# Effect of temperature on development and reproduction of *Spodoptera frugiperda* (Lepidoptera: Noctuidae)

**M Schlemmer**

orcid.org/0000-0001-8852-2716

Dissertation submitted in fulfilment of the requirements for the *Masters* degree in *Environmental Science* at the North-West University

Supervisor: Prof MJ du Plessis

Co-supervisor: Prof J van den Berg

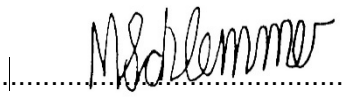
Graduation May 2018

23479523

NWU®
NORTH-WEST UNIVERSITY
NOORDWES-UNIVERSITEIT
UNIBESITI YA BOKONE-BOPHIRIMA

## DECLARATION

I declare that this dissertation is my own work. This dissertation complies with the requirements of Master of Science degree. It is being submitted at the North-West University in Potchefstroom. This has not been submitted before for any degree or at any other university.

Signature of Student .. 

November 2017

## ACKNOWLEDGEMENTS

This project was made possible by the kindness and generosity of many people and it is a great pleasure to thank everyone who has inspired and guided me throughout this journey.

Firstly, I want to thank Prof Johnnie van den Berg, my co-supervisor. You took a big chance accepting me into the Plant Protection course in 2015 and I will be forever grateful to you for believing in me before you even knew me. I have learnt and grown so much during the last years and have enjoyed it immensely. Thank you for your support, encouragement and leadership during the coursework, and for your insightful comments on the project.

The best supervisor every student could wish for, Prof. Hannalene du Plessis. Thank you for everything, words cannot describe what I learned from you. All your patience, positive attitude, strong work ethic, always the time to encouragement me and always believing in me. I want to thank you for the last stretch of the dissertation and for your great help with the statistics and editing work.

I would like to thank my family for their unwavering love, support and encouragement. Thank you for always showing an interest in my work. Thank you for always believing in me. I also want to thank my devoted colleagues for their unconditional support, for standing by me through thick and thin. Finally, I would like to thank my God for the many blessings I received throughout the years and for Your presence in everything I did.

## ABSTRACT

*Spodoptera frugiperda* (Lepidoptera: Noctuidae) is a polyphagous pest with a preference for crops which belong to the Poaceae family. *Spodoptera frugiperda* is native to the tropical and sub-tropical regions of South America and is one of the most serious maize pests in the Americas. This pest recently invaded the tropical regions of Africa, where it is considered to be a serious threat to food security. Due to the absence of diapause in *S. frugiperda*, its biology and distribution is strongly influenced by low temperatures. The aim of this study was to evaluate the effect of temperature on the development and reproduction of this species. The effect of temperature on the development and reproduction of *S. frugiperda* was studied at five different temperature regimes, namely 18, 22, 26, 30 and 32 ± 1 °C, at 65 ± 5 % relative humidity (RH) and a 14L: 10D photoperiod. Fertility was found to be high with all eggs that hatched at temperatures ranging from 18 to 32 °C. Development of eggs at a constant temperature of 18 °C was, however, slow and the percentage of eggs that survived very low. Continuous low temperatures, although above the lower thermal limit, will therefore slow development down and may reduce population dynamics as a result of high mortality. The optimal range for egg, larval and egg-to-adult development of *S. frugiperda* in South Africa was determined to be between 26 and 32 °C. The development rate of *S. frugiperda* increased linearly with increasing temperatures between 18 and 30 °C and larval survival was also the highest between 26 and 30 °C. The optimum temperature with the most rapid development rate and lowest mortality for larvae was at 30 °C. Pupal development time varied from 7.82 to 30.68 days (32 - 18 °C) with a mean pupal development time of 17.06 days at 22 °C, but only 11.43 days at 26 °C. The development period of the egg-to-adult stage decreased from 71.35 days at 18 °C to 20.27 days at 32 °C. Based on linear regression analysis of development rate at all temperatures, a minimum temperature threshold of 13.01 °C was calculated for egg development and 12.12 °C for larvae, 13.24 °C for pupae and 12.57 °C for egg-to-adult development. Degree-day requirements for *S. frugiperda* egg and larval development was determined at 35.72 ± 1.30 °D and 202.67 ± 4.45 °D respectively when larvae were reared on sweet corn kernels. Pupae needed 147.06 °D for development and development of the life cycle (egg-to-adult), 391.01 ± 1.22 °D. The number of larval instars was determined by using head capsule widths that ranged from 0.30, 0.46, 0.80, 1.40, 1.90, and 2.60 mm. All successive instars increased in size according to Dyar's ratio. The threshold temperatures determined in this study can be used in a model to estimate the number of generations at specific localities where the crop host plants are cultivated. It can also be used in a model to determine areas suitable for cultivation to which *S. frugiperda* can migrate from its overwintering sites, as well as areas with suitable environmental conditions for persistent

occurrence. Oviposition occurred at all the temperatures and the mean number of eggs laid by *S. frugiperda* was 224.4 and 979.2 at 32 and 22 °C respectively. There was a strong negative correlation between temperature, oviposition period and longevity of moths. The optimum temperature for oviposition was determined to be between 18 and 26 °C. Results from this study on the thermal constants and lower and upper threshold temperatures of *S. frugiperda* can be used to predict the impact of climate change on the distribution and population growth of this pest. This knowledge can contribute to the development of integrated pest management strategies for this pest in Africa.

**Key words:** degree-days, development rate, instars, oviposition, longevity, *Spodoptera frugiperda,* temperature

## TABLE OF CONTENTS

## LIST OF FIGURES

# LIST OF TABLES

# CHAPTER 1

# Introduction

## 1.1 General introduction

Maize is the staple food of about 900 million people (FAO, 2010). It is also important as fodder for livestock and the main ingredient of bioethanol (Shiferaw *et al.,* 2011). The demand for maize in the developing world will double from 2009 to 2050, due to the increase in population growth (Rosegrant *et al.,* 2009). Maize is currently planted around the globe in 125 developing countries and produced on 100 million hectares (FAO, 2010). The top ten maize production countries in the world are the United States of America, China, Brazil, Mexico, Argentina, India, France, Indonesia, South Africa and Ukraine (Figure 1.1) (FAO, 2017).

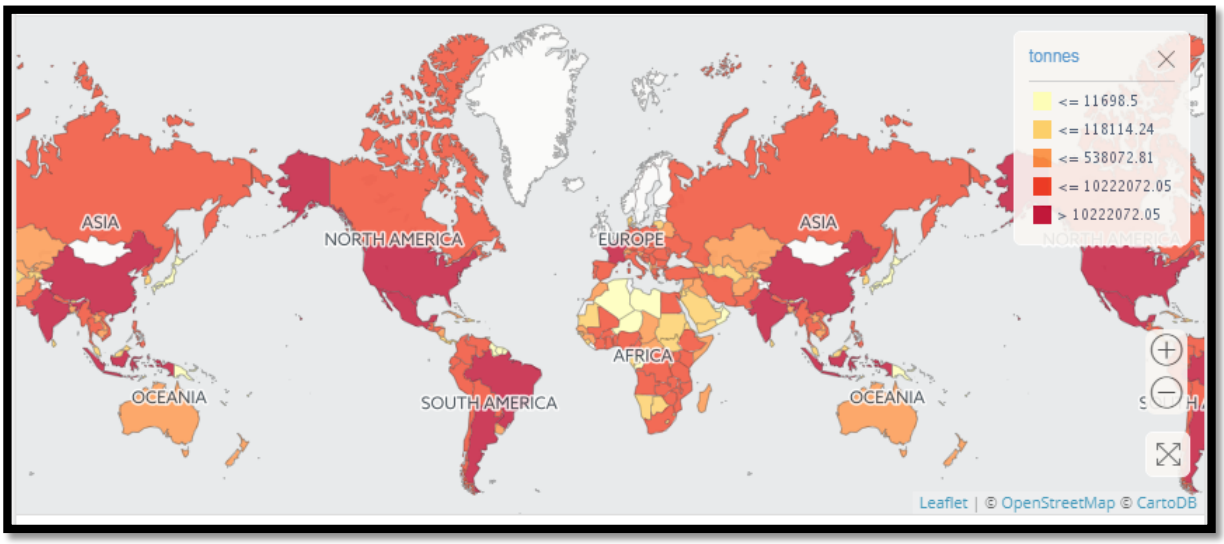
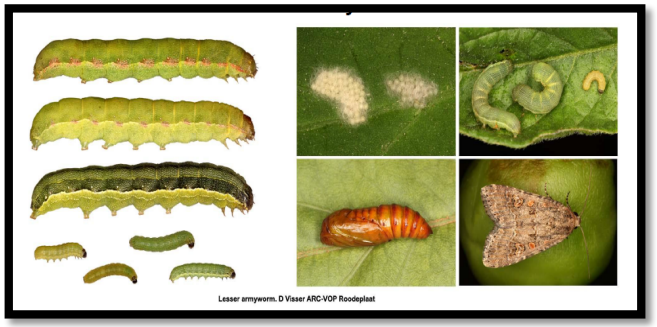



**Figure 1.1:** Maize production per country from 1994 - 2014 (FAO, 2017).

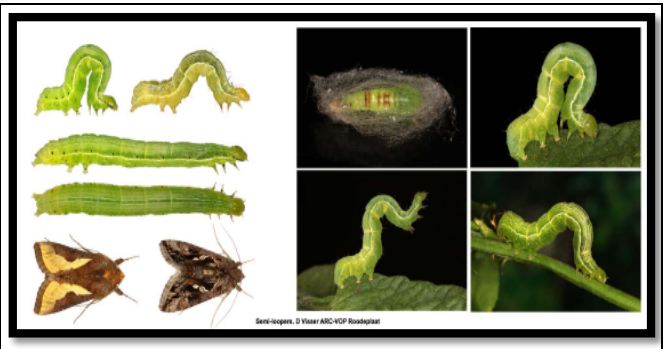
Maize production in Africa (Abrahams *et al*., 2017) is threatened by the native economically important stemborers, *i.e.* the African maize stemborer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae); spotted stemborer, *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae); pink stemborer, *Sesamia calamistis* (Hampson) (Lepidoptera: Noctuidae); sugarcane stemborer *Eldana saccharina* (Walker) (Lepidoptera: Pyralidae) and the coastal stemborer, *Chilo orichalcociliellus* (Strand) (Lepidoptera: Crambidae) (Kfir, 2002; Addo-Bediako & Thanguane, 2012). Mwalusepo *et al.* (2015) reported *B. fusca* and *C. partellus* as the most important biotic factors affecting maize production in East Africa. It was, however, before the invasion of the

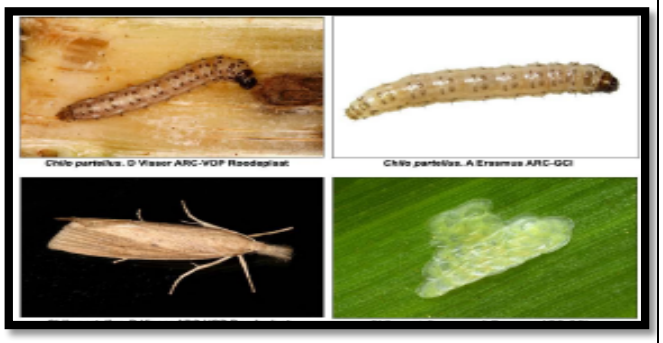
fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), which has only recently invaded Africa (Goergen *et al.,* 2016). It has been reported in Nigeria, Sao Tomoé, Benin and Togo (Abrahams *et al.,* 2017). Since then, *S. frugiperda* moved southwards to Ghana (CABI, 2017), Zimbabwe (FAO, 2017), Swaziland (IPPC, 2017), Kenya (Abrahams *et al*., 2017), Zambia (IPPC, 2017) and the Democratic Republic of the Congo (Abrahams *et al.,* 2017), Malawi, Mozambique, Namibia and South Africa (BBC, 2017). This pest attacks the most important staple crops in developing countries, namely maize and rice (Ramirez-Cabral *et al.,* 2017). A list of the most important lepidopteran maize pests in South Africa is provided in table 1.1, and amongst others, also include stem borers and *Spodoptera* species.

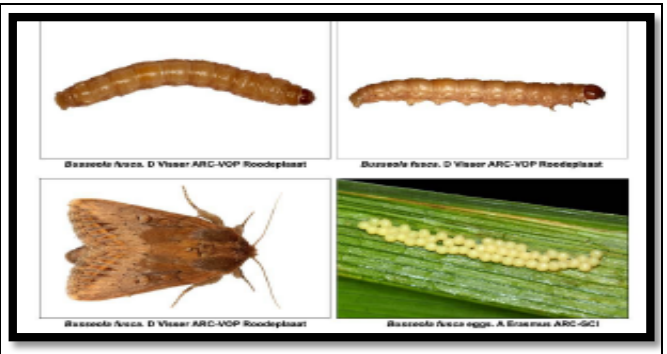
**Table 1.1:** Most important lepidopteran pests of maize in South Africa.

| Common name | Scientific name | Host plants | Descriptive larval characteristics | Visual characteristics |
|---|---|---|---|---|
| African bollworm | *Helicoverpa armigera* (Hübner) | This is the most polyphagous pest in southern Africa (Kroon, 1999). | Larval colour varies (Kroon, 1999). Older larvae are darker than younger larva. Characterised by a longitudinal white or beige stripe along each side of the body (Kroon, 1999). |   (Visser, 2017) |
| Lesser armyworm | *Spodoptera exigua* (Hübner) | A polyphagous pest on poaceous plants, as well as on broad-leaf crops such as *Amaranthus*, cotton, groundnut, lucerne and tobacco (Van Rensburg, 2000). | Larvae are usually olive green, but can also be darker or lighter (yellow). Darker larvae appear when overcrowding is experienced. A characteristic pink line or spots are present laterally on the body (Van Rensburg, 2000). |   (Visser, 2017) |

| | | | | |
|---|---|---|---|---|
| Tomato moth caterpillar | *Spodoptera littoralis* (Boisduval) | A highly polyphagous species. Preference for tomato and sweet potato (Visser, 2011). | Larvae vary in colour, but are usually brown. Black individuals are also common. Characteristic black spots are present on the dorsal side of the last apical segments of the larval body (Visser, 2011). |  (Visser, 2017) |
| African armyworm | *Spodoptera exempta* (Walker) | Feed exclusively on poaceous plants (Van Rensburg, 2000). | Larval colour varies between black, brown and green. The head has a characteristic Y-mark and a white line is present alongside the body similar to that of *S. frugiperda* (Rose, 2000). |  (Visser, 2017) |

| | | | | |
|---|---|---|---|---|
| Semi-loopers | Plusia semi-looper (*Thysanoplusia orichalcea*) (Fabricius)<br><br>Tomato semi-looper (*Chrysodeixes acuta)* (Walker) | The Plusia semi-looper is polyphagous and the tomato semi-looper feeds on tomato, potato, beans, banana, cotton, chrysanthemums and certain weed species (Visser, 2011). | Larvae are usually greenish in colour, but yellow individuals may also be recorded.<br>Apically the body becomes narrower (Visser, 2011). |  <br>(Visser, 2017) |
| Common cutworm | *Agrotis segetum* (Hampson) | A polyphagous pest which attacks vegetables, maize, sorghum, grain legumes, strawberries, cherries, cotton, tobacco and garden flowers (Drinkwater & Van Rensburg, 1992; Du Plessis, 2000). | Larvae are greyish or brown in colour, hairless, smooth, with a waxy appearance, with a length of 30-40 mm when mature (Drinkwater & Van Rensburg, 1992; Du Plessis, 2000). |  <br>(Visser, 2017) |

| | | | | |
|---|---|---|---|---|
| False armyworm | *Leucania loreyi* (Hill, 1983) | Essentially polyphagous, but with a preference for poaceae plants, mostly maize and barley (Hill, 1983). | Larvae vary in colour, usually pale pinkish, with longitudinal stripes (Hill, 1983). |  (Visser, 2017) |
| *Chilo* borer | *Chilo partellus* (Swinhoe) | Larvae attack sorghum, maize, millet, sugarcane and rice (Van den Berg, 1997). | The head is dark brown and the body creamy-white to yellowish-brown with dark brown spots on each segment. Brown spots are sometimes lighter or absent in overwintering larvae (Van den Berg, 1997). |  (Visser, 2017) |

| | | | | |
|---|---|---|---|---|
| Maize stem borer | *Busseola fusca* (Fuller) | Larvae oligophagous and feed mostly on maize, millet, sorghum and sugarcane (Kruger *et al.,* 2012). | Neonate larvae are dark brown, but become lighter as they get older. Older larvae vary from creamy white, light brown to pinkish with a row of small black spots laterally on the body. Head capsules dark brown (Van den Berg, 1997). |  (Visser, 2017) |

The global geographic distribution of *S. frugiperda* overlaps with some of the top ten maize production areas, namely the southern states of the United States of America, Mexico, Brazil, Argentina and South Africa. FAW, previously known as *Laphygma frugiperda* (Guenee) (Vickery, 1929; Wilson, 1933) was first recorded in 1797 in the United States (Johnson, 1987). This pest is indigenous to the tropical and subtropical regions of the western hemisphere from South America (Brazil, Argentina, Chile), Caribbean Islands, Mexico, some southern states of the USA (Texas, southern Georgia, Florida, Alabama, Louisiana, Mississippi) and southern Canada (Luginbill, 1928; Sparks, 1979; Andrews, 1980; Knipling, 1980; Pashley *et al.,* 1985; Adamczyk *et al.,* 1999; Sena *et al.,* 2003; Prowell *et al.,* 2004; Clark *et al.,* 2007), but it is now widely distributed.

Most of the available literature with regard to overwintering and migration of *S. frugiperda* is from North and South America. With regard to its distribution in the northern hemisphere, it has been reported that, due to the lack of diapause, overwintering occurs and year-round survival is possible in the tropical regions, such as southern Florida, southern Texas in the USA and northern Mexico, where its host plants occur (Luginbill, 1928; Mitchell, 1979; Sparks, 1979; Andrews, 1980; Barfield *et al.,* 1980; Mitchell, 1986; Pair *et al.,* 1986; Raulston *et al.,* 1986). The adults are strong fliers and their seasonal migration is influenced by seasonal changes in rainfall, temperature, prevailing winds and host plant availability (Luginbill, 1928; Hogg *et al.,* 1982). The prevailing winds and frontal systems in spring are the main factors that determine the extent and the direction of *S. frugiperda* migration (Pair *et al.,* 1986). During summer months, the moths migrate northward to southeastern Canada (Luginbill, 1928; Mitchell, 1979; Sparks, 1979; Pair *et al.,* 1986), as well as northern Argentina and Chile (Ortega, 1974) (Fig. 1.2). In southern Florida population densities increase during spring and rapidly decline during summer (Pair *et al.,* 1986; Mitchell *et al.*, 1991). This rapid decline indicates the northward migration to northern Florida and southern Georgia during April and May in the USA (Snow & Copeland, 1969; Greene *et al.*, 1971). In this part of the world *S. frugiperda* continues to migrate northward during July and August (Mitchell, 1979) and is then subjected to both climatic variation in terms of temperature and moisture, and different soil types (Luginbill, 1928).


**Figure 1.2:** Seasonal distribution of *Spodoptera frugiperda* in the Americas. The solid line indicates year-round presence and the dotted line indicates presence during summer months (Map adopted from Johnson, 1987).

Due to this migratory behaviour, *S. frugiperda* is classified as a sporadic pest (Jarrod *et al.,* 2015). The number of generations that *S. frugiperda* can complete per year largely depends on the latitude of specific habitats (Luginbill, 1928) and more generations are predicted in tropical regions where the conditions are more favourable (Sparks, 1979; Randall, 1986; Bale *et al.,* 2002). This pest can complete six or more generations in a year (Luginbill, 1928) in areas of the United States where it occurs throughout the year (Figure 1.2). In regions with colder climates, such as Canada, Northern USA and Chile, fewer generations are completed per annum (Ramirez-Cabral, 2017). The estimated number of *S. frugiperda* generations per annum in Cuba is 11.4 (Andrews, 1980).

Maize is produced in most parts of South Africa, but the main production areas are in the Free State, North-West and Mpumalanga provinces (Crops estimates committee, 2017). The outbreak areas of *S. frugiperda* in South Africa during 2017 (Figure 1.3), overlapped with this main production area, but it has also been reported from the Limpopo, Northern Cape and Eastern Cape provinces.

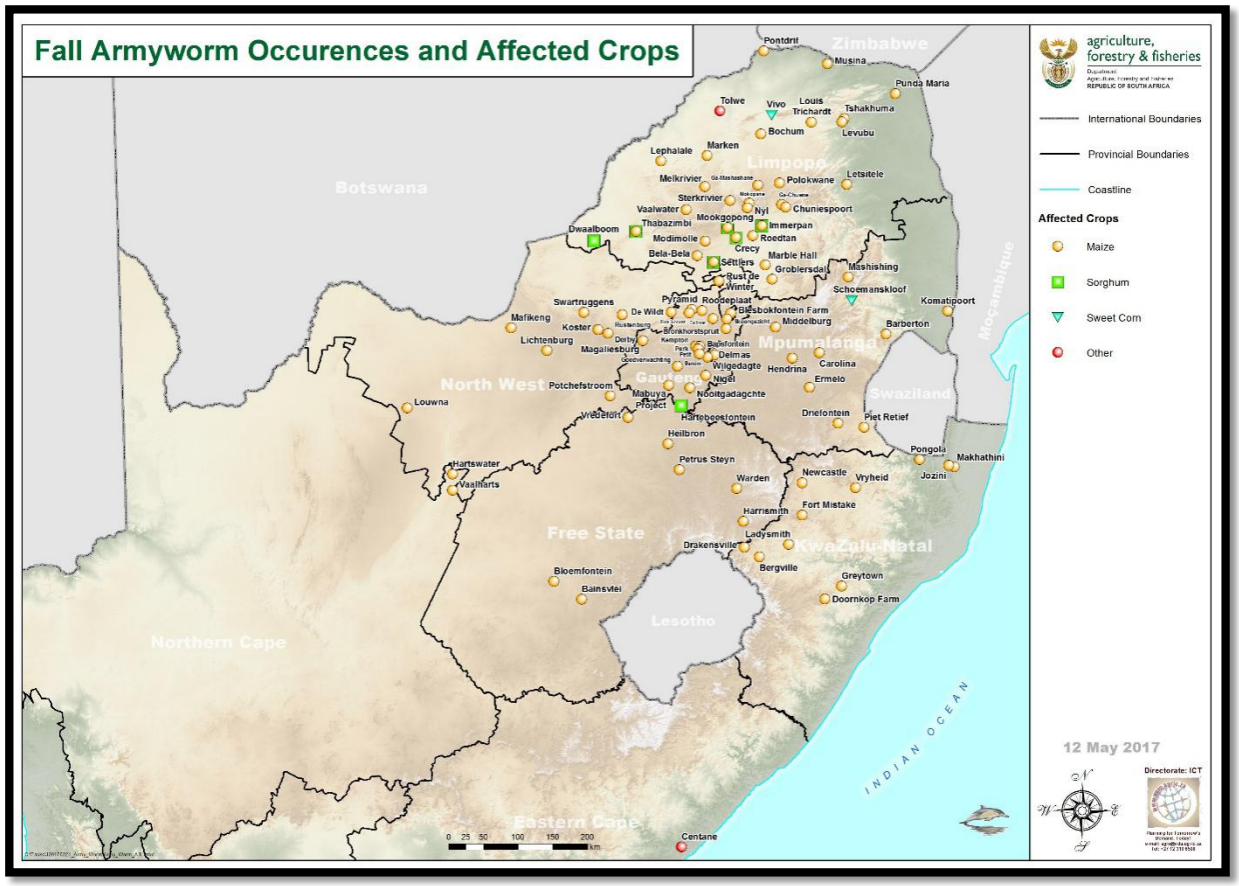



**Figure 1.3:** Map indicating areas where *Spodoptera frugiperda* has been reported on crops in South Africa (source: Mr J. Venter, Department of Agriculture, Forestry and Fisheries, South Africa).

