Kfir, R. (1997). Competitive Displacement of *Busseola fusca* (Lepidoptera: Noctuidae) by *Chilo partellus* (Lepidoptera: pyralidae). *Ecology and Population Biology* 90:619-624.

Kfir, R., Overholt, W.A., Khan, Z.R. & Polaszek, A. (2002). Biology and management of economically important lepidopteran cereal stemborers in Africa. *Annual Review of Entomology* 47:701-731.

Khan, Z.R., Midega, C.A.O., Bruce, T.J.A., Hooper, A.M. & Pickett, J.A. (2010). Exploiting phytochemicals for developing a ‘push–pull’ crop protection strategy for cereal farmers in Africa. *Journal of Experimental Botany* 61:4185-4196.

Kindlmann, P. & Dixon, A.F.G. (2003). Insect predator-prey dynamics and the biological control of aphids by ladybirds;In *First international symposium on biological control of arthropods*, Driesche R. V. (ed), USDA Forest Service, USA, pp 118-124.

Klomp, H. (1964). Intraspecific competition and the regulation of insect numbers. *Annual Review of Entomology* 9:17-40.

Krüger, W., Van den Berg, J. & Van Hamburg, H. (2008) The relative abundance of maize stem borers and their parasitoids at the Tshiombo irrigation scheme in Venda, South Africa. *South African Journal of Plant and Soil* 25:144-151.

Lale, N.E.S. & Vidal, S. (2001). Intraspecific and interspecific competition in *Callosobruchus maculatus* (F.) and *Callosobruchus subinnotatus* (Pic) on stored bambara groundnut, *Vigna subterranea* (L.) Verdcourt. *Journal of Stored Products Research* 37:329-338.

Lawton, J.H. (1982). Vacant niches & unsaturated communities: a comparison of bracken herbivores at sites on two continents. *Journal of Animal Ecology* 51:573-595.

Lawton, J.H. & Strong Jr, D.R. (1981). Community patterns and competition in folivorous insects. *The American Naturalist* 118:317-338.

Le Ru, B.P., Ong'amo, G.O., Moyal, P., Muchugu, E., Ngala, L. Musyoka, B., Abdullah, Z., Matama-Kauma, T., Lada, V.Y., Pallangyo, B., Omwega, C.O., Schulthess, F., Calatayud, P.-A. & Silvain, J.-F. (2006a). Geographic distribution and host plant ranges of East African noctuid stem borers. *Annales de la Société Entomologique de France (Nouvelle série)* 42:353-361.

Le Ru, B.P., Ong'amo, G.O., Moyal, P., Ngala, L. Musyoka, B., Abdullah, Z., Cugala, D., Defabachew, B., Haile, T.A., Kauma Matama, T., Lada, V.Y., Negassi, B., Pallangyo, K., Ravolonandrianina, J., Sidumo, A., Omwega, C.O., Schulthess, F., Calatayud, P.-A. & Silvain, J.-F. (2006b). Diversity of Lepidopteran stemborers on monocotyledonous plants in Eastern Africa and the islands of Madagascar and Zanzibar revisited. *Bulletin of Entomological Research* 96:555-563.

Leibold, M.A. (1995). The niche concept revisited: mechanistic models and community context. *Ecology* 76:1371-1382.

Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature* 461:254-257.

Lill, J.T. & Marquis, R.J. (2003). Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology* 84:682-690.

Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72-76.

Lounibos, L.P., Suárez, S., Menéndez, Z., Nishimura, N., Escher, R.L., O'Connell, S.M. & Rey, J.R. (2002). Does temperature affect the outcome of larval competition between *Aedes aegypti* and *Aedes albopictus*? *Journal of Vector Ecology* 27:86-95.

Lynch, M.E., Kaplan, I., Dively, G.P. & Denno, R.F. (2006). Host-plant-mediated competition via induced resistance: interactions between pest herbivores on potatoes. *Ecological Applications* 16:855-864.

Maes, K.V.N. (1998a). Lepidoptera: Introduction; In *African Cereal Stemborers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford, UK. pp 75-78.

Maes, K.V.N. (1998b). Pyraloidea: Crambidae, Pyralidae; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford, UK. pp 87-98.

Mangla, S., Sheley, R.L., James, J.J. & Radosevich, S.R. (2011). Intra and interspecific competition among invasive and native species during early stages of plant growth. *Plant Ecology* 212:531-542.

Mason, N.W.H., de Bello, F., Doležal, J. & Leps, J. (2011). Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology* 99:788-796.

Masters, G.J., Brown, V.K., Clarke, I.P., Whittaker, J.B. & Hollier, J.A. (1998). Direct and indirect effects of climate change on insect herbivores: Auchenorrhyncha (Homoptera). *Ecological Entomology* 23:45-52.

Memmott, J., Alonso, D., Berlow, E., Dobson, A. P., Dunne, J.A., Sole, R. & Weitz, J.S. (2006). Biodiversity loss and ecological network structure; In *Ecological Networks: Linking Structure to Dynamics in Food Webs*, Pascual, M. & Dunne, J. A. (eds). Oxford University Press, Oxford, pp 325-347.

Memmott, J., Gibson, R., Carvalheiro, L.G., Henson, K., Heleno, R.H., Mikel, L.M. & Pearce, S. (2007). The conservation of ecological interactions; In *Insect Conservation Biology,* Stewart, A.J.A., New, T.R. & Lewis, O.T. (eds), pp 226-244.

Midega, C.A.O., Khan, Z.R., Pickett, J.A. & Nylin, S. (2011). Host plant selection behaviour of *Chilo partellus* and its implication for effectiveness of a trap crop. *Entomologia Experimentalis et Applicata* 138:40-47.

Moon, D.C. & Stiling, P. (2002). Top-down, bottom-up, or side to side? within-trophic-level interactions modify trophic dynamics of a salt marsh herbivore. *Oikos* 98: 480-490.

Morris, R.J., Lewis, O.T. & Godfray, H.C.J. (2005). Apparent competition and insect community structure: towards a spatial perspective. *Annales Zoologici Fennici* 42:449-462.

Moya-Laraño, J., El-Sayyid, M.E.T & Fox, C.W. (2007). Smaller beetles are better scramble competitors at cooler temperatures. *Biology Letters* 3:475-478.

Mucheru, O.M., Jiang, N., Kongoro, J., Bruce, A.Y. & Schulthess, F. (2009). Intrinsic competition between two oligophagous parasitoids, *Sturmiopsis parasitica* and *Cotesia sesamiae*, attacking the same life stages of lepidopteran cereal stemborers. *Entomologia Experimentalis et Applicata* 130:10-20.

Ndemah, R., Schulthess, F., Korie, S., Borgemeister, C. & Cardwell, K.F. (2001). Distribution, relative importance & effect of Lepidopterous borers on maize yields in the forest zone and mid-altitude of Cameroon. *Journal of Economic Entomology* 94:1434-1444.

Nufio, C.R. & Papaj, D.R. (2001). Host marking behavior in phytophagous insects and parasitoids. *Entomologia Experimentalis et Applicata* 99:273-293.

Ofomata, V.C., Overholt, W.A.  Lux, S.A., Van Huis, A. & Egwuatu, R.I. (2000). Comparative studies on the fecundity, egg survival, larval feeding, and development of *Chilo partellus* and *Chilo orichalcociliellus* (Lepidoptera: Crambidae) on five grasses. *Ecology and Population Biology* 93:492-499.

Ofomata, V.C., Overholt, W.A., Van Huis, A., Egwuatu, R.I. & Ngi-Song, A.J. (1999). Niche overlap and interspecific association between *Chilo partellus* and *Chilo orichalcociliellus* on the Kenya coast. *Entomologia Experimentalis et Applicata* 93:141-148.

Ohgushi, T. (2008). Herbivore-induced indirect interaction webs on terrestrial plants: the importance of non-trophic, indirect and facilitative interactions. *Entomologia Experimentalis et Applicata* 128:217-229.

Ong'amo, G.O., Le Ru, B.P., Dupas, S., Moyal, P., Calatayud, P.-A. & Silvain, J.-F. (2006a). Distribution, pest status and agro-climatic preferences of lepidopteran stemborers of maize in Kenya. *Annales de la Société Entomologique de France (Nouvelle série)* 42:171-177.

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 lepidopteran stemborers along altitudinal gradient in Kenya. *Annales de la Société Entomologique de France (Nouvelle série)* 42:1-9.

Ong'amo, G.O., Le Ru, B.P., Moyal, P., Calatayud, P.-A., Le Gall, P., Ogol, C.K.P.O., Kokwaro, E.D., Capdevielle-Dulac, C. & Silvain, J.-F. (2008). Host plant diversity of *Sesamia calamistis*: cytochrome b gene sequences reveal local genetic differentiation. *Entomologia Experimentalis et Applicata* 128:154-161.

Otieno, N.A., Le Ru, B.P., Ong'amo, G.O., Dupas, S., Calatayud, P.-A., Makobe, M., Ochora, J. & Silvain, J.-F. (2006). Diversity and abundance of wild host plants of lepidopteran stem borers in two different agroecological zones of Kenya. *Annales de la Société Entomologique de France (Nouvelle série)* 42:371-380.

Ovadia, O. & Schmitz, O.J. (2004). Weather variation and trophic interaction strength: sorting the signal from the noise. *Oecologia* 140:398-406.

Overholt, W.A., Maes, K.V.N. & Goebel, F.R. (2001). *Field guide to the stemborer larvae of maize, sorghum and sugarcane in Eastern and Southern Africa*. ICIPE science press, Nairobi, Kenya. 31pp.

Peacor, S.D. & Werner, E.E. (2004). How dependent are species-pair interaction strengths on other species in the food web. *Ecology* 85:2754-2763.

Petersen, M.K. & Sandström, J.P. (2001). Outcome of indirect competition between two aphid species mediated by responses in their common host plant. *Functional Ecology* 15:525-534.

Pianka, E.R. (1974). Niche overlap and diffuse competition. *PNAS* 71:2141-2145.

Poelman, E.H., Broekgaarden, C., Van Loon, J.J. & Dicke, M. (2008). Early season herbivore differentially affects plant defence responses to subsequently colonizing herbivores and their abundance in the field. *Molecular Ecology* 17:3352-3365.

Polaszek, A. & Khan, Z.R. (1998). Host plants; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford. pp 3-10.

Prokopy, R.J. (1981). Epideictic pheromones that influence spacing patterns of phytophagous insects; In *Semiochemicals: their role in pest control*, Nordlund, D. A., Jones, R.L. & Lewis, W.J. (eds), John Wiley & Sons, New York. pp 181-213.

Pulliam, H.R. (2000). On the relationship between niche and distribution. *Ecology Letters* 3:349-361.

Rathcke, B.J. (1976). Competition and coexistence with a guild of herbivorous insects. *Ecology* 57:76-87.

Redman, A.M. & Scriber, J.M. (2000). Competition between the gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: interactions mediated by host plant chemistry, pathogens and parasitoids. *Oecologia* 125:218-228.

Reitz, S.R. & Trumble, J.T. (2002). Competitive displacement among insects and arachnids. *Annual Review of Entomology* 47:435-465.

Renwick, J.A.A. & Chew, F.S. (1994). Oviposition behavior in Lepidoptera. *Annual Review of Entomology* 39:377-400.

Resetarits, Jr., W.J. & Wilbur, H.M. (1989). Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. *Ecology* 70:220-228.

Sallam, M.N., Overholt, W.A. & Kairu, E. (2002). Intraspecific and interspecific competition between *Cotesia flavipes* and *Cotesia sesamiae* (Hymenoptera: Braconidae), gregarious larval endoparasitoids of lepidopteran stemborers. *Biocontrol Science and Technology* 12:493-506.

Sato, Y., Yano, S., Takabayashi, J. & Ohsaki, N. (1999). *Pieris rapae* (Lepidoptera: Pieridae) females avoid oviposition on *Rorippa indica* plants infested by conspecific larvae. *Applied Entomology and Zoology* 34:333-337.

Schoener, T.W. (1974). Resource partitioning in ecological communities. *Science* 185:27-39.

Schoener, T.W. (1983). Field experiments on interspecific competition. *The American Naturalist* 122:240-285.

Schowalter, T.D. (2011). *Insect ecology: an ecosystem approach,* 3rd edition. Academic Press, San Diego, USA. 650p.

Sezonlin, M., Dupas, S., Le Ru, B., Le Gall, P., Moyal, P., Calatayud, P.-A., Giffard, I., Faure, N. & Silvain, J.-F. (2006). Phylogeography and population genetics of the maize stalk borer *Busseola fusca* (Lepidoptera; Noctuidae) in sub-Saharan Africa. *Molecular Ecology* 15:407-420.

Shea, P.J. (1989). Interactions among phytophagous insect species colonizing cones of white fir (*Abies concolor*). *Oecologia* 81:104-110.

Shiojiri, K., Takabayashi, J., Yano, S. & Takafuji, A. (2002). Oviposition preferences of herbivores are affected by tritrophic interaction webs. *Ecology Letters* 5:186-192.

Singh, S.P. (1991). Biometrical observations on sorghum stemborer, *Chilo partellus* (Swinhoe) under fluctuating and constant temperature conditions. *International Journal of Tropical Insect Science* 12:419-422.

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10:1115-1123.

Soberón, J. & Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. *PNAS* 106:19644-19650.

Sparks, T.H., Dennis, R.L.H., Croxton, P.J. & Cade, M. (2007). Increased migration of Lepidoptera linked to climate change*. European Journal of Entomology* 104:139-143.

Speight, M.R., Hunter, M.D. & Watt, A.D. (2008). *Ecology of insects: concepts and applications.* Second edition. John Wiley & Sons Ltd, UK*.* 628pp.

Sporleder, M., Kroschel, J., Quispe, M.R.G. & Lagnaoui, A. (2004). A temperature-based simulation model for the potato tuberworm, *Phthorimaea operculella* Zeller (Lepidoptera; Gelechiidae). *Environmental Entomology* 33:477-486.

Stachowicz, J.J. (2001). Mutualism, facilitation, and the structure of ecological communities. *BioScience* 51:235-246.

Stiling, P.D. & Strong, D.R. (1983). Weak competition among spartina stemborers, by means of murder. *Ecology* 64:770-778.

Stiling, P.D. & Strong, D.R. (1984). Experimental density manipulation of stem-boring insects: some evidence for interspecific competition. *Ecology* 65:1683-1685.

Sugiura, S., Yamazak, K. & Yamaura, Y. (2007). Intraspecific competition as a selective pressure on the choice of oviposition site in a phytophagous insect. *Biological Journal of the Linnean Society* 92:641-650.

Taylor, L.R. (1963). Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology* 32:99-117.

Teder, T. & Tammaru, T. (2003). Short-term indirect interactions between two moth (Lepidoptera: Noctuidae) species mediated by shared parasitoids: The benefit of being scarce. *European Journal of Entomology* 100:323-328.

Thompson, J.N. & Pellmyr, O. (1991). Evolution of oviposition behavior and host preference in Lepidoptera. *Annual Review of Entomology* 36:65-89.

Tonkel, K.C. & Piper, G.L. (2009). Patterns in resource partitioning by insect biological control agents of yellow starthistle (*Centaurea solstitialis* L.) in Washington. *Northwest Science* 83:16-24.

Van den Berg, J. (2006). Oviposition preference and larval survival of *Chilo partellus* (Lepidoptera: Pyralidae) on Napier grass (*Pennisetum purpureum*) trap crops. *International Journal of Pest Management* 52:39-44

Van den Berg, J., Van Rensburg, J.B.J. & Van der Westhuizen, M.C. (1991). The effect of single and mixed populations of *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Pyralidae) on damage to grain sorghum. *Journal of the Entomological Society of Southern Africa* 54:231-242.Van Rensburg, J.B.J. & Van den Berg, J. (1990). Host plant preference by the maize stalk borer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). *South African Journal of Plant and Soil* 7:117-120.

Van Rensburg, J.B.J. & Van den Berg, J. (1992). Infestation patterns of the stalk borers *Busseola fusca* Fuller (Lep.: Noctuidae) and *Chilo partellus* Swinhoe (Lep.: Pyralidae) in grain sorghum. *Journal of the Entomological Society of Southern Africa* 55:197-212.

Van Rensburg, J.B.J., Walters, M.C. & Giliomee, J.H. (1987). Ecology of the maize stalk borer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* 77:255–269.

Van Veen, F.J. F., Morris, R.J. & Godfray, H.C.J. (2006). Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology* 51:187-208.

Viswanathan, D.V., Narwani, A.J. & Thaler, J.S. (2005). Specificity in induced plant responses shapes patterns of herbivore occurrence on *Solanum dulcamara*. *Ecology* 86:886-896.

Von Wirén, N., Römheld, V., Shioiri, T. & Marschner, H. (1995). Competition between micro-organisms and roots of barley and sorghum for iron accumulated in the root apoplasm. *New Phytologist* 130:511-521.

Wise, M.J. & Weinberg, A.M. (2002). Prior flea beetle herbivory affects oviposition preference and larval performance of a potato beetle on their shared host plant. *Ecological Entomology* 27:115-122.

Woiwod, I.P. (1997). Detecting the effects of climate change on Lepidoptera. *Journal of insect conservation* 1:149-158.

Zalucki, M.P., Clarke, A.R. & Malcolm, S.B. (2002). Ecology and behavior of first instar larval Lepidoptera. *Annual Review of Entomology* 47:361-393.

# CHAPTER THREE

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

## 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; Onga'mo *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

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

### 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.

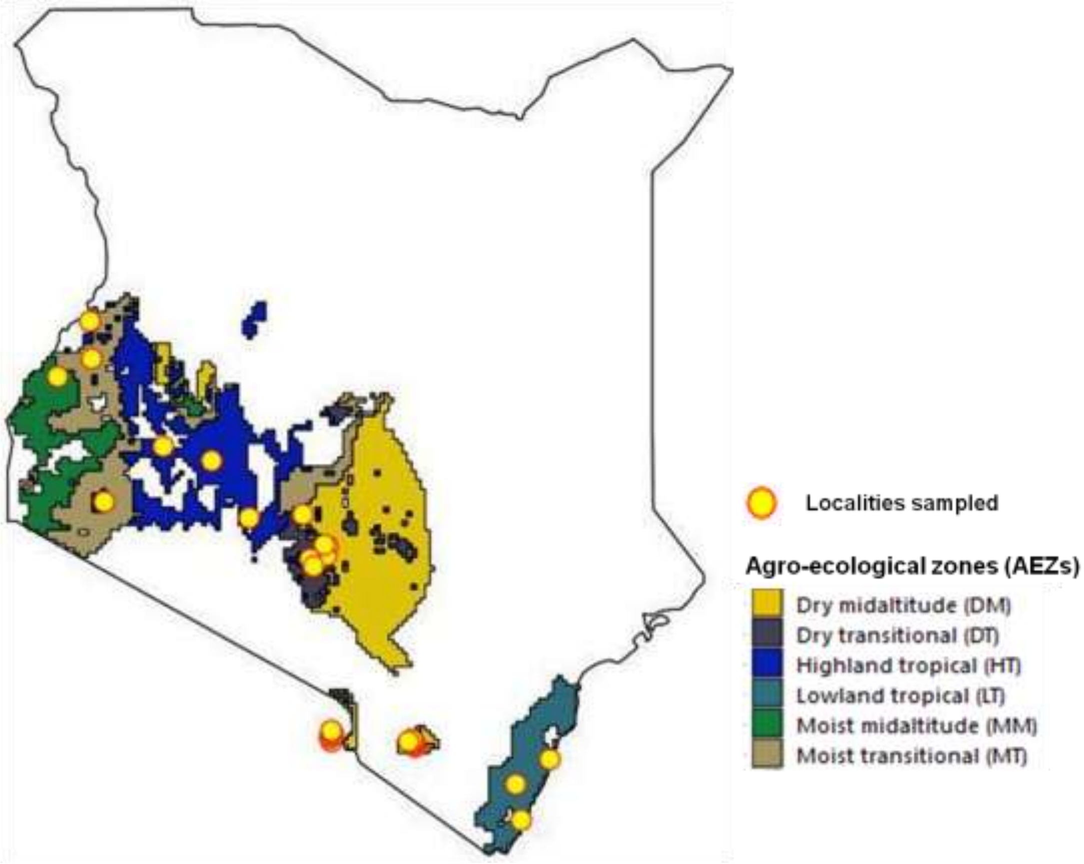


**Figure 3.1.** Map of sampling localities in the different agro-ecological zones

## 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).

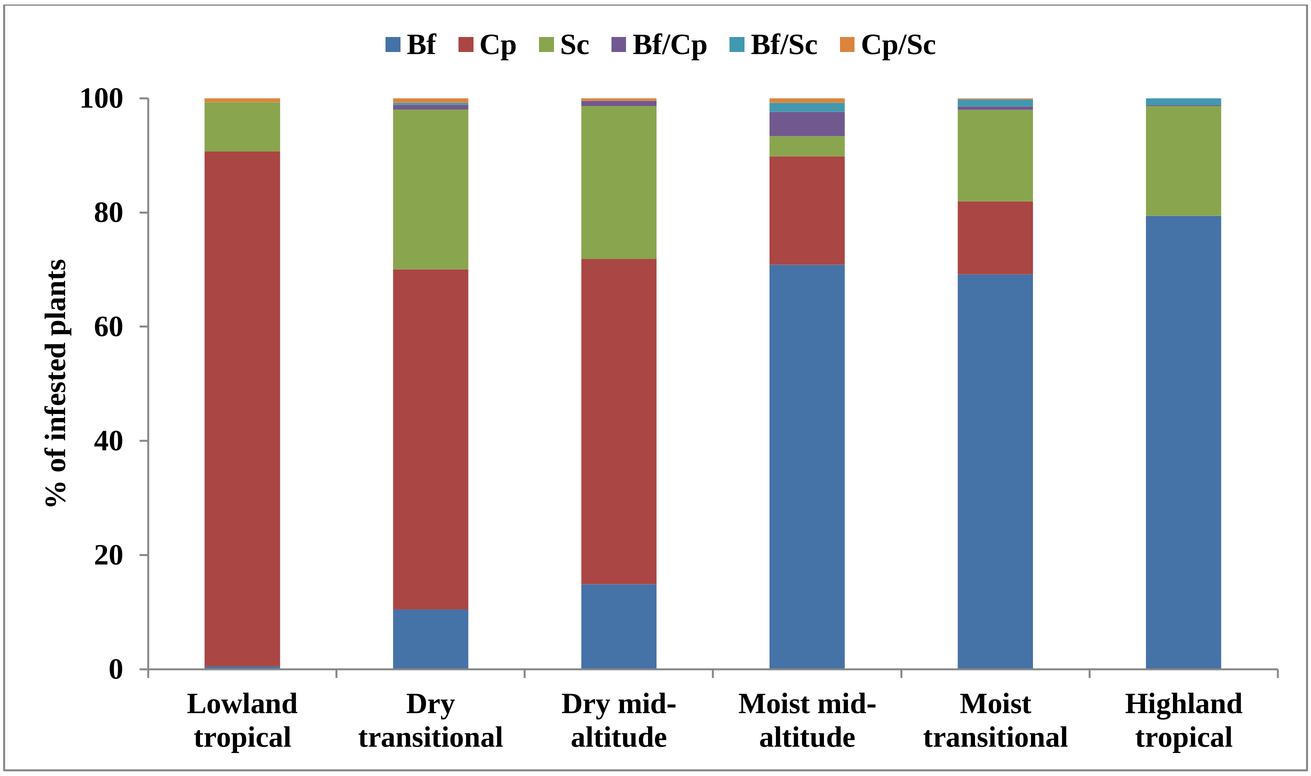


**Figure 3.2.** Percentage of maize plants with single- and multi-species infestations of *Busseola fusca* (Bf), *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) in each Agro-ecological zone