## 1.2. Life cycle and description of *Spodoptera frugiperda* moths

*Spodoptera frugiperda* moths appear similar to the moths of the common cutworm (*Agrotis segetum*), with whitish spots at the tips of the forewings (Metcalf *et al.,* 1965). *Spodoptera frugiperda* moths have a wing span of ± 3.81 cm. The male moth has white spots near the dorsal tip of the wing, while the lower portion of the forewings is light grey to brown in colour (Oliver & Chapin, 1981). The forewings of the female moth are not so distinctly marked as that

of the male and have a greyish brown to fine mottling of grey and brown (Oliver & Chapin, 1981) (Figure 1.4). The hind wings of both sexes are shining silver-white, with a narrow dark border (Figure 1.5). The moths are nocturnal, feed on nectar and prefer maize over sorghum for oviposition (Van Huis, 1981). Males are attracted by the female sex pheromone and they may mate several times (Sparks, 1979).

Temperature and humidity are the main factors that influence longevity of the adults (Luginbill, 1928). Adult longevity is about 10 days, but may range between 7 and 21 days (Vickery, 1929).

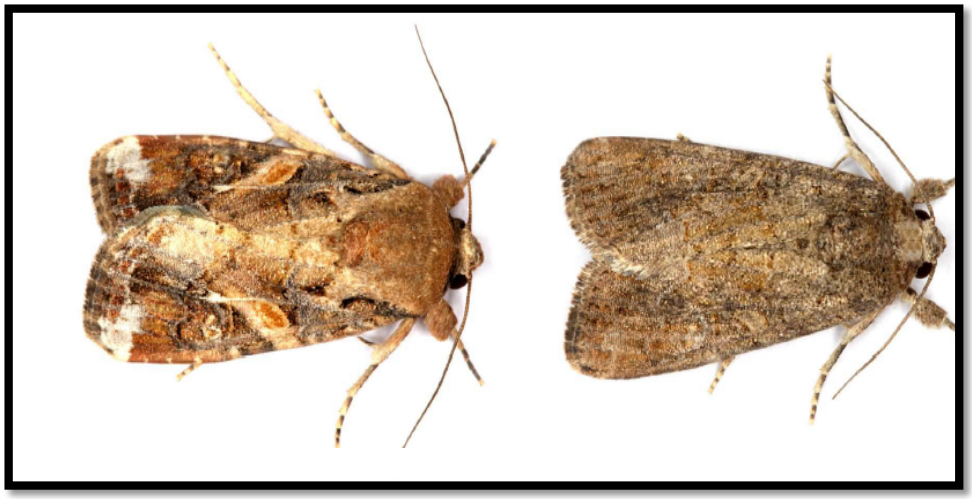


**Figure 1.4:** *Spodoptera frugiperda* male (left) and female moths (right) (Visser, 2017).

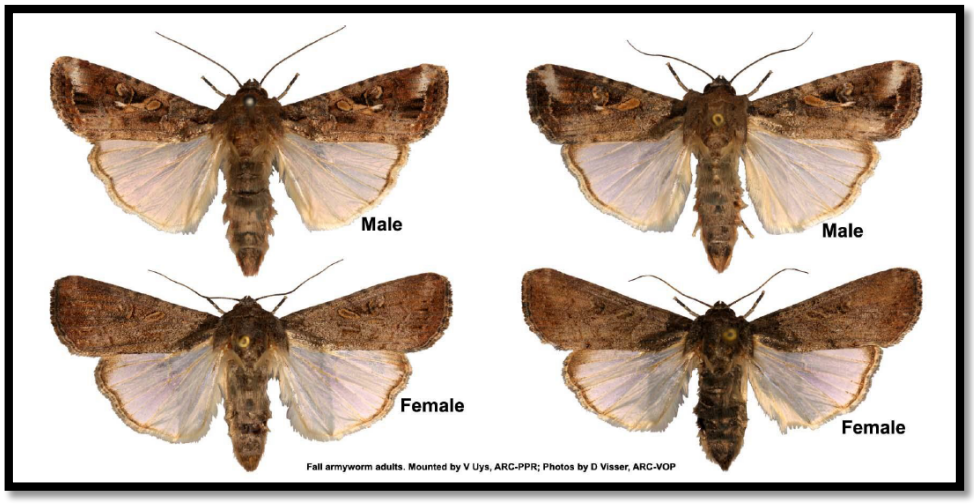



**Figure 1.5:** Variation in the wing patterns of *Spodoptera frugiperda* moths (Visser, 2017).

Newly emerged moths can mate locally or migrate up to 480 km before mating and oviposition (Ashley *et al.*, 1989). The length of the oviposition period depends on temperature, but the majority of eggs are laid in the first four to five days of this period, in the first four hours shortly

after dark (Luginbill, 1928). Moths lay eggs in batches of 100 - 200, usually on the underside of the host plant leaves if the population densities are low. They do, however, also oviposit over the entire plant under high population densities (Luginbill, 1928). According to Ali *et al.* (1990), the most preferred location for oviposition is on the leaves or the lower portion of the plant canopy. The female often deposits eggs in masses of two to three layers on top of each other (Luginbill, 1928). The average egg production per female varies between 1500 and 2000, with a fecundity approaching 100%. The eggs are oblate-spheroidal shaped, 0.39 mm in length and 0.47 mm in diameter (Luginbill, 1928). Newly laid eggs are pink to greenish grey in colour and become darker with age towards larval eclosion (Luginbill, 1928). Eggs (Figure 1.6 a, b, c) are covered with greyish scales (Figure 1.6b) by the female moth, giving them a downy appearance (Sparks, 1979) (Figure 1.6b).

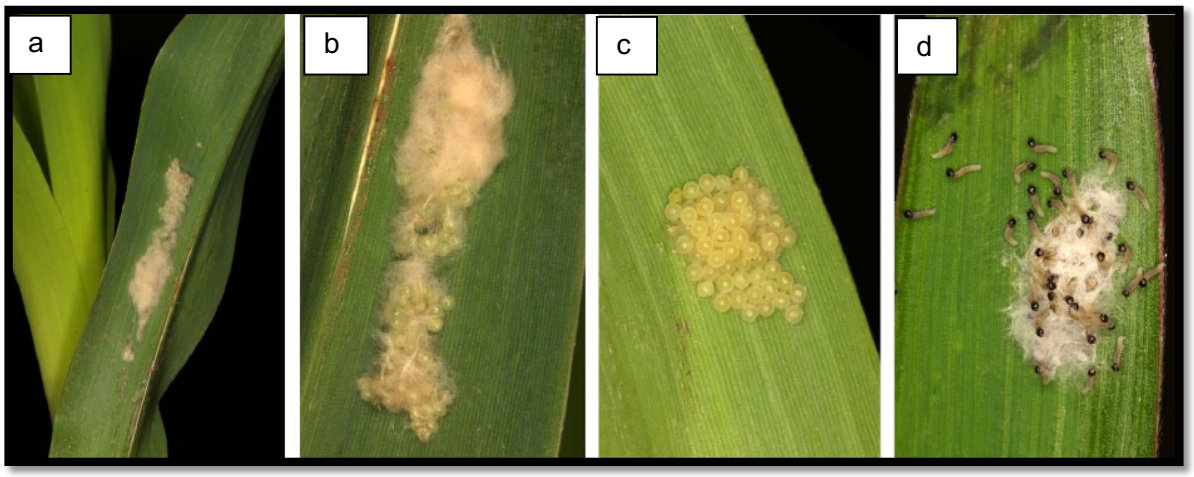



**Figure 1.6:** (a) Egg batch (b): Eggs covered with scales, (c) eggs without scales and (d) newly hatched first instar larvae (Visser, 2017).

Newly hatched larvae consume the egg shells and then disperse to vegetative tissue of the host crop to start feeding. Developmental time of eggs ranges between 2 - 11 days depending on the climatic conditions (Luginbill, 1928).

*Spodoptera frugiperda* larvae normally complete six larval instars), but it may range between six and seven depending on the temperature and host plant availability (Luginbill, 1928). Newly emerged first instar larvae (L1) are off-white to yellow in colour with black head capsules (Figure 1.7a) and small black spots from which primary setae protrude. Neonate larvae balloon from plants to disperse (F1.7b). Larvae become darker and greenish in colour as they feed. Larvae of instars two and three (L2 and L3) are similar in colour and the last three instars (L4 - L6) are typically darker with a varying colour pattern depending on the diet and environmental conditions (Luginbill, 1928). The dorsal white line forms during the third instar (Capinera,

1999). The head varies in colour, from yellowish to very dark brown and the thoracic shield is the same colour as the head. Older larvae vary in colour from light green, brown or even black (Luginbill, 1928).

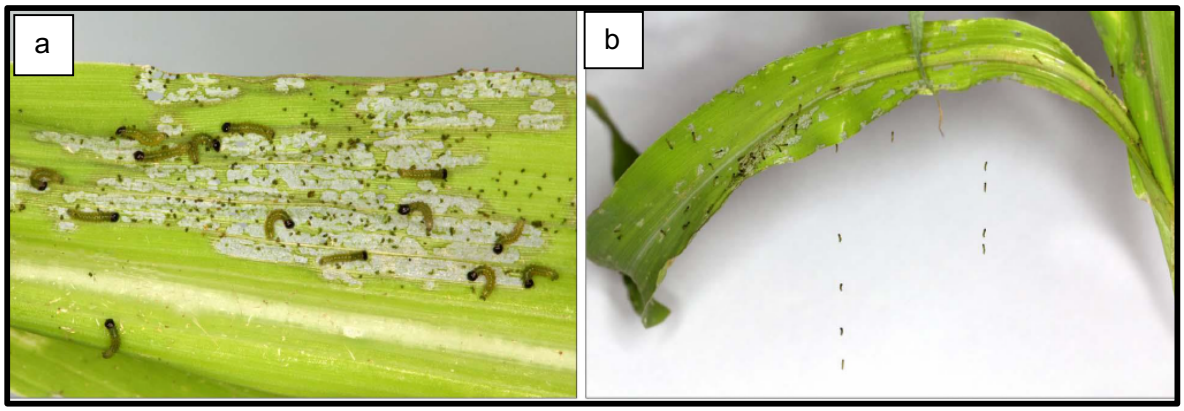



**Figure 1.7:** a) Larvae (L1 - L3) feed near the oviposition site and (b) balloon to disperse (Visser, 2017).

Larval feeding and adult activity usually occur at night, but can also occur during the late evening or early morning. Young larvae (L1 - L3) feed near the oviposition site and eat the green tissue from one side of the leaf, leaving the membranous epidermis on the other side of the leaf intact. The second and third instars feed on both sides of the leaves, making holes, while L4 - L6 larvae eat holes in leaves (Luginbill, 1928). The larvae become cannibalistic from the third instar (L3) onwards, after which they dominate interspecific competitors and reduce their numbers of intraspecifically (Chapman *et al.,* 2000).

The larvae can be distinguished from those of other noctuids by characteristics such as the inverted white Y on the head capsule, the white line in the mid-dorsal area, the yellow and red “flecking” on the abdomen, the four black dots on the eighth abdominal segment and more predominant long hairs arising from the black tubercles which gives them a rough or granular texture (Metcalf *et al.,* 1965) (Figure 1.8).

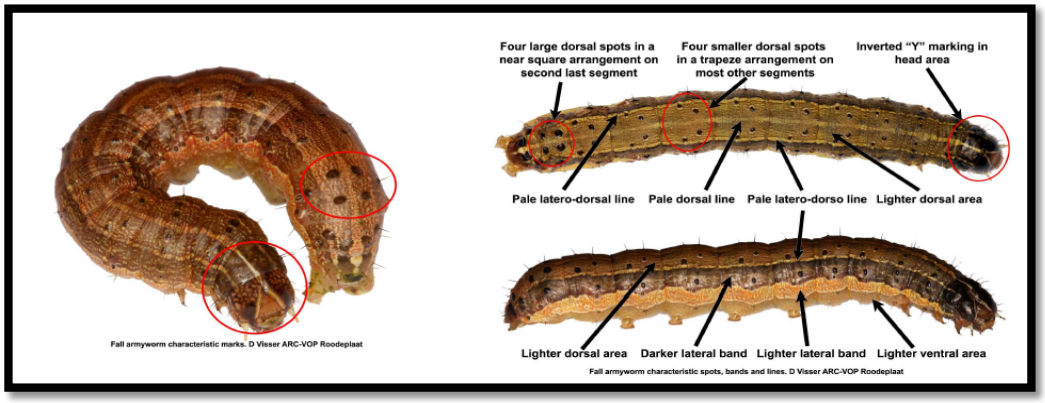



**Figure 1.8:** Characteristic markings on larvae (red circles) of *Spodoptera frugiperda* (Visser, 2017).

Final instar larvae enter the soil and become prepupae before they pupate two to four days later (Luginbill, 1928). Differences between sexes are illustrated in figure 1.9, e.g. the visible genital scars on sternum 9 of male and sternum 8 of female pupae. Pupation occurs in the soil (Figure 1.10a) if the densities are low, but pupation can also occur on the plant if larval densities are high (Figure 1.10b) (Luginbill, 1928). The soil depth at which pupation occurs depends on the physical structure, moisture and temperature of the soil (Sparks, 1979). Duration of the pupal stage depends on the temperature of the environment (Luginbill, 1928). The orange-brown pupae are 14 - 18 mm long and 4.5 mm wide and similar to other noctuids. The pupal period ranges between 8 - 9 days in summer and 20 - 30 days in winter (Capinera, 2001).

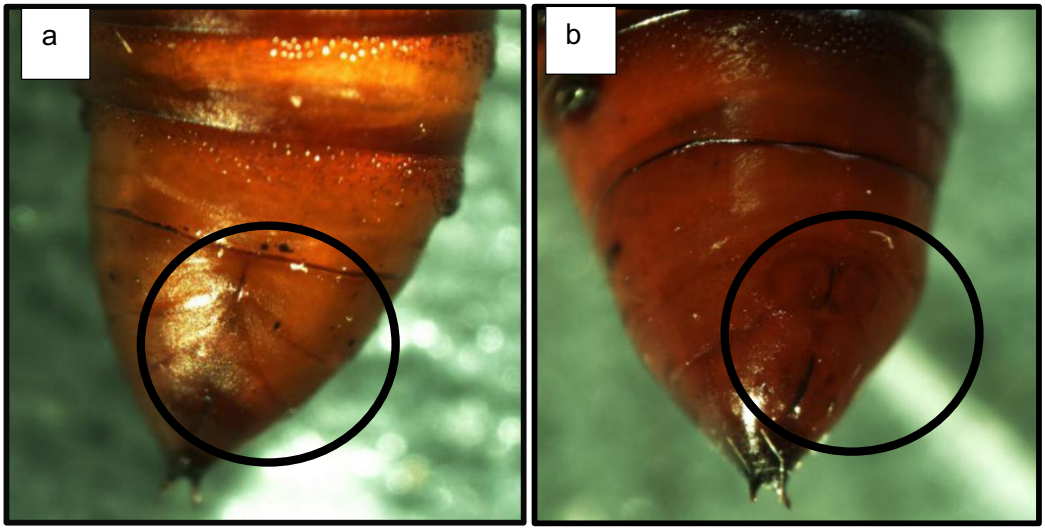



**Figure 1.9:** Pupae of *Spodoptera frugiperda* showing visible genital scars (a) female and (b) male.


**Figure 1.10:** *Spodoptera frugiperda* pupae, a) in the soil, b) on a plant (Visser, 2017).

## 1.3 *Spodoptera frugiperda* damage on maize

The most damage by *Spodoptera frugiperda* on maize is caused by the last three larval instars (L4 - L6) based on their high consumption rate (98%) (Luginbill, 1928). These larval stages prefer to feed on the reproductive structures of the host plant (Jarrod *et al.,* 2015). Feeding during the late whorl stage of maize may prevent the tassel from developing or it does not develop properly (Hanway, 1969). Larval feeding and damage to the silk reduces pollination which causes a decrease in the number of kernels formed per ear (Morril & Greene, 1974; Gross *et al.*, 1982). Larvae also feed on kernels by tunnelling through the ear (Vickery, 1929).

Larvae can also tunnel in at the base of the ear, causing ears to drop (Burkhardt, 1952). During heavy infestations, larvae have been found at the base of leaves where they feed on the stalk, sheaths and leaves (Burkhardt, 1952). An entire leaf may be excised as a result of this activity and stalk injury may render the plant more susceptible to lodging (Burkhardt, 1952). Larvae from infestations late in the season attack the whorl, leaf base or ear (Morrill & Greene, 1973), which allows for entry of humidity and pathogens that may result in ear rot (Avila *et al.,* 1997). This pattern of feeding on leaves and tunnelling into ears by *S. frugiperda* is similar to feeding by *Helicoverpa zea* (Vickery, 1929).

## 1.4 Host plants of *Spodoptera frugiperda*

The host plant range of this polyphagous pest (Ruíz-Nájera *et al*., 2007) includes numerous important crops (Andrews, 1980), but is primarily those that belong to the Poaceae, namely maize (*Zea mays* L.*)*, sorghum (*Sorghum bicolor* (L.) Moench), Bermuda grass (*Cynodon dactylon),* wheat (*Triticum aestivum*) rice (*Oryza sativa*) and Johnson grass (*Sorghum*

*halepense*). Other affected plant groups include the Malvaceae (with cotton *Gossypium hirsutum*), the Fabaceae, (with soybean *Glycine max*), peanut (*Arachis hypogaea*) and lucerne (*Medicago sativa*). In the Solanaceae tobacco (*Nicotiana tabacum*) and in the Amaranthaceae sugarbeet (*Beta vulgaris*) are attacked (Luginbill, 1928; Sparks, 1979; Andrews, 1980; Martin *et al.,* 1980).

The wide host range of *S. frugiperda* is due to the occurrence of two sympatric and morphologically identical strains, *i.e.* the maize and rice strains, that are defined by their host plant preferences (Pashley *et al.*, 1985; Pashley, 1986). Larvae of the maize strain largely feed on large grasses, such as maize and sorghum, while those of the rice strain feed on small grasses, such as rice and Bermuda grass (McMichael & Prowell, 1999). Not only do these strains differ in host plant preference, they also have differential physiological and behavioural characteristics (Pashley *et al.,* 1986; Pashley *et al.,* 1995; Prowell *et al.,* 2004). Differences between strains have also been reported in terms of susceptibility and resistance to pesticides (Pashley *et al.,* 1987b) and mating behaviour (Pashley & Martin, 1987a; Pashley *et al.*, 1992).

Control difficulties are also ascribed to this wide host plant range of *S. frugiperda,* which enable easy migration from one crop to another (Capinera, 2001). Lower mortality of the larvae and a faster development rate for *S. frugiperda* was, however, reported on maize compared to cotton and soybean (Pitre & Hogg, 1983). Afrotropical armyworms (such as *Spodoptera exempta*) first have to build up a dense population on wild grasses before older larvae move into cultivated Poaceae crops (Rose *et al.*, 2000), while *S. frugiperda* females oviposit directly on maize (Rose *et al.*, 2000). Larvae feeding on plants with a high silica content is facilitated by the sharp cutting edges of the mandibles which are strongly serrated (Brown, 1975).

## 1.5 Pest status of *Spodoptera frugiperda*

*Spodoptera frugiperda* has been reported as the most destructive and economically important insect pest on maize in Brazil (Sena *et al.,* 2003*).* The larvae of *S. frugiperda* are also reported to be more damaging to maize than that of other noctuids in Africa (Goergen *et al.,* 2016). Pest status of *S. frugiperda* depends on the specific developmental stages of the larvae and the host plants (Barros, 2010). Sporadic outbreaks of *S. frugiperda* on maize crops can easily reach the economic injury level (Cruz, 2008), before visible evidence of infestation occurs (Linduska & Harrison, 1986) and between 20 - 87% yield reduction can be caused during outbreaks (Henderson *et al*., 1966; Andrews, 1980). *Spodoptera frugiperda* is a highly successful pest due to characteristics such as its high reproductive rate, a relatively short generation period of approximately 30 days under favourable temperature conditions, high

dispersal ability (Luginbill, 1928, Dingle, 1972), wide host range and multi-voltinism (Knipling, 1980). Outbreaks of *S. frugiperda* are attributed to the egg laying habit of the moths and larval migration behaviour (Vickery, 1929).

The larvae attack all growth stages of maize but prefer younger vegetative-stage plants for oviposition (Harrison, 1984). *Spodoptera frugiperda* colonises maize mainly during the vegetative whorl stage, feeding on the young leaves, but it can also feed on the reproductive parts (ears and tassels) depending on the larval developmental stage and the host crop stage (Melo & Silva, 1987). Overall this damage often causes devastating crop losses (Jarrod *et al.,* 2015).

Gross *et al.* (1982) reported that plant injury during the fourth to eight leaf stages cause significant reductions in plant height, stalk diameter, ear length and mass. They also reported a substantial reduction in yield due to damage caused by *S. frugiperda* during the very late whorl stage (14 - leaf stage) during which tassel development is taking place. They reported yield loss resulting from larval feeding damage during the 14 - leaf stage to be more affected by defoliation of the leaves surrounding the tassel, which is important for grain yield (Hanway, 1969), rather than direct feeding on the tassel (Gross *et al.,* 1982). Although yield reductions were not found to be consistent, Buntin (1986) concluded that plants in the late-whorl stage were less sensitive to *S. frugiperda* injury than plants in the early to mid-whorl and early tassel stages.