### 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).

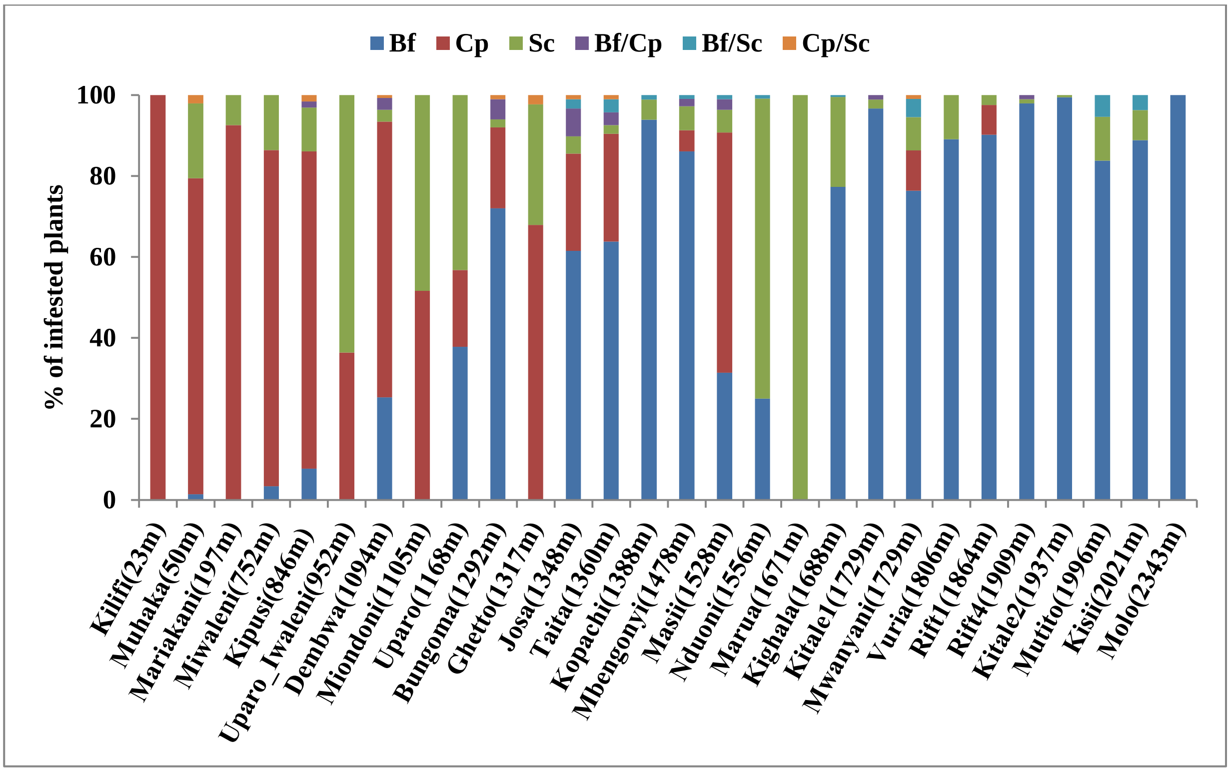


**Figure 3.3.** Percentage of maize plants with single- and multi-species infestations of *Busseola fusca* (Bf), *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) in different localities along altitudinal gradients

### 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)

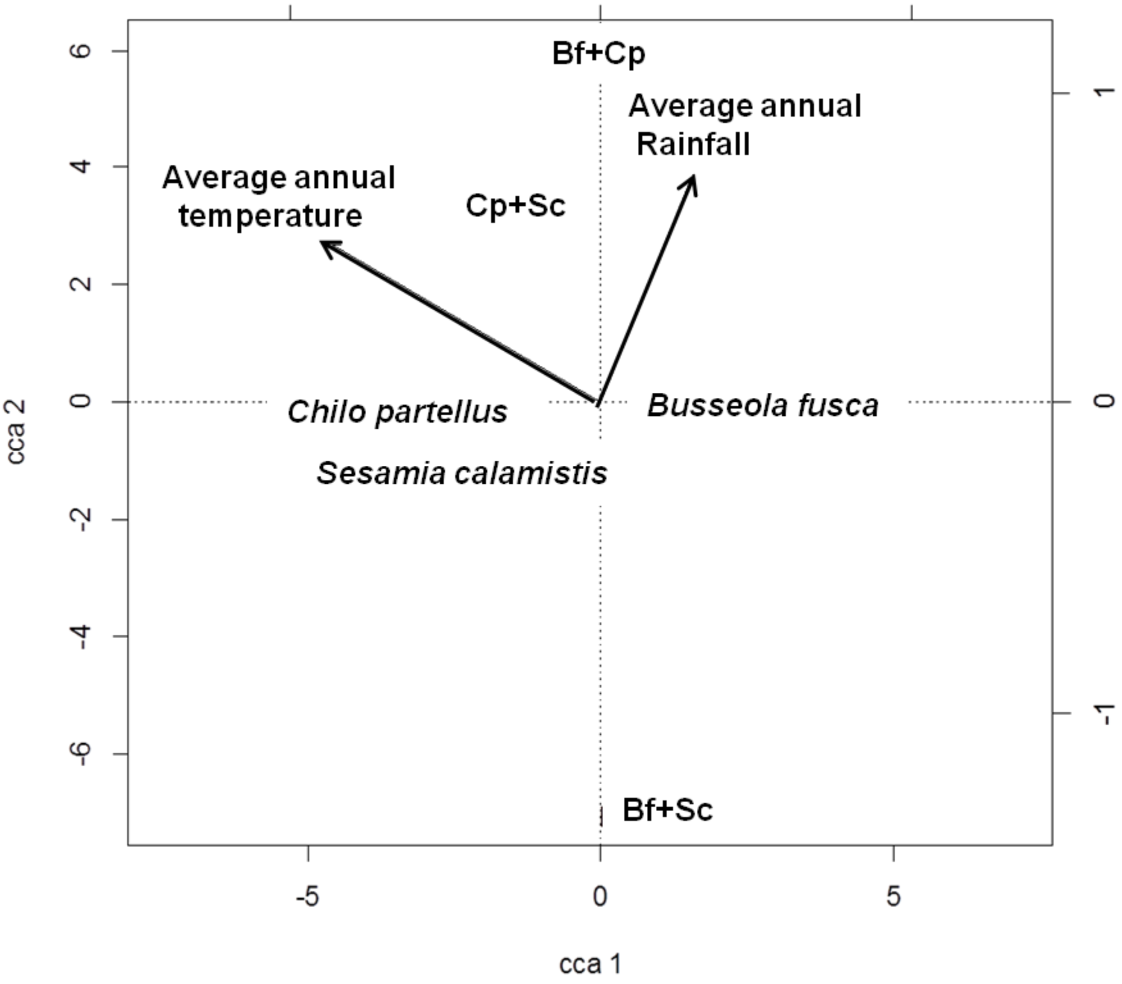


**Figure 3.4.** Biplot showing the relationship between average annual temperature and average annual rainfall and the occurrence of single- and multi-species communities consisting of *Busseola fusca* (Bf), *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc)

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)

| | **Inertia** | **Proportion** |
|---|---|---|
| **Total** | 0.877 | 1 |
| **Constrained** | 0.492 | 0.561 |
| **Unconstrained** | 0.385 | 0.439 |

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

| **Importance of components** | **CCA1** | **CCA2** |
|---|---|---|
| **Eigenvalue** | 0.490 | 0.002 |
| **Proportion explained** | 0.558 | 0.003 |
| **Cumulative proportion** | 0.558 | 0.561 |

**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

| | **F** | **P-value** |
|---|---|---|
| **Average annual temperature** | 18.5 | 0.001 |
| **Average annual rainfall** | 2.4 | 0.29 |

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).

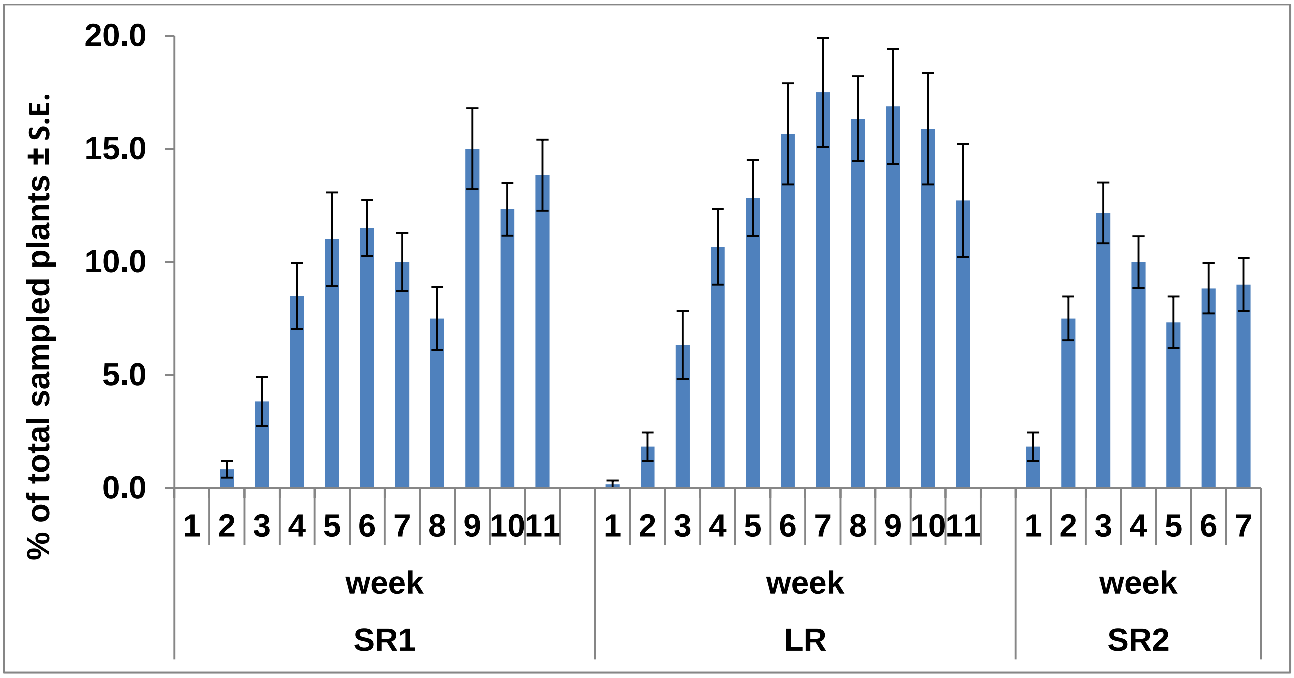


**Figure 3.5.** Percentage of stemborer infested plants over time in each season in Makuyu. SR=short rain season, LR=long rain season

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

| Seasons | Odd Ratios (95%CI) | P-value |
|---|---|---|
| Short Rain 1 | 1 | |
| Long Rain | 1.25 (0.87-1.78) | 0.24 |
| Short Rain 2 | 0.85 (0.58-1.25) | 0.42 |

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).

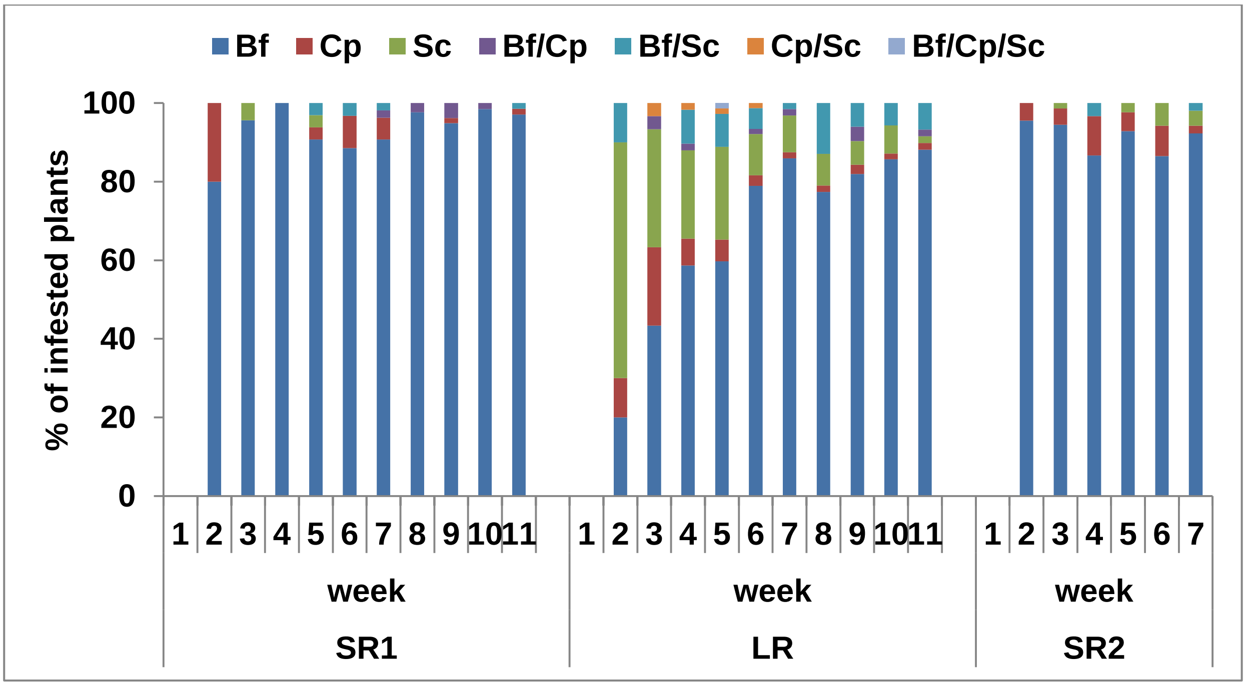


**Figure 3.6.** The percentage of plants infested with single-species and combinations of of *Busseola fusca* (Bf), *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) over time in three growing seasons at Makuyu. SR=short rain season, LR=long rain season

### 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).

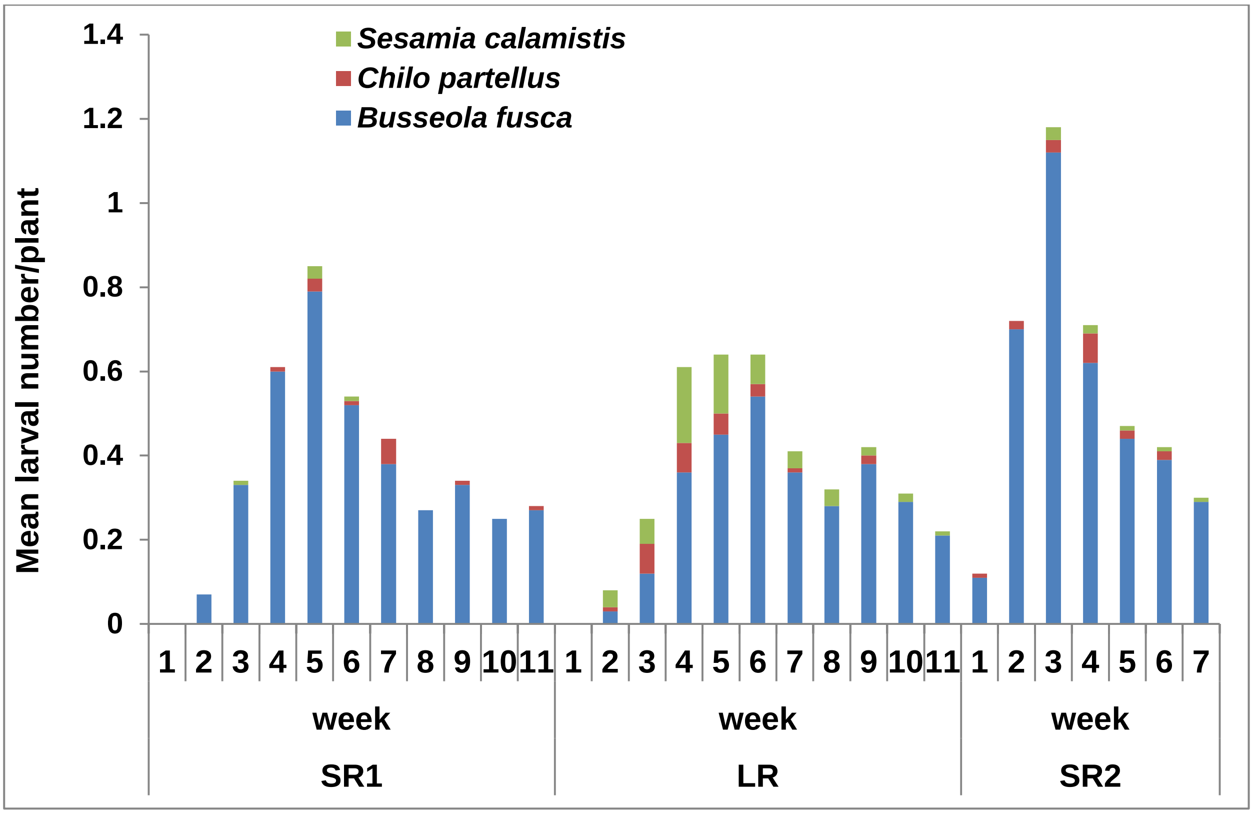


**Figure 3.7.** Larval numbers of *Busseola fusca, Chilo partellus* and *Sesamia calamistis* per plant over time in three growing seasons. SR=short rain season, LR=long rain season

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

| | **Species** | | | | | |
|---|---|---|---|---|---|---|
| | ***Busseola fusca*** | | ***Chilo partellus*** | | ***Sesamia calamistis*** | |
| **Seasons** | **Z** | **P-value** | **Z** | **P-value** | **Z** | **P-value** |
| Short Rain 1 | 47.7 | <0.001 | 3.7 | <0.001 | 3.7 | <0.001 |
| Long Rain | 6.7 | <0.001 | 5.2 | <0.001 | 13.4 | <0.001 |
| Short Rain 2 | 0.9 | 0.38 | 1.9 | 0.05 | 1.8 | 0.07 |

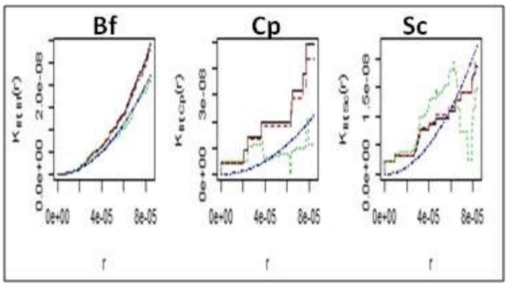
**Table 3.7**. GLMM results on the larval density between *Busseola fusca*, *Chilo partellus* and *Sesamia calamistis* in each season

| | **Seasons** | | | | | |
|---|---|---|---|---|---|---|
| | **Short rain 1** | | **Long rain** | | **Short rain 2** | |
| **Species** | **Z** | **P-value** | **Z** | **P-value** | **Z** | **P-value** |
| ***Busseola fusca*** | 35.13 | <0.001 | 28.12 | <0.001 | 33.74 | <0.001 |
| ***Chilo partellus*** | 29.16 | <0.001 | 29.41 | <0.001 | 30.89 | <0.001 |
| ***Sesamia calamistis*** | 23.88 | <0.001 | 27.74 | <0.001 | 26.54 | <0.001 |

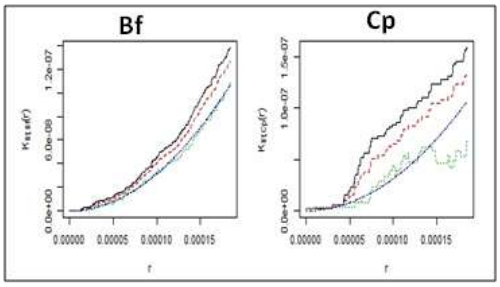
#### 3.3.4.4. Spatial distribution of species among plants

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).