## 1.6 Effect of climate on *Spodoptera frugiperda*

The larval development cycle takes approximately 14 days during the summer and 30 days during cool weather (Capinera, 2001). For each larval stage, there is an active feeding period and an inactive period which occurs just before each moult (Luginbill, 1928). Although temperature can affect the length of both these periods of the larval stage, lower temperatures result in a longer extension of the inactive period than the active period, and during the active period, food supply is more important (Vickery, 1929).

## 1.7 Control of *Spodoptera frugiperda*

Monitoring the presence and density of the pest population is important to facilitate optimum timing of management practices such as insecticide applications. *Spodoptera frugiperda* monitoring can be done by means of pheromone traps which indicate the presence or absence

of the pest, as well as moth flight patterns over time (Starrat & McLeod, 1982). This pest is difficult to control because of its wide host range, wide geographic distribution, development of resistance to insecticides, as well as its rapid and long distance movement ability which can serve as an escape mechanism from natural enemies (Knipling, 1980).

In the USA area-wide management can be applied through control of the different *S. frugiperda* strains at the overwintering sites by using information on the distribution of these strains between host plants (Meagher & Nagoshi, 2004). Control of the pest at overwintering sites can delay or reduce the northward migration of moths (Meagher & Nagoshi, 2004).

### 1.7.1 Chemical control

Knowledge of pest biology is important to ensure effective and timely application of pesticides (Cruz, 2007). Chemical control may be ineffective due to incorrect use which, in the long term, may contribute to resistance development and decreased numbers of natural enemies (Gómez-Valderrama *et al.,* 2010). The classes of insecticides to which *S. frugiperda* is known to have developed resistance to are carbamates (methomyl, carbaryl and thiodicarb), organophosphates (chlorpyrifos, methyl parathion, diazinon, malathion and trichlorfon) and pyrethroids (cypermethrin, fenvalerate, fluvalinate and permethrin) (Wood *et al.,* 1981, Yu 1991, Adamczyk *et al.,* 1999, Al-Sarar *et al.,* 2006) and benzoylureas, spinosyns, indoxacarb, diamides and *Bacillus thuringiensis* (FAO, 2017).

Chemical control can be applied during the vegetative and reproductive stages of maize. A chemical control strategy alone often provides unsuccessful control of *S. frugiperda*. Newly hatched larvae move directly into the whorl of maize plants where they are protected from insecticide sprays (Harrison, 1986; Castro, 2002; Siebert *et al.*, 2008). Knowledge about pest biology and identification of different instars is also important, since larval size has been reported to be strongly related to the efficacy of certain insecticides. First to fourth instar *S. frugiperda* larvae can be effectively parasitised and predated upon by natural enemies and the use of insecticides could be minimized if natural enemy diversity and abundance is high (Cruz, 2007).

### 1.7.2 Biological control

*Spodoptera frugiperda* can be controlled by a number of pathogens including viruses, fungi, protozoa, nematodes and bacteria (All *et al.,* 1996). The effectiveness of natural enemies may result in reduced numbers of pesticide applications for control of *S. frugiperda* (Cruz, 2007).

There are 53 species of parasites, from 43 genera and 10 families that attack *S. frugiperda* globally (Ashley, 1979; Sparks, 1986). Entomophagous pathogens can be used to suppress *S. frugiperda* populations in at least three ways, namely optimisation of naturally occurring diseases, introduction and colonisation of pathogens into insect populations as natural regulatory agents, and repeated applications of pathogens as microbial insecticides (Gardner & Fuxa, 1980). With regard to pathogens, *B. thuringiensis* (All *et al.,* 1996) and a nucleopolyhedrovirus (NPV) (Gardner & Fuxa, 1980) were reported to be the most prevalent and potent in natural populations of this pest. *Spodoptera frugiperda* spends its prepupal and pupal stages in the soil which make them highly susceptible to soil-inhabiting pathogens and entomopathogenic nematodes that occur naturally (Barbercheck, 1993). Egg parasitoids, such as *Telenomus remus* Nixon (Hymenoptera: Platygastridae) and *Trichogramma* spp. (Hymenoptera: Trichogrammatidae), have been used as biological control agents in Venezuela (Ferrer, 2001) and Colombia (Garcia-Roa *et al.,* 2002). In Argentina, 13 hymenopteran and eight dipteran parasitoids are known to parasitise *S. frugiperda* larvae (Murúa *et al.,* 2003; Murúa & Virla, 2004). Higher temperatures cause an increase in the development rate of natural enemies, but they are often absent in newly colonised areas due to their poor ability to migrate together with their hosts (Ashley, 1979).

### 1.7.3 Cultural control

According to Andrews (1988), plants growing in fields where low or no-tilling is practiced, as well as those in polyculture cropping systems, are less attacked by *S. frugiperda* compared to those in monoculture cropping systems. Polyculture cropping systems are likely to support more predators which disrupt oviposition and larval migration between plants (Labrador, 1967). Changing planting dates of the crops can also contribute to crops escaping from high *S. frugiperda* infestation levels (Mitchell, 1978). Intercropping monoculture maize fields with sorghum may also lead to a reduction in the infestation levels of *S. frugiperda* on the maize crop (Castro & Pitre, 1988).

Pheromone traps can be used to disrupt mating of moths, but this has not been attempted before for *S. frugiperda*. The sex pheromone used in these traps contains tetradecenyl acetate which also occurs in the pheromones of *S. exigua* and *Agrotis ipsilon* (Klun *et al.,* 1996).

### 1.7.4 Host plant resistance

With the development of resistance by *S. frugiperda* to insecticides of different groups, transgenic maize varieties were introduced to provide another control option. It has, however, been reported that the concentration of Bt toxins in GM Bt maize plants decrease with plant age, making the crop more susceptible to insect pests at late growth stages (Kranthi *et al.,* 2005). Development of resistance is also a concern (Moar *et al.,* 1995). The first field resistance by *S. frugiperda* larvae to Bt maize (Cry1F) in the world, was reported during 2006 in Puerto Rico (Matten *et al.,* 2008; Storer *et al.,* 2010). Breeding for conventional host plant resistance is also possible by breeding maize varieties with thicker leaves (Davis *et al.,* 1995).

## 1.8 Temperature dependent development and reproduction

Temperature is the most important abiotic factor affecting the performance of insects (Bale *et al.,* 2002). The range of temperatures at which insects can develop and reproduce is referred to as the thermal range (Jarosík *et al.,* 2002; 2004). Based on theoretical studies the thermal range for each insect species should be about 20 °C (Gillooly *et al.,* 2002). Insects are poikilothermic species and their body temperature is reliant on the ambient surrounding temperature making them sensitive to changes in temperature (Rosenzweig *et al.,* 2001; Bale *et al.,* 2002; Menéndez, 2007). An increase in body temperature of insects progressively increases the physiological performance up to a maximum value at the optimum temperature ($T_O$), after which it decreases rapidly (Briere *et al.,* 1999). Huey and Stevenson (1979) illustrated this temperature-performance relationship hypothetically, as can be seen in Figure 1.11. The non-linear asymmetric curve defines the optimum temperature and the temperature range between the critical minimum and critical maximum temperatures (Paaijmans *et al.,* 2013). The optimum temperature is the most favourable temperature for development and reproduction of insect species. Temperature increases to the thermal optimum of a species where an acceleration of metabolism is caused, leading to increases in activity and feeding behaviour (Jaworski & Hilszczański, 2013). Development and reproduction rates decrease at temperatures above the optimum, and eventually reach an upper threshold (Briere *et al.,* 1999). The lower and upper threshold levels are the restricted temperatures for development and reproduction of insect species (Sharpe & DeMichele, 1977).

Insects have the ability to withstand thermal fluctuations and unfavourable temperatures (Scharf *et al.,* 2015). Fitness is the ability of a species to remain active during extreme temperatures (Loeschcke & Hoffmann, 2007). It is important to determine the temperature limits of a species in order to understand the fitness and dynamics of a specific population (Terblanche *et al.,* 2007). Individual fitness of insect species can also be evaluated as the ability to produce offspring (next generation) (Kolberg, 2013). Insects are, however, restricted by critical thermal minima ($CT_{min}$) and maxima ($CT_{max}$) which are defined as the statistical means of the temperatures at which individual animals are immobilized by temperature and where they are incapable of escaping conditions that will lead to death (Whitford & Ettershank, 1975).

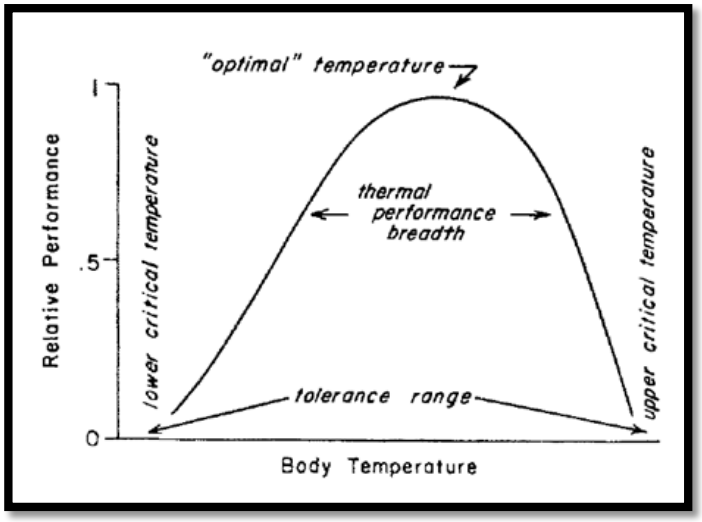



**Figure 1.11:** Hypothetical performance curve of poikilothermic species as a function of body temperature (Huey & Stevenson, 1979).

Insect development rate, reproduction, number of generations in a season, survival, mortality, density, feeding behaviour and distribution are strongly influenced by temperature (Bale *et al.,* 2002; Harrington *et al.,* 2007; Hassal *et al.,* 2007). Poikilothermic species are known to develop faster under warmer environmental conditions (Atkinson & Silby, 1997). Development of insect species may therefore benefit from a temperature increase through a faster development rate, higher reproduction and better survival (Zheng *et al.,* 2015). Higher development rates of insect species shorten the time spent in unfavourable environmental conditions that decrease their ability to survive (Jaworski & Hilszczański, 2013). The number of generations of multivoltine insect species, such as *S. frugiperda*, could increase due to an increase in temperature (Pollard *et al.,* 1995; Bale *et al.,* 2002). Temperature also influences the time of emergence and overwintering mortality of insect species (Porter *et al.,* 1991).

Warmer winter temperatures result in decreased overwintering mortality, which may, in turn, result in increased spring population numbers (Bale & Hayward, 2010).

Life tables containing survival rate, fecundity and mean generation period of insect species (Ma *et al.,* 2017) are used in ecological studies of insect populations. These studies include the development of insect mass-rearing techniques (Chi & Getz, 1988; Jha *et al.,* 2012), timing of pest control actions (Yu *et al.,* 2013), as well as studies on host preferences and fitness of insect species (Naseri *et al.,* 2014). Temperature records can be helpful in pest management and for the prediction of the occurrence of the various life stages of a pest (Logan, 1988). Information on host specific development, survival of immature stages, longevity and fecundity is important for understanding the dynamics of pest populations (Carey, 1984). This information is important in determining the seasonal occurrence of pest species and for use in integrated pest management (IPM) strategies (Wagner *et al.,* 1984). The susceptibility of insect species and natural enemies to pesticides differs between their development stages (Chi, 1990) and the thermal requirements and biological parameters of insect species vary among different populations (Lee & Elliot, 1998).

Degree-degree or phenology-based models are used for prediction of developmental dynamics and migration of insects (Bryant *et al.,* 1998; Roltech *et al.*, 1999). Temperature is not the only variable that influences pest status, but parameters such as rainfall, humidity, radiation and $CO_2$ concentrations also play a role (Bale *et al.,* 2002). The relationship between temperature and larval development can be estimated using degree-days, which can be determined by observation of insect development under constant temperature conditions (Garcia-Salazar *et al.,* 1988). Degree-day estimation is difficult under field conditions because of the many factors such as fluctuating temperatures, absence or presence of food sources and larval density that may influence developmental rates (Gu & Novak, 2005). Degree-day values are based on the threshold temperatures of insects and are specific for each species (Miller, 1977).

Non-linear models simulate the development period of an insect in a population (Wagner *et al.,* 1984). Linear models describe the relationship between temperature and development (Milonas & Savopoulou-Soultani, 2000). Development of insect species occurs linearly at favourable temperatures, but becomes non-linear at low and high temperatures (Honěk, 1996). These curves can also be used to represent the sensitivity of insect species to climate change (Amarasekare & Savage, 2012).

The linear degree-day model is the most widely used approach to determine temperature-dependent development and requires minimal data for formulation and is easy to calculate and apply (Fan *et al*., 1992). Estimating the relationship between temperature and life history parameters (development rate, survival and reproduction) is important for the prediction of suitable establishment areas for species under different climate change scenarios (Cammell & Knight, 1992; Bale *et al.,* 2002; Estay *et al.,* 2009; Régnière *et al.,* 2012). Climate change alters the mean temperatures that may be experienced in certain environments and which will affect the daily and seasonal temperature ranges (Easterling *et al.,* 1997). The effects of climate change on insects can be estimated by the use of bioclimatic models to determine their distribution (Acevedo *et al.,* 2011). Predicting the potential geographic distribution and abundance of agricultural pests could assist farmers to adapt to climate change by having enough pest management tools available to protect crops against such biotic crop production constraints (Kroschel *et al*., 2013).

## 1.9 Climate change

Impacts of climate change and global warming will, amongst others, affect the ecosystem, water availability, crop production and food security (Sharma, 2014). With the current increasing levels of carbon dioxide ($CO_2$), an increase in the average temperature of between 1.4 and 5.8 °C can be expected by 2100 (Sharma, 2014). Climate change can have both direct and indirect impacts on agricultural productivity. These impacts are unequivocal changes in average temperature, rainfall patterns, droughts, flooding and the geographical distribution of pests and diseases (FAO, 2015).

Agriculture contributes an average of 30% to the gross domestic product (GDP) and 40% of exports from Africa (Commission for Africa, 2005). It is very important in sub-Saharan Africa where approximately 70% of the population depends on agriculture for their livelihoods (World Bank, 2007). Developing countries, such as those in sub-Saharan Africa, may be the most vulnerable to climate change because of their high dependency on agriculture, natural resources, warmer baseline climates and limited ability to adapt (Kurukulasuriya & Mendelsohn, 2007; 2008; Hassan & Nhemachena, 2008; Thornton *et al.,* 2008). Agriculture in sub-Saharan Africa is a vulnerable sector due to its dependency on rainfall, lack of infrastructure, unpredictable markets, agro-ecological complexities and heterogeneity of the region, low use of fertilizers and degraded soils (World Bank, 2007). Only 4% of crop production in sub-Sahara Africa is under irrigation, while the rest is rain-fed (Shah *et al.,* 2008).

The economic growth, income distribution, agricultural demand (Scmidhuber & Tubiello, 2007) and changes in markets and food prices (FAO, 2008) are all influenced by climate change. The amount of land available for crop production decreases, while the world population increases, and this has serious implications for food security, especially in developing countries (Sharma, 2014).

Crop production is directly influenced by precipitation and temperature (Calzadilla *et al.*, 2013). A rise in average temperature can increase the growing period of crops and the change in precipitation levels can affect evaporation, soil erosion rates and availability of fresh water for agricultural production (IFAD, 2009), which can alter crop yields and the profitability of production of several staple food crops (Prato *et al.,* 2010). Maize farming systems face many challenges, including low soil fertility and pests, both in the field and in storage (De Groote, 2002; Kfir, 2002). A decrease in cereal crop production in Africa is projected due to heat and water stress shortening the growing season, more diseases, and pest and weed outbreaks (Niang *et al.,* 2014). People living in the tropics and subtropics will be the most affected because of their high dependency on agriculture for their livelihoods (IPCC, 2001).

The activity, diversity, abundance, geographical distribution, overwintering, development and population dynamics of insects will in future all be affected by climate change (Sharma, 2014). The response of insect species to climate change will be distinctive and will depend on the flexibility of their life history characteristics, different growth rates and diapause requirements that will influence their geographic distribution and population increase (Bale *et al.,* 2002). Successful adaptation of insects to conditions of their host plants and the climate of the environment are represented by their ability to complete their life cycle under certain conditions (Bale *et al.*, 2002). Temperature can have a significant and rapid impact on species distribution and abundance because the main eco-physical traits of insects (*e.g.* life cycle duration, mobility, reproduction), are all sensitive to the thermal environment (Piyaphongkul, 2013). An increase in temperature enables migratory insects (*e.g. S. frugiperda*) to establish in new regions (Pollard *et al.,* 1995; Bale *et al.,* 2002). The distribution ranges of insects in future are therefore expected to move within the range of approximately 200 km from their current areas of distribution as a result of climate change (Watt *et al.,* 1990), but it may also cause a decrease or elimination from certain areas (Ramirez-Cabral *et al.,* 2017).

Pest management will become more challenging in future due to an increase in temperature and the variability of climatic events (Ramirez-Cabral *et al.,* 2017). The effectiveness of crop protection control strategies will be affected by climate change through the effect it has on the expression of host plant resistance, natural enemies, bio-pesticides and synthetic insecticides

(Sharma, 2014). Pest management will therefore become more challenging in future due to the increase in temperature and the variability of climatic events (Ramirez-Cabral *et al.,* 2017). Knowledge of the effect of *S. frugiperda* on their host crops under current and future climatic conditions is therefore important for sustainable crop production and to ensure food security.

An increase in temperature causes an increased risk of invasion by migrant pests (Porter *et al.,* 1991, Parmesan, 2007; Memmott *et al.*, 2010). Sharma (2014) projected greater yield losses due to insect damage as a result of a reduction in crop diversity and increased incidence of insect pests resulting from global warming. Climate change affects insects directly and indirectly (Cannon, 1998; Patterson *et al.,* 1999; Bale *et al.,* 2002). Indirect effects of climate change on insects are, for example, the relationships between natural enemies, interspecies interactions, their environments and availability of host crops (Bowler & Terblanche, 2008). Species that only occur in small areas or at low densities may distribute to wider areas and reach population densities which can result in economic damage (Porter *et al.,* 1991; Bale *et al*., 2002).

An increase in temperature decreases the immature stages developmental time of insects which make them less vulnerable to predation and increases their chances for survival (Bernays, 1997). Earlier emergence of adults due to temperature increases will lead to changes in flight activity patterns (Sharma, 2014). A change in temperature also changes the longevity of insects (Rosenzweig *et al.,* 2001). An increase in average temperature results in a decrease in winter mortality, which have an effect on population dynamics (Ayres & Lombardero, 2000; Bale & Hayward, 2010). The size of adult insects has, however, been reported to decrease at higher temperatures, causing lower fecundity (Atkinson, 1994). Insects respond faster to climate change due to their high reproductive rates and short generation times when compared to vertebrates (Bale *et al.,* 2002; Menéndez, 2007). Insect species that are not dependent on low temperatures to induce diapause and that have short life cycles will respond to warming by expanding their geographic distributions, whereas species that are dependent on cold temperatures to induce diapause and slow development will have fewer favourable environments (Sharma, 2014).

Shifting in ecosystem boundaries is a major indicator of the influence of climate change and implies that new areas become more suitable for species to invade (Parmesan, 1996). New species that arrive may compete interspecifically with native species and this could lead to additional challenges in terms of pest management (Berggren *et al.,* 2009). The increase in temperature will extend the distribution of insect species to higher altitudes and latitudes (Pollard *et al.,* 1995; Hill *et al.,* 1999), due to these environments that become more suitable

(Sharma, 2014). *Spodoptera frugiperda* outbreaks are also predicted to increase in regions with higher altitudes as a result of climate change (Ramirez-Cabral *et al.,* 2017) (Fig. 1.12), a phenomenon which can have a major impact on maize production. Maize is grown over the widest range of altitudes and latitudes compared to any other food crop (Shiferaw *et al.,* 2011). The CLIMEX model of Ramirez-Cabral *et al.* (2017) forecasts the distribution of *S. frugiperda* to expand to 30 °N latitude and to below the Tropic of Capricorn. They also forecast a decrease or elimination from Mexico to the Tropic of Capricorn (Ramirez-Cabral *et al.,* 2017) (Fig. 1.12).

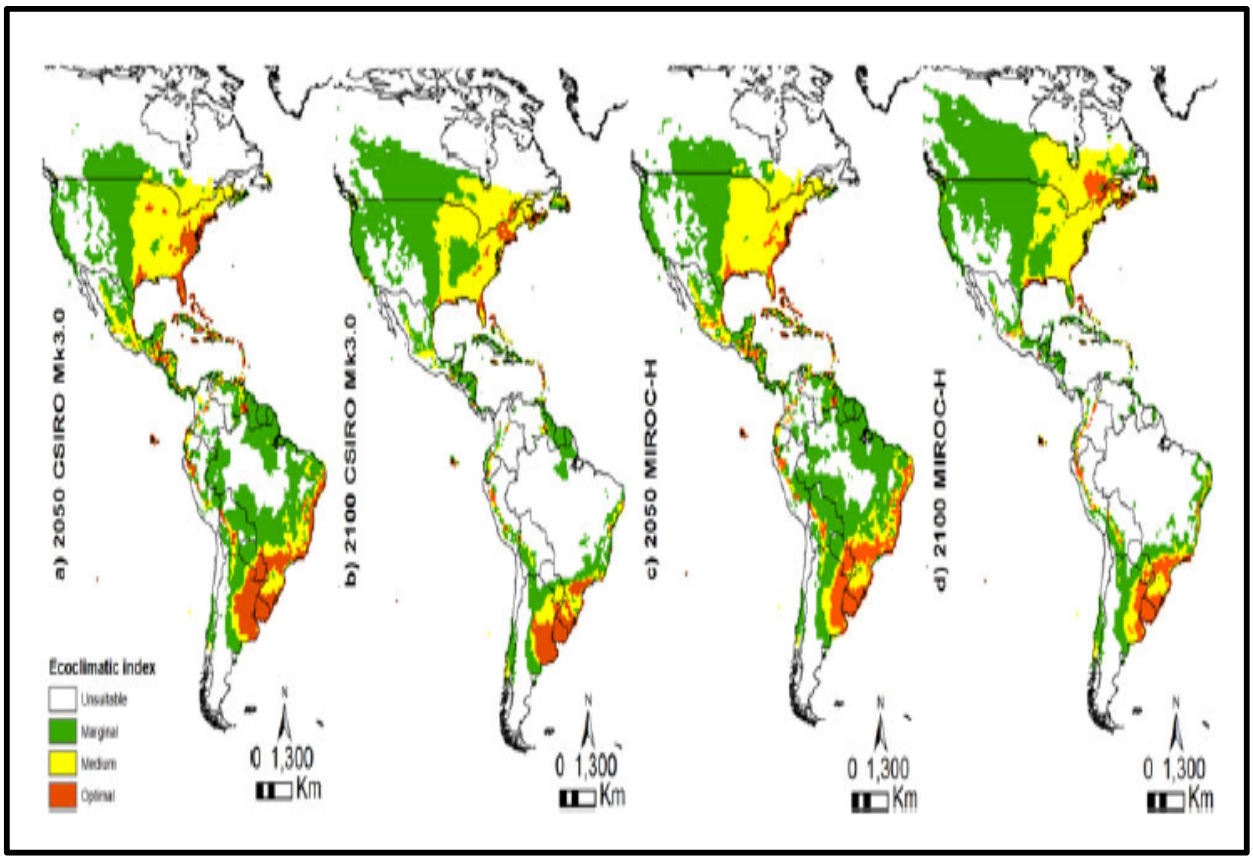



**Figure 1.12:** Ecoclimatic index for future climate conditions of *Spodoptera frugiperda* in the Americas (a) by 2050 under CSIRO-Mk3.0, (b) by 2100 under CSIRO-Mk3.0, (c) by 2050 under MIROC-H and (d) by 2100 under MIROC-H (Ramirez-Cabral *et al.,* 2017).