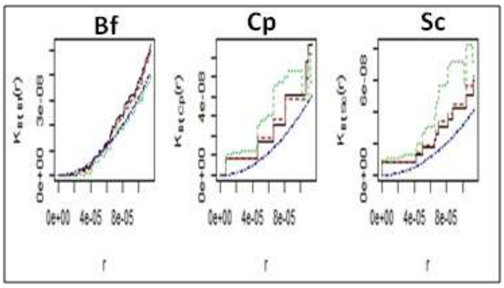
(a)



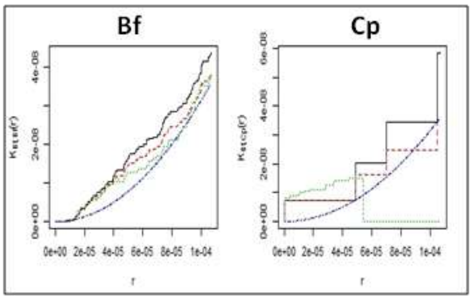
Field A



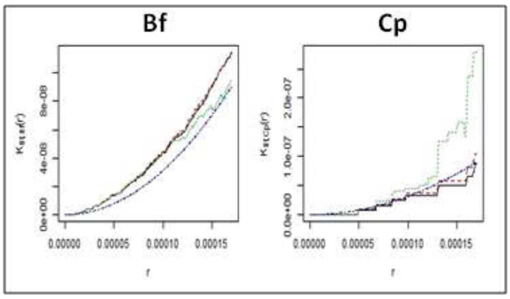
Field B



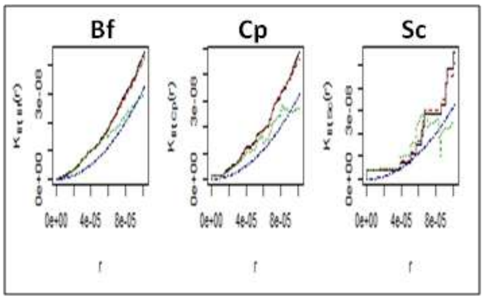
Field C



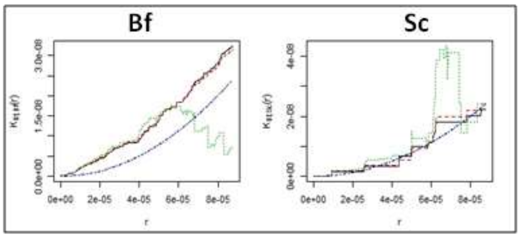
Field D



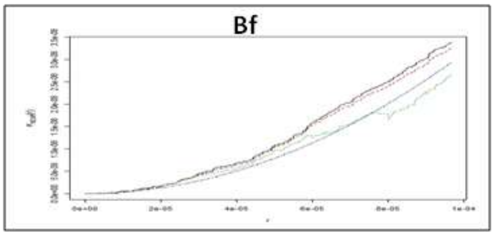
Field E



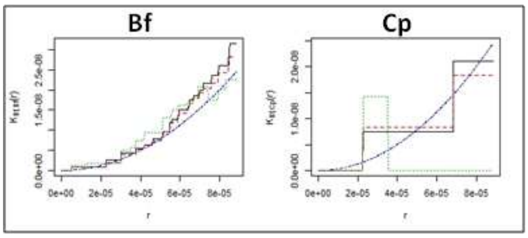
Field F



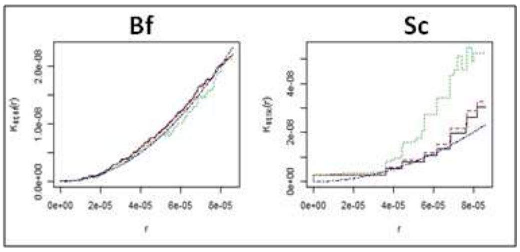
Field G



Field H



Field I



Field J

(b)

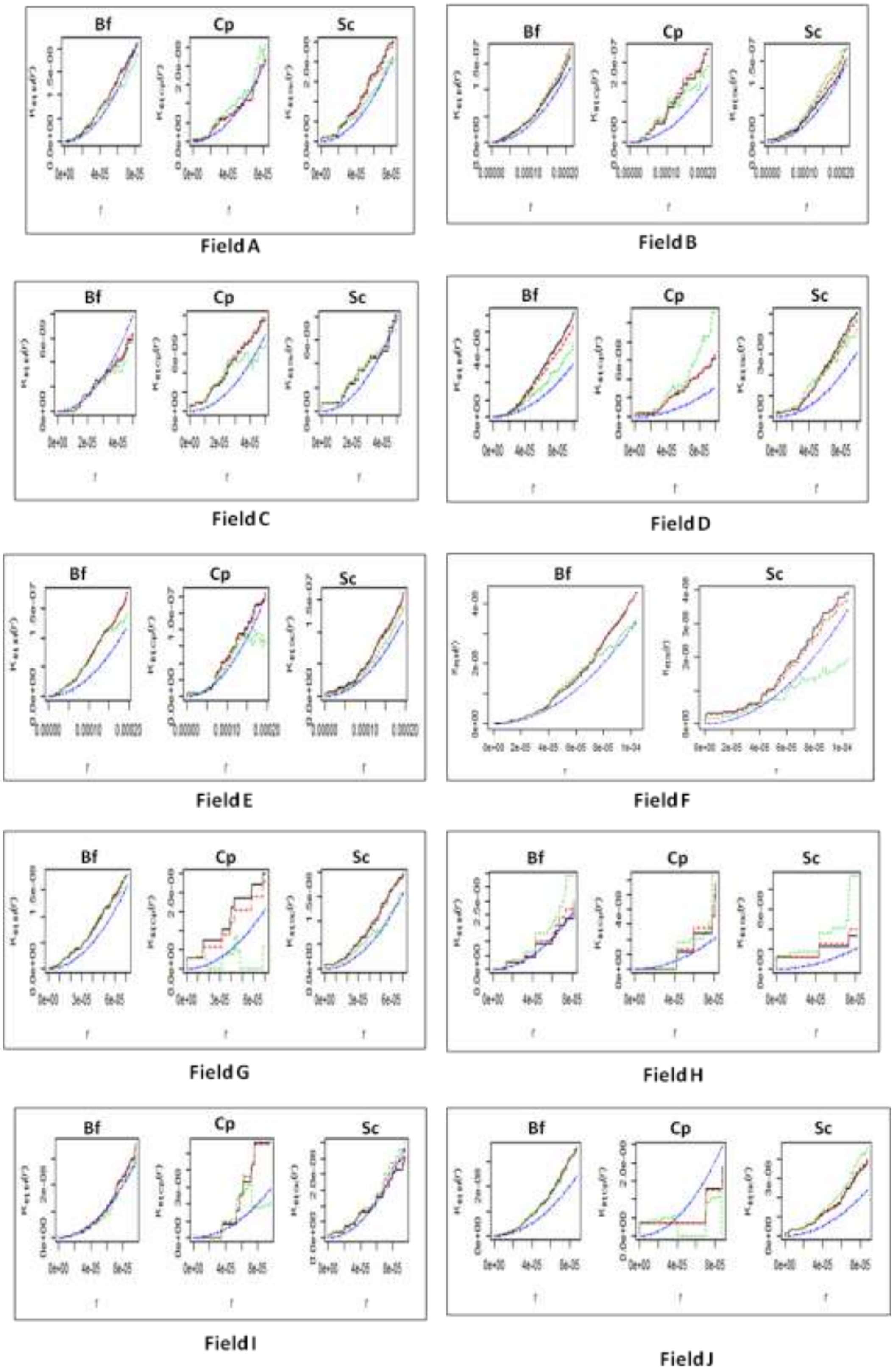


**Figure 3.8.** Clustered distribution pattern of *Busseola fusca* (Bf) intra-specifically and inter-specifically with *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) in each field in the (a) short rain season and (b) long rain season

### 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

| | ***Species*** | | | | | |
|---|---|---|---|---|---|---|
| | ***Busseola fusca*** | | ***Chilo partellus*** | | ***Sesamia calamistis*** | |
| **Environmental factors** | **Z** | **P-value** | **Z** | **P-value** | **Z** | **P-value** |
| **Temperature** | 7.4 | <0.001 | 5.9 | <0.001 | 7.3 | <0.001 |
| **Rainfall** | 17.2 | <0.001 | 7.5 | <0.001 | 7.6 | <0.001 |

### 3.4. Discussion

This study showed that the composition of lepidopteran stemborers 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 stemborers in Kenya and Tanzania (Kalule, 1997; Guofa *et al.,* 2001; Tefera, 2004; Onga'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 stemborer 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 stemborer species composition from the lower to higher altitudes (Guofa *et al.,* 2001; Ong'amo *et al.,* 2006b; 2013). This study, however, also contradicts other studies which indicated that *C. partellus* dominates the stemborer 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

Baddeley, A. (2008). *Analysing spatial point patterns in R*: Technical report, CSIRO, 2010. Version 4. Available at www. csiro. au/resources/pf16h. html

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. & Whittaker, J.B. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1-16.

Bivand, R.S., Pebesma, E.J., Gómez-Rubio, V. & Pebesma, E.J. (2008). *Applied spatial data analysis with R* . Springer, USA., 374pp.

Connell, J.H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122:661-696.

Cornelissen, T. (2011). Climate change and its effects on terrestrial insects and herbivory patterns. *Neotropical Entomology* 40:155-163.

Cugala, D. & Omwega, C. (2001). Cereal stemborer distribution and abundance, and introduction and establishment of *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) in Mozambique. *International Journal of Tropical Insect Science* 21:281-287.

Damos, P. & Savopoulou-Soultani, M. (2011). Temperature-driven models for insect development and vital thermal requirements. *Psyche: A Journal of Entomology* 2012:13pp.

Dangles, O., Carpio, C., Barragan, A.R., Zeddam, J.-L. & Silvain, J.-F. (2008). Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. *Ecological Applications* 18:1795-1809.

Denno, R.F., McClure, M.S. & Ott, J.R. (1995). Interspecific interactions in phytophagous insects: competition re-examined and resurrected. *Annual Review of Entomology* 40:297-331.

Dunson, W.A. & Travis, J. (1991). The role of abiotic factors in community organization. *American Naturalist* 138:1067-1091.

Gounou, S. & Schulthess, F. (2004). Spatial distribution of lepidopterous stem borers on indigenous host plants in West Africa and its implications for sampling schemes. *African Entomology* 12:171-178.

Guofa, Z., Overholt, W.A. & Mochiah, M.B. (2001). Changes in the distribution of lepidopteran maize stemborers in Kenya from the 1950s to 1990s. *International Journal of Tropical Insect Science* 21:395-402.

Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992). A meta-analysis of competition in field experiments. *The American Naturalist* 140:539-572.

Hodkinson, I.D. (2005). Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80:489-513.

Howe, R.W. (1967). Temperature effects on embryonic development in insects. *Annual Review of Entomology* 12:15-42.

Hudson, E.E. & Stiling, P. (1997). Exploitative competition strongly affects the herbivorous insect community on *Baccharis halimifolia*. *Oikos* 79:521-528.

Imura, O. (2003). Herbivorous arthropod community of an alien weed *Solanum carolinense* L. *Applied Entomology and Zoology* 38:293-300.

Jiang, N., Zhou, G., Overholt, W.A., Muchugu, E. & Schulthess, F. (2006). The temporal correlation and spatial synchrony in the stemborer and parasitoid system of Coast Kenya with climate effects. *Annales de la Société Entomologique de France* 42:381-387

Kalule, T., Ogenga-Latigo, M. & Okoth, V. (1997). Seasonal fluctuations and damage of lepidopteran stemborers of maize in a major agroecozone of Uganda. *African Crop Science Journal* 5:385-393.

Kaplan, I. & Denno, R.F. (2007). Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecology Letters* 10:977-994.

Kaplan, I. & Eubanks, M.D. (2005). Aphids alter the community-wide impact of fire ants. *Ecology* 86:1640-1649.

Karban, R. (1986). Interspecific competition between folivorous insects on *Erigeron glaucus*. *Ecology* 67:1063-1072.

Kfir, R. (1997). Competitive displacement of *Busseola fusca* (Lepidoptera: Noctuidae) by *Chilo partellus* (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* 90:619-624.

Kfir, R., Overholt, W., Khan, Z. & Polaszek, A. (2002). Biology and management of economically important lepidopteran cereal stem borers in Africa. *Annual Review of Entomology* 47:701-731.

Krüger, W., Van den Berg, J. & Van Hamburg, H. (2008) The relative abundance of maize stem borers and their parasitoids at the Tshiombo irrigation scheme in Venda, South Africa. *South African Journal of Plant and Soil* 25:144-151

Le Ru, B.P., Ong'amo, G.O., Moyal, P., Ngala, L. Musyoka, B., Abdullah, Z., Cugala, D., Defabachew, B., Haile, T.A., Kauma Matama, T., Lada, V.Y., Negassi, B., Pallangyo, K., Ravolonandrianina, J., Sidumo, A., Omwega, C.O., Schulthess, F., Calatayud, P.-A. & Silvain, J.-F. (2006b). Diversity of lepidopteran stemborers on monocotyledonous plants in eastern Africa and the islands of Madagascar and Zanzibar revisited. *Bulletin of Entomological Research* 96:555-563.

Lewinsohn, T.M., Novotny, V. & Basset, Y. (2005). Insects on plants: diversity of herbivore assemblages revisited. *Annual Review of Ecology, Evolution, and Systematics* 597-620.

Liss, W., Gut, L. & Westigard, P. (1986). Perspectives on arthropod community structure, organization, and development in agricultural crops. *Annual Review of Entomology* 31:455-478.

Moolman, J., Van den Berg, J., Conlong, D., Cugala, D., Siebert, S. & Le Ru, B. (2014). Species diversity and distribution of lepidopteran stem borers in South Africa and Mozambique. *Journal of Applied Entomology* 138:52-66.

Ndemah, R., Schulthess, F., Poehling, M. & Borgemeister, C. (2001). Spatial dynamics of lepidopterous pests on *Zea mays* (L.) and *Pennisetum purpureum* (Moench) in the forest zone of Cameroon and their implications for sampling schemes. *Journal of Applied Entomology* 125:507-514.

Ofomata, V., Overholt, W., Huis, A.V., Egwuatu, R. & Ngi-Song, A. (1999). Niche overlap and interspecific association between *Chilo partellus* and *Chilo orichalcociliellus* on the Kenya coast. *Entomologia Experimentalis et Applicata* 93:141-148.

Ong'amo, G.O., Le Ru, B.P., Dupas, S., Moyal, P., Calatayud, P.-A. & Silvain, J.-F. (2006a). Distribution, pest status and agro-climatic preferences of lepidopteran stemborers of maize in Kenya. *Annales de la Société Entomologique de France (Nouvelle série)* 42:171-177.

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 lepidopteran stemborers along altitudinal gradient in Kenya. *Annales de la Société Entomologique de France (Nouvelle série)* 42:1-9.

Ong'amo, G., Le Ru, B., Calatayud, P.-A., & Silvain, J.-F. (2013). Composition of stem borer communities in selected vegetation mosaics in Kenya. *Arthropod-Plant Interactions* 7:267-275.

Ovadia, O. & Schmitz, O.J. (2004). Weather variation and trophic interaction strength: sorting the signal from the noise. *Oecologia* 140:398-406.

Overholt, W., Ogedah, K. & Lammers, P. (1994). Distribution and sampling of *Chilo partellus* (Lepidoptera: Pyralidae) in maize and sorghum on the Kenya coast. *Bulletin of Entomological Research* 84:367-378.

Polaszek, A. & Khan, Z.R. (1998). Host plants; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford. pp 3-10.

R Development Team (2014). R*: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Reddy, K. (1998). Maize and Sorghum: East Africa; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford, pp 25-28.

Rocca, M. & Greco, N. (2011). Diversity of herbivorous communities in blueberry crops of different regions of Argentina. *Environmental Entomology* 40:247-259.

Sánchez-Galván, I.R., Quinto, J., Micó, E., Galante, E. & Marcos-García, M.A. (2014). Facilitation among saproxylic insects inhabiting tree hollows in a mediterranean forest: the case of cetonids (Coleoptera: Cetoniidae) and syrphids (Diptera: Syrphidae). *Environmental Entomology* 43:336-343.

Sanders, N. J., Belote, R. T. & Weltzin, J. F. (2004). Multitrophic effects of elevated atmospheric $CO_2$ on understory plant and arthropod communities. *Environmental Entomology* 33:1609-1616.

Soler, R., Badenes-Pérez, F.R., Broekgaarden, C., Zheng, S.J., David, A., Boland, W. & Dicke, M. (2012). Plant-mediated facilitation between a leaf-feeding and a phloem-feeding insect in a brassicaceous plant: from insect performance to gene transcription. *Functional Ecology* 26:156-166.

Speight, M.R., Hunter, M.D. & Watt, A.D. (2008). *Ecology of insects: concepts and applications.* Second edition. John Wiley & Sons Ltd, UK. 628pp.

Sporleder, M., Kroschel, J., Quispe, M.R.G. & Lagnaoui, A. (2004). A temperature-based simulation model for the potato tuberworm, *Phthorimaea operculella* Zeller (Lepidoptera; Gelechiidae). *Environmental Entomology* 33:477-486.

Stam, J.M., Kroes, A., Li, Y., Gols, R., van Loon, J.J.A., Poelman, E.H. & Dicke, M. (2014). Plant Interactions with multiple insect herbivores: from community to genes. *Annual Review of Plant Biology* 65:689-713.

Stiling, P., Rossi, A.M., Cattell, M. & Bowdish, T.I. (1999). Weak competition between coastal insect herbivores. *Florida Entomologist* 82:599-608.

Strong, D.R., Lawton, J.H. & Southwood, S.R. (1984). *Insects on plants. Community patterns and mechanisms:* Blackwell Scientific Publications.

Tefera, T. (2004). Lepidopterous stem borers of sorghum and their natural enemies in eastern Ethiopia. *Tropical Science* 44:128-130.

Truter, J., Van Hamburg, H. & Van den Berg, J. (2014). Comparative diversity of arthropods on Bt Maize and Non-Bt Maize in two different cropping systems in South Africa. *Environmental Entomology* 43:197-208.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351-1363

Van den Berg, J., Van Rensburg, J. & Pringle, K. (1991). Comparative injuriousness of *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Pyralidae) on grain sorghum. *Bulletin of Entomological Research* 81:137-142.

Van Rensburg, J.B.J, Van Rensburg, G.D.J., Giliomee, J.H. & Walters, M.C. (1987a). The influence of rainfall on the seasonal abundance and flight activity of the maize stalk borer, *Busseola fusca* in South Africa. *South African Journal of Plant and Soil* 4:183-187.

Van Rensburg, J.B.J., Walters, M.C. & Giliomee, J.H. (1987b). Ecology of the maize stalk borer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* 77:255-269.

Wale, M. (1999). Population dynamics of the stemborers *Chilo partellus* (Swinhoe), *Busseola fusca* (Fuller) and *Sesamia calamistis* attacking sorghum in central Ethiopia. *International Journal of Tropical Insect Science* 19:149-156.

Woiwod, I.P. (1997). Detecting the effects of climate change on Lepidoptera. *Journal of Insect Conservation* 1:149-158.

Wootton, J.T. & Emmerson, M. (2005). Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics* 36:419-444.

Zuur, A., Ieno, E.N. & Smith G.M. (2007). *Analysing ecological data*: Springer Science & Business Media, 672pp.

# CHAPTER FOUR

# OVIPOSITION RESPONSES OF DIFFERENT STEMBORER 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; Onga'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 heterospecifc 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).

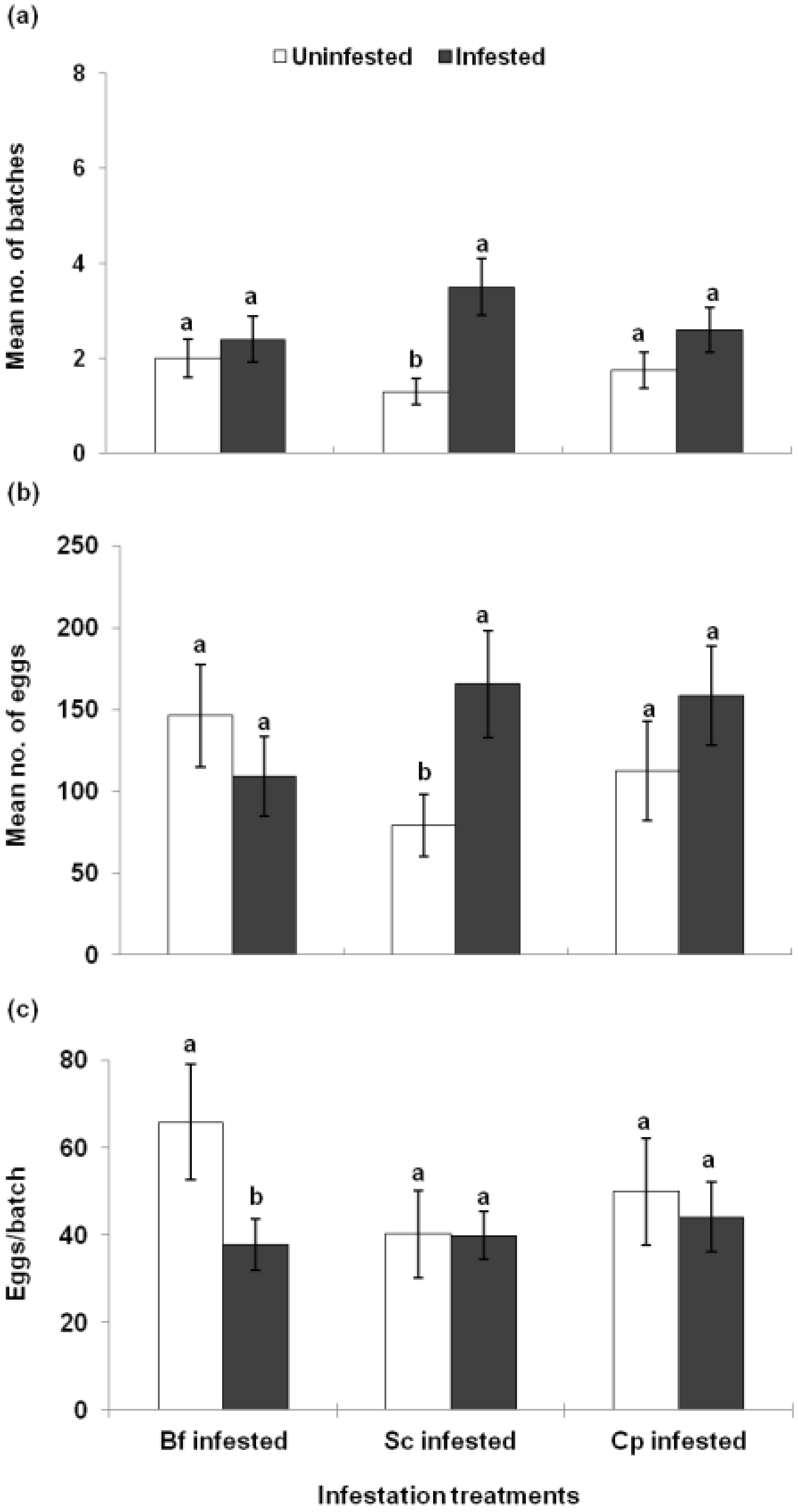


**Figure 4.1.** (a) Mean number of egg batches per female, (b) Mean number of eggs per female and (c) Mean number of eggs per batch, ovposited on uninfested and infested maize plants by *Busseola fusca* (Bf), *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) moths. Bars indicate S.E.

### 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).

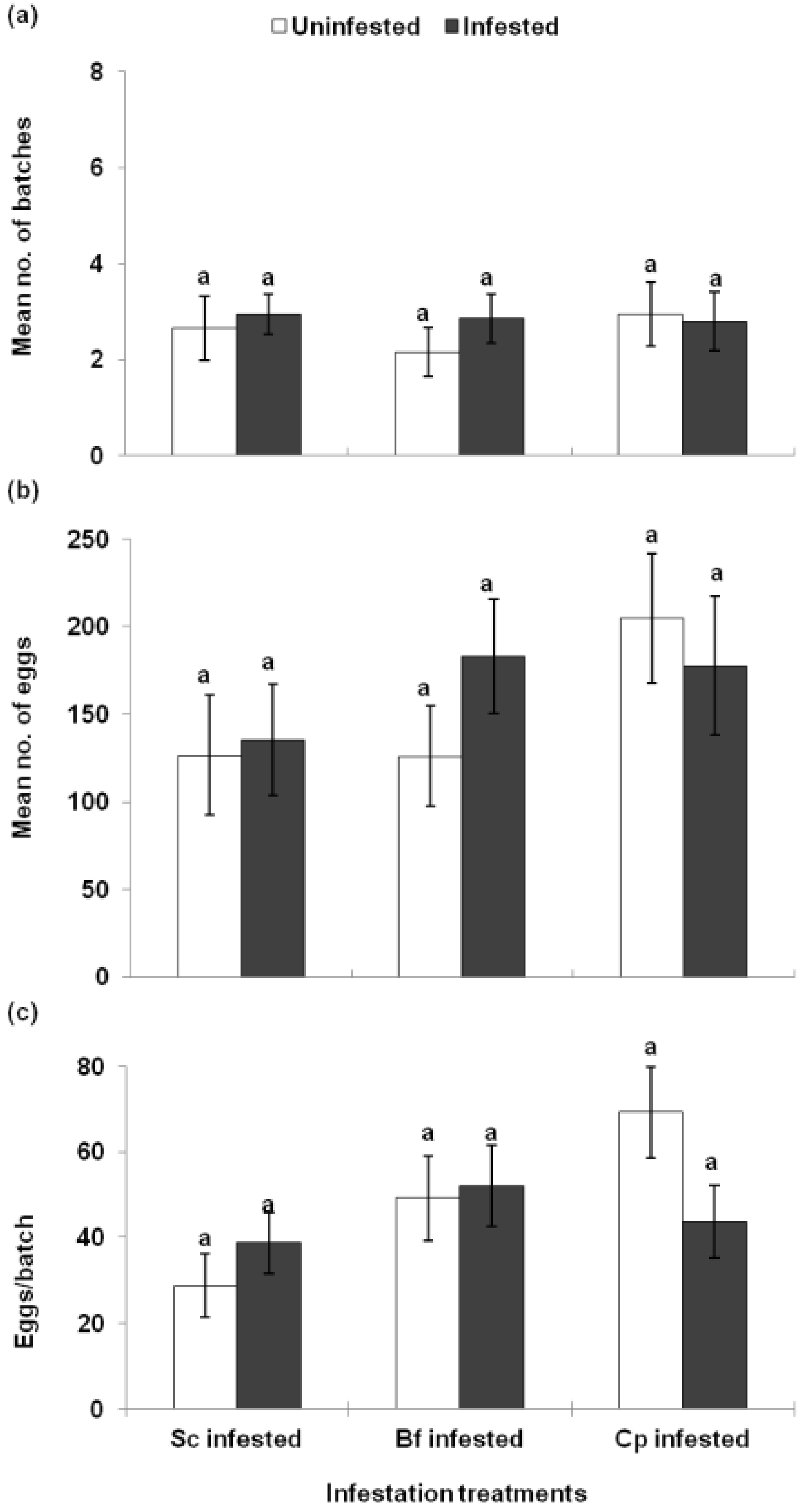


**Figure 4.2.** (a) Mean number of egg batches per female, (b) Mean number of eggs per female and (c) Mean number of eggs per batch ovposited on uninfested and infested maize plants by *Sesamia calamistis* (Sc), *Busseola fusca* (Bf) and *Chilo partellus* (Cp) moths. Bars indicate S.E.

### 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).

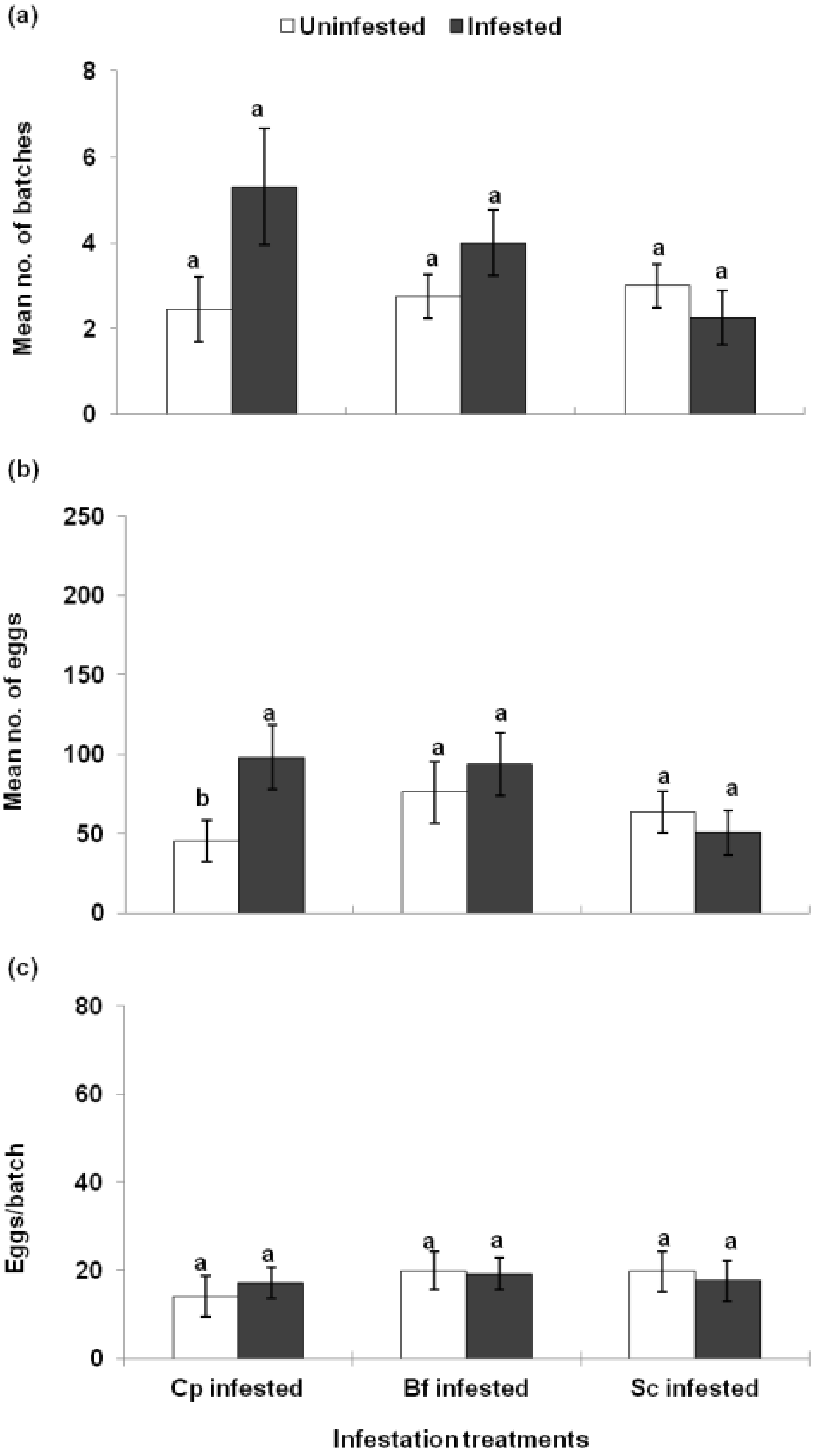


**Figure 4.3.** (a) Mean number of egg batches per female, (b) Mean number of eggs per female and (c) Mean number of eggs per batch ovposited on uninfested and infested maize plants *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) moths. Bars indicate S.E.

**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

| | **Mean number of egg batches** | | **Mean number of eggs** | | **Mean number of eggs / batch** | |
|---|---|---|---|---|---|---|
| **Treatments** | **t** | **p-value** | **t** | **p-value** | **t** | **p-value** |
| *B. fusca*-infested + *B. fusca* moth | 0.67 | 0.51 | 2.14 | 0.35 | 2.03 | 0.04 |
| *S. calamistis*-infested + *B. fusca* moth | 3.42 | 0.001 | 2.31 | 0.02 | 0.03 | 0.98 |
| *C. partellus*-infested + *B. fusca* moth | 1.35 | 0.18 | 1.06 | 0.30 | 0.40 | 0.69 |
| *S. calamistis*-infested + *S. calamistis* moth | 0.38 | 0.71 | 0.19 | 0.85 | 0.96 | 0.34 |
| *B. fusca*-infested + *S. calamistis* moth | 0.95 | 0.35 | 1.30 | 0.20 | 0.21 | 0.83 |
| *C. partellus*-infested + *S. calamistis* moth | 0.16 | 0.87 | 0.50 | 0.62 | 1.86 | 0.07 |
| *C. partellus*-infested + *C. partellus* moth | 1.86 | 0.07 | 2.14 | 0.03 | 0.50 | 0.62 |
| *B. fusca*-infested + *C. partellus* moth | 1.37 | 0.18 | 0.64 | 0.52 | 0.13 | 0.90 |
| *S. calamistis*-infested + *C. partellus* moth | 0.91 | 0.37 | 0.67 | 0.51 | 0.36 | 0.72 |

## 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 obseved 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

Anderson, P. & Alborn, H. (1999). Effects on oviposition behaviour and larval development of *Spodoptera littoralis* by herbivore-induced changes in cotton plants. *Entomologia Experimentalis et Applicata* 92:45-51.

Awmack, C.S. & Leather, S.R. (2002). Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* 47:817-844.

Baur, R., Patrian, B. & Städler, E. (1996). Preference for plants damaged by conspecific larvae in ovipositing cabbage root flies: influence of stimuli from leaf surface and roots. *Entomologia Experimentalis et Applicata* 81:353-364.

Bernays, E.A. & Chapman, R.E. (1994). *Host-plant selection by phytophagous insects*. Chapman and Hall, New York, USA. 312pp.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119-125.

Calatayud, P.-A., Guénégo, H., Ahuya, P., Wanjoya, A., Le Ru, B., Silvain, J-.F. & Frérot, B. (2008a). Flight and oviposition behaviour of the African stem borer, *Busseola fusca*, on various host plant species. *Entomologia experimentalis et applicata 129*:348-355.

Calatayud, P.-A., Juma, G., Njagi, P.G.N., Faure, N., Calatayud, S., Dupas, S., Le Ru, B.P., Magoma, G., Silvain, J.-F. & Frérot, B. (2008b). Differences in mate acceptance and host plant recognition between wild and laboratory-reared *Busseola fusca* (Fuller). *Journal of Applied Entomology* 132:255-264.

Courtney, S.P., Chen, G.K. & Gardner, A. (1989). A general model for individual host selection. *Oikos* 55:55-65.

Craig, T.P., Itami, J.K., Shantz, C., Abrahamson, W.G., Horner, J. & Craig, J.V. (2000). The influence of host plant variation and intraspecific competition on oviposition preference and offspring performance in the host races of *Eurosta solidaginis*. *Ecological Entomology* 25:7-18.

Cunningham, J.P., Jallow, M.F., Wright, D.J. & Zalucki, M.P. (1998). Learning in host selection in *Helicoverpa armigera* (Hübner)(Lepidoptera: Noctuidae). *Animal Behaviour* 55:227-234.

Cunningham, J.P., Zalucki, M.P. & West, S.A. (1999). Learning in Helicoverpa armigera (Lepidoptera: Noctuidae): a new look at the behaviour and control of a polyphagous pest. *Bulletin of Entomological Research* 89:201-207.

De Moraes, C.M., Mescher, M.C. & Tumlinson, J.H. (2001). Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* 410: 577-580.

Denno, R.F. & Kaplan, I. (2007). Plant-mediated interactions in herbivorous insects: mechanisms, symmetry, and challenging the paradigms of competition past; In *Ecological Communities: Plant Mediation in Indirect Interaction Webs*, Ohgushi, T., Craig, T. P. & Price, P. W. (eds) Cambridge University Press, UK. pp 19-50.

Denno, R.F., McClure, M.S. & Ott, J.R. (1995). Interspecific interactions in phytophagous insects: competition re-examined and resurrected. *Annual Review of Entomology* 40:297-331.

Facknath, S. (2012). Study of herbivore response to the presence of conspecifics and heterospecifics in an insect-host plant relationship. *University of Mauritius Research Journal* 18:250-274.

Faeth, S.H. (1986). Indirect interactions between temporally separated herbivores mediated by the host plant. *Ecology* 67:479-494.

Fatouros, N.E., Lucas-Barbosa, D., Weldegergis, B.T., Pashalidou, F.G., van Loon, J.J., Dicke, M., Harvey, J.A., Gols, R. & Huigens, M.E. (2012). Plant volatiles induced by herbivore egg deposition affect insects of different trophic levels. *PLoS ONE* 7:e43607.

Fisher, A.E.I., Hartley, S.E. & Young, M. (2000). Direct and indirect competitive effects of foliage feeding guilds on the performance of the birch leaf-miner *Eriocrania*. *Journal of Animal Ecology* 69:165-176.

Glas, J., Van den Berg, J. & Potting, R. (2007). Effect of learning on the oviposition preference of field-collected and laboratory-reared *Chilo partellus* (Lepidoptera: Crambidae) populations. *Bulletin of Entomological Research* 97:415-420.

Gripenberg, S., Mayhew, P.J., Parnell, M. & Roslin, T. (2010). A meta-analysis of preference-performance relationships in phytophagous insects. *Ecology Letters* 13:383-393.

Groot, A., Heijboer, A., Visser, J. & Dicke, M. (2003). Oviposition preference of *Lygocoris pabulinus* (Het., Miridae) in relation to plants and conspecifics. *Journal of Applied Entomology* 127:65-71.

Guofa, Z., Overholt, W.A. & Mochiah, M.B. (2001) Changes in the distribution of lepidopteran maize stemborers in Kenya from the 1950s to 1990s. *International Journal of Tropical Insect Science* 21:395-402.

Hausmann, S. & Miller, J. (1989). Ovipositional preference and larval survival of the onion maggot (Diptera: Anthomyiidae) as influenced by previous maggot feeding. *Journal of Economic Entomology* 82:426-429.

Jaenike, J. (1978). On optimal oviposition behavior in phytophagous insects. *Theoretical Population Biology* 14:350-356.

Kaplan, I. & Denno, R.F. (2007). Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecology Letters* 10:977-994.

Kfir, R. (1997). Competitive displacement of *Busseola fusca* (Lepidoptera:Noctuidae) by *Chilo partellus* (Lepidoptera: Pyralidae). *Ecology and Population Biology* 90:619-624.

Kfir,R., Overholt, W.A., Khan, Z.R. & Polaszek, A. (2002). Biology and management of economically important lepidopteran cereal stemborers in Africa. *Annual Review of Entomology* 47:701–731.

Klomp, H. (1964). Intraspecific competition and the regulation of insect numbers. *Annual Review of Entomology* 9:17-40.

Krüger, W., Van den Berg, J., & Van Hamburg, H. (2008) The relative abundance of maize stem borers and their parasitoids at the Tshiombo irrigation scheme in Venda, South Africa. *South African Journal of Plant and Soil* 25:144-151.

Lum, P. (1979). Degeneration of ova in the bulla seminalis of Lepidoptera. *Journal of Insect Physiology* 25:595-599.

Lynch, M.E., Kaplan, I., Dively, G.P. & Denno, R.F. (2006). Host-plant-mediated competition via induced resistance: interactions between pest herbivores on potatoes. *Ecological Applications* 16:855-864

Memmott, J., Gibson, R., Carvalheiro, L.G., Henson, K., Heleno, R.H., Mikel, L.M. & Pearce, S. (2007). The conservation of ecological interactions. In *Insect Conservation Biology*, Stewart, A.J.A., New, T.R. & Lewis, O.T. (eds), pp 226-244.

Miller, C.W., Fletcher Jr, R.J. & Gillespie, S.R. (2013). Conspecific and heterospecific cues override resource quality to influence offspring production. *PLoS ONE* 8:e70268.

Minkenberg, O.P., Tatar, M. & Rosenheim, J.A. (1992). Egg load as a major source of variability in insect foraging and oviposition behavior. *Oikos* 65:134-142.

Ochieng, R., Onyango, F. & Bungu, M. (1985). Improvement of techniques for mass-culture of *Chilo partellus* (Swinhoe). *International Journal of Tropical Insect Science* 6:425-428.

Ohgushi, T. (2005). Indirect interaction webs: herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution, and Systematics* 36:81-105.

Oliver, T., Timms, J., Taylor, A. & Leather, S. (2006). Oviposition responses to patch quality in the larch ladybird *Aphidecta obliterata* (Coleoptera: Coccinellidae): effects of aphid density, and con- and heterospecific tracks. *Bulletin of Entomological Research* 96:25-34.