Pest outbreaks will occur more regularly in environments with higher temperatures because the conditions are better for development and reproduction of pest outbreaks (Boggs, 2016; Ramsfield *et al.,* 2016). In general changes in climate may result in changes in geographical distribution, increased overwintering, changes in population growth rates, increases in the number of generations, extension of the development season, changes in crop-pest synchrony, changes in interspecific interactions and increased risk of invasion by migrant pests (Porter *et al.,* 1991).

## 1.10 Objectives of this study

### 1.10.1 General objective

The main objective of the study was to evaluate the effect of temperature on the development and reproduction of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) under South African conditions.

### 1.10.2 Specific objectives

The specific objectives were to determine:

- the development rate of *S. frugiperda* at different constant temperatures
- the number of degree-days (°D) required for each stage to complete development, as well as for the overall egg-to-adult development
- the number of larval instars and to develop criteria for identifying specific instars of *S. frugiperda*
- the effect of different constant temperatures on the reproduction of *S. frugiperda*

## 1.11 References


Abrahams, P., Beale, T., Cock, M., Corniani, N., Day, R., Godwin, J., Murphy, S., Richards, G. & Vos, J. 2017. Fall armyworm status. Impacts and control options in Africa: CABI Preliminary Evidence Note (April 2017). 14 p.

Acevedo, P., Ruiz-Fons, F., Estrada, R., Márquez, A.L., Miranda, M.A., Gortázar, C. & Lucientes, J. 2011. A broad assessment of factors determining *Culicoides imicola* abundance: modelling the present and forecasting its future in climate change scenarios. *PLoS ONE* 5(12): e14236.

Adamczyk Jr, J.J., Leonard, B.R. & Graves, J.B. 1999. Toxicity of selected insecticides to fall armyworm (Lepidoptera: Noctuidae) in laboratory bioassay studies. *Florida Entomologist* 82: 230-236.

Addo-Bediako, A. & Thanguane, N. 2012. Stem borer distribution in different sorghum cultivars as influenced by soil fertility. *Agricultural Science Research Journal* 2(4): 189-194.

Ali, A., Luttrell, R.G. & Schneider, J.C. 1990. Effects of temperature and larval diet on development of the fall army worm (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America.* 83(4): 725-733.

All, J.N., Stancil, J.D., Johnson, T.B. & Gouger, R. 1996. Controlling fall armyworm infestations in whorl stage corn with genetically modified *Bacillus thuringiensis* formulations. *Florida Entomologist* 79: 311-317.

Al-Sarar, A., Hall, F.R. & Downer, R.A. 2006. Impact of spray application methodology on the development of resistance to cypermethrin and spinosad by fall armyworm *Spodoptera frugiperda* (JE Smith). *Pest Management Science* 62: 1023-1031.

Amarasekare, P. & Savage, V. 2012. A framework for elucidating the temperature dependence of fitness. *American Naturalist* 179: 178-191.

Andrews, K.L. 1980. The whorlworm, *Spodoptera frugiperda*, in the Central America and neighboring areas. *Florida Entomologist* 63: 456-467.

Andrews, K.L. 1988. Latin American research on *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Florida Entomologist* 71(4): 630-653.

Ashley, T.R. 1979. Classification and distribution of fall armyworm parasites. *Florida Entomologist* 62: 114-122.

Ashley, T.R., Wiseman, B.R., Davis, F.M. & Andrews, K.L. 1989. The fall armyworm: a bibliography. *Florida Entomologist* 72: 152-202.

Atkinson, D. 1994. Temperature and organism size - a biological law for ectotherms? *Advances in Ecological Research* 25: 1-58.

Atkinson, D. & Sibly, R.M. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology & Evolution* 12: 235-239.

Avila, C.J., De Grande, P.E. & Gomez, S.A. 1997. Insetos-pragas: reconhecimento, comportamento, danos e controle, pp. 168-180. *In*: *Milho: informações técnicas*. EMBRAPA, Circular Técnica, 5, Dourados.

Ayres, M.P. & Lombardero, M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* 262(3): 263-286.

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.

Bale, J.S. & Hayward, S.A. 2010. Insect overwintering in a changing climate. *Journal of Experimental Biology* 213: 980-994.

Barbercheck, M.E. 1993. Tritrophic level effects on entomopathogenic nematodes. *Environmental Entomology* 22(5): 1166-1171.

Barfield, C.S., Stimac, J.L. & Keller, M.A. 1980. State of the art for predicting damaging infestations of fall armyworm. *Florida Entomologist* 63: 364-375.

Barros, E., Torres, J.B., Ruberson, J.R. & Oliveira, M.D. 2010. Development of *Spodoptera frugiperda* on different hosts and damage to reproductive structures in cotton. *Entomologia Experimentalis et Applicata* 137: 237-245.

BBC (British Broadcasting Corporation). 2017. Fall armyworm 'threatens African farmers' livelihoods'. UK: BBC.http://www.bbc.co.uk/news/science-environment-38859851. Date of access: 17 Oct. 2017.

Bennett, A.F. & Huey, R.B. 1990. Studying the evolution of physiological performance. *Oxford Surveys in Evolutionary Biology* 6: 251-284.

Berggren, A., Björkman, C., Bylund, H. & Ayres, M.P. 2009. The distribution and abundance of animal populations in a climate of uncertainty. *Oikos* 118: 1121-1126.
Bernays, E.A. 1997. Feeding by lepidopteran larvae is dangerous. *Ecological Entomology* 22: 121-123.

Boggs, C.L. 2016. The fingerprints of global climate change on insect populations. *Current Opinion in Insect Science* 17: 69-73.

Bowler, K. & Terblanche, J.S. 2008. Insect thermal tolerance: what is the role of ontogeny, ageing and senescence? *Biological Reviews of the Cambridge Philosophical Society* 83(3): 335-339.

Briere, J.F., Pracros, P., Le Roux, A.Y. & Pierre, S. 1999. A novel rate model of temperature dependent development for arthropods. *Environmental Entomology* 28: 22-29.

Brown, E.S. & Dewhurst, C.F. 1975. The genus *Spodoptera* (Lepidoptera: Noctuidae) in Africa and the near East. *Bulletin of Entomological Research* 65: 221-262.

Bryant, S.R., Bale, J.S. & Thomas, C.D. 1998. Modification of the triangle method of degree-day accumulation to allow for behavioural thermoregulation in insects. *Journal of Applied Ecology* 35: 921-927.

Buntin, G.D. 1986. A review of plant response to fall armyworm, *Spodoptera frugiperda* (J.E. Smith), injury in selected field and forage crops. *The Florida Entomologist* 69(3): 549-559.

Burkhardt, C.C. 1952. Feeding and pupating habits of the fall armyworm. *Journal of Economic Entomology* 45(6): 1035-1037.

CABI. Datasheet. *Spodoptera frugiperda* (fall army worm). Invasive Species Compendium http://www.cabi.org/isc/datasheet/29810 (2016). Date of access: 23 Oct. 2017.

Calzadilla, A., Rehdanz, K., Betts, R., Falloon, P., Wiltshire, A. & Tol, R.S.J. 2013. Climate change impacts on global agriculture. *Climate Change* 120: 357-374.

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.

Cannon, R.J.C. 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology* 4: 785-796.

Capinera, J.L. 1999. Fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Insecta: Lepidoptera: Noctuidae). University of Florida, IFAS Extension, 6 pp.

Capinera, J.L. 2001. Handbook of Vegetable Pests. Academic Press, San Diego, USA, 727 pp.

Carey, J.R. 1984. Host-specific demographic studies of the Mediterranean fruit fly *Ceratitis capitata. Ecological Entomology* 9: 26-270.

Castro, M.T. & Pitre, H.N. 1988. Development of fall armyworm, *Spodoptera frugiperda*, from Honduras and Mississippi on sorghum or corn in the laboratory. *The Florida Entomologist* 7: 49-56.

Castro, B.A. 2002. Evaluation of *Bacillus thuringiensis* field corn for management of Louisiana corn pests. Ph.D. Dissertation, Louisiana State University, Baton Rouge, LA., pp. 189.

Chapman, J.W., Williams, T., Martínez, A.M., Cisneros, J., Caballero, P., Cave, R.D. & Goulson, D. 2000. Does cannibalism in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) reduce the risk of predation? *Behavioural Ecology and Sociobiology* 48: 321-327.

Chi, H. & Getz, W.M. 1988. Mass rearing and harvesting based on an age-stage, two-sex life table: a potato tuber worm (Lepidoptera: Gelechiidae) case study. *Environmental Entomology* 17: 18-25.

Chi, H. 1990. Timing of control based on the stage structure of pest population: A simulation approach. *Journal of Economic Entomology* 83: 1143-1150.

Chi, H. & Su, H.Y. 2006. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. *Environmental Entomology* 35: 10-21.

Clark, P.L., Molina-Ochoa, J., Martinelli, S., Skoda, S.R., Isenhour, D.J., Lee, D.J., Krumm, J.T. & Foster, J.E. 2007. Population variation of the fall armyworm, *Spodoptera frugiperda*, in the Western Hemisphere. *Journal of Insect Science* 7: 1536-2442.

Commission for Africa. 2005. Our common interest-report of the Commission for Africa. Commission for Africa, London.

Crops Estimates Committee. 2017. Summer crops-Final production estimate (2017) and winter cereals: Revised area planted and second production forecast (2017). National Department of Agriculture, South Africa, 28 September 2017.

Cruz, I. 2007. Alternativas para o controle da lagarta-do-cartucho, *Spodoptera frugiperda* e principais cuidados no uso de milhos transgênicos resistentes a insetos. In: FANCELLI, A. L.; DOURADO NETO, D. (Ed.). Milho - Fatores determinantes da produtividade. Piracicaba: USP-ESALQ.

Cruz, I. 2008. Manejo de pragas da cultura do milho. In: Galvão JCC, Miranda GV, editors, Tecnologias de produção do milho. Viçosa: UFV. p. 311-366.

Davis, F.M., Baker, G.T. & Williams, W.P. 1995. Anatomical characteristics of maize resistant to leaf feeding by southwestern corn borer (Lepidoptera: Pyralidae) and fall armyworm (Lepidoptera: Noctuidae). *Journal of Agricultural Entomology* 12: 55-65.

De Groote, H. 2002. Maize yield losses from stem borers in Kenya. *Insect Science and its Application* 22(2): 89-96.

Dingle, H. 1972. Migration strategies of insects. *Science* 175(4028): 1327-1335.

Drinkwater, T. W. & Van Rensburg, J.B.J. 1992. Association of common cutworm, *Agrotis segetum* (Lepidoptera: Noctuidae), with winter weeds and volunteer maize. *Phytophylactica* 24: 25-28.

Du Plessis, H. 2000. Common cutworm - a pest of grain crops. Crop Protection Series No. 9. ARC-Grain Crops Institute, Potchefstroom.

Easterling, D.R., Horton, B., Jones, P.D., Peterson, T.C., Karl, T.R., Parker, D.E., Salinger, M.J., Razuvayev, V., Plummer, N., Jamason, P. & Folland, C.K. 1997. Maximum and minimum temperature trends for the globe. *Science* 277: 364-367.

Estay, S.A., Lima, M. & Harrington, R. 2009. Climate mediated exogenous forcing and synchrony in populations of the oak aphid in the UK. *Oikos* 118: 175-182.

Fan, Y.Q., Groden, E. & Drummond, F.A. 1992. Temperature-dependent development of Mexican bean beetle (Coleoptera: Coccinellidae) under constant and variable temperatures. *Journal of Economic Entomology* 85(5): 1762-1770.

FAO (Food and Agricultural Organization of the United Nations). 2008. Climate change and food security: A conceptual document. Rome, Italy: Food and Agricultural Organisation of the United Nations.

FAO (Food and Agricultural Organization of the United Nations). 2010. Statistical Database of the Food and Agriculture Organization of the United Nations. FAO, Rome.

FAO (Food and Agricultural Organization of the United Nations). 2017. Fall army worm outbreak, a blow to prospects of recovery for Southern Africa. Rome, Italy.

Ferrer, F. 2001. Biological control of agricultural insect pests in Venezuela; advances, achievements, and future perspectives. *Biocontrol News and Information* 22(3): 67-74.

García-Roa, F., Mosquera-E, M.T., Vargas-S, C.A. & Rojas, A L. 2002. Control biológico,microbiológico y físico de *Spodoptera frugiperda* (Lepidoptera: Noctuidae), plaga del maíz y otros cultivos em Colombia. *Revista Colombiana de Entomología* 28: 53-60.

Garcia-Salazar, C., Podoler, H. & Whalon, M.E. 1988. Effects of temperature on diapause induction in the codling moth, *Cydia pomonella*. *Environmental Entomology* 17: 626-628.

Gardner, W.A. & Fuxa, J.R. 1980. Pathogens for the suppression of the fall armyworm. *The Florida Entomologist* 63: 439-447.

Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M. & Brown, J.H. 2002. Effects of size and temperature on developmental time. *Nature* 417(6884): 70-73.

Goergen, G., Kumar, P.L., Sankung, S.B., Togola, A. & Tamo, M. 2016. First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in west and Central Africa *PLoS one* 11(10): e0165632.

Gómez-Valderrama, J.A., Guevara-Agudelo, E.J., Barrera-Cubillos, G.P., Cotes-Prado, A.M. & Villamizar-Rivero, L.F. 2010. Aislamiento, identificación y caracterización de *Nucleopoliedrovirus* nativos de *Spodoptera frugiperda*en Colombia. *Revista Facultad Nacional de Agronomía, Medellín* 63(2): 5511-5520.

Greene, G.L., Janes, M.J. & Mead, F.W. 1971. Fall armyworm, *Spodoptera frugiperda,* males captured at three Florida locations in traps baited with virgin females. *The Florida Entomologist* 54: 165-166.

Gross Jr, H.R., Young, J.R. & Wiseman, B.R. 1982. Relative susceptibility of summer-planted dent and tropical flint corn variety to whorl stage damage by the fall armyworm (Lepidoptera: Noctuidae). *Journal of Economic Entomology* 75(6): 1153-1156.

Gu, W. & Novak, R.J. 2005. Statistical estimation of degree days of mosquito development under fluctuating temperatures in the field. *Journal of Vector Ecology* 31: 107-112.

Hanway, J.J. 1969. Defoliation effect on different corn (*Zea mays* L.) hybrids as influenced by plant population and stage of development. *Agronomy Journal* 61: 534-538.

Harrington, R., Clark, S.J., Welham, S.J., Verrier, P.J., Denholm, C.H., Hullé, M., Maurice, D., Rounsevell, M.D. & Cocu, N. 2007. European Union Examine Consortium. Environmental change and the phenology of European aphids. *Global Change Biology* 13: 1550-1564.

Harrison, F.P. 1984. Observations on the infestation of corn by fall armyworm (Lepidoptera: Noctuidae) with reference to plant maturity. *The Florida Entomologist* 67: 333-335.

Harrison, F.P. 1986. Oviposition and subsequent infestations of corn by fall armyworm. *The Florida Entomologist* 69: 588-592.

Hassall, C., Thompson, D.J., French, G.C. & Harvey, I.F. 2007. Historical changes in the phenology of British Odonata are related to climate. *Global Change Biology* 13: 933-941.

Hassan, R. & Nhemachena, C. 2008. Determinants of African farmers' strategies for adapting to climate change: Multinomial choice analysis. *African Journal of Agricultural and Resource Economics* 2: 83-104.

Henderson, C.F., Kinzer, H.G. & Thompson. E.G. 1966. Growth and yield of grain sorghum infested in the whorl with fall armyworm. *Journal of Economic Entomology* 59(4): 1001-1003.

Hill, D.S. 1983. Agricultural Insect Pests of the Tropics and their Control. Second edition. Cambridge University Press, Cambridge, UK, 746 pp.

Hill, J.K., Thomas, C.D. & Huntley, B. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margins. *Proceedings of the Royal Society of London, Series B* 266: 1197-1206.

Hogg, D.B., Pitre, H.N. & Anderson, R.E. 1982. Assessment of early-season phenology of the fall armyworm (Lepidoptera: Noctuidae) in Mississippi. *Environmental Entomology* 11: 705-710.

Honěk, A. 1996. The relationship between thermal constants for insect development: a verification. *Acta Societatis Zoologicae Bohemicae* 60: 115-152.

Honěk, A., Jarosik, V. & Martinkova, Z. 2003. Effect of temperature on development and reproduction in *Gastrophysa viridula* (Coleoptera: Chrysomelidae). *European Journal of Entomology* 100: 295-300.

Huey, R.B. & Stevenson, R.D. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist* 19: 357-366.

IFAD (International Fund for Agricultural Development). 2009. Research and innovation for smallholder farmers in the context of climate change. Discussion paper for Round Table 3, thirty-second session of the Governing Council, Rome, 18-19 February. https://www.uncclearn.org/sites/default/files/inventory/ifad57.pdf. Date of access: 17 Oct. 2017.

IPCC (Intergovernmental Panel on Climate Change). 2001. Climate change Impacts, adaptations and vulnerability. Contribution of Working Group Fourth Assessment Report of the IPCC. In McCarthy, J.J., Canziani, F.O., Leary, N.A., Dokken, D.J. & White, K.S. (Eds.), Cambridge: Cambridge University Press.

IPPC (Intergovernmental Panel on Climate Change). 2017. Detection of Fall Army Worm *Spodoptera frugiperda* in Swaziland. IPPC Official Pest Report, No. SWZ-02/1. Rome, Italy: FAO.https://www.ippc.int/

Jarošík, V., Honek, A. & Dixon, A.F. 2002. Developmental rate isomorphy in insects and mites. *American Naturalist* 160(4): 497-510.

Jarošík, V., Kratochvíl, L., Honek, A. & Dixon, A.F.G. 2004. A general rule for the dependence of developmental rate on temperature in ectotherms. *Proceedings of the Royal Society, London B (Supplementum)* 271: S219-S221.

Jarrod, T.H., Lorenz, G.M. & Leonard, R.B. 2015. Fall Armyworm (Lepidoptera: Noctuidae) ecology in Southeastern cotton. *Journal of Integrated Pest Management* 6 (1): 10.

Jaworski, T. & Hilszczański, J. 2013. The effect of temperature and humidity on insect development and their impact on forest ecosystems in the context of expected climate change. *Forest Research Papers* 74(4): 345-355.

Jha, K.R., Chi, H. & Li, C.T. 2012. A comparison of artificial diet and hybrid sweet corn for the rearing of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) based on life table characteristics. *Environmental Entomology* 41: 30-39.

Johnson, S.F. 1987. Migration and the life history strategy of fall armyworm, *Spodoptera frugiperda* in the western hemisphere. *Insect Science and its Application* 8: 543-549.

Kannan, R. & James, D.A. 2009. Effects of climate change on global diversity: a review of key literature. *Tropical Ecology* 50: 31-39.

Kfir, R. 2002. Increase in cereal stem borer populations through partial elimination of natural enemies. *Entomologia Experimentalis et Applicata* 104: 299-306.

Klun, J.A., Potts, W.J.E. & Oliver, J.E. 1996. Four species of noctuid moths degrade sex pheromone by a common antennal metabolic pathway. *Journal of Entomological Science* 31(4): 404-413.

Knipling, E.F. 1980. Regional management of the fall armyworm-a realistic approach? *The Florida Entomologist* 63: 468-480.

Kolberg, I. 2013. The effect of temperature on trophic Interactions. Unpublished PhD thesis. University of Uppsala, Sweden.

Kranthi, K.R., Naidu, S., Dhawad, C.S., Tatwawadi, A., Mate, K., Patil, E., Bharose, A.A., Behere, G.T., Wadaskar, R.M. & Kranthi, S. 2005. Temporal and intra-plant variability of *Cry*1Ac expression Bt-cotton and its influence on the survival of the cotton bollworm, *Helicoverpa armigera* Hübner (Noctuidae: Lepidoptera). *Current Science* 89(2): 291-298.

Kroon, D.M. 1999. Lepidoptera of southern Africa, host plants and other associations. Lepidopterists' Society of Southern Africa. Kroon, D.M. Jukskei Park & Sasolburg, South Africa.

Kroschel, J., Sporleder, M., Tonnang, H.E.Z., Juarez, H., Carhuapoma, P., Gonzales, J.C. & Simon, R. 2013. Predicting climate-change-caused changes in global temperature on potato tuber moth *Phthorimaea operculella* (Zeller) distribution and abundance using phenology modelling and GIS mapping. *Agricultural and Forest Meteorology* 170: 228-241.

Kruger, M., Van Rensburg, J.B.J. & Van den Berg, J. 2012. Transgenic Bt maize farmers' perceptions, refuge compliance and reports of stem borer resistance in South Africa. *Journal of Applied Entomology* 136: 38-50.

Kurukulasuriya, P. & Mendelsohn, R. 2007. A Ricardian analysis of the impact of climate change on Africa cropland. *World Bank Policy Research Working Paper No*. 4305.