Ong'amo, G.O., Le Ru, B.P., Dupas, S., Moyal, P., Calatayud, P.-A. & Silvain, J.-F. (2006). Distribution, pest status and agro-climatic preferences of Lepidopteran stem borers of maize in Kenya. *Annales de la Société Entomologique de France* (Nouvelle série) 42:171-177.

Ong'amo, G.O., Le Ru, B.P., Moyal, P., Calatayud, P.-A., Le Gall, P., Ogol, C.K.P. O., Kokwaro, E.D., Capdevielle-Dulac, C. & Silvain, J.-F. (2008). Host plant diversity of *Sesamia calamistis*: cytochrome b gene sequences reveal local genetic differentiation. *Entomologia Experimentalis et Applicata* 128:154-161.

Onyango F.O. & Ochieng'-Odero, J.P.R. (1994). Continuous rearing of the maize stemborer *Busseola fusca* on an artificial diet. *Entomologia Experimentalis et Applicata* 73:139-144.

Päts, P. & Ekbom, B. (1994). Distribution of *Chilo partellus* (Lepidoptera: Pyralidae) egg batches on maize. *Journal of Insect Behavior* 7:29-41.

Poelman, E.H., Broekgaarden, C., Van Loon, J.J. & Dicke, M. (2008). Early season herbivore differentially affects plant defence responses to subsequently colonizing herbivores and their abundance in the field. *Molecular Ecology* 17:3352-3365.

R Development Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Reddy, K. (1998). Maize and Sorghum: East Africa; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford, pp 25-28.

Rostás, M. & Hilker, M. (2002). Feeding damage by larvae of the mustard leaf beetle deters conspecific females from oviposition and feeding. *Entomologia Experimentalis et Applicata* 103:267-277.

Sato, Y., Yano, S., Takabayashi, J. & Ohsaki, N. (1999). *Pieris rapae* (Lepidoptera: Pieridae) females avoid oviposition on *Rorippa indica* plants infested by conspecific larvae. *Applied Entomology and Zoology* 34:333-337.

Scheirs, J. & De Bruyn, L. (2002). Integrating optimal foraging and optimal oviposition theory in plant–insect research. *Oikos* 96:187-191.

Schowalter, T.D. (2011). *Insect ecology: an ecosystem approach*, 3rd edition. Academic Press, San Diego, USA. 650p.

Shiojiri, K., Takabayashi, J., Yano, S. & Takafuji, A. (2002). Oviposition preferences of herbivores are affected by tritrophic interaction webs. *Ecology Letters* 5:186-192.

Sigsgaard, L. (2004). Oviposition preference of *Anthocoris nemorum* and *A. nemoralis* for apple and pear. *Entomologia Experimentalis et Applicata* 111:215-223.

Singer, M.C. (2004). Oviposition preference: its definition, measurement and correlates, and its use in assessing risk of host shifts. Paper presented at the XI International Symposium on Biological Control of Weeds.

Speight, M.R., Hunter, M.D. & Watt, A.D. (2008). *Ecology of insects: concepts and applications*. Second edition. John Wiley & Sons Ltd, UK. 628pp.

Tefera, T. (2004). Lepidopterous stem borers of sorghum and their natural enemies in eastern Ethiopia. *Tropical Science* 44:128-130.

Thompson, J.N. (1988). Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata* 47:3-14.

Van den Berg, J. (2006). Oviposition preference and larval survival of *Chilo partellus* (Lepidoptera: Pyralidae) on Napier grass (*Pennisetum purpureum*) trap crops. *International Journal of Pest Management* 52:39-44.

Van den Berg, J., De Bruyn, A. & Van Hamburg, H. (2006). Oviposition preference and survival of the maize stemborer, *Busseola fusca* (Lepidoptera: Noctuidae), on Napier grasses, *Pennisetum spp*., and maize. *African Entomology* 14:211-218.

Viswanathan, D.V., Narwani, A.J. & Thaler, J.S. (2005). Specificity in induced plant responses shapes patterns of herbivore occurrence on *Solanum dulcamara*. *Ecology* 86:886-896.

Wise, M.J. & Weinberg, A.M. (2002). Prior flea beetle herbivory affects oviposition preference and larval performance of a potato beetle on their shared host plant. *Ecological Entomology* 27:115-122.

Wootton, J.T. & Emmerson, M. (2005). Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics* 36:419-444.

Yasuda, H., Takagi, T. & Kogi, K. (2000). Effects of conspecific and heterospecific larval tracks on the oviposition behaviour of the predatory ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology* 97:551-554.

# CHAPTER FIVE

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

### 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**

Ntiri, E.S., Calatayud, P.-A., Van den Berg, J., Schulthess, F. & Le Ru, B.P. (2015). Influence of temperature on intra- and interspecific resource utilization within a community of lepidopteran maize stemborers.

## 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; Onga'mo *et al.*, 2006a; Krüger *et al.*, 2008), although differences exist in the ranges of their wild host plants (Rebe *et al.,* 2000; Ong'amo *et al.,* 2006b). While *B. fusca* and *C. partellus* were identified as oligophagous, *S. calamistis* was found to be polyphagous (Le Ru *et al.*, 2006a; 2006b; Moolman *et al*., 2014). 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

### 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): RGR=(Total mass of surviving larvae-initial mass of larvae)/30 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).

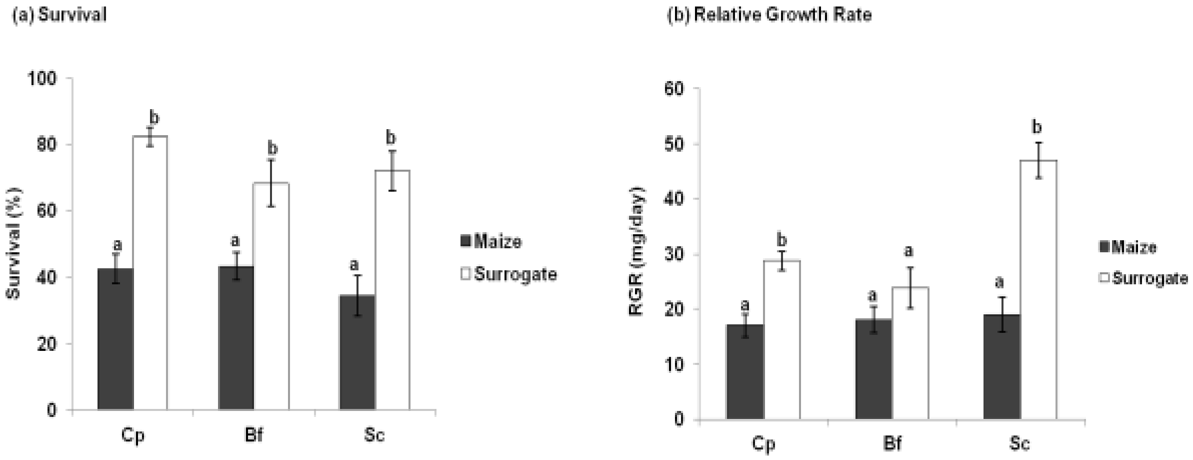


**Figure 5.1**. Survival (a) and relative growth rates (b) of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae on maize and surrogate stems under fluctuating temperatures. Means (± SE) with different letters are significantly different at 5% level according to the GLM 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).

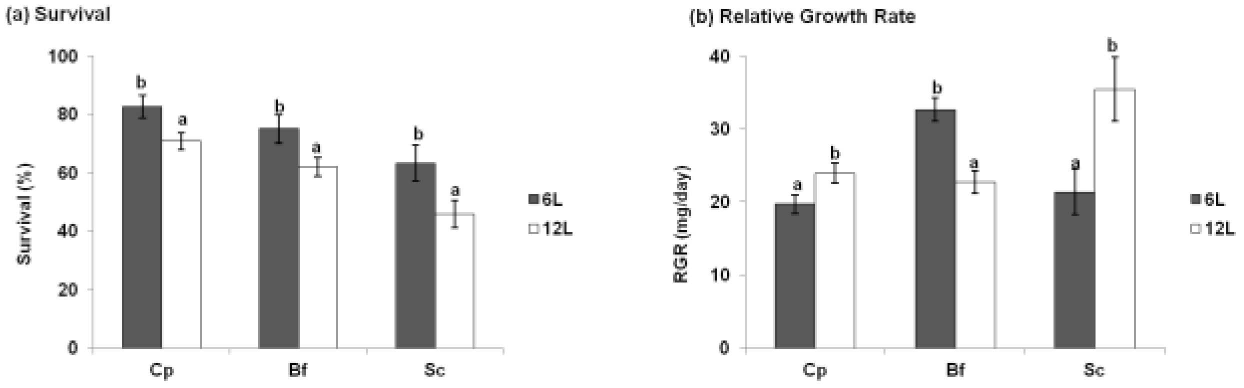


**Figure 5.2**. Survival (a) and relative growth rates (b) of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) at densities of 6 (6L) and 12 (12L) larvae per stem at 25°C. Means (± SE) with different letters are significantly different at 5% level according to the GLM for survival 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).

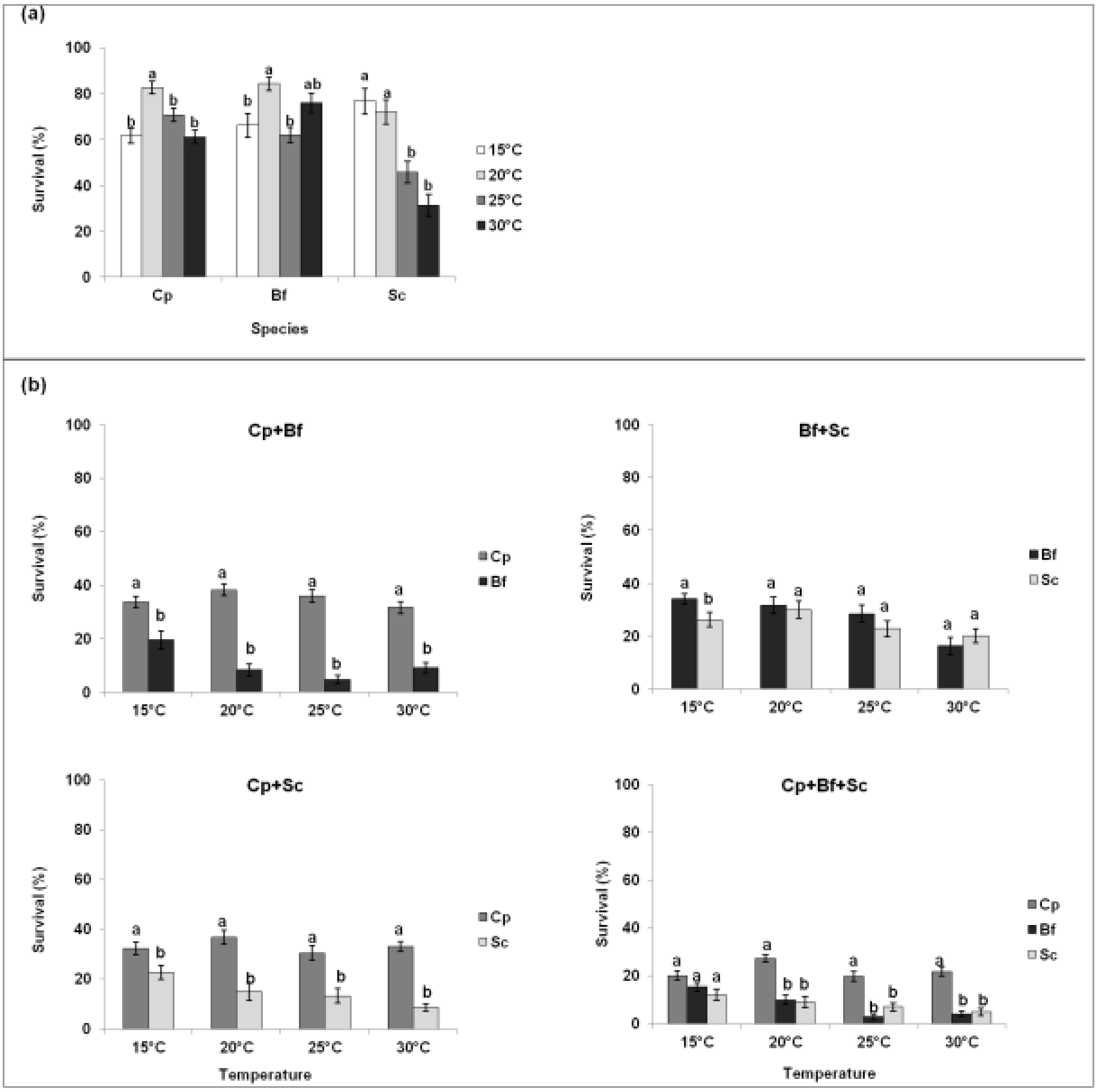


**Figure 5.3.** Comparison of survival of *Chilo partellus* (Cp)*, Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae between (a) different constant temperatures in single-species communities, and between (b) borer species in multi-species communities at different constant temperatures

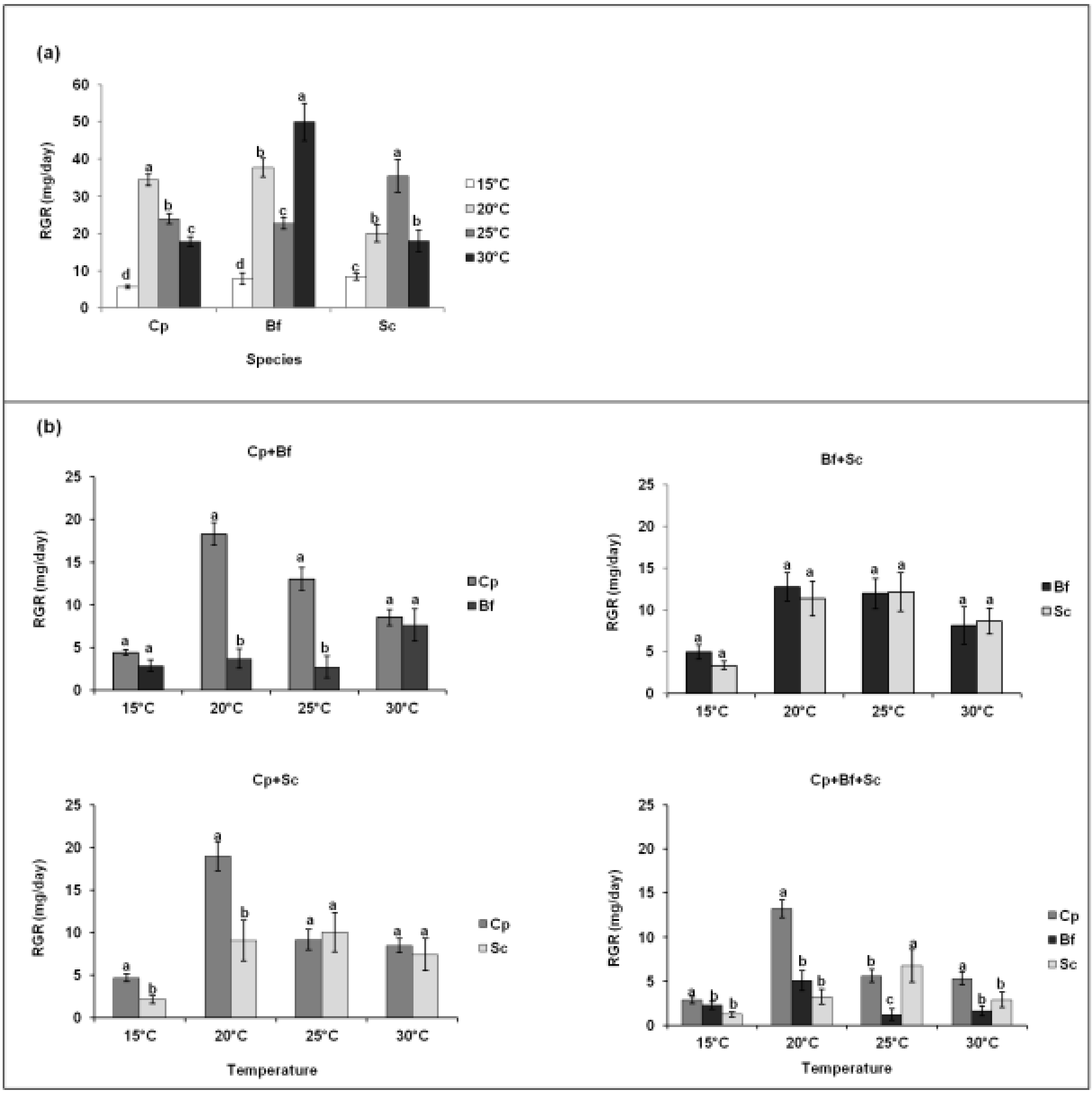


**Figure 5.4.** Comparison of the relative growth rates (RGR) of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae between (a) different constant temperatures in single-species communities, and between (b) borer species in multi-species communities at different constant 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 where 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).

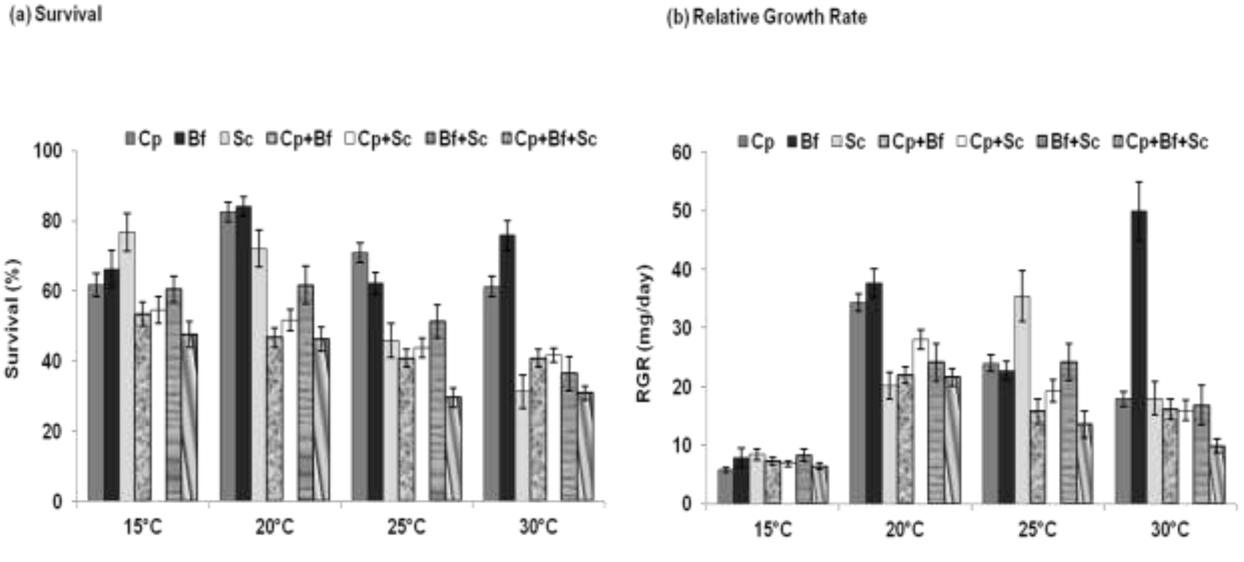


**Figure 5.5**. Comparative survival and RGR between single-species and multi-species communities under different constant temperatures. *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc). Statistical comparisons were only made between single- and the corresponding multi-species 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** | | | | | |
|---|---|---|---|---|---|---|
| | ***Chilo partellus*** | | ***Busseola fusca*** | | ***Sesamia calamistis*** | |
| **Temperature** | **O.R. (95% CI)** | **P-value** | **O.R. (95% CI)** | **P-value** | **O.R. (95% CI)** | **P-value** |
| **15°C** | 1 | | 1 | | 1 | |
| **20°C** | 2.9 (1.9-4.6) | <0.001 | 2.7 (1.5-5.0) | 0.002 | 0.8 (0.4-1.6) | 0.51 |
| **25°C** | 1.5 (1.0-2.2) | 0.04 | 0.8 (0.5-1.4) | 0.49 | 0.3 (0.1-0.5) | <0.001 |
| **30°C** | 1 (0.7-1.4) | 0.93 | 1.6 (0.9-2.8) | 0.1 | 0.1 (0.1-0.3) | <0.001 |

| | **Multi-species communities** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Cp+Bf** | | **Cp+Sc** | | **Bf+Sc** | | **Cp+Bf+Sc (Cp *vs* Bf)** | | **Cp+Bf+Sc (Bf *vs* Sc)** | |
| **Temperature** | **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).

| **Single species** | | |
|---|---|---|
| **Species** | **F** | **P-value** |
| Cp | 94.1 | <0.001 |
| Bf | 36.5 | <0.001 |
| Sc | 15.0 | <0.001 |

| **Multi-species communities** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Cp+Bf** | | **Cp+Sc** | | **Bf+Sc** | | **Cp+Bf+Sc** | |
| **Temperature** | **F** | **P-value** | **F** | **P-value** | **F** | **P-value** | **F** | **P-value** |
| 15°C | 4.1 | 0.04 | 17.3 | <0.001 | 2.4 | 0.13 | 5.1 | 0.009 |
| 20°C | 70.2 | <0.001 | 11.0 | 0.002 | 0.3 | 0.61 | 27.4 | <0.001 |
| 25°C | 31.6 | <0.001 | 0.1 | 0.74 | 0.01 | 0.94 | 6.0 | 0.004 |
| 30°C | 0.1749 | 0.6781 | 0.3 | 0.62 | 0.04 | 0.84 | 6.4 | 0.003 |

**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).

| | **Temperature** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **15°C** | | **20°C** | | **25°C** | | **30°C** | |
| **Treatments comparisons** | **O.R. (95% CI)** | **P-value** | **O.R. (95% CI)** | **P-value** | **O.R. (95% CI)** | **P-value** | **O.R. (95% CI)** | **P-value** |
| Cp *vs* Cp+Bf | 1.4 (1.0-2.1) | 0.08 | 5.4 (3.6-8.2) | <0.001 | 3.5 (2.4-5.2) | <0.001 | 2.3 (1.6-3.3) | <0.001 |
| Cp *vs* Cp+Sc | 0.7 (0.5-1.1) | 0.17 | 0.2 (0.1-0.3) | <0.001 | 0.3 (0.2-0.5) | <0.001 | 0.5 (0.3-0.6) | <0.001 |
| Cp *vs* Cp+Bf+Sc | 1.8 (1.2-2.7) | 0.007 | 5.5 (3.5-8.5) | <0.001 | 5.8 (3.9-8.6) | <0.001 | 3.5 (2.4-5.2) | <0.001 |
| Bf *vs* Cp+Bf | 1.7 (1.0-2.9) | 0.05 | 6.1 (3.9-9.6) | <0.001 | 2.4 (1.6-3.5) | <0.001 | 4.5 (2.9-7.3) | <0.001 |
| Bf *vs* Bf+Sc | 0.8 (0.4-1.3) | 0.37 | 0.3 (0.2-0.6) | <0.001 | 0.6 (0.4-1.0) | 0.06 | 0.2 (0.1-0.3) | <0.001 |
| Bf *vs* Cp+Bf+Sc | 2.2 (1.3-3.7) | 0.007 | 6.2 (3.8-10.2) | <0.001 | 3.9 (2.7-5.7) | <0.001 | 7.0 (4.4-11.3) | <0.001 |
| Sc *vs* Bf+Sc | 2.2 (1.1-4.1) | 0.02 | 1.6 (0.8-3.2) | 0.17 | 0.8 (0.5-1.4) | 0.4 | 0.8 (0.4-1.4) | 0.4 |
| Sc *vs* Cp+Sc | 2.7 (1.5-5.3) | 0.003 | 2.4 (1.4-4.2) | 0.002 | 1.1 (0.7-1.7) | 0.71 | 0.6 (0.4-1.0) | 0.05 |
| Sc *vs* Cp+Bf+Sc | 3.6 (1.9-6.9) | <0.001 | 3.0 (1.7-5.3) | <0.001 | 2.0 (1.3-3.2) | 0.005 | 1.0 (0.6-1.6) | 0.9 |

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).

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

## 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-occuring 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 scenarious and will contribute to the development of possible mitigation and adaption strategies.

## 5.5. References

Agnew, P., Hide, M., Sidobre, C. & Michalakis, Y. (2002). A minimalist approach to the effects of density-dependent competition on insect life-history traits. *Ecological Entomology* 27:396-402.

Agrawal, A.A. (2005). Future directions in the study of induced plant responses to herbivory. *Entomologia Experimentalis et Applicata* 115:97-105.

Alexandrou, M.A., Cardinale, B.J., Hall, J.D., Delwiche, C.F., Fritschie, K., Narwani, A., Venail, P.A., Bentlage, B., Pankey, M.S. & Oakley, T.H. (2015). Evolutionary relatedness does not predict competition and co-occurrence in natural or experimental communities of green algae. *Proceedings of the Royal Society B: Biological Sciences* 282:20141745.

Applebaum, S. & Heifetz, Y. (1999). Density-dependent physiological phase in insects. *Annual Review of Entomology* 44:317-341.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E. G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. & Whittaker, J.B. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1-16.

Berger, A. (1992). Larval movements of *Chilo partellus* (Lepidoptera: Pyralidae) within and between plants: timing, density responses and survival. *Bulletin of Entomological Research* 82:441-448.

Best, R., Caulk, N. & Stachowicz, J. (2013). Trait vs. phylogenetic diversity as predictors of competition and community composition in herbivorous marine amphipods. *Ecology Letters* 16:72-80.

Bezemer, T. M., Jones, T. H. & Knight, K. J. (1998). Long-term effects of elevated CO2 and temperature on populations of the peach potato aphid *Myzus persicae* and its parasitoid *Aphidius matricariae*. *Oecologia* 116:128-135.

Breeuwer, A., Heijmans, M.M., Robroek, B.J. & Berendse, F. (2008). The effect of temperature on growth and competition between *Sphagnum* species. *Oecologia* 156:155-167.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* 18:119-125.

Buse, A., Dury, S., Woodburn, R., Perrins, C. & Good, J. (1999). Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology* 13:74-82.

Calderón-Cortés, N., Quesada, M. & Escalera-Vázquez, L.H. (2011). Insects as stem engineers: interactions mediated by the twig-girdler *Oncideres albomarginata* Chamela enhance arthropod diversity. *PLoS ONE* 6:1-9.

Cammell, M.E. & Knight, J.D. (1992). Effects of climatic-change on the population dynamics of crop pests. *Advances in Ecological Research* 22:117-162.

Cardinale, B. J., Palmer, M. A. & Collins, S. L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426-429.

Carmona-Catot, G., Magellan, K. & García-Berthou, E. (2013). Temperature-specific competition between invasive mosquitofish and an endangered cyprinodontid fish. *PLoS ONE* 8:e54734.

Connell, J.H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122:661-696.

Craig, T.P., Itami, J.K., Shantz, C., Abrahamson, W.G., Horner, J. & Craig, J.V. (2000). The influence of host plant variation and intraspecific competition on oviposition preference and offspring performance in the host races of *Eurosta solidaginis*. *Ecological Entomology* 25:7-18**.**

Damos, P. & Savopoulou-Soultani, M. (2012). Temperature-driven models for insect development and vital thermal requirements. *Psyche*: *A Journal of Entomology* 2012:13 pp.

Dangles, O., Carpio, C., Barragan, A., Zeddam, J.-L. & Silvain, J.-F. (2008). Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. *Ecological Applications* 18:1795-1809.

Davis, A.J., Lawton, J.H., Shorrocks, B. & Jenkinson, L.S. (1998). Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology* 67:600-612.

De Moraes, C.M., Mescher, M.C. & Tumlinson, J.H. (2001). Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* 410:577-580.

Denno, R.F., McClure, M.S. & Ott, J.R. (1995). Interspecific interactions in phytophagous insects: competition re-examined and resurrected. *Annual Review of Entomology* 40:297-331

Duyck, P.-F., David, P. & Quilici, S. (2004). A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). *Ecological Entomology* 29:511-520.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution* 25:325-331.

Gounou, S. & Schulthess, F. (2004). Spatial distribution of lepidopterous stem borers on indigenous host plants in West Africa and its implications for sampling schemes. *African Entomology* 12:171-178**.**

Guofa, Z., Overholt, W.A. & Mochiah, M.B. (2001). Changes in the distribution of lepidopteran maize stemborers in Kenya from the 1950s to 1990s*. International Journal of Tropical Insect Science* 21: 395-402.

Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992). A meta-analysis of competition in field experiments. *The American Naturalist* 140:539-572.

Hodkinson, I.D. (2005). Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* 80:489-513.

Holway, D.A. (1999). Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80:238-251.

Howe, R. (1967). Temperature effects on embryonic development in insects. *Annual Review of Entomology* 12:15-42.

Inbar, M., Eshel, A. & Wool, D. (1995). Interspecific competition among phloem-feeding insects mediated by induced host-plant sinks. *Ecology* 76:1506-1515.

Intergovernmental Panel on Climate Change (2014). *Climate Change 2014: Synthesis Report*. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri & L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Jiang, L. & Morin, P.J. (2004). Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. *Journal of Animal Ecology* 73:69-576.

Jiang, N., Zhou, G., Overholt, W.A., Muchugu, E. & Schulthess, F. (2006). The temporal correlation and spatial synchrony in the stemborer and parasitoid system of Coast Kenya with climate effects. *Annales de la Société entomologique de France* 42:381-387.

Kaplan, I. & Denno, R.F. (2007). Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecology Letters* 10: 977-994.

Kaplan, I. & Eubanks, M.D. (2005). Aphids alter the community-wide impact of fire ants. *Ecology* 86:1640-1649.

Karban, R. (1986). Interspecific competition between folivorous insects on *Erigeron glaucus. Ecology* 67:1063-1072.

Kaufmann, T. (1983). Behavioral biology, feeding habits, and ecology of three species of maize stem-borers: *Eldana saccharina* (Lepidoptera: Pyralidae), *Sesamia calamistis* and *Busseola fusca* (Noctuidae) in Ibadan, Nigeria, West Africa [*Zea mays*]. *Journal of the Georgia Entomological Society* 18:259-272.

Kfir, R. (1997). Competitive Displacement of *Busseola fusca* (Lepidoptera: Noctuidae) by *Chilo partellus* (Lepidoptera: pyralidae). *Ecology and Population Biology* 90:619-624.

Kfir, R., Overholt, W.A., Khan, Z.R. & Polaszek, A. (2002). Biology and management of economically important Lepidopteran cereal stemborers in Africa. *Annual Review of Entomology* 47:701–731.

Khadioli, N., Tonnang, Z.E.H., Ong'amo, G., Achia, T., Kipchirchir, I., Kroschel, J. & Le Ru, B. (2014a). Effect of temperature on the life history parameters of noctuid lepidopteran stem borers, *Busseola fusca* and *Sesamia calamistis*. *Annals of Applied Biology* 165:373-386.

Khadioli, N., Tonnang, Z.E.H., Muchugu, E., Ong'amo, G., Achia, T., Kipchirchir, I., Kroschel, J. & Le Ru, B. (2014b). Effect of temperature on the phenology of *Chilo partellus* (Swinhoe) (Lepidoptera, Crambidae); simulation and visualization of the potential future distribution of *C. partellus* in Africa under warmer temperatures through the development of life-table parameters. *Bulletin of Entomological Research* 104:809-822.

Krüger, W., Van den Berg, J. & Van Hamburg, H. (2008). The relative abundance of maize stemborers and their parasitoids at the Tshiombo irrigation scheme in Venda, South Africa. *South African Journal of Plant and Soil* 25:144-151.

Lactin, D.J., Holliday, N., Johnson, D. & Craigen, R. (1995). Improved rate model of temperature-dependent development by arthropods. *Environmental Entomology* 24:68-75.

Laws, A.N. & Belovsky, G.E. (2010). How will species respond to climate change? Examining the effects of temperature and population density on an herbivorous insect. *Environmental Entomology* 39:312-319.

Le Ru, B.P., Ong'amo, G.O., Moyal, P., Muchugu, E., Ngala, L. Musyoka, B., Abdullah, Z., Matama-Kauma, T., Lada, V.Y., Pallangyo, B., Omwega, C.O., Schulthess, F., Calatayud, P.-A. & Silvain, J.-F. (2006a). Geographic distribution and host plant ranges of East African noctuid stem borers. *Annales de la Société Entomologique de France* (Nouvelle série) 42:353-361.

Le Ru, B.P., Ong'amo, G.O., Moyal, P., Ngala, L. Musyoka, B., Abdullah, Z., Cugala, D., Defabachew, B., Haile, T.A., Kauma Matama, T., Lada, V.Y., Negassi, B., Pallangyo, K., Ravolonandrianina, J., Sidumo, A., Omwega, C.O., Schulthess, F., Calatayud, P.-A. & Silvain, J.-F. (2006b). Diversity of Lepidopteran stemborers on monocotyledonous plants in Eastern Africa and the islands of Madagascar and Zanzibar revisited. *Bulletin of Entomological Research* 96:555-563.

Leibold, M.A. (1995). The niche concept revisited: mechanistic models and community context. *Ecology* 76:1371-1382.

Lill, J.T. & Marquis, R.J. (2003). Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology* 84:682-690.

Logan, J., Wollkind, D., Hoyt, S. & Tanigoshi, L. (1976). An analytic model for description of temperature dependent rate phenomena in arthropods. *Environmental Entomology* 5:1133-1140.

Lounibos, L.P., Suárez, S., Menéndez, Z., Nishimura, N., Escher, R.L., O'Connell, S.M. & Rey, J.R. (2002). Does temperature affect the outcome of larval competition between *Aedes aegypti* and *Aedes albopictus*? *Journal of Vector Ecology* 27:86-95.

Matama-Kauma, T., Kyamanywa, S., Ogwang, J., Omwega, C. & Willson, H. (2001). Cereal stemborer species complex and establishment of *Cotesia flavipes* Cameron in eastern Uganda. *International Journal of Tropical Insect Science* 21:317-325.

Moolman, J., Van den Berg, J., Conlong, D., Cugala, D., Siebert, S. & Le Ru, B. (2014). Species diversity and distribution of lepidopteran stem borers in South Africa and Mozambique. *Journal of Applied Entomology* 138:52-66.

Moya-Laraño, J., El-Sayyid, M.E.T. & Fox, C.W. (2007). Smaller beetles are better scramble competitors at cooler temperatures. *Biology Letters* 3:475-478.

Ndemah, R., Schulthess, F., Korie, S., Borgemeister, C., Poehling, H.-M. & Cardwell, K. (2003). Factors affecting infestations of the Stalk Borer *Busseola fusca* (Lepitoptera: Noctuidae) on maize in the forest zone of Cameroon with special reference to Scelionid Egg Parasitoids. *Environmental Entomology* 32:51-60.

Ofomata, V.C., Overholt, W.A., Lux, S.A., Van Huis, A. & Egwuatu, R.I. (2000). Comparative studies on the fecundity, egg survival, larval feeding, and development of *Chilo partellus* and *Chilo orichalcociliellus* (Lepidoptera: Crambidae) on five grasses. *Ecology and Population Biology* 93:492-499.

Ofomata, V.C., Overholt, W.A., Van Huis, A., Egwuatu, R.I. & Ngi-Song, A.J. (1999). Niche overlap and interspecific association between *Chilo partellus* and *Chilo orichalcociliellus* on the Kenya coast. *Entomologia Experimentalis et Applicata* 93:141-148.

Ojeda-Avila, T., Woods, H.A. & Raguso, R. (2003). Effects of dietary variation on growth, composition, and maturation of *Manduca sexta* (Sphingidae: Lepidoptera). *Journal of Insect Physiology* 49:293-306.

Ong’amo, G.O., Le Ru, B.P., Dupas, S., Moyal, P., Calatayud, P.-A. & Silvain, J.-F. (2006a). Distribution, pest status and agro-climatic preferences of lepidopteran stem borers of maize in Kenya. *Annales de la Société Entomologique de France* (Nouvelle série) 42:171-177.

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 lepidopteran stem borers along altitudinal gradient in Kenya. *Annales de la Société Entomologique de France* (Nouvelle série) 42:1-9.

Onyango F.O. & Ochieng’-Odero, J.P.R. (1994). Continuous rearing of the maize stemborer *Busseola fusca* on an artificial diet. *Entomologia Experimentalis et Applicata* 73:139-144.

Pascual, S. & Callejas, C. (2004). Intra-and interspecific competition between biotypes B and Q of *Bemisia tabaci* (Hemiptera: Aleyrodidae) from Spain. *Bulletin of Entomological Research* 94:369-375.

R Development Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Rebe, M., Van Den Berg, J. & McGeoch, M. (2004). Colonization of cultivated and indigenous graminaceous host plants by *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) and *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) under field conditions. *African Entomology* 12:187-199.

Reddy, K. (1998). Maize and Sorghum: East Africa; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford pp 25-28.

Rwomushana, I., Ekesi, S., Ogol, C.K. & Gordon, I. (2009). Mechanisms contributing to the competitive success of the invasive fruit fly *Bactrocera invadens* over the indigenous mango fruit fly, *Ceratitis cosyra*: the role of temperature and resource pre-emption. *Entomologia Experimentalis et Applicata* 133:27-37.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. & Weller, S.G. (2001). The population biology of invasive species. *Annual Review of Ecology and Systematics* 32:305-332.

Schoonhoven, L.M., van Loon, J.J.A. & Dicke, M. (2005). *Insect-plant biology*. Second Edition. Oxford University Press, 421pp.

Shanower, T., Schulthess, F. & Bosque-Perez, N. (1993). Development and fecundity of *Sesamia calamistis* (Lepidoptera: Noctuidae) and *Eldana saccharina* (Lepidoptera: Pyralidae). *Bulletin of Entomological Research* 83:237-243.

Shiojiri, K., Takabayashi, J., Yano, S. & Takafuji, A. (2002). Oviposition preferences of herbivores are affected by tritrophic interaction webs. *Ecology Letters* 5:186-192.

Speight, M.R., Hunter, M.D. & Watt, A.D. (2008). *Ecology of insects: concepts and applications.* Second edition. John Wiley & Sons Ltd, UK. 628pp.

Sporleder, M., Kroschel, J., Quispe, M.R.G. & Lagnaoui, A. (2004). A temperature-based simulation model for the potato tuberworm, *Phthorimaea operculella* Zeller (Lepidoptera; Gelechiidae). *Environmental Entomology* 33:477-486.

Stachowicz, J.J. (2001). Mutualism, facilitation, and the structure of ecological communities. *BioScience* 51:235-246.

Stiling, P.D. & Strong, D.R. (1983). Weak competition among spartina stem borers, by means of murder. *Ecology* 64:770-778.

Stokes, K. & Stiling, P. (2015). Indirect competitive effects of stemborers on a gall community. *Entomologia Experimentalis et Applicata* 154:23-27.

Taniguchi, Y. & Nakano, S. (2000). Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology* 81:2027-2039.

Taniguchi, Y., Rahel, F.J., Novinger, D.C. & Gerow, K.G. (1998). Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1894-1901.

Tefera, T. (2004). Lepidopterous stem borers of sorghum and their natural enemies in eastern Ethiopia. *Tropical Science* 44:128-130.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351-1363.

Van den Berg, J., Van Rensburg, J.B.J. & Pringle, K.L. (1991). Comparative injuriousness of *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Pyralidae) on grain sorghum. *Bulletin of Entomological Research* 82:137-143.

Van Rensburg, J.B.J, Van Rensburg, G.D.J, Giliomee, J. & Walters, M. (1987). The influence of rainfall on the seasonal abundance and flight activity of the maize stalk borer, *Busseola fusca* in South Africa. *South African Journal of Plant and Soil* 4:183-187.

Venail, P.A., Narwani, A., Fritschie, K., Alexandrou, M.A., Oakley, T.H. & Cardinale, B.J. (2014). The influence of phylogenetic relatedness on species interactions among freshwater green algae in a mesocosm experiment. *Journal of Ecology* 102:1288-1299.

Violle, C., Nemergut, D.R., Pu, Z. & Jiang, L. (2011). Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters* 14:782-787.

Wang, H., Reitz, S.R., Xiang, J., Smagghe, G. & Lei, Z. (2014). Does temperature-mediated reproductive success drive the direction of species displacement in two invasive species of leafminer fly? *PLoS ONE* 9:e98761.

Wilson, D.S., Knollenberg, W. & Fudge, J. (1984). Species packing and temperature dependent competition among burying beetles (Silphidae: Nicrophorus). *Ecological Entomology* 9:205-216.

Zilli, A., Ronkay, L. & Fibiger, M. (2005). Noctuidae Europaeae. 8. Apameini: Entomological Press Sorø.

# 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 2nd 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 = (Total mass of surviving larvae - Initial mass of surviving larvae)/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).

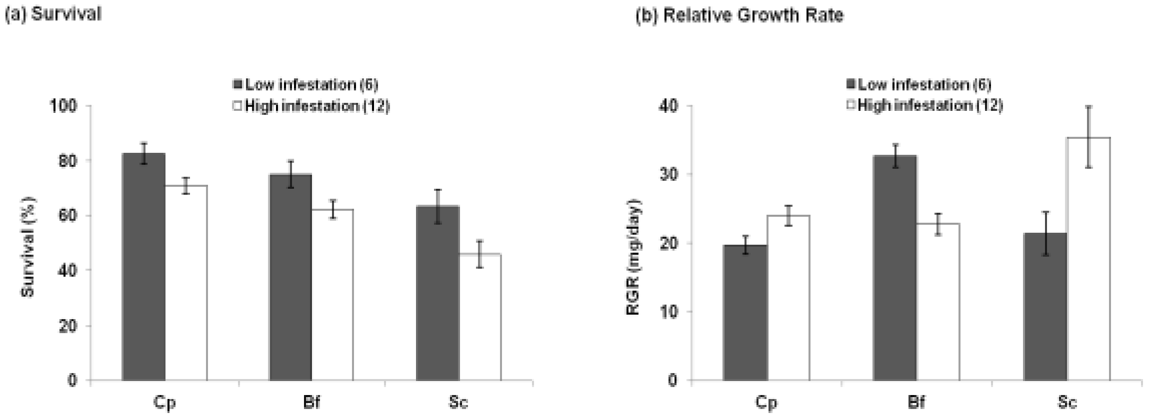


**Figure 6.1.** Survival (a) and relative growth rate (b) of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae at low (6) and high (12) single species infestations. Bars indicate S.E.