Kurukulasuriya, P. & Mendelsohn, R. 2008. How will climate change shift agro-ecological zones and impact African agriculture? *World Bank Policy Research Working Paper* 4717, Washington, D.C, USA: World Bank.

Labrador, J.R. 1967. Estudios de biologia y combate del gusano cogollero del maiz, *Laphygma frugiperda* (S. and A.) University of Zulia. Maracaibo, Venezuela. 83 pp.

Lanciani, C., Lipp, K.E. & Giesel, J.T. 1992. The effect of photoperiod on cold tolerance in Drosophila melanogaster. *Journal of Thermal Biology* 17: 147-148.

Lee, J.H. & Elliott, N.C. 1998. Comparison of developmental responses to temperature in *Aphelinus asychis* (Walker) from two different geographic regions. *Southwestern Entomologist* 23: 77-82.

Linduska, J.J. & Harrison, F.P. 1986. Adult sampling as a means of predicting damage levels of fall armyworm (Lepidoptera: Noctuidae) in grain corn. *The Florida Entomologist.* 69: 487-491.

Loeschcke, V. & Hoffmann, A.A. 2007. Consequences of heat hardening on a field fitness component in *Drosophila* depend on environmental temperature. *The American Naturalist* 169: 175-183.

Logan, J.A. 1988. Toward an expert system for development of pest simulation models. *Environmental Entomology* 17: 359-376.

Luginbill, P. 1928. The fall armyworm. U.S. Department of Agricultural *Technical Bulletin* 34: 1-91.

Ma, L., Wang, X., Liu, Y., Su, M-Z. &Huang, G-H. 2017. Temperature effects on development and fecundity of *Brachmia macroscopa* (Lepidoptera: Gelechiidae). *PLoS ONE* 12(3): 1-12.

Martin, P.B., Wiseman, B.R. & Lynch, R.E. 1980. Action thresholds for fall armyworm on grain sorghum and coastal Bermuda grass. *The Florida Entomologist* 63: 375-405.

Matten, S.R., Head, G.P. & MacIntosh, S.C. 2008. How government regulation can help or hinder the integration of Bt crops within IPM programs. In: Romeis, J., Shelton, A.M.,

Kennedy, G.G. (Eds.), Integration of Insect Resistant Genetically Modified Crops with IPM Programs. Springer Science þ Business Media B. V., New York, USA, pp. 27-39.

McMichael, M. & Prowell, D.P. 1999. Differences in amplified fragment-length polymorphisms in fall armyworm (Lepidoptera: Noctuidae) host strains. *Annals of the Entomological Society America* 92: 175-181.

Meagher, R.L. & Nagoshi, R.N. 2004. Population dynamics and occurrence of *Spodoptera frugiperda* host strains in southern Florida. *Ecological Entomology* 29 (5): 614-620.

Melo, M. & Silva, R.F.P. 1987. Influência de três cultivares de milho no desenvolvimento de *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera: Noctuidae). *Anais da Sociedade Entomológica do Brasil* 16: 37-49.

Memmott, J., Carvell, C., Pywell, R.F. & Craze, P.G. 2010. The potential impact of global warming on the efficacy of field margins sown for the conservation of bumble-bees. *Philosophical Transactions Royal Society of London, B Biological Science* 365(1549): 2071-2079.

Menéndez, R. 2007. How are insects responding to global warming. *Tijdschrift voor Entomologie* 150: 355-365.

Metcalf, C.L., Metcalf, R.L. & Flint, W.P. 1965. Insectos destructivos e insectos utiles: sus costumbres y su control. Compa nia Editorial ~ Continental, p. 1208.

Miller, G.W. 1977. Mortality of *Spodoptera littoralis* at non-freezing temperatures. *Bulletin of Entomological Research* 67: 143-152.

Milonas, P.G. & Savopoulou-Soultani, M. 2000. Development, survivorship, and reproduction of *Adoxophyes orana* (Lepidoptera: Tortricidae) at constant temperatures. *Annals of the Entomological Society of America* 93: 96-102.

Mitchell, E.R. 1978. Relationship of planting date to damage by earworms in commercial sweet corn in north central Florida. *The Florida Entomologist* 61: 251-255.

Mitchell, E.R. 1979. Migration by *Spodoptera exigua* and *Spodoptera frugiperda,* North American style. pp. 386–393. *IN* R.L. Rabb and G.G. Kennedy (eds.), Movement of Highly

Mobile Insects: Concepts and Methodology in Research. Raleigh, North Carolina State University, North Carolina, USA.

Mitchell, E.R. 1986. USDA Technical Bulletin No. 34-The legacy of Philip Luginbill. *The Florida Entomologist* 69: 452-455.

Mitchell, E.R., McNeil, J.N., Westbrook, J.K., Silvain, J.F., Lalanne-Cassou, B., Chalfant, R.B., Pair, S.D., Waddill, V.H., Sotomayor-Rios, A. & Proshold, F.I. 1991. Seasonal periodicity of fall armyworm, (Lepidoptera: Noctuidae) in the Caribbean basin and northward to Canada. *Journal of Entomological Science* 26: 39-50.

Moallem, Z., Karimi-Malati, A., Sahragard, A. & Zibaee, A. 2017. Modeling temperature-dependent development of *Glyphodes pyloalis* (Lepidoptera: Pyralidae). *Journal of Insect Science* 17(2): 37: 1-8.

Moar, W.J., Pusztai-Carey, M., Van Faassen, H., Bosch, D., Frutos, R., Rang, C., Luo, K. & Adang, M.J. 1995. Development of *Bacillus thuringiensis* CryIC Resistance by *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae). *Applied and Environmental Microbiology* 61(6): 2086-2092.

Morrill, W.L. & Greene, G.L. 1973. Distribution of fall armyworm larvae. Regions of field corn plants infested by larvae. *Environmental Entomology* 2: 195-198.

Morrill, W.L. & Greene, G.L. 1974. Survival of fall armyworm larvae and yields of field corn after artificial infestations. *Journal of Economic Entomology* 67: 119-123.

Murúa, M., Fidalgo, G.P. & Virla, E. 2003. First record of *Trichogramma atopovirilia* Otman y Platner (Hymenoptera: Trichogrammatidae), for Argentina, attacking the eggs of *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae) on corn. *Vedalia* 9(10): 25-26.

Murúa, M.G. & Virla, E.G. 2004. Contribution to the knowledge of the biology of *Euplectrus platyhypenae* (Hymenoptera: Eulophidae), parasitoid of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Argentina. *Folia Entomologica Mexicana* 43(2): 171-180.

Mwalusepo, S., Tonnang, H.E.Z., Massawe, E.S., Okuku, G.O., Khadioli, N., Johansson, T., Calatayud, P. & Le Ru, B.P. 2015. Predicting the impact of temperature change on the future distribution of maize stem borers and their natural enemies along east African mountain gradients using phenology models. *PLoS ONE*: 1-23.

Naseri, B., Golparvar, Z., Razmjou, J. & Golizadeh, A. 2014. Age-stage, two-sex life table of *Helicoverpa armigera* (Lepidoptera: Noctuidae) on different bean cultivars. *Journal of Agriculture Science and Technology*-Iran. 16(1): 19-32.

Niang, I., Ruppel, O.C., Abdrabo, M.A., Essel, A., Lennard, C., Padgham, J. & Urquhart, P. 2014. Africa. In: *Climate Change 2014*: *Impacts, Adaptation, and Vulnerability*. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change Cambridge, Cambridge University Press.

Oliver, A.D. & Chapin, J.B. 1981. Biology and illustrated key for the identification of twenty species of economically important noctuid pests. *Louisiana Agricultural Experiment Station Bulletin No.* 733.

Ortega, A. 1974. Maize diseases and pests. In: *Proceedings World Wide Maize Improvement in the 70s and the Role of C1MMYT.* 7: 1-41.

Paaijmans, K.P., Heinig, R.L., Seliga, R.A., Blanford, J.I., Blanford, S., Murdock, C.C. & Thomas, M.B. 2013. Temperature variation makes ectotherms more sensitive to climate change. *Global Change Biology* 19: 2373-2380.

Pair, S.D., Raulston, J.R., Sparks, A.N., Westbrook, J.K. & Dounce, G.K. 1986. Fall armyworm distribution and population dynamics in the southeastern states. *The Florida Entomologist* 69: 468-487.

Parmesan, C. 1996. Climate and species' range. *Nature* 382: 765-766.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phonological response to global warming. *Global Change Biology* 13: 1860-1872.

Pashley, D.P., Johnson, S.J. & Sparks, A.N. 1985. Genetic population structure of migratory moths: the fall armyworm (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* 78: 756-762.

Pashley, D.P. 1986. Host-associated genetic differentiation in fall armyworm (Lepidoptera: Noctuidae): a sibling species complex? *Annals of the Entomological Society of America* 79: 898-904.

Pashley, D.P. & Martin, J.A. 1987a. Reproductive incompatibility between host strains of the fall armyworm (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* 80: 731-733.

Pashley, D.P., Sparks, T.C., Quisenberry, S.S., Jamjanya, T. & Dowd, P.F. 1987b. Two fall armyworm strains feed on corn, rice and bermudagrass. *Louisiana Agriculture* 30: 8-9.

Pasley, D.P., Hammond, A.N. & Hardy, T.N. 1992. Reproductive isolating mechanisms in fall armyworm host strains (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* 80: 400-405.

Pashley, D.P., Hardy, T.N. & Hammond, A.M. 1995. Host effects on development and reproductive strains. (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* 88: 748-755.

Patterson, D.T., Westbrook, J.K., Joyce, R.J.C., Lingren, P.D. & Rogasik, J. 1999. Weeds, insect and diseases. *Climate Change* 43: 711-727.

Pitre, H.N. & Hogg, D.B. 1983. Development of the fall armyworm on cotton, soybean and corn. *Journal of Georgia Entomological Society* 18: 182-187.

Piyaphongkul, J., Pritchard, J. & Bale, J. 2012. Can tropical insects stand the heat? A case study with the brown planthopper *Nilaparvata lugens* (Stal). *PLoS ONE* 7: 1-6.

Pollard, E., Moss, D. & Yates, T.J. 1995. Population trends of common British butterflies at monitored sites. *Journal of Applied Ecology* 32: 9-16.

Porter, J.H., Parry, M.L. & Carter, T.R. 1991. The potential effects of climatic change on agricultural insect pests. *Agricultural and Forest Meteorology* 57: 221-240.

Prato, T., Zeyuan, Q., Pederson, G., Fagre, D., Bengtson, L.E. & Williams, J.R. 2010. Potential economic benefits of adapting agricultural production systems to future climate change. *Environmental Management* 45: 577-589.

Prowell, D.P., McMichael, M. & Silvain, J.F. 2004. Multilocus genetic analysis of host use, introgression, and speciation in host strains of fall armyworm (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* 97: 1034-1044.

Ramirez-Cabral, N.Y.Z., Kumar, L. & Shabani, F. 2017. Global alterations in areas of suitability for maize production from climate change and using a mechanistic species distribution model (CLIMEX). *Scientific Reports* 7: 1-12.

Ramsfield, T.D., Bentz, B.J., Faccoli, M., Jactel, H. & Brockerhoff, E.G. 2016. Forest health in a changing world: effects of globalization and climate change on forest insect and pathogen impacts. *Forestry* 89: 245-252.

Randall, M.G.M. 1986. The predation of predispersed *Juncus squarrosus* seeds by *Coleophora alticolella* (Lepidoptera) larvae over a range of altitudes in northern England. *Oecologia* 69(3): 460-465.

Raulston, J.R., Pair, S.D., Sparks, A.N., Loera, J.G., Pedraza, F.A.M., Palamon, A.T., Ortega, A.A., Sanchez Ruiz, A.J.M., Marquez, A.P.C., Rueles, A.H.A., Perez, A.J.M., Rodriguez, A.R.R., Carrillo, A.H.R., Archundia, A.R.R. & Herrera, R.F. 1986. Fall armyworm distribution and population dynamics in the Texas-Mexico Gulf coast area. *The Florida Entomologist* 68: 686-691.

Régnière, J., St-Amant, R. & Duva, I.P. 2012. Predicting insect distributions under climate change from physiological responses: spruce budworm as an example. *Biological Invasions.* 14: 1571-1586.

Roltech, W.J., Zalom, F.G., Strawn, A.J., Strand, A.J.F. & Pitcairn, M.J. 1999. Evaluation of several degree-day estimation methods in California climates. *International Journal of Biometeorol*ogy 42: 169-176.

Rose, D.J.W., Dewhurst, C.F. & Page, W.W. 2000. The African Armyworm handbook. The Status, Biology, Ecology, Epidemiology and Management of *Spodoptera exempta* (Lepidoptera: Noctuidae) Second edition Chatham: Natural Resources Institute, University of Greenwich, Greenwich, UK.

Rosegrant, M.R., Ringler, C., Sulser, T.B., Ewing, M., Palazzo, A., Zhu, T., Nelson, G.C., Koo, J., Robertson, R., Msangi, S. & Batka, M. 2009. Agriculture and food security under global change: Prospects for 2025/2050. International Food Policy Research Institute Washington, D.C.

Rosenzweig, C., Iglesias, A., Yang, X.B., Epstein, P.R. & Chivian, E. 2001. Climate change and extreme weather events; Implications for food production, plant diseases and pests. *Global Change & Human Health* 2: 90-104.

Ruíz-Nájera, R.E., Molina-Ochoa, J., Carpenter, J.E., Espinosa-Moreno, J.A., Ruíz-Nájera, J.A., Lezama-Gutiérrez, R. & Foster, J.E. 2007. Survey for hymenopteran and dipteran parasitoids of the fall armyworm (Lepidoptera: Noctuidae) in Chiapas, Mexico. *Journal of Agricultural and Urban Entomology* 24: 35-42.

Sarfraz, M., Dosdall, L.M. & Keddie, B.A. 2006. Diamondback moth-host plant interactions: implications for pest management. *Crop Protection* 25: 625-636.

Scharf, I., Braf, H., Ifrach, N., Rosenstein, S. & Subach, A. 2015. The effects of temperature and diet during development, adulthood, and mating on reproduction in the Red Flour Beetle. *PLoS ONE* 10(9): 1-15.

Schmidhuber, J. & Tubiello, N.F. 2007. Global food security under climate change. *Proceedings of the National Academy of Science USA* 104(50): 19703-19708.

Sena Jr, D.G., Pinto, F.A.C., Queiroz, D.M. & Viana, P.A. 2003. Fall armyworm damaged maize plant identification using digital images. *Biosystems Engineering* 85: 449-454.

Shah, M.M., Fischer, G. & Van Velthuizen, H. 2008. Food security and sustainable agriculture: The challenges of climate change in Sub-Saharan Africa. International Institute for Applied Systems Analysis, Laxenburg, Austria.

Sharma, H.C. 2014. Climate change effects on insects: Implications for crop protection and food security. *Journal of Crop Improvement* 28: 229-259.

Sharpe, P.J.H. & De Michele, D.W. 1977. Reaction kinetics of poikilotherm development. *Journal of Theoretical Biol*ogy 64: 649-670.

Shiferaw, B., Prasanna, B.M., Hellin, J. & Bänziger, M. 2011. Crops that feed the world. Past successes and future challenges to the role played by maize in global food security. *Food Security* 3(3): 307-327.

Siebert, M.W., Tindall, K.V., Leonard, B.R., Van Duyn, J.W. & Babcock, J.M. 2008. Evaluation of corn hybrids expressing Cry1F (Herculex® I insect protection) against fall armyworm (Lepidoptera: Noctuidae) in the Southern United States. *Journal of Entomological Science* 43: 41-51.

Snow, J.W. & Copeland, W.W. 1969. Fall armyworm: use of virgin female traps to detect males and to determine seasonal distribution. USDA *Production Research Report* 110: 9.

Sparks, A.N. 1979. A review of the biology of the fall armyworm. *The Florida Entomologist* 62: 82-87.

Sparks, A.N. 1986. Fall armyworm (Lepidoptera: Noctuidae): Potential for area-wide management. *The Florida Entomologist* 69: 603-614.

Starrat, A.N. & McLeod, G.R. 1982. Monitoring of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), moth population in southwestern Ontario with sex pheromone traps. *Canadian Entomologist* 114: 545-549.

Storer, N.P., Babcock, J.M., Schlenz, M., Meade, T., Thompson, G.D., Bing, J.W. & Huckaba, R.M. 2010. Discovery and characterization of field resistance to Bt maize: *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Puerto Rico. *Journal of Economic Entomology* 103: 1031-1038.

Terblanche, J.S., Deere, J.A., Clusella-Trullas, S., Janion, C. & Chown, S.L. 2007. Critical thermal limits depend on methodological context. *Proceedings of the Royal Society of London,* B 274: 2935-2942.

Thornton, P.K., Jones, P.G., Owiyo, T., Kruska, R.L., Herrero, M., Orindi, V., Bhadwal, S., Kristjanson, P., Notenbaert, A., Bekele, N. & Omolo, A. 2008. Climate change and poverty in Africa: Mapping hotspots of vulnerability. *African Journal of Agricultural and Resource Economics* 2: 24-44.

Van den Berg, J. 1997. Stemborers in sorghum. Crop Protection Series no. 3. ARC-Grain Institute, Potchefstroom.

Van Huis, A. 1981. Integrated pest management in the small farmer's maize crop in Nicaragua. *Mededelingen Landbouwhogeschool Wageningen* 81(6): 221.

Van Rensburg, J.B.J. 2000. The army worm complex. In: McDonald, A.H. & Van Rensburg, J.B.J (Eds). *Protection of Grain Crops*: *Principles and Practices*. 20. ARC-Grain Crops Institute, Potchefstroom.

Vickery, R.A. 1929. Studies on the fall armyworm in the Gulf coast district of Texas. United Sates Department of Agriculture, Washington, D.C. USA. *Technical Bulletin* 138: 64.

Visser, D. 2011. A complete Guide to Vegetable Pests in South Africa. Agricultural Research Council, Roodeplaat Vegetable and Ornamental Plant Institute, Pretoria.

Visser, D. 2017. An identification guide in relation to other common caterpillars, a South African perspective. http://sana.co.za/wp-content/uploads/2017/06/Fall-Armyworm-Identification.-DAFF-Presentation-v1.2-secured-Published....pdf Date of access: 14 June 2017.

Wagner, T.L., Wu, H.I., Sharpe, P.J.H., Schoolfield, R.M. & Coulson, R.N. 1984. Modelling insect development rates: a literature review and application of a biophysical model. *Annals of the Entomological Society of America* 77: 208-225.

Watt, A.D., Ward, L.K. & Eversham, B.C. 1990. Effects on animals: invertebrates. *The Greenhouse Effect and Terrestrial Ecosystems of the UK* (Eds Cannell, M.G.R. & Hooper, M.D.), pp. 32-37. *ITE Research Publication no*. 4. HMSO London.

Whitford, W.O. & Ettershank, O. 1975. Factors affecting foraging activity in Chihuahuan Desert harvester ants. *Environmental Entomology* 4: 689-696.

Wilson, J.W. 1933. The biology of parasites and predators of *Laphygma exigua* Huebner reared during the season of 1932. *The Florida Entomologist* 17: 1-15.

Wood, K.A., Wilson, B.H. & Graves, J.B. 1981. Influence of host plant on the susceptibility of the fall armyworm to insecticides. *Journal of Economic Entomology* 74: 96-98.

World Bank. 2007. World Development Report 2008: Agriculture for Development. Washington D.C: The World Bank.

Yu, S.J. 1991. Insecticide resistance in the fall armyworm, *Spodoptera frugiperda* (J. E. Smith). *Pesticide Biochemistry and Physiology* 39: 84-91.

Yu, J.Z., Chi, H. & Chen, B.H. 2013. Comparison of the life tables and predation rates of *Harmonia dimidiata* (F.) (Coleoptera: Coccinellidae) fed on *Aphis gossypii* Glover (Hemiptera: Aphididae) at different temperatures. *Biological Control* 64: 1-9.

Zheng, X., Huang, Q., Cao, W., Lu, W., Wang, G., Yu, S., Yang, Z. & Wang, X. 2015. Modelling climate change impacts on overwintering of *Spodoptera exigua* Hübner in regions of China. *Chilean Journal of Agricultural Research* 75(3): 328-333.

# CHAPTER 2

## The effect of temperature on the development of *Spodoptera frugiperda* (Lepidoptera: Noctuidae)

### 2.1 Abstract

The fall armyworm, *Spodoptera frugiperda*, is a polyphagous pest and native to the tropical and sub-tropical regions of America which recently invaded Africa. The effect of temperature on the development of *S. frugiperda* was studied at five different temperature regimes, namely 18, 22, 26, 30 and 32 ± 1 °C. Fertility was found to be high with all eggs that hatched at temperatures ranging from 18 to 32 °C. Development of eggs at a constant temperature of 18 °C was, however, slow and the percentage of eggs that survived, very low. Continuous low temperature, although above the lower thermal limit, will therefore slow development down and may reduce population numbers as a result of high mortality. The optimal range for egg, larval and egg-to-adult development of *S. frugiperda* in South Africa was determined to be between 26 and 32 °C. Development rate of *S. frugiperda* increased linearly with increasing temperatures between 18 and 30 °C and larval survival was also the highest between 26 and 30 °C. The optimum temperature with the fastest development rate and lowest mortality for larvae was at 30 °C. Pupal development time varied from 7.82 to 30.68 days (32 – 18 °C) with a mean pupal development time of 17.06 days at 22 °C, but only 11.43 days at 26 °C. Development period of the egg-to-adult stage decreased from 71.3 at 18 °C to 20.2 days at 32 °C. Based on linear regression analysis of development rate at all temperatures, a minimum temperature threshold of 13.01 °C was calculated for egg development and 12.12 °C for larvae, 13.24 °C for pupae and 12.57 °C for egg-to-adult development. Degree-day requirements for *S. frugiperda* egg and larval development was 35.72 ± 1.30 and 202.67 ± 4.45 °D respectively when larvae were reared on sweet corn kernels. Pupae needed 147.06 °D for development and development of the life cycle (egg-to-adult), 391.01 ± 1.22 °D. The six larval instars were determined by using head capsule widths that ranged from 0.3, 0.46, 0.8, 1.4, 1.9, and 2.69 mm. All successive instars increased in size according to Dyar's ratio.

**Key words:** degree-days, development, head capsule widths, *Spodoptera frugiperda*, temperature

## 2.2 Introduction

Pest biology, distribution and abundance are influenced by the relationship between temperature and the rate of development (Tobin *et al*., 2003). Development of insects occurs within a specific temperature range and a change in temperature will therefore influence the rate of development, duration of the life-cycle and ultimately, survival (Howe, 1967). An increase in ambient temperature to near the thermal optimum of insects cause an increase in their metabolism and therefore also their activity (Jaworski & Hilszczański, 2013). Since thermal and biological requirements of insect species can differ between populations (Lee & Eliot, 1998), it is important to study these relationships in order to understand and possibly predict invasion patterns and areas where pests may establish.

The thermal optimum is the temperature at which a species develops, reproduces and survives optimally (Begon *et al.,* 2006). Temperatures lower or higher than the optimum temperature lead to a decrease in development rate (Begon *et al.,* 2006). Temperature influences the duration of each instar, as well as the number of instars that larvae go through before reaching the adult stage (Aguilon *et al.,* 2015). A faster development rate can be advantageous to insects since it results in less time spent in vulnerable stages during which they can be attacked by predators, parasitoids and entomopathogens (Jaworski & Hilszczański, 2013). The status of crop pest species is therefore affected by changes in climate and weather (Porter *et al.,* 1991).

Temperatures fluctuate in natural environments and affect insect population dynamics differently from conditions where insects would only be exposed to constant temperatures. However, studies of insect pest species at constant temperatures can be used to predict their seasonal and phenological development (Mironidis, 2014), pest population dynamics and timing of control strategies (Shanower *et al.,* 1993). Insects develop faster under fluctuating temperatures when the maximum and minimum temperatures are within the optimal range of development of the species (Hagstrum & Hagstrum, 1970).

The fall armyworm, *Spodoptera frugiperda*, a lepidopteran pest that recently invaded Africa, is expected to be a lasting threat to several important crops (Goergen *et al*., 2016). It is likely that this pest will have the ability to colonise the tropical areas of Africa (Goergen *et al*., 2016). Furthermore, the effect of temperature on the development of target insect speces under the current changing climatic conditions should be known for risk analysis purposes, forecasting and management strategies in order to minimize pest infestation levels (Calvo & Molina, 2005). It is important to determine number of and difference between larval instars correctly,

not only for ecological studies, but also for pest management strategies, since the effectiveness of insecticides may differ between instars (Drooz, 1965).

The objectives of this study were to determine the development rate of *S. frugiperda* at different constant temperatures, to determine the number of degree-days (DD) required for each stage to complete development, as well as for overall egg-to-adult development. Larval instar demarcation were also determined by measuring the head capsule widths for use as criteria to be applied in decision making for control of *S. frugiperda.*

## 2.3 Materials and Methods

### 2.3.1 *Spodoptera frugiperda* stock colony

*Spodoptera frugiperda* larvae ($F_0$ generation) were collected from maize fields at Delmas (26.1575° S, 28.5915° E), Mpumalanga province, South Africa. These larvae were reared in plastic containers (40 x 20 x 15 cm) with aerated lids and provided with maize leaves from the non-Bt maize cultivar PAN 6Q-121, as food. Food was replaced at three-day intervals. Larvae were reared separately from the 3$^{rd}$ instar onwards. This was done in small plastic containers (52 mm high x 30 mm in diameter) with a steel mesh infused lid. Larvae were kept in a rearing room at 26 ± 1 °C, 65 ± 5% RH, and 14L: 10D photoperiod until pupation. Pupae were sexed and kept in the same rearing room as the larvae. Pupae were observed daily until moths emerged.

After the emergence of moths, single male-female pairs were confined to oviposition chambers in a rearing room at 26 ± 1 °C, 65 ± 5 % RH and a 14L : 10D photoperiod. The chambers and method used are according to that described by Kruger *et al*. (2012). A plastic bottle (22 cm in height and 10 cm in diameter) was cut open at the top and filled with small crusher stones up to a height of 5 cm. One maize stem (25 - 30 mm diameter) with the whorl intact and 18 cm in length were placed in an upright position in the bottle. The stem was inserted 3 - 4 cm into the crusher stones to keep it upright. Water was added up to a level three-quarter of the height of the stones to provide humidity and to keep the plant parts fresh. The containers were covered with a fine gauze mesh to prevent the moths from escaping (Fig. 2.1a, b). The maize leaves and stems were observed daily for egg batches and replaced every day.

### 2.3.2 Temperature-dependent egg development

Egg batches from the stock colony were removed from maize plants within 12 hours of oviposition by cutting off the piece of leaf sheath or leaf to which the egg batches were attached. About 50 eggs were placed in a small plastic container (52 mm high and 30 mm in diameter) with a steel mesh infused lid. These plastic containers were kept in a glass desiccator (150 mm diameter) in which RH was maintained at 70 ± 5 % using a potassium hydroxide solution according to the method of Solomon (1951) (Fig. 2.1c). The desiccators were kept at 18, 22, 26, 30 and 32° ± 1 °C in incubators with a 14L: 10D photoperiod. The temperature and RH in each desiccator were recorded at 30-minute intervals using iButtons® from ColdChain Thermo Dynamics (Fairbridge Technologies). The eggs were checked daily until they hatched and the number of days to hatching was recorded.

### 2.3.3 Temperature-dependent larval and pupal development

Eggs were collected from moths kept at 26 ± 1 °C, 65 ± 5 % RH and a 14L: 10D photoperiod and husbandry was as described above. After hatching, neonate larvae ($F_6$ generation) were transferred and kept individually in Petri dishes (9 cm diameter) with sweetcorn kernels (cultivar NK603) in the soft dough stage as food (Fig. 2.1d). Larval and pupal development was studied under the same conditions of constant temperature and photoperiod used for egg development (see 2.3.2). The developmental time of the pre-pupal and pupal stages were combined and provided as development time for pupae.

The Petri dishes were checked daily for head capsules and exuviae. Head capsule and exuviae found were removed daily to avoid confusion. Daily observations of the larvae were done and moulting, as well as survival, were recorded. Food was also replaced and the Petri dishes cleaned daily. Pupae were checked daily until the emergence of the moths. The number of days to emergence of moths was recorded. The temperature and RH in the container at each temperature regime were recorded at 30-minute intervals using iButtons® from ColdChain Thermo Dynamics (Fairbridge Technologies).

### 2.3.4 Number of instars

First instar larvae were collected within 24 hours of hatching from small plastic containers kept in a glass desiccator at 26 ± 1 °C and 14L :10D and transferred individually to Petri dishes (9 cm diameter). These larvae were provided with sweetcorn (NK603) kernels as food. After

moulting, thirty larvae of each consecutive instar were fixed in 70% ethanol. Head capsules were measured under a stereo microscope (Nikon SMZ 1500) equipped with a camera and the NIS-Elements D 3.1, Microscope Imaging Software. The head capsule widths were measured as the distance between the most distant lateral sides of the head capsule margins.

### 2.3.5 Data analysis

The relationship between temperature (x) and development rate (y) was determined by using a simple linear regression analysis. The lower threshold temperature (t) and the number of degree-days (k) required to complete development for each of the stages, as well as their standard errors, were calculated using the equations of Campbell *et al*. (1974). The lower threshold temperature was estimated by setting y = 0 and solving x for the regression equation, y = a + bx, where y = 1/days, x = temperature, a = intercept and b = slope. The lower temperature threshold was calculated as t = -a/b and the thermal constant for development in number of degree-days (ºD): k = 1/b. The standard error of means was calculated as: S.E. of $t = \bar{y}/b \sqrt{(s^2/N\bar{y}^2)} + [\text{S.E. of } b/b]^2$ and standard error of the day degrees as: S.E. of k = (S.E. of $b)/b^2$. The mean number of degree-days (ºD) needed for the development of the egg, larval and pupal stage were estimated using the equation of Jackson and Elliot (1988): $ºD = T(c - T_{min})$, where T is the number of days taken to complete development at a constant temperature (c) and $T_{min}$ is the minimum temperature for development. The thermal constant was used and the mean number of ºD required for the development of each life stage at the set constant temperatures were compared. The effect of temperature on development was analysed by means of one-way ANOVA followed by Tukey's HSD test (P = 0.05).

The number of instars was reported by means of the frequency distribution of head capsule width and ranges were assigned to individual instars based on larval instar head capsule width. The possibility of assigning specimens to instars by means of Dyar's rule (Dyar, 1890) as [post moult size/pre-moult size (moult increment) = constant], was determined. Linear regression analysis was used to establish relationships between temperature and growth ratios. All statistical analyses were done using STATISTICA 12 (Statsoft, Inc., 2013).

## 2.4 Results

Egg, larval and pupal development times of *S. frugiperda* were inversely related to temperature between 18 and 30 °C (Table 2.1). Development time of eggs ($F_{4, 134}$ = 10902.3; P < 0.001) and all larval instars differed significantly at temperatures between 18 and 32 °C (Table 2.1). [First instar ($F_{4, 134}$ = 70.47; P < 0.001); second instar ($F_{4, 134}$ = 139.09; P < 0.001); third instar ($F_{4, 134}$ = 293.47; P < 0.001); fourth instar ($F_{4, 134}$ = 238.67; P < 0.001); fifth instar ($F_{4, 134}$ = 191.40; P < 0.001); sixth instar ($F_{4, 134}$ = 325.32; P < 0.001)]. The time for total larval development also differed significantly at the respective temperatures ($F_{4, 134}$ = 1463.94; P < 0.001). Development times for all the above-mentioned stages were significantly longer at a constant temperature of 18 °C compared to 22, 26, 30 and 32 °C. Mortality of larvae at 18 °C was also very high (70%) indicating a constant temperature of 18 °C not to be suitable for development of *S. frugiperda* larvae. Development time of eggs and all instars, except for instar 2 did not differ significantly at 30 and 32 °C (Table 2.1). Development time for instars 2 and 5 was not significantly different at 26 and 30 °C, but decreased at 32 °C. Development time was significantly longer at 32 °C for instar 2 larvae, but this decrease in development time was not significant for instar 5 larvae at 32 °C (Table 2.1). This suggests that the optimum temperature for development of larvae from these two instars should be between 26 and 30 °C. Therefore, for a more accurate estimation of the lower threshold temperature for development, times where development did not fit the linear model, were omitted from the calculations, *viz.* 32 °C for eggs and larval instars 1, 3, 4 and 6, and 30 and 32 °C for instars 2 and 5. Development time for the total larval development period was also inversely related to temperature between 18 and 30 °C, with no difference in development time at 30 and 32 °C (Table 2.1). Development time of larvae at 26 °C decreased by half compared to the development time at 22 °C. However, larvae developed significantly faster at 30 °C compared to 26 °C and there was no significant difference in development time between 30 and 32 °C. The lowest larval mortality (4%) occurred at a constant temperature of 30 °C (Table 2.1). Larval mortality at 26 °C was 15% and 29% at a constant temperature of 32 °C. The optimum temperature range for larval development is therefore between 26 and 30 °C and the optimum temperature 30 °C. Development time of pupae was also inversely related at temperatures from 18 to 32 °C (Table 2.1). Development time of pupae was significantly shorter at 32 than at 30 °C, suggesting that the optimum temperature for pupal development is closer to 32 °C. Development rate at this temperature was therefore also included in the calculations of the lower threshold temperature for pupae, as well as for egg-to-adult development.

The relationship between development rate and temperature for *S. frugiperda* is illustrated in figure 2.2. Replication means were used to calculate development rate (1/days) curves. Rearing temperatures where development rate did not fit the linear portion of the graphs from the least square linear regression analyses, (also indicated as development times not significantly different from those at subsequent rearing temperatures indicated above), were excluded. High $R^2$ values for the linear models (Figures 2.2 and 2.3) indicated that the model represented the data accurately. Linear regression equations describing these relationships and estimates of the lower temperature threshold (t) and the number of degree-days (°D) for each life stage are summarized in table 2.2.

The thermal constant (k) for egg development was calculated as 35.73, for development of larvae and pupae, 202.67 and 147.06, respectively (Table 2.2) and 391.01 °D for egg-to-adult development (Table 2.3). For first instar larvae, the lower temperature threshold temperature was calculated as 8.5 °C, which seems to be too low. A very high overall mortality rate of larvae (70%) occurred at 18 °C, most of which occurred during first instar development. Therefore, recording of the development rate of only the 30% larvae that did survive to adulthood, might be a possible reason for this low estimation of lower temperature threshold. Based on linear regression analysis of development rate at all temperatures, a minimum temperature threshold of 13.01 °C was calculated for egg development and 12.12 °C for larval instars. The lower minimum threshold temperature for the larval stage was lower than that of the egg stage and eggs will therefore not develop and hatch at temperatures which are not suitable for larval development.

In figure 2.4 the head capsule width distribution of *S. frugiperda* was illustrated by a linear regression analysis indicating a relationship between larval instars and head capsule width (log value) with an r-value of 0.976. Instar 7 did not fit the linear line because the larvae did not increase in size and head capsule width of instar 7 remained the same as that of instar 6 (Figure 2.4). Head capsule widths of larvae ranged between 0.27 mm and 2.90 mm (Table 2.4). No distinction could be made between instars 6 and 7 in terms of head capsule width. All successive instars increased in size according to Dyar's ratio (Table 2.4).

## 2.5 Discussion

The development rate of species at their favourable range of temperatures increase linearly, but at unfavourable temperatures the rate becomes nonlinear (Wagner *et al.,* 1984). *Spodoptera frugiperda* fertility was found to be high in this study with all eggs that hatched at temperatures ranging between 18 and 32 °C. This favourable range was also reported by Ali

*et al.* (1990), namely 17 to 38 °C. Egg development rate was similar at 30 and 32 °C, which is in contrast to the findings of Ali *et al.* (1990) who reported non-linearity in egg development at 35.5 and 38 °C, where the development rate declined. Development of eggs at a constant temperature of 18 °C was, however, slow and the percentage of eggs that hatched, very low. Continuous low temperature, although above the lower thermal limit, will therefore slow down development and may reduce population growth rate as a result of high mortality.

Development rate of *S. frugiperda* increased linearly with temperatures increasing from 18 to 30 °C. Ali *et al*. (1990), who studied development of *S. frugiperda* at temperatures from 17 to 38 °C, reported development at temperatures ranging between 21 and 33 °C to increase linearly, but excluded 17 °C and temperatures higher than 33 °C from his analysis. They therefore regarded 21 to 33 °C to be suitable for *S. frugiperda* development. In the present study, development at 32 °C was found not to be linear for egg and larval development, but linear for pupal development up to 32 °C. The optimal temperature range is a specific temperature range within the suitable range, at which insect species can successfully develop and reproduce (Jarošík *et al.,* 2002). Species that occur in environments where temperatures are greater than or below the optimum temperature take longer to develop and survival is lower (Dixon *et al.,* 2009). The optimal range for egg, larval and egg-to-adult development of *S. frugiperda* in South Africa was therefore determined to be between 26 and 32 °C. Larval survival was the highest between 26 and 30 °C and the optimum temperature with the fastest development and lowest mortality for larvae was at 30 °C. Although larval development does not increase at a linear rate at 32 °C, pupal development was linear with increasing temperatures up to 32 °C. *Spodoptera frugiperda* pupae develop at a depth of 2 to 8 cm below the soil surface under field conditions (Sparks, 1979; Capinera, 2001) and are therefore exposed to changes in the daily temperature (Simmons, 1993). Soil temperature can be very high (>30 °C) during summer months in South Africa, which also coincides with the maize production season and *S. frugiperda* infestation of maize. The ability of *S. frugiperda* pupae to survive and develop at high temperatures in the soil therefore provides an advantage for this pest in terms of survival and development. The estimated lower development threshold of 13.01 ± 0.10 °C for eggs, is near the thresholds estimated by Ali *et al*. (1990) (12.69 ± 1.37 °C) and Hogg *et al*. (1982) (13.4 °C), but lower than the 16.95 ± 1.35 °C threshold reported by Barfield *et al*. (1978). Larval mortality was the lowest at 26 – 30 °C, with 70 % of larvae that died at 18 °C and 28% at 32 °C. Barfield *et al*. (1978) also reported *S. frugiperda* larval mortality to be higher at 18 °C and 37 °C than at 26.7 °C.

Development period of the egg-to-adult stage decreased from 71.3 at 18 °C to 20.2 days at 32 °C, which is slightly slower than the total development period for *S. frugiperda* of 66.5 days

at 18.3 °C and 18.3 days at 35.0 °C reported by Barfield *et al.* (1978). The rate of successive generations can be determined by using the duration of the egg-to-adult period (Campbell *et al.,* 1974). Degree-day requirements for *S. frugiperda* larval development is 202.67 ± 4.45 °D when reared on sweetcorn kernels and 147.06 °D for pupae, which is near the larval degree-day requirement of 197.60 ± 0.54 °D reported by Ali *et al*. (1990), but differed from their 112.86 ± 9.25 °D reported for pupal development. Ali *et al*. (1990) found degree-day requirements for pupae to be independent of larval diet. However, they did report the degree-days needed for completion of the larval stage to be affected by larval diet, since they found larvae fed with cotton to require 37 % more day-degrees compared to larvae that were reared on an artificial diet or maize. Mortality of larvae on a cotton diet was also the highest.

Temperature related development studies have also been conducted on other *Spodoptera* species, e.g. *Spodoptera exigua* (Lepidoptera: Noctuidae) in Iran (Karimi-Malati *et al.,* 2014) and *Spodoptera litura* (Lepidoptera: Noctuidae) in India (Fand *et al.,* 2015).. The lower threshold, optimum and upper threshold temperatures of the beet armyworm, *S. exigua* fed on sugar beet, were 13.1, 32.2 and 34.1 °C, respectively (Karimi-Malati *et al.,* 2014). No development was reported at 12 and 36 °C (Karimi-Malati *et al.,* 2014). The lower and upper developmental threshold temperatures predicted for immature life stages of *S. litura* (Lepidoptera: Noctuidae) reared on soybean are 10.2 °C and 36.3 °C for eggs, 9.9 °C and 38.7 °C for larvae and 9.8 °C and 38.2 °C for pupae, respectively (Fand *et al.,* 2015). The optimum temperatures for immature development of *S. litura* are 24.6 °C, 26.7 °C and 26.5 °C for eggs, larvae and pupae, respectively (Fand *et al.,* 2015). The developmental periods reported for *S. litura* larvae is 17.1 days, and for pupae, 8.4 days at 27 ± 0.5 °C (Hashmat & Khan, 1977).

The 29.3 days required for completion of the life cycle by *S. frugiperda* determined in this study is in agreement with the completion of its life cycle in 30 days at 25 °C reported by Sparks (1979). Development rate is, however, affected by larval diet (Sparks, 1979; Ali *et al*., 1990). Pitre and Hogg (1983) reared *S. frugiperda* on maize at 25 °C compared to this study where larvae were reared on sweetcorn kernels at 26 °C and reported mean development times for instars 1 to 6 to be 3.3, 1.7, 1.5, 1.5, 2.0 and 3.7 days compared to this study where these development times were 3.0, 2.1, 2.0, 2.2, 2.3 and 3.4 days, respectively. Similar development in these two studies was therefore recorded, taking into account the difference in food and temperature.

*Spodoptera frugiperda* pupal development time varied between 7.82 and 30.68 days (32 - 18 °C), while pupae kept at 15 and 35 °C by Simmons (1993) took approximately 37.2 and 5.6

days respectively to complete the pupal stage. Luginbill (1928) reported the pupal stage to be completed in nine to 45 days depending on the temperature, and 17 days at mean temperatures of 22.3 to 26.6 °C. Capinera (2001) reported the pre-pupae and pupal stage to range between two and four days and between eight to 30 days, respectively depending on the temperature conditions. A mean pupal development time of 17.06 days was recorded at 22 °C, but only 11.43 days at 26 °C. *Spodoptera frugiperda* pupae kept at 10 °C by Wood *et al.* (1979) survived for 50 days and by Simmons (1993) for 62 days, but they did not eclose. Pupae kept at 40 °C did not survive (Simmons, 1993). The lower threshold temperature for the pupal development in this study was 13.24 °C, which is similar to that of 13.3 °C reported by Vickery (1929). According to Simmons (1993), 90% of the pupae eclosed at temperatures of 20, 25, 30 and 35 °C, but only 58 to 78 % eclosed at 15 °C, with no difference in percentage pupal eclosion between fluctuating and constant temperatures.

Insect species from temperate regions cannot survive year round due to unfavourable environmental conditions and strategies need to be developed to overcome these unfavourable conditions (Nylin & Gotthard, 1928). *Spodoptera frugiperda* do not diapause and therefore migrates to regions which have a more favourable environmental temperature (Luginbill, 1928). Temperatures below 13 °C at the overwintering sites of *S. frugiperda* will not allow survival of larvae and pupae (Perkins, 1979), but Sparks (1979) estimated this minimum temperature for survival to be 10 °C. With regard to the northern hemisphere, survival of *S. frugiperda* occurs in the southern regions of Florida and Texas and during mild winters along the Gulf Coast (Luginbill, 1928; Barfield *et al.,* 1978; Sparks, 1979). *Spodoptera frugiperda* can, however, not survive periods of extreme cold, as well as periods with mild cold and rainfall (Luginbill, 1928). The eggs, pupae and adults can tolerate cold without developing cold hardiness, but not the larval stages (Morrill, 1971). Cold hardiness is a slow process that increases the tolerance of an insect to better survive in cold environments (Kelty & Lee, 2001; Denlinger & Lee, 2010).

Insects exposed to stressful conditions, such as an increase in its thermal tolerance level caused by high temperatures, can result in a rapid response to hardening (inducible thermo-tolerance) (Dahlgaard *et al*., 1998). Hardening in terms of high temperatures is more associated with rapid responses to short term moderately stressful exposures (Denlinger *et al*., 1991, Dahlgaard *et al*., 1998). Insects at high temperatures may avoid overheating through shade-seeking, avoidance behaviour, increased evaporation, cooling or biochemical reactions. Rapid biochemical protection can be created, such as heat shock proteins that will cause cell function to stop (Denlinger & Lee, 2010; Terblanche, 2013). This is an aspect which should be further investigated for *S. frugiperda*, taking into account the effect of climate change

and the very high summer temperatures during the maize production season in the temperate zones of South Africa.