### 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 species in combination (Cp+Bf+Sc) differed significantly from each other at high infestation levels (Figure 6.2b, Table 6.2).

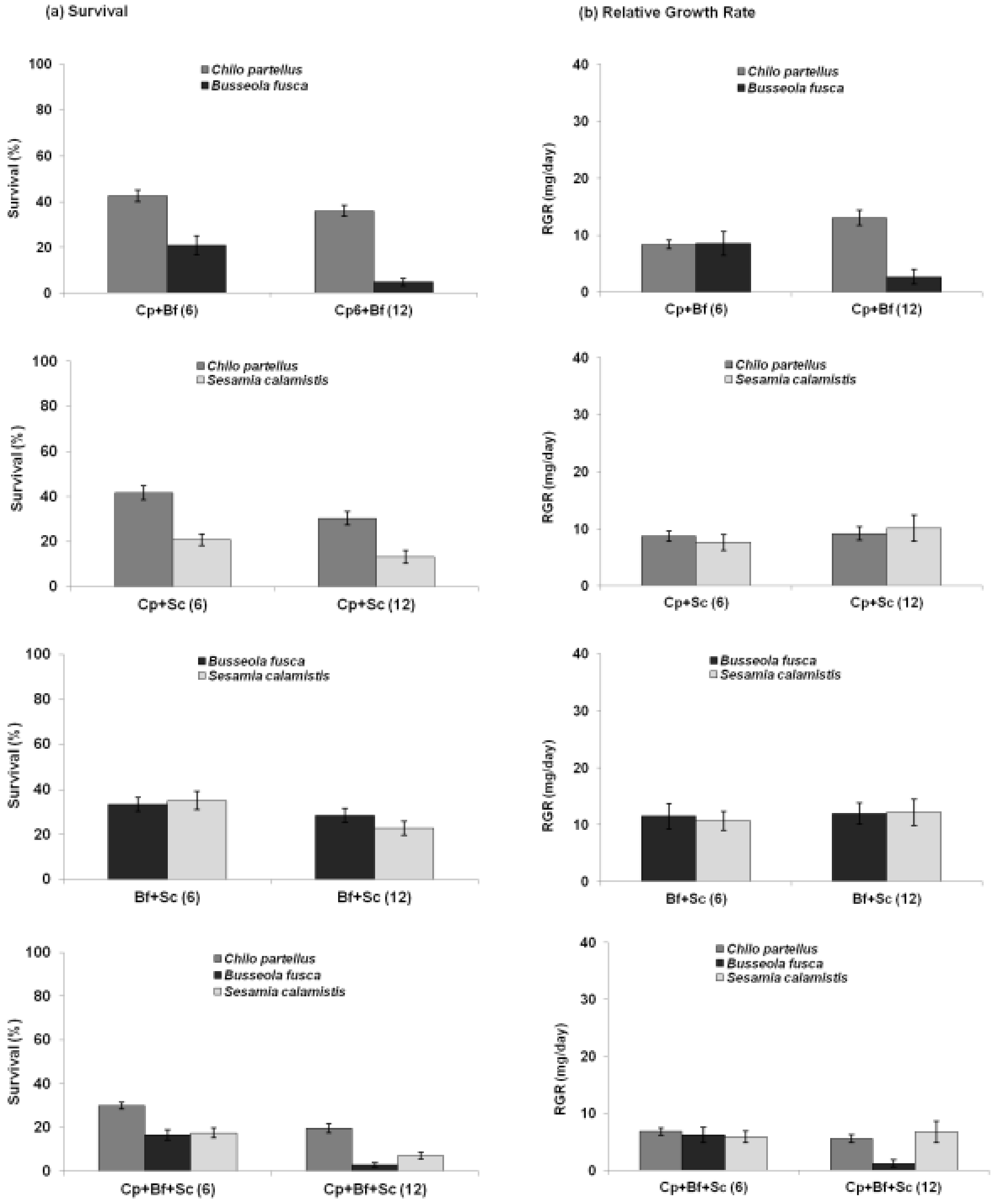
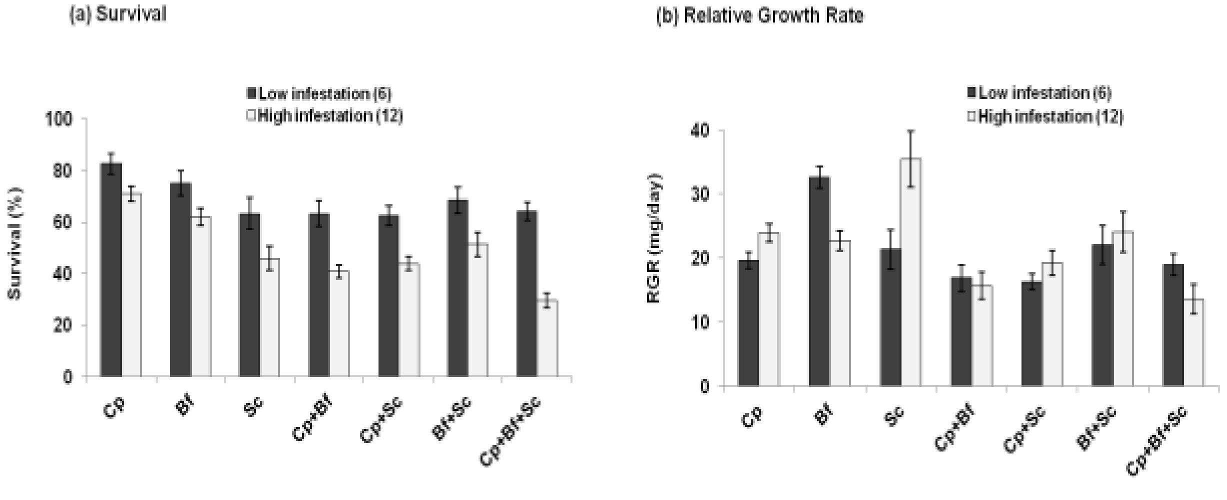


**Figure 6.2.** Survival (a) and relative growth rate (b) of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae in different species combinations at low (6) and high (12) infestation levels. Bars indicate S.E.

### 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).


(a) Survival

(b) Relative Growth Rate

**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).

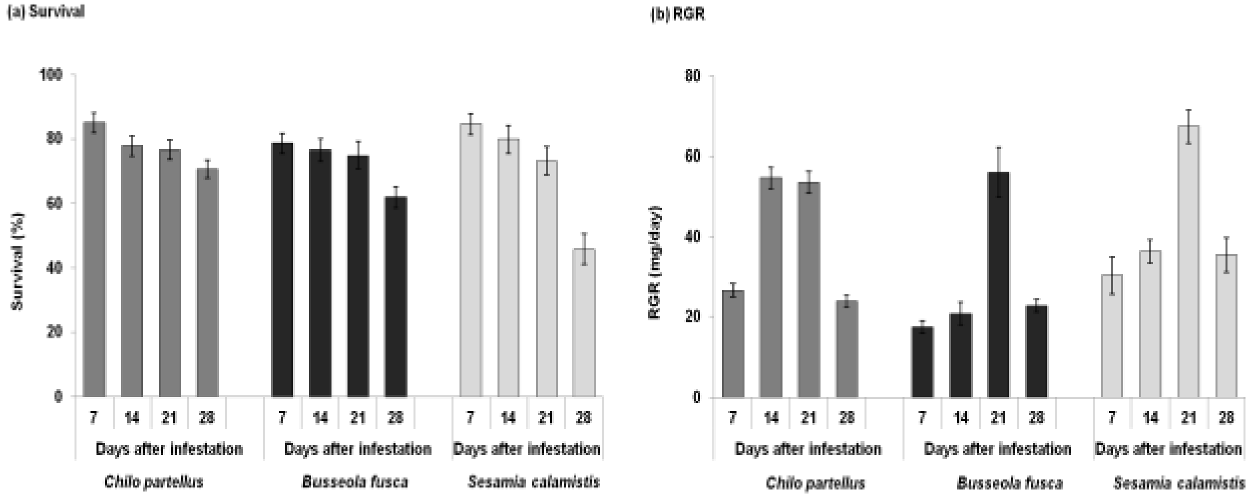


**Figure 6.4.** Survival (a) and relative growth rate (RGR) (b) of single-species infestations of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae on different days after infestation. Bars indicate S.E.

### 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).

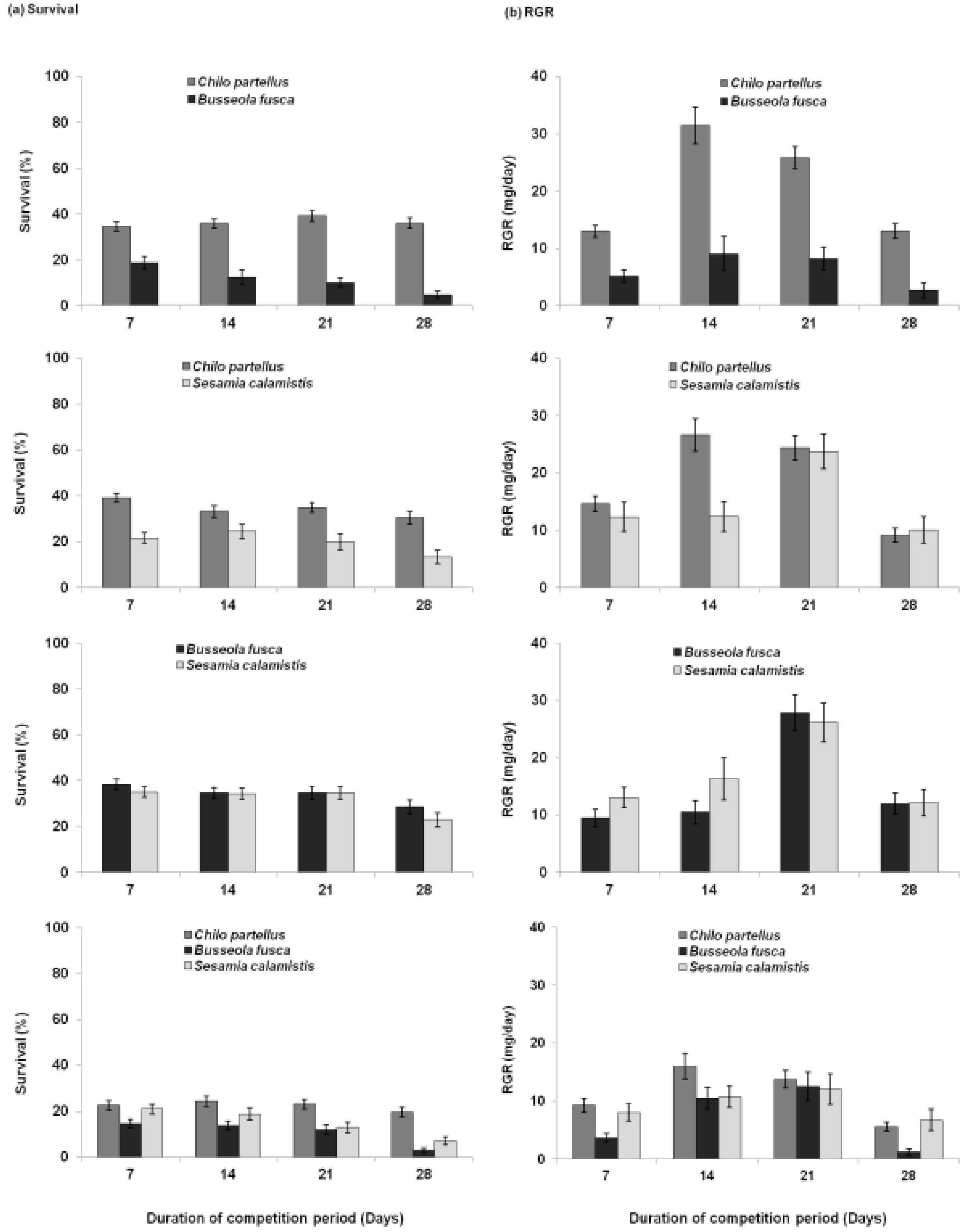


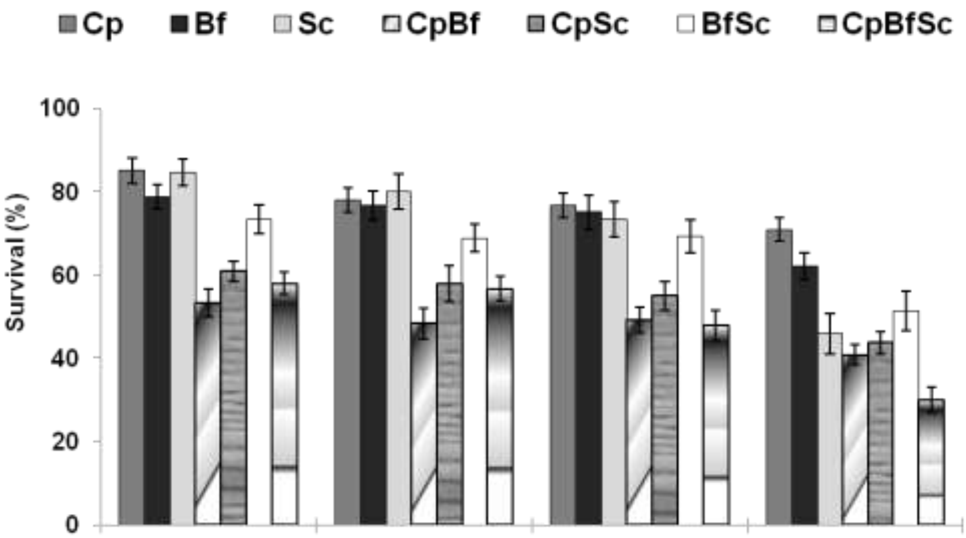
**Figure 6.5.** Survival (a) and relative growth rate (RGR) (b) of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) larvae in multi-species communities on different days after infestation. Bars indicate S.E.

### 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).

(a) Survival



(b) RGR

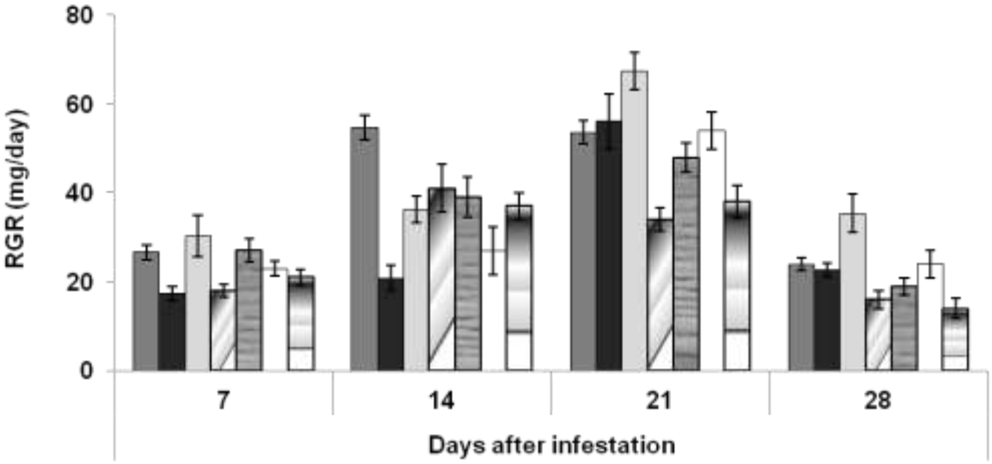


**Figure 6.6.** Survival (a) and relative growth rate (RGR) (b) of larvae in single- and multi-species communities of *Chilo partellus* (Cp), *Busseola fusca* (Bf) and *Sesamia calamistis* (Sc) on different days after infestation

**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

| | Single-species treatments | |
|---|---|---|
| **Treatments** | **O.R. (95%CI)** | **P-value** |
| Cp (6) & Cp (12) | 1.9 (1.1-3.5) | 0.02 |
| Bf (6) & Bf (12) | 1.8 (1.1-3.2) | 0.03 |
| Sc (6) & Sc (12) | 2.0 (1.1-3.9) | 0.03 |

| | Multi-species treatments | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Cp+Bf** | | **Cp+Sc** | | **Bf+Sc** | | **Cp+Bf+Sc (Bf vs Cp)** | | **Cp+Bf+Sc (Bf vs Sc)** | |
| **Treatments** | **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** |
| Low infestation level | 7.9 (2.9-24.7) | <0.001 | 0.14 (0.05-0.35) | <0.001 | 1.18 (0.46-3) | 0.73 | 9 (2.9-34.3) | <0.001 | 1.1 (0.5-2.7) | 0.82 |
| High infestation level | 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 |

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

| | **Single-species treatments** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Treatments** | **F** | **P-value** | | | | | | |
| Cp (6) & Cp (12) | 4.9 | 0.03 | | | | | | |
| Bf (6) & Bf (12) | 19.3 | <0.001 | | | | | | |
| Sc (6) & Sc (12) | 6.9 | 0.01 | | | | | | |
| | **Multi-species treatments** | | | | | | | |
| | **Cp+Bf** | | **Cp+Sc** | | **Bf+Sc** | | **Cp+Bf+Sc** | |
| **Treatment density** | **F** | **P-value** | **F** | **P-value** | **F** | **P-value** | **F** | **P-value** |
| Low larval density (6) | 0.01 | 0.94 | 0.47 | 0.5 | 0.09 | 0.76 | 0.19 | 0.82 |
| High larval density (12) | 32 | <0.001 | 0.1 | 0.74 | 0.01 | 0.94 | 6 | 0.004 |

**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

| | **Low larval numbers (6)** | | **High larval numbers (12)** | |
|---|---|---|---|---|
| **Treatments** | **O.R. (95%CI)** | **P-value** | **O.R. (95%CI)** | **P-value** |
| Bf *vs* Cp+Bf | 0.6 (0.3-1.1) | <0.001 | 2.4 (1.6-3.5) | <0.001 |
| Bf *vs* Bf+Sc | 0.7 (0.4-1.4) | <0.001 | 0.6 (0.4-1.0) | 0.06 |
| Bf *vs* Cp+Bf+Sc | 0.6 (0.3-1.0) | <0.001 | 3.9 (2.7-5.7) | <0.001 |
| | | | | |
| Cp *vs* Cp+Bf | 0.4 (0.2-0.7) | 0.006 | 3.5 (2.4-5.2) | <0.001 |
| Cp *vs* Cp+Sc | 0.4 (0.2-0.6) | 0.001 | 0.3 (0.2-0.5) | <0.001 |
| Cp *vs* Cp+Bf+Sc | 0.4 (0.2-0.7) | 0.002 | 5.8 (3.9-8.6) | <0.001 |
| | | | | |
| Sc *vs* Bf+Sc | 0.8 (0.4-1.6) | 0.52 | 0.8 (0.5-1.4) | 0.4 |
| Sc *vs* Cp+Sc | 1.0 (0.6-1.9) | 0.91 | 1.1 (0.7-1.7) | 0.71 |
| Sc *vs* Cp+Bf+Sc | 1.0 (0.5-1.7) | 0.90 | 2.0 (1.3-3.2) | 0.005 |

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

| | **Low larval numbers (6)** | | **High larval numbers (12)** | |
|---|---|---|---|---|
| **Treatments** | **F** | **P-value** | **F** | **P-value** |
| Bf *vs* Cp+Bf | 36.3 | <0.001 | 3.9 | 0.05 |
| Bf *vs* Bf+Sc | 9.6 | 0.003 | 31.7 | <0.001 |
| Bf *vs* Cp+Bf+Sc | 32.6 | <0.001 | 10.9 | 0.002 |
| | | | | |
| Cp *vs* Cp+Bf | 1.3 | 0.26 | 5.6 | 0.02 |
| Cp *vs* Cp+Sc | 3.6 | 0.07 | 30.3 | <0.001 |
| Cp *vs* Cp+Bf+Sc | 0.1 | 0.75 | 12.5 | 0.001 |
| | | | | |
| Sc *vs* Bf+Sc | 0.0 | 0.86 | 0.9 | 0.35 |
| Sc *vs* Cp+Sc | 2.3 | 0.14 | 0.5 | 0.51 |
| Sc *vs* Cp+Bf+Sc | 0.5 | 0.50 | 0.8 | 0.37 |

**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)

| | **Single-species treatments** | | | | | |
|---|---|---|---|---|---|---|
| **Duration (DAI)** | ***Chilo partellus*** | | ***Busseola fusca*** | | ***Sesamia calamistis*** | |
| | **O.R. (95% CI)** | **P-value** | **O.R. (95% CI)** | **P-value** | **O.R. (95% CI)** | **P-value** |
| 7 | 1 | | 1 | | 1 | |
| 14 | 0.6 (0.4-1.0) | 0.08 | 0.9 (0.5-1.5) | 0.66 | 0.7 (0.3-1.5) | 0.4 |
| 21 | 0.6 (0.3-1.0) | 0.04 | 0.8 (0.5-1.4) | 0.43 | 0.5 (0.2-0.9) | 0.02 |
| 28 | 0.4 (0.3-0.7) | 0.001 | 0.4 (0.3-0.7) | 0.001 | 0.2 (0.1-0.3) | <0.001 |

**Multi-species treatments**

| **Duration (DAI)** | **Cp+Bf** | | **Cp+Sc** | | **Bf+Sc** | | **Cp+Bf+Sc (Bf vs Cp)** | | **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** |
| 7 | 3.7 (2.0-6.8) | <0.001 | 0.2 (0.1-0.4) | <0.001 | 0.7 (0.4-1.3) | 0.3 | 2.7 (1.3-5.6) | 0.01 | 2.1 (1.0-4.5) | 0.04 |
| 14 | 7.6 (3.6-16.7) | <0.001 | 0.5 (0.2-0.3) | 0.03 | 1.0 (0.5-1.7) | 0.9 | 3.8 (1.6-9.0) | 0.003 | 1.8 (0.8-4.1) | 0.14 |
| 21 | 14.5 (7.4-29.8) | <0.001 | 0.3 (0.1-0.6) | 0.001 | 1.0 (0.5-2.0) | 1 | 3.9 (1.8-8.5) | 0.001 | 1.1 (0.5-2.4) | 0.78 |
| 28 | 26.5 (11.8-65.9) | <0.001 | 0.2 (0.1-0.5) | <0.001 | 0.6 (0.3-1.3) | 0.2 | 14.9 (6.0-43.1) | <0.001 | 2.8 (1.1-8.5) | 0.05 |

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)

| **Single-species treatments** | | |
|---|---|---|
| **Single species** | **F** | **P-value** |
| *Chilo partellus* | 57.3 | <0.001 |
| *Busseola fusca* | 25.7 | <0.001 |
| *Sesamia calamistis* | 16.9 | <0.001 |

| **Multi-species treatments** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Cp+Bf** | | **Cp+Sc** | | **Bf+Sc** | | **Cp+Bf+Sc** | |
| **Duration (DAI)** | **F** | **P-value** | **F** | **P-value** | **F** | **P-value** | **F** | **P-value** |
| 7 | 26.7 | <0.001 | 0.6 | 0.43 | 2.47 | 0.12 | 6.43 | 0.003 |
| 14 | 26.6 | <0.001 | 14.0 | <0.001 | 1.93 | 0.17 | 2.50 | 0.09 |
| 21 | 41.2 | <0.001 | 0.03 | 0.87 | 0.13 | 0.72 | 0.15 | 0.86 |
| 28 | 31.6 | <0.001 | 0.1 | 0.74 | 0.01 | 0.94 | 5.99 | 0.004 |

**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)

| | **7DAI** | | **14DAI** | | **21DAI** | | **28DAI** | |
|---|---|---|---|---|---|---|---|---|
| **Treatments** | **O.R. (95% CI)** | **P-value** | **O.R. (95% CI)** | **P-value** | **O.R. (95% CI)** | **P-value** | **O.R. (95% CI)** | **P-value** |
| Bf *vs* Cp+Bf | 0.3 (0.2-0.5) | <0.001 | 0.3 (0.2-0.5) | <0.001 | 0.3 (0.2-0.4) | <0.001 | 2.4 (1.6-3.5) | <0.001 |
| Bf *vs* Bf+Sc | 0.7 (0.4-1.2) | 0.25 | 0.7 (0.4-1.2) | 0.25 | 0.7 (0.4-1.1) | 0.16 | 0.6 (0.4-1.0) | 0.06 |
| Bf *vs* Cp+Bf+Sc | 0.4 (0.2-0.6) | <0.001 | 0.4 (0.3-0.7) | 0.001 | 0.3 (0.2-0.4) | <0.001 | 3.9(2.7-5.7) | <0.001 |
| Cp *vs* Cp+Bf | 0.2 (0.1-0.3) | <0.001 | 0.3 (0.2-0.4) | <0.001 | 0.3 (0.2-0.4) | <0.001 | 3.5(2.4-5.2) | <0.001 |
| Cp *vs* Cp+Sc | 0.2 (0.1-0.4) | <0.001 | 0.3 (0.2-0.5) | <0.001 | 0.5 (0.3-0.7) | <0.001 | 0.3(0.2-0.5) | <0.001 |
| Cp *vs* Cp+Bf+Sc | 0.2 (0.1-0.4) | <0.001 | 0.4 (0.2-0.6) | <0.001 | 0.3 (0.2-0.4) | <0.001 | 5.8(3.9-8.6) | <0.001 |
| Sc *vs* Bf+Sc | 2.0 (1.1-3.7) | 0.02 | 1.8 (1.0-3.3) | 0.05 | 1.2 (0.7-2.1) | 0.47 | 0.8(0.5-1.4) | 0.4 |
| Sc *vs* Cp+Sc | 4.0 (2.2-7.4) | <0.001 | 3.3 (1.9-5.8) | <0.001 | 1.8 (1.1-2.8) | 0.01 | 1.1(0.7-1.7) | 0.71 |
| Sc *vs* Cp+Bf+Sc | 4.0 (2.4-6.7) | <0.001 | 3.1 (1.8-5.3) | <0.001 | 3.0 (1.8-5.0) | <0.001 | 2.0(1.3-3.2) | 0.005 |

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)

| | **Days after infestation** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 7 | | 14 | | 21 | | 28 | |
| | **F** | **P-value** | **F** | **P-value** | **F** | **P-value** | **F** | **P-value** |
| Bf *vs* Cp+Bf | 0.14 | 0.71 | 10.7 | 0.002 | 10.8 | 0.002 | 7.3 | 0.01 |
| Bf *vs* Bf+Sc | 4.9 | 0.03 | 0.98 | 0.33 | 0.08 | 0.78 | 0.2 | 0.69 |
| Bf *vs* Cp+Bf+Sc | 2.19 | 0.15 | 15.6 | <0.001 | 6.2 | 0.01 | 10.9 | 0.002 |
| Cp *vs* Cp+Bf | 13.8 | <0.001 | 5.5 | 0.02 | 26.75 | <0.001 | 10.8 | 0.002 |
| Cp *vs* Cp+Sc | 0.01 | 0.91 | 8.9 | 0.004 | 1.6 | 0.22 | 3.9 | 0.05 |
| Cp *vs* Cp+Bf+Sc | 4.80 | 0.03 | 18.8 | <0.001 | 11.4 | 0.001 | 14.9 | <0.001 |
| Sc *vs* Bf+Sc | 2.5 | 0.12 | 2.5 | 0.13 | 5.1 | 0.02 | 4.3 | 0.04 |
| Sc *vs* Cp+Sc | 0.4 | 0.53 | 0.26 | 0.61 | 12.8 | <0.001 | 11.5 | 0.001 |
| Sc *vs* Cp+Bf+Sc | 3.4 | 0.07 | 3.4 | 0.07 | 27.3 | <0.001 | 19.6 | <0.001 |

### 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., 2*002). 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

Agnew, P., Hide, M., Sidobre, C. & Michalakis, Y. (2002). A minimalist approach to the effects of density-dependent competition on insect life-history traits. *Ecological Entomology* 27:396-402.

Berger, A. (1992). Larval movements of *Chilo partellus* (Lepidoptera: Pyralidae) within and between plants: timing, density responses and survival. *Bulletin of Entomological Research 82*:441-448.

Breden, F. & Chippendale, G.M. (1989). Effect of larval density and cannibalism on growth and development of the southwestern corn borer, *Diatraea grandiosella* and the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Journal of the Kansas Entomological Society* 62:307-315.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* 18:119-125.

Connell, J.H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122:661-696.

DeLong, J.P., Hanley, T.C. & Vasseur, D.A. (2014). Competition and the density dependence of metabolic rates. *Journal of Animal Ecology* 83:51-58.

Denno, R.F., McClure, M.S. & Ott, J.R. (1995). Interspecific interactions in phytophagous insects: competition re-examined and resurrected. *Annual Review of Entomology* 40:297-331.

Dezfuli, B., Volponi, S., Beltrami, I. & Poulin, R. (2002). Intra-and interspecific density-dependent effects on growth in helminth parasites of the cormorant, *Phalacrocorax carbo* sinensis. *Parasitology* 124:537-544.

Duan, J.J., Larson, K., Watt, T., Gould, J. & Lelito, J.P. (2013). Effects of host plant and larval density on intraspecific competition in larvae of the emerald ash borer (Coleoptera: Buprestidae). *Environmental Entomology* 42:1193-1200.

Fantinou, A.A., Perdikis, D.C. & Stamogiannis, N. (2008). Effect of larval crowding on the life history traits of *Sesamia nonagrioides* (Lepidoptera: Noctuidae). *European Journal of Entomology* 105:625-630.

Flockhart, D.T., Martin, T.G. & Norris, D.R. (2012). Experimental examination of intraspecific density-dependent competition during the breeding period in monarch butterflies (*Danaus plexippus*). *PLoS ONE* 7:e45080.

Fordyce, J.A. (2006). The evolutionary consequences of ecological interactions mediated through phenotypic plasticity. *Journal of Experimental Biology* 209:2377-2383.

Futuyma, D.J. & Peterson, S.C. (1985). Genetic variation in the use of resources by insects. *Annual Review of Entomology* 30:217-238.

Gibbs, M., Lace, L.A., Jones, M.J. & Moore, A.J. (2004). Intraspecific competition in the speckled wood butterfly *Pararge aegeria*: effect of rearing density and gender on larval life history. *Journal of Insect Science* 4:16.

Gibson, K., Fischer, A., Foin, T. & Hill, J. (2002). Implications of delayed *Echinochloa* spp. germination and duration of competition for integrated weed management in water-seeded rice. *Weed Research* 42:351-358.

Guofa, Z., Overholt, W.A. & Mochiah, M.B. (2001). Changes in the distribution of lepidopteran maize stemborers in Kenya from the 1950s to 1990s. *International Journal of Tropical Insect Science* 21:395-402.

Hemphill, N. (1991). Disturbance and variation in competition between two stream insects. *Ecology* 72:864-872.

Kfir, R., Overholt, W., Khan, Z. & Polaszek, A. (2002). Biology and management of economically important lepidopteran cereal stem borers in Africa. *Annual Review of Entomology* 47:701-731.

Khadioli, N., Tonnang, Z.E.H., Ong'amo, G., Achia, T., Kipchirchir, I., Kroschel, J. & Le Ru, B. (2014a). Effect of temperature on the life history parameters of noctuid lepidopteran stem borers, *Busseola fusca* and *Sesamia calamistis*. *Annals of Applied Biology* 165:373-386.

Khadioli, N., Tonnang, Z.E.H., Muchugu, E., Ong'amo, G., Achia, T., Kipchirchir, I., Kroschel, J. & Le Ru, B. (2014b). Effect of temperature on the phenology of *Chilo partellus* (Swinhoe) (Lepidoptera, Crambidae); simulation and visualization of the potential future distribution of *C. partellus* in Africa under warmer temperatures through the development of life-table parameters. *Bulletin of Entomological Research* 104:809-822.

Kirkland, K.J. (1993). Spring wheat (*Triticum aestivum*) growth and yield as influenced by duration of wild oat (*Avena fatua*) competition. *Weed Technology* 7:890-893.

Krüger, W., Van den Berg, J. & Van Hamburg, H. (2008) The relative abundance of maize stem borers and their parasitoids at the Tshiombo irrigation scheme in Venda, South Africa. *South African Journal of Plant and Soil* 25:144-151.

Leisnham, P.T. & Juliano, S.A. (2009). Spatial and temporal patterns of coexistence between competing *Aedes* mosquitoes in urban Florida. *Oecologia* 160:343-352.

Manly, B.F., McDonald, L. & Thomas, D. (1993). *Resource selection by animals: statistical design and analysis for field studies*: Springer Science & Business Media. pp 1-4.

Middendorf III, G. (1984). The effects of population density on patterns of resource utilization by Yarrow's spiny lizard. *Journal of the Washington Academy of Sciences* 74:51-60.

Miner, B.G., Sultan, S.E., Morgan, S.G., Padilla, D.K. & Relyea R.A. (2005). Ecological consequences of phenotypic plasticity. *Trends in Ecology & Evolution* 20:685-692.

Muriu, S.M., Coulson, T., Mbogo, C.M. & Godfray, H.C.J. (2013). Larval density dependence in *Anopheles gambiae* ss, the major African vector of malaria. *Journal of Animal Ecology* 82:166-174.

Ojeda-Avila, T., Woods, H.A. & Raguso, R. (2003). Effects of dietary variation on growth, composition, and maturation of *Manduca sexta* (Sphingidae: Lepidoptera). *Journal of Insect Physiology* 49:293-306.

Ong’amo, G.O., Le Ru, B.P., Dupas, S., Moyal, P., Calatayud, P.-A. & Silvain, J.-F. (2006a). Distribution, pest status and agro-climatic preferences of lepidopteran stemborers of maize in Kenya. *Annales de la Société Entomologique de France* (Nouvelle série) 42:171-177.

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 lepidopteran stemborers along altitudinal gradient in Kenya. *Annales de la Société Entomologique de France* (Nouvelle série) 42:1-9.

Onyango F.O. & Ochieng’-Odero, J.P.R. (1994). Continuous rearing of the maize stemborer *Busseola fusca* on an artificial diet. *Entomologia Experimentalis et Applicata* 73:139-144.

R Development Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Reddy, K. (1998). Maize and Sorghum: East Africa; In *African Cereal Stem Borers: Economic importance, taxonomy, natural enemies and control*, Polaszek A. (ed), Wallingford, pp 25-28.

Schneider, P., Takken, W. & McCall, P. (2000). Interspecific competition between sibling species larvae of *Anopheles arabiensis* and *An. gambiae*. *Medical and Veterinary Entomology* 14:165-170.

Schoener, T.W. (1974). Resource partitioning in ecological communities. *Science* 185:27-39.

Schoener, T.W. (1983). Field experiments on interspecific competition. *The American Naturalist* 122:240-285.

Smallegange, I.M. & Tregenza, T. (2008). Local competition between foraging relatives: growth and survival of bruchid beetle larvae. *Journal of Insect Behavior* 21:375-386.

Stachowicz, J.J. (2001). Mutualism, facilitation, and the structure of ecological communities. *BioScience* 51:235-246.

Svensson, E., Sinervo, B. & Comendant, T. (2001). Density-dependent competition and selection on immune function in genetic lizard morphs. *Proceedings of the National Academy of Sciences* 98:12561-12565.

Tamado, T., Ohlander, L. & Milberg, P. (2002). Interference by the weed *Parthenium hysterophorus* L. with grain sorghum: influence of weed density and duration of competition. *International Journal of Pest Management* 48:183-188.

Tardy, O., Massé, A., Pelletier, F., Mainguy, J. & Fortin, D. (2014). Density-dependent functional responses in habitat selection by two hosts of the raccoon rabies virus variant. *Ecosphere* 5:art132-art132.

Tefera, T. (2004). Lepidopterous stemborers of sorghum and their natural enemies in eastern Ethiopia. *Tropical Science* 44:128-130.

Teng, H.-J. & Apperson, C.S. (2000). Development and survival of immature *Aedes albopictus* and *Aedes triseriatus* (Diptera: Culicidae) in the laboratory: effects of density, food, and competition on response to temperature. *Journal of Medical Entomology* 37:40-52.

Thompson, J.N. (1988). Variation in interspecific interactions. *Annual Review of Ecology and Systematics* 19:65-87.

Underwood, N. (2010). Density dependence in insect performance within individual plants: induced resistance to *Spodoptera exigua* in tomato. *Oikos* 119:1993-1999.

Van Hamburg, H. & Hassell, M. (1984). Density dependence and the augmentative release of egg parasitoids against graminaceous stalk borers. *Ecological Entomology* 9:101-108.

Van Hamburg, H. (1980). The grain-sorghum stalk-borer, *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae): survival and location of larvae at different infestation levels in plants of different ages. *Journal of the Entomological Society of southern Africa* 43:71-76.

Wissinger, S.A. (1989). Seasonal variation in the intensity of competition and predation among dragonfly larvae. *Ecology* 70:1017-1027.

Yoshioka, M., Couret, J., Kim, F., McMillan, J., Burkot, T.R., Dotson, E.M., Kitron, U. & Vazquez-Prokopec, G.M. (2012). Diet and density dependent competition affect larval performance and oviposition site selection in the mosquito species *Aedes albopictus* (Diptera: Culicidae). *Parasites & Vectors* 5:225.

# 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

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* 18:119-125.

Dangles, O., Mesías, V., Crespo-Perez, V. & Silvain, J.-F. (2009). Crop damage increases with pest species diversity: evidence from potato tuber moths in the tropical Andes*. Journal of Applied Ecology* 46:1115-1121.

De Moraes, C.M., Mescher, M.C. & Tumlinson, J.H. (2001). Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* 410:577-580.

Denno, R.F., McClure, M.S. & Ott, J.R. (1995). Interspecific interactions in phytophagous insects: competition re-examined and resurrected. *Annual Review of Entomology* 40:297-331.

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E. & Loreau, M. (2007). The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522-538.

Guofa, Z., Overholt, W.A. & Mochiah, M.B. (2001). Changes in the distribution of lepidopteran maize stemborers in Kenya from the 1950s to 1990s*. International Journal of Tropical Insect Science* 21:395-402.

Jaenike, J. (1978). On optimal oviposition behavior in phytophagous insects. *Theoretical Population Biology* 14:350-356.

Jaenike, J. (1990). Host specialization in phytophagous insects. *Annual Review of Ecology and Systematics* 21:243-273.

Kfir, R. (1997). Competitive displacement of *Busseola fusca* (Lepidoptera: Noctuidae) by *Chilo partellus* (Lepidoptera: Pyralidae). *Ecology and Population Biology* 90:619-624.

Kfir, R., Overholt, W.A., Khan, Z.R. & Polaszek, A. (2002). Biology and management of economically important Lepidopteran cereal stemborers in Africa. *Annual Review of Entomology* 47:701–731.

Khadioli, N., Tonnang, Z.E.H., Muchugu, E., Ong'amo, G., Achia, T., Kipchirchir, I., Kroschel, J. & Le Ru, B. (2014). Effect of temperature on the phenology of *Chilo partellus* (Swinhoe) (Lepidoptera, Crambidae); simulation and visualization of the potential future distribution of *C. partellus* in Africa under warmer temperatures through the development of life-table parameters. *Bulletin of Entomological Research* 104:809-822.

Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72-76

Memmott, J., Alonso, D., Berlow, E., Dobson, A. P., Dunne, J.A., Sole, R. & Weitz, J.S. (2006). Biodiversity loss and ecological network structure; In *Ecological Networks: Linking Structure to Dynamics in Food Webs*, Pascual, M. & Dunne, J. A. (eds). Oxford University Press, Oxford, pp 325-347.

Memmott, J., Gibson, R., Carvalheiro, L.G., Henson, K., Heleno, R.H., Mikel, L.M. & Pearce, S. (2007). The conservation of ecological interactions; In *Insect Conservation Biology,* Stewart, A.J.A., New, T.R. & Lewis, O.T. (eds), pp 226-244.

Ofomata, V.C., Overholt, W.A. Lux, S.A., Van Huis, A. & Egwuatu, R.I. (2000). Comparative studies on the fecundity, egg survival, larval feeding, and development of *Chilo partellus* and *Chilo orichalcociliellus* (Lepidoptera: Crambidae) on five grasses. *Ecology and Population Biology* 93:492-499.

Ofomata, V.C., Overholt, W.A., Van Huis, A., Egwuatu, R.I. & Ngi-Song, A.J. (1999). Niche overlap and interspecific association between *Chilo partellus* and *Chilo orichalcociliellus* on the Kenya coast. *Entomologia Experimentalis et Applicata* 93:141-148.

Ong'amo, G.O., Le Ru, B.P., Dupas, S., Moyal, P., Calatayud, P.-A. & Silvain, J.-F. (2006a). Distribution, pest status and agro-climatic preferences of lepidopteran stem borers of maize in Kenya. *Annales de la Société Entomologique de France* (Nouvelle série) 42:171-177.

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 lepidopteran stem borers along altitudinal gradient in Kenya. *Annales de la Société Entomologique de France* (Nouvelle série) 42:1-9

Rebe, M., Van den Berg, J. & McGeoch, M. (2004). Colonization of cultivated and indigenous graminaceous host plants by *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) and *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) under field conditions. *African Entomology* 12:187-199.

Scheirs, J. & De Bruyn, L. (2002). Integrating optimal foraging and optimal oviposition theory in plant–insect research. *Oikos* 96:187-191.

Strong, D.R., Lawton, J.H. & Southwood, S.R. (1984). *Insects on plants. Community patterns and mechanisms:* Blackwell Scientific Publications. CABI, London, UK.

Thompson, J.N. (1988). Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata*, 47:3-14.

Van den Berg, J., Van Rensburg, J.B.J. & Van der Westhuizen, M.C. (1991a). The effect of single and mixed populations of *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Pyralidae) on damage to grain sorghum. *Journal of the Entomological Society of Southern Africa* 54:231-242.

Van den Berg, J., Van Rensburg, J.B.J. & Pringle, K.L. (1991b). Comparative injuriousness of *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Pyralidae) on grain sorghum. *Bulletin of Entomological Research* 82:137-143.

Van Veen, F.J.F., Morris, R.J. & Godfray, H.C.J. (2006). Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology* 51:187-208.