Climate change affects temperature on a seasonal and daily basis and insect species must therefore have the ability to withstand thermal fluctuations and unfavourable temperatures (Scharf *et al.,* 2015). Changes in temperature affect the physiological traits of insects based on body-size and it also affects metabolic rates, as well as water and feeding requirements (Speight *et al.,* 2008). Some insects go through extra or fewer moultings to withstand the effects of low or high temperature, and low quality and availability of food sources (Ali *et al.,* 1990). Development of *S. frugiperda* larvae during this study was also affected in terms of the number of larval instars. At a constant temperature of 18 °C, 30 % of larvae completed development to the adult stage in seven instars. This is in accordance with the findings of Yarro (1985) that the African armyworm, *Spodoptera exempta* (Lepidoptera: Noctuidae) and the fall armyworm, *S. frugiperda*, can go through extra moults to reach the optimal final body size when reared on poor quality crops and at unfavourable environmental conditions. Luginbill (1928) also reported the developmental period and number of instars of *S. frugiperda* to be temperature and diet dependent. Ali *et al.* (1990) indicated that the number of larval instars of *S. frugiperda* increase with decreasing temperature. The general number of *S. frugiperda* larval instars is six (Luginbill, 1928), but it can reduce to five (Ali *et al*., 1990; Santos *et al.,* 2003). Ali *et al.* (1990) reported five instars for larvae reared on artificial diet at 25 to 29 °C, but six larval instars at rearing temperatures between 21 and 35 °C on maize. It is a common occurrence in the USA that larvae go through seven instars during late fall (Luginbill, 1928). The number of larval instars of *S. frugiperda* larvae that feed on different phenological stages of maize which have different nutritive value, also increases to seven (Barfield & Ashley, 1987). Nine larval instars occurred at 17 °C for larvae that were reared on cotton (Ali *et al.,* 1990) and also when they were reared on low nutritive value grasses such as *Cyperus globulosus* (Cyperaceae) at 27 °C (Pencoe & Martin, 1981). Eight *S. litura* larval instars were reported by Bhat and Bhattacharya (1978) for larvae kept at 15 °C. The same trend was also reported for other noctuids, with the Lesser armyworm, *S. exigua* which goes through six instars, instead of five, before reaching the critical final body size at extreme temperatures of 15 and 34 °C (Karimi-Malati *et al*., 2014). An increase in the number of moults of *Sesamia nonagrioides* (Lepidoptera: Noctuidae) results in an increase in body mass that is necessary during diapause (Esperk & Tammaru, 2004).

Larval development and feeding cease during moulting, which decreases the development rate (Sehnal, 1985), but mouthparts, a sclerotised body part, increase in size as a result of moulting (Esperk & Tammaru, 2004). According to Dyar's rule, a straight line should result if

the logarithm of the measurement of a sclerotised body part in different instars is plotted against the instar number, and any deviation from a straight line indicates missing instars (Gullan & Cranston, 2005). A linear progression therefore exists if the growth ratio is constant between the head capsule widths of each instar for a given species where the ratio ranges between 1.3 - 1.7 (Gullan & Cranston, 2005). The larval instars of *S. frugiperda* in this study followed Dyar's rule up to the sixth instar. The head capsule widths ranged from 0.27 mm (first instar) to 2.9 mm (instar six), which differed from the head capsule widths of 0.314 mm (first instar) to 2.78 mm (sixth instar), reported by Luginbill (1928) and 0.35 mm (first instar) to 2.6 mm (sixth instar) by Kondidie (2011). Larvae reared at 18 °C on sweetcorn kernels, went through seven larval instars. However, head width measurements indicated that there was no difference in head capsule widths between instars six and seven, which is therefore not a true extra instar.

Knowledge of the temperature thresholds of insects is important for predicting their potential distribution (Cammell & Knight, 1992; Marco *et al.,* 1997). The respective developmental stages have specific temperature requirements which is important for survival in specific environments (Cammell & Knight, 1992). The threshold temperatures determined in this study can be used in a model to estimate the number of generations at specific localities where the crop hosts are cultivated. It can also be used in a model to determine areas suitable for crop cultivation to which *S. frugiperda* can migrate from it's over wintering sites, as well as areas with suitable environmental conditions for persistent occurrence.

## 2.6 References

Addo-Bediako, A., Chown, S.L., Gaston, K.J. 2000. Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society B* 267(1445): 739-745.

Aguilon, D.J.D., Medina, C.dR. & Velasco, L.R.I. 2015. Effects of larval rearing temperature and host plant condition on the development, survival, and coloration of African armyworm, *Spodoptera exempta* Walker (Lepidoptera: Noctuidae). *Journal of Environmental Science and Management* 18(1): 54-60.

Ali, A., Luttrell, R.G. & Schneider, J.C. 1990. Effects of temperature and larval diet on development of the fall army worm (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America.* 83(4): 725-733.

Barfield, C.S. & Ashley, T.R. 1987. Effects of corn phenology and temperature on the life cycle of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Florida Entomologist* 70: 110-116.

Barfield, C.S., Mitchell, E.R. & Poe, S.L. 1978. A temperature-dependent model for fall armyworm development. *Annals of the Entomological Society of America* 71: 70-74.

BBC (British Broadcasting Corporation), 2017. Fall armyworm 'threatens African farmers' livelihoods'. UK: BBC.http://www.bbc.co.uk/news/science-environment-38859851. Date of access: 17 Nov. 2017.

Begon, M., Townsend, C.R. & Harper, J.L. 2006. Ecology: From individuals to Ecosystems, fourth edition Blackwell Publishing Ltd Oxford, United Kingdom.

Bhat, N.S. & Bhattacharya, A.K. 1987. Consumption and utilization of soybean by *Spodoptera litura* at different temperatures *Indian Journal of Entomology* 40: 16-25.

Calvo, D. & Molina, J.M. 2005. Developmental rates of the lappet moth *Streblote panda* Hübner (1820) (Lepidoptera: Lasiocampidae) at constant temperatures. *Spanish Journal of Agricultural Research* 3: 1-8.

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.

Campbell, A., Frazer, B.D., Gilbert, N., Gutierrez, A.P. & Mackauer, M. 1974. Temperature requirements of some aphids and their parasites. *Journal of Applied Ecology* 11: 431-438.

Capinera, J.L. 2001. Handbook of Vegetable Pests. Academic Press, San Diego, USA, 727 pp.

Dahlgaard, J., Loeschcke, V., Michalak, P. & Justesen, J. 1998. Induced thermotolerance and associated expression of the heat-shock protein Hsp70 in adult *Drosophila melanogaster*. *Functional Ecology* 12: 786-793.

Dahlgaard, J., Loeschcke, V., Michalak, P. & Justesen, J. 1998. Induced thermotolerance and associated expression of the heat-shock protein Hsp70 in adult *Drosophila melanogaster*. *Functional Ecology* 12: 786-793.

Denlinger, D.L. & Lee, R.E. 2010. Low temperature biology of insects. Cambridge University Press: Cambridge, UK.

Denlinger, D.L., Joplin, K.H., Chen, C.P. & Lee, R.E. 1991. Cold shock and heat shock. (*In* Lee, R.E. & Denlinger, D.L., *eds*. Insects at low temperatures. Chapman and Hall: New York. p. 131-148).

Dixon, A.F.G., Honěk, A., Keil, P., Kotela, M.A.A., Šizling, A.L. & Jarošík, V. 2009. Relationship between the minimum and maximum temperature thresholds for development in insects. *Functional Ecology* 23(2): 257-264.

Drooz, A.T. 1965. Elm spanworm head capsule widths and instars. *Journal of Economic Entomology* 58: 629-631.

Dyar, H.G. 1890. The number of molts of lepidopterous larvae. *Psyche* 5: 420-422.

Esperk, T. & Tammaru, T. 2004. Does the 'investment principle' model explain moulting strategies in Lepidopteran larvae? *Physiological Entomology* 29: 56-66.

Fand, B.B., Sul, N.T., Bal, S.K. & Minhas, P.S. 2015. Temperature impacts the development and survival of common cutworm (*Spodoptera litura*): simulation and visualization of potential population growth in India under warmer temperatures through life cycle modelling and spatial mapping. *PLoS ONE* 10(4): 1-25.

Goergen, G., Kumar, P.L., Sankung, S.B., Togola, A. & Tamo, M. 2016. First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera: Noctuidae), a new alien invasive pest in west and Central Africa *PLoS ONE* 11(10): 1-15.

Gullan, P.J. & Cranston, P.S. 2005. The insects: an outline of entomology. 3rd ed. Oxford: Blackwell Publishing. 505 pp.

Hagstrum, D.W. & Hagstrum, W.R. 1970. A simple device for producing fluctuating temperatures, with an evaluation of the ecological significance of fluctuating temperatures. *Annual Entomological Society of America* 63: 1385-1389.

Hashmat, M. & Khan, M.A. 1977. The effect of temperature on the fecundity and fertility of *Spodoptera litura* (Fabricius.) (Lepidoptera: Noctuidae). *Journal of Animal Morphology and Physiology* 24: 203-210.

Hogg, D.B., Pitre, H.N. & Anderson, R.E. 1982. Assessment of early-season phenology of the fall armyworm (Lepidoptera: Noctuidae) in Mississippi. *Environmental Entomology* 11: 705-710.

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

Jackson, J.J. & Elliot, N.C. 1988. Temperature-dependent development of immature stages of the western corn rootworm, *Diabrotica virgifera* (Coleoptera: Chrysomelidae). *Environmental Entomology* 17: 166-171.

Jarošík, V., Honek, A. & Dixon, A.F.G. 2002. Developmental rate isomorphy in insects and mites. *American Naturalist* 160: 497-510.

Jaworski, T. & Hilszczański, J. 2013. The effect of temperature and humidity changes on insect development and their impact on forest ecosystems in the context of expected climate change. *Forest Research Papers* 74(4): 345-355.

Karimi-Malati, A., Fathipour, Y., Talebi, A.A. & Bazoubandi, M. 2014. Life table parameters and survivorship of *Spodoptera exigua* (Lepidoptera: Noctuidae) at constant temperatures. *Environmental Entomology* 43(3): 795-803.

Kelty, J.D. & Lee, R.E. 2001. Rapid cold-hardening of *Drosophila melanogaster* (Diptera: Drosophilidae) during ecologically based thermoperiodic cycles. *Journal of Experimental Biology* 204: 1659-1666.

Kondidie, D.B. 2011. Genetic variability and gene flow of the fall armyworm *Spodoptera frugiperda* (J.E. SMITH) in the western hemisphere and susceptibility to insecticides. Lincoln, Nebraska. (Thesis-PhD).

Kruger, M., Van Rensburg, J.B.J. & Van den Berg, J. 2012. Transgenic Bt maize: farmers' perceptions refuge compliance and reports of stem borer resistance in South Africa. *Journal of Applied Entomology* 136: 38-50.

Lee, J.H. & Elliott, N.C. 1998. Comparison of developmental responses to temperature in *Aphelinus asychis* (Walker) from two different geographic regions. - *Southwestern Entomologist* 23: 77-82.

Luginbill, P. 1928. The Fall Army Worm. Washington, DC: USDA.

Marco,V., Taberner, A. & Castañera, P. 1997. Development and survival of immature *Aubeonymus mariaefranciscae* (Coleoptera: Curculionidae) at constant temperatures. *Annals of the Entomological Society of America* 90: 169-176.

Mironidis, G.K. 2014. Development, survivorship and reproduction of *Helicoverpa armigera* (Lepidoptera: Noctuidae) under fluctuating temperatures. *Bulletin of Entomological Research* 104: 751-764.

Morrill, W.L. 1971. *Ecology, Economics and Behavior of the Fall Armyworm in Field Corn*. Ph.D. Dissertation, University of Florida, USA.

Nylin, S. & Gotthard, K. 1998. Plasticity in life-history traits. *Annual Review of Entomology* 43: 63-83.

Pencoe, N.L. & Martin, P.B. 1981. Development and reproduction of fall armyworms on several wild grasses. *Environmental Entomology* 10: 999-1002.

Perkins, W.D. 1979. Laboratory rearing of the fall armyworm. *Florida Entomologist* 62: 87-91.

Pitre, H.N. & Hogg, D.B. 1983. Development of the fall armyworm on cotton, soybean and corn. *Journal of the Georgia Entomological Society* 18: 187-194.

Porter, J.H., Parry, M.L. & Carter, T.R. 1991. The potential effects of climatic change on agricultural insect pests. *Agricultural and Forest Meteorology* 57: 221-240.

Santos, L.M., Redaelli, L.R., Diefenbach, L.M.G. & Efrom, C.F.S. 2003. Larval and pupal stage of *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) in sweet and field corn genotypes. *Brazilian Journal of Biology* 63(4): 627-633.

Scharf, I., Braf, H., Ifrach, N., Rosenstein, S. & Subach, A. 2015. The effects of temperature and diet during development, adulthood, and mating on reproduction in the red flour beetle. *PLoS ONE* 10(9): 1-15.

Sehnal, F. 1985. Growth and life cycles. In: Kerkut GA, Gilbert LI., editors. Comprehensive insect physiology biochemistry and pharmacology, vol. 2. Oxford: Pergamon Press. p 129-152.

Shanower, T.G., Schulthess, F. & Bosque-Pérez, N.A. 1993. The effect of larval diet on the growth and development of *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) and *Eldana saccharina* Walker (Lepidopetera: Pyralidae*). Insect Science and its Application* 14: 681-685.

Simmons, A.M. 1993. Fall armyworm symposium: effects of constant and fluctuating temperatures and humidities on the survival of *Spodoptera frugiperda* pupae (Lepidoptera: Noctuidae). *Florida Entomologist* 76(2): 333-340.

Solomon, M.E. 1951. Control of humidity with potassium hydroxide, sulphuric acid or other solutions. *Bulletin of Entomological Research* 42: 543-554.

Sparks, A.N. 1979. A review of the biology of the fall armyworm. *The Florida Entomologist* 62: 82-87.

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

StatSoft, Inc. 2013. STATISTICA (data analysis software system), version 12. www.statsoft.com.

Terblanche, J.S. 2013. Thermal relations. (*In* Chapman, R.F., Simpson, S.J. & Douglas, A.E., *eds*. The insects: structure and function. 5th ed. Cambridge University Press: Cambridge, UK. p. 588-621).

Tobin, P.C., Nagarkatti, S. & Saunders, M.C. 2003. Phenology of Grape Berry Moth (Lepidoptera: Tortricidae) in cultivated grape at selected geographic locations. *Environmental Entomology* 32(2): 340-346.

Vickery, R.A. 1929. Studies on the fall armyworm in the Gulf coast district of Texas. United Sates Department of Agriculture, Washington, D.C. *Technical Bulletin* 138: 64.

Wagner, T.L., Wu, H., Sharpe, P.J.H., Schoolfield, R.M. & Coulson, R.M. 1984. Modeling distributions of insect development time: a literature review and application of the Weibull function. *Environmental Entomology* 77: 475-487.

Wood, J.R., Poe, S.L. & Leppla, N.C. 1979. Winter survival of fall armyworm pupae in Florida. *Environmental Entomology* 8: 249-252.

Yarro, J.G. 1985. Effect of host plant on moulting in the African armyworm *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae) at constant temperature and humidity conditions. *Insect Science and its Application* 6: 171-175.

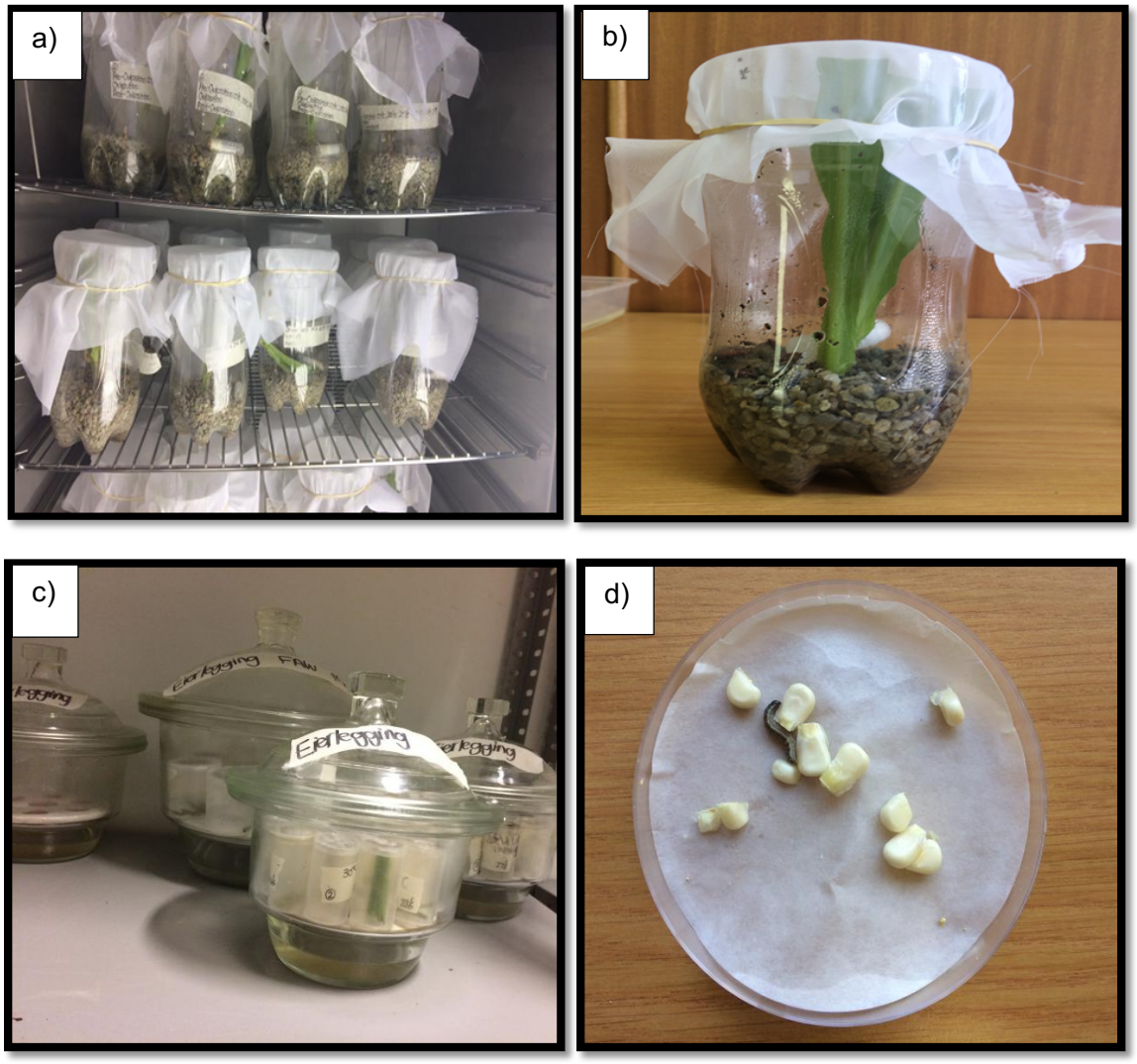



**Figure 2.1:** Containers used for *Spodoptera frugiperda* rearing: a and b) Oviposition chambers with one maize stem with the whorl intact per moth pair, c) desiccator with small plastic containers with eggs, d) Petri dishes lined with moist filter paper and sweetcorn kernels provided as larval food.

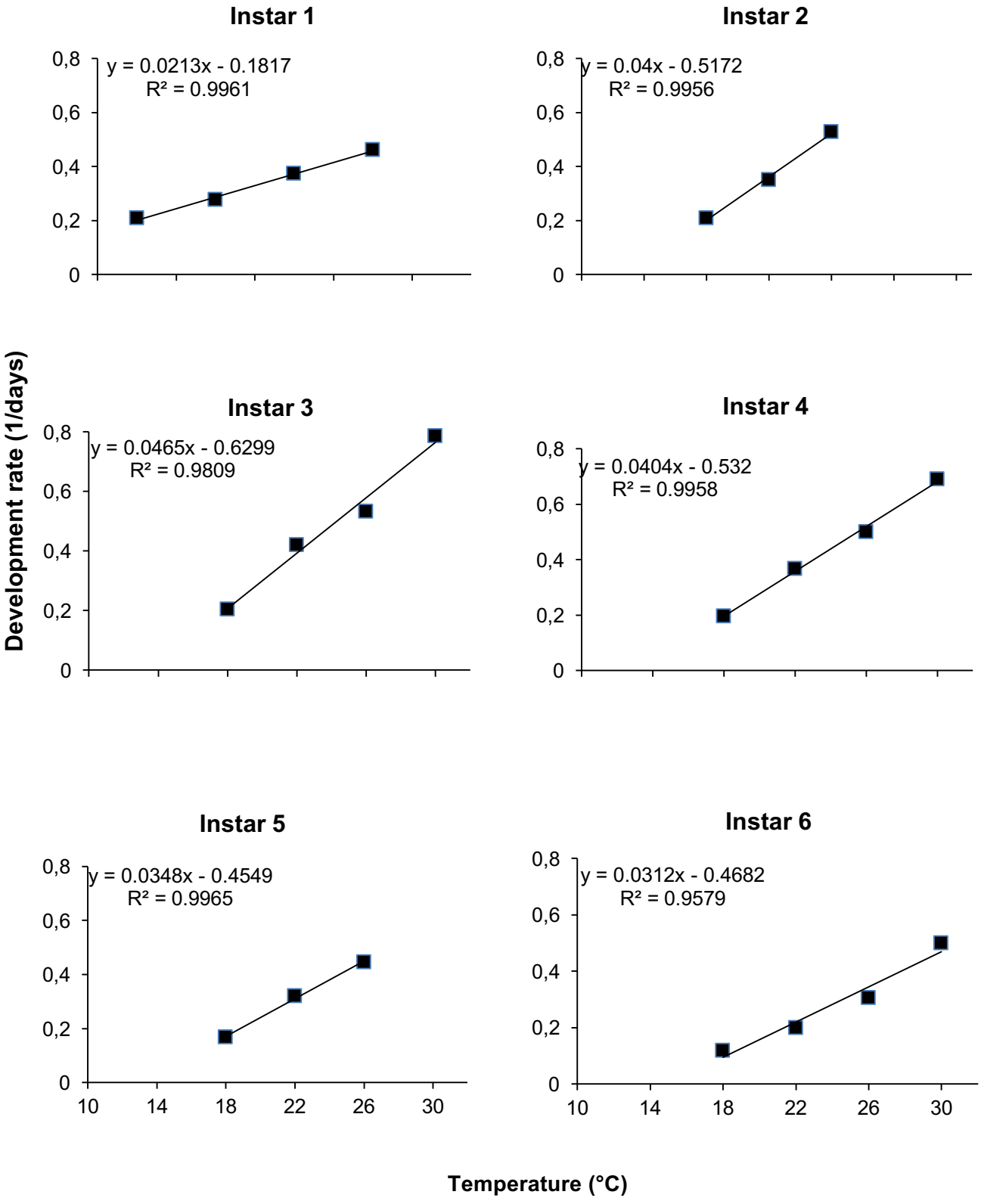



**Figure 2.2:** The relationship between *Spodoptera frugiperda* development rates and rearing temperature for larval instar one to six. Development rate at 30 °C omitted for instars 2 and 5 due to non-linear development.

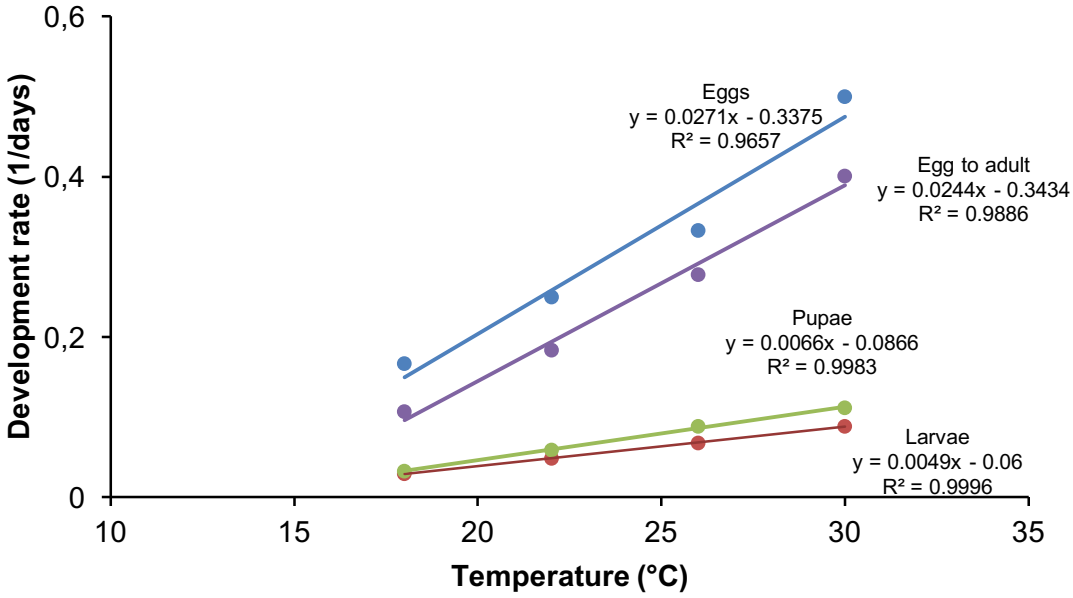



**Figure 2.3:** The relationship between development rates and rearing temperature for eggs, larvae, pupae and egg-to-adult stages of *Spodoptera frugiperda.*

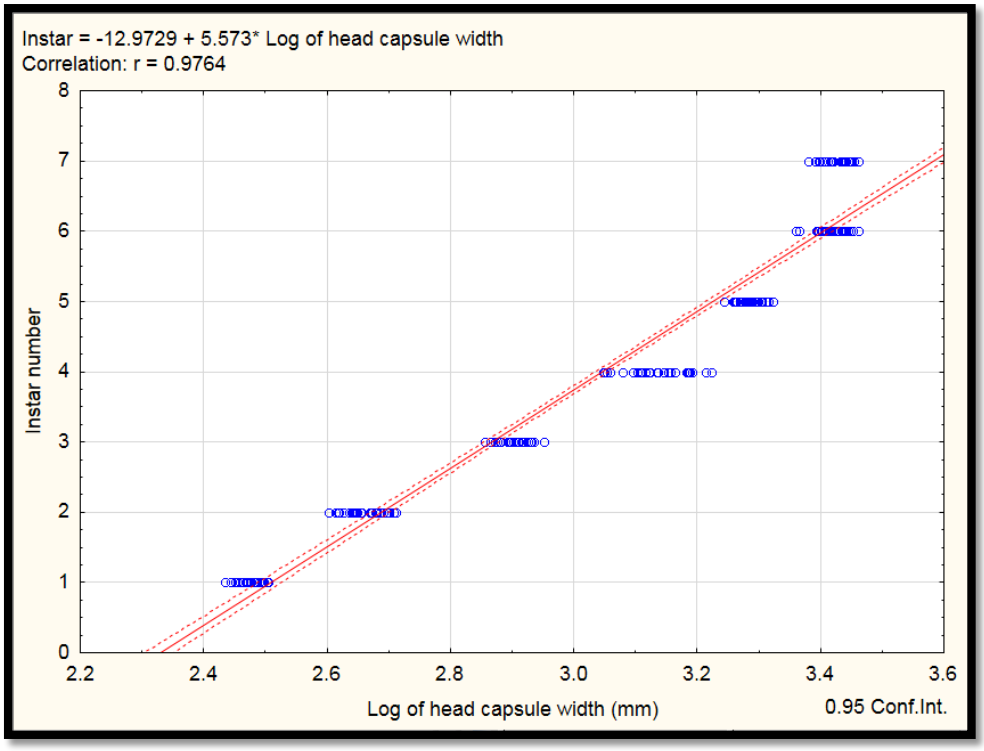



**Figure 2.4:** Relationship between head capsule width and instar of *Spodoptera frugiperda* larvae, demonstrating the presence of six clearly defined instars. The linear regression shows a straight line which fitted Dyar's rule.

**Table 2.1:** Mean development time (days ± S.E.) of different life stages and larval survival of *Spodoptera frugiperda* at constant temperatures. The range of days taken to complete a stage is shown in brackets.

| Development stage | Temperature (±1 °C) | | | | |
|---|---|---|---|---|---|
| | **18** | **22** | **26** | **30** | **32** |
| **Egg** | 6.3 ± 0.1 a (6 - 7) | 4 ± 0 b (4) | 3 ± 0 c (3) | 2 ± 0 d (2) | 2 ± 0 d (2) |
| **Instar 1** | 4.9 ± 0.1 a (3 - 7) | 3.7 ± 0.1 b (3 - 5) | 3.0 ± 0.2 c (2 - 6) | 2.2 ± 0.1 d (2 - 3) | 2.7 ± 0.1 cd (1 - 3) |
| **Instar 2** | 4.9 ± 0.2 a (3 - 7) | 3 ± 0.1 b (2 - 5) | 2.1 ± 0.2 d (1 - 4) | 1.9 ± 0.1 d (1 - 3) | 1.3 ± 0.1 c (1 - 2) |
| **Instar 3** | 5 ± 0.1 a (4 - 6) | 2.5 ± 0.1 b (2 - 3) | 2 ± 0.1 c (1 - 3) | 1.4 ± 0.11 d (1- 2) | 1.1 ± 0.04 d (1 - 2) |
| **Instar 4** | 5.2 ± 0.1 a (4 - 6) | 2.8 ± 0.1 b (2 - 5) | 2.2 ± 0.1 c (2 - 3) | 1.7 ± 0.1 d (1 - 2) | 1.5 ± 0.1 d (1 - 2) |
| **Instar 5** | 6.2 ± 0.2 a (4 - 8) | 3.4 ± 0.2 b (1- 5) | 2.3 ± 0.1 c (2 - 3) | 2.2 ± 0.1 c (1 - 4) | 1.8 ± 0.1 c (1 - 2) |
| **Instar 6** | 8.6 ± 0.2 a (6 - 12) | 5.1 ± 0.2 b (4 - 9) | 3.4 ± 0.17 c (3- 6) | (2 ± 0) d (2) | 2.1 ± 0.04 d (2 - 3) |
| | | | | | |
| **Larvae** | 34.39 ± 0.41 a (28 - 37) | 30.58 ± 0.15 b (19 - 22) | 14.86 ± 0.31 c (13 - 19) | 11.38 ± 0.25 d (10 -14) | 10.45 ± 0.10 d (10 - 12) |
| **Pupae** | 30.68 ± 0.28 a (28 - 34) | 17.06 ± 0.24 b (14 - 20) | 11.43 ± 0.22 c (10 - 13) | 9 ± 0.12 d (8 - 10) | 7.82 ± 0.1 e (7 - 9) |
| **Egg-to-adult** | 71.35 ± 0.42 a (67 - 78) | 41.64 ± 0.32 b (38 - 46) | 29.29 ± 0.29 c (27 - 32) | 22.38 ± 0.27 d (20 - 25) | 20.27 ± 0.15 e (19 - 22) |
| **Larval mortality (%)** | 71 | 37 | 15 | 4 | 28 |

Means within the same row followed by the same letter do not differ significantly at P = 0.05 (Tukey's HSD).

**Table 2.2:** Linear regression equations describing the relationship between development rate (1/days) and temperature (18 - 30 °C) and the thermal requirements of different developmental stages of *Spodoptera frugiperda.*

| Development stage | Regression model | k ± S.E. | t ± S.E. | r - value |
|---|---|---|---|---|
| **Eggs** | y = 0.0280x - 0.32641 | 35.73 ± 0.31 | 13.01 ± 0.10 | 0.99 |
| **First instar** | y = 0.0212x - 0.1801 | 47.14 ± 3.13 | 8.49 ± 0.970 | 0.83 |
| ***Second instar** | y = 0.0372x - 0.4530 | 26.86 ± 2.99 | 12.17 ± 1.05 | 0.69 |
| **Third instar** | y = 0.0463x - 0.6242 | 21.58 ± 1.49 | 13.47 ± 0.67 | 0.82 |
| **Fourth instar** | y = 0.0404x - 0.5293 | 24.78 ± 1.80 | 13.11 ± 0.74 | 0.80 |
| ***Fifth instar** | y = 0.0351x - 0.4600 | 28.53 ± 2.73 | 13.13 ± 1.05 | 0.75 |
| **Sixth instar** | y = 0.0307x - 0.4560 | 32.57 ± 0.94 | 14.85 ± 0.24 | 0.96 |
| **[#]Pupal stage** | y = 0.0068x - 0.0900 | 147.06 ± 4.45 | 13.24 ± 0.19 | 0.98 |
| **All Instars** | y = 0.0049x - 0.0598 | 202.67 ± 4.45 | 12.12 ± 0.22 | 0.98 |
| **[$]Egg- to-adult** | y = 0.0026x - 0.0322 | 390.42 ± 4.84 | 12.57 ± 0.00 | 0.99 |

t = estimated lower temperature threshold, k = estimated thermal requirement in degree-days

*Development rate at 30 °C was omitted

[#]Development rate at 32 °C also included

[$] Development rate at temperatures included as per development stages above

**Table 2.3:** Mean development time in days and degree-days (°D) for *Spodoptera frugiperda* at constant temperatures. Degree-days were calculated using the lower threshold temperature for development for each developmental stage (eggs = 13.01 °C, larvae = 12.12 °C, pupae = 13.24 °C and egg-to-adult = 12.57 °C).

| Developmental stage | Temperature (°C) | n | Development time (days ± S.E.) | Range | °D ± S.E. |
|---|---|---|---|---|---|
| **Egg** | 18 | 93 | 6.38 ± 0.05 | 6 - 7 | 31.82 ± 0.25 |
| | 22 | 130 | 4.0 ± 0 | 4 | 35.96 ± 0.00 |
| | 26 | 151 | 3 ± 0 | 3 | 38.97 ± 0.00 |
| | 30 | 128 | 2 ± 0 | 2 | 33.98 ± 0.00 |
| | 32 | 162 | 2 ± 0 | 2 | 37.98 ± 0.00 |
| **[$]Mean** | | | | | 35.72 ± 1.30 |
| | | | | | |
| **Larvae** | 18 | 31 | 34.39 ± 0.41 | 28 - 37 | 202.20 ± 2.43 |
| | 22 | 33 | 20.58 ± 0.15 | 19 - 22 | 168.56 ± 2.39 |
| | 26 | 21 | 14.86 ± 0.31 | 13 - 19 | 158.63 ± 3.11 |
| | *30 | 21 | 11.38 ± 0.25 | 10 - 14 | 160.92 ± 2.14 |
| | [#]32 | 33 | 6.64 ± 0.16 | 6 - 10 | 155.43 ± 2.02 |
| **[$]Mean** | | | | | 172.58 ± 10.10 |
| | | | | | |
| **Pupae** | 18 | 31 | 30.68 ± 0.28 | 28 - 34 | 146.02 ± 1.31 |
| | 22 | 33 | 17.06 ± 0.24 | 14 - 20 | 149.45 ± 2.12 |
| | 26 | 21 | 11.43 ± 0.22 | 10 - 13 | 145.82 ± 2.86 |
| | 30 | 21 | 9 ± 0.12 | 8 - 10 | 150.84 ± 2.00 |
| | 32 | 33 | 7.82 ± 0.10 | 7 - 9 | 146.67 ± 1.91 |
| **Mean** | | | | | 147.76 ± 1.01 |
| | | | | | |
| **Egg-to-adult** | 18 | 31 | 71.45 ± 0.42 | 67 - 77 | 387.98 ± 2.31 |
| | 22 | 33 | 41.64 ± 0.32 | 38 - 46 | 392.63 ± 2.98 |
| | 26 | 21 | 29.29 ± 0.29 | 27 - 32 | 393.31 ± 3.84 |
| | 30 | 21 | 22.38 ± 0.27 | 20 - 25 | 390.10 ± 4.73 |
| | 32 | 33 | 16.45 ± 0.15 | 15 - 19 | 319.71 ± 2.94 |
| **[$]Mean** | | | | | 391.01 ± 1.22 |

*Instar 2 and 5 omitted due to non-linearity; [#]All instars included

[$]32 °C not included for calculation of mean number of degree days

**Table 2.4:** Mean head capsule widths and ranges for each *Spodoptera frugiperda* larval instar and Dyar's ratio.

| Instar | n | Range (mm) | Range Size | Mean ± S.E. | Dyar's ratio |
|---|---|---|---|---|---|
| **1** | 32 | 0.27 - 0.32 | 0.05 | 0.30 ± 0.002 | - |
| **2** | 30 | 0.40 - 0.51 | 0.11 | 0.46 ± 0.006 | 1.53 |
| **3** | 30 | 0.72 - 0.89 | 0.17 | 0.8 ± 0.008 | 1.74 |
| **4** | 30 | 1.12 - 1.67 | 0.55 | 1.36 ± 0.027 | 1.7 |
| **5** | 35 | 1.75 - 2.1 | 0.35 | 1.94 ± 0.014 | 1.43 |
| **6** | 36 | 2.29 - 2.90 | 0.61 | 2.63 ± 0.021 | 1.36 |
| **7** | 31 | 2.40 - 2.90 | 0.5 | 2.69 ± 0.0 | 1.02 |

# CHAPTER 3

## The effect of temperature on reproduction of *Spodoptera frugiperda* (Lepidoptera: Noctuidae)

### 3.1 Abstract

The effect of temperature on the reproduction parameters of *Spodopetra frugiperda* was evaluated at five different constant temperatures namely 18, 22, 26, 30 and 32 ± 1 °C, 65 ± 5% RH and 14L: 10D photoperiod. The recorded parameters were: duration of the pre-oviposition, oviposition and post-oviposition periods, as well as the number of eggs laid and longevity of the parent moths. Oviposition occurred at all the temperatures and 100% of eggs were fertile. Significantly more eggs were laid at 22 °C, compared to all the other temperatures. The total number of eggs laid by per *S. frugiperda* female ranged between 224.4 at 32 °C and 979.2 at 22 °C. Longevity and fecundity of female moths were inversely related to temperature. The pre-oviposition period, oviposition period and longevity was the longest at 18 °C compared to other temperatures. The lowest number of eggs laid per female was at 32 °C and the most eggs per female, as well as the maximum number of eggs laid per female, was at 22 °C. Many females died at 32 °C before ovipositing. The upper threshold for reproduction is therefore lower than 32 °C. Female moths lived significantly longer at 18 °C compared to 22, 26, 30 and 32 °C, but female longevity was similar at 22 and 26 °C. The optimum temperature for oviposition of moths of the *S. frugiperda* population used in this study, was 22 °C.

**Key words:** fertility, longevity, reproduction, *Spodoptera frugiperda,* temperature

## 3.2 Introduction

### 3.2.1 The effect of temperature on reproduction

Insect reproduction is governed by interactions between intrinsic life history traits and factors such as temperature, food, moisture gradients, light intensity, chemicals and pathogens (Danks, 1994). Of the many abiotic factors that may influence the reproduction of insect species, temperature is usually the most important (Andrewartha, 1952).

Temperature affects the fecundity and longevity of species, which in turn affects the rate of increase in population density (Andrewartha & Birch, 1954) and pest status (Son & Lewis, 2005). Insect species have a specific temperature range at which they reproduce (Davidson, 1944). Temperature is also the most important abiotic factor which influences development, reproduction and the survival of an insect population (Ratte, 1985; Liu *et al.,* 1995). Fitness levels of insect species can be determined by their reproductive success. The impact of temperature on reproductive success can be determined by the total fecundity per female, duration of the pre-oviposition and oviposition periods, life-span and egg viability (Kim & Lee, 2003). Temperature is also a limiting factor in the geographic distribution of species (Krebs & Loeschke, 1994). However, thermal tolerance and requirements for development and reproduction of a specific species may differ between populations from different geographical regions (Lee & Elliott, 1998). The optimum temperature range for egg production differs greatly among species (Engelmann, 1970). Temperatures below or above the optimum for a specific insect species can be used to predict the impact of climate change on pest population growth. Often these temperatures reflect what the species normally encounters during reproductive periods (Engelmann, 1970), which may act to regulate the timing of many life history events.

Knowledge of the effect of temperature on the reproduction parameters of insect species enables prediction of moth flight periods and periods during which crops will most likely be infested by a particular pest species (Shahout *et al.,* 2011). Reproduction parameters are important to consider in the study of population dynamics and management of pest populations (Ims & Steen, 1990). Mathematical models can be used to predict population dynamics (Sporleder *et al*., 2004) and species distribution (Hauptfleisch *et al*., 2014). It is also used in the application of the sterile insect technique and implementation of trapping techniques for monitoring or suppression of insect populations (Shatout *et al.,* 2011).

An increase in temperature affects the physiological parameters of insects and causes a decrease in body size, which results in lower fecundity (Atkinson, 1994). This effect of higher temperatures was demonstrated by Ernsting and Isaaks (1997), who found the fecundity parameters of *Notiophilus biguttatus* (Coleoptera: Carabidae) to be inversely related to temperature with higher numbers, but smaller eggs, produced at higher temperatures. Populations which are adapted to warmer temperatures may have a higher optimal temperature and seem to be able to survive better than populations from colder environments (Kolberg, 2013). The impact of climate change on insect species can therefore be measured by their longevity and fecundity success (Coulson *et al.,* 2001).

Information on the temperature-dependent population growth potential of insect pests is critical for understanding population dynamics and for implementing agro-ecosystem specific pest control strategies, especially in the context of climate change predictions (Kroschel *et al.,* 2013). A 2.7 - 4.7 °C increase in the average temperature due to climate change (IPCC, 2013) and climate variability can affect the fecundity and longevity of *S. frugiperda.* It is therefore important to understand the possible impacts of climate change on pests to be able to develop integrated pest management strategies (Ju *et al.,* 2010; Fernandes *et al.,* 2013).

### 3.2.2 Objectives

The objective of this study was to determine the effect of different temperature regimes on the reproduction of *S. frugiperda*. The pre-oviposition period, oviposition period, post-oviposition period, longevity, number of oviposition quiescence days, maximum number of eggs laid, minimum number of eggs laid and mean number of eggs laid per female, were determined at different temperature regimes.

## 3.3 Materials and Methods

### 3.3.1 *Spodoptera frugiperda* collection sites

The collection sites are those described in Chapter 2 (see 2.3.1).

### 3.3.2 Fecundity and longevity of female moths

Within 24 hours of emergence of the moths, single male-female pairs were confined to oviposition chambers (Fig. 2.1a, b). Between 40 and 70 oviposition chambers were used per

temperature regime. The temperature regimes used were 18, 22, 26, 30 and 32 ± 1 °C, RH of 65 ± 5% and a 14L: 10D photoperiod. The temperature and RH at each regime were recorded at 30-minute intervals using iButtons® from ColdChain Thermo Dynamics (Fairbridge Technologies).

The chambers and methods used are similar to those described in Chapter 2 (see 2.3.3). The pre- and post-oviposition periods, oviposition period, days without oviposition, longevity, number of egg batches laid, and egg production of each female moth were determined at each temperature regime. Egg batches were removed and kept in small plastic containers (52 mm high and 30 mm in diameter) with a steel mesh infused lid. The containers were marked and kept in glass desiccators (150 mm in diameter) in which RH was maintained at 70 ± 5% using a potassium hydroxide solution according to the method of Solomon (1951). The eggs were observed daily until no more larvae hatched. The neonate larvae in each container were fixed with 70% alcohol and quantified.

### 3.3.3 Statistical analysis

The effect of temperature on pre-oviposition, post-oviposition, and oviposition periods, the longevity of moths and egg production were analysed by means of one-way ANOVA, followed by Tukey's HSD test for unequal N (P = 0.05). The relationships between temperature and the oviposition period of *S. frugiperda,* as well as between female longevity and temperature, were determined by means of correlation analyses. All analyses were done with STATISTICA 12 (Statsoft, Inc., 2013).

## 3.4 Results

Temperature had a significant effect on all reproduction parameters *viz*. the duration of the pre-oviposition, oviposition and post-oviposition periods, as well as the number of eggs laid and longevity of the moths (Table 3.1). Moths laid eggs at all temperatures and all the eggs were fertile. There was, however, a significant difference between the numbers of eggs laid at the respective temperatures ($F_{4, 120} = 18.3$; $P < 0.001$). Significantly more eggs were laid at 22 °C, compared to all other temperatures. There was no significant difference in the total number of eggs laid per female at 18 and 26 °C, while significantly fewer eggs were laid at 32 °C compared to 18, 22 and 26 °C (Table 3.1).

The pre-oviposition period of *S. frugiperda* differed significantly at the different temperatures ($F_{4, 120} = 17.3$; $P < 0.0001$). The pre-oviposition period at 18 °C was significantly longer than at 22, 26 and 30 °C, but it did not differ from that at 32 °C. The pre-oviposition periods at 22, 26 and 30 °C did not differ significantly (Table 3.1). The oviposition period of *S. frugiperda* was inversely related to temperature (Figure 3.1a), with significant differences between the duration of oviposition periods at the respective temperatures ($F_{4, 120} = 24.0$; $P < 0.0001$). It did not differ significantly between 18 and 22 °C, and there were also no differences between the duration of oviposition periods at 22 and 26 °C. The duration at 18 °C was, however, significantly longer than at 26, 30 and 32 °C (Table 3.1). The duration of the post-oviposition periods also differed significantly at the different temperatures ($F_{4, 120} = 3.9$; $P = 0.005$). However, the post hoc test used to differentiate between the means, *viz*. Tukey's unequal N test, did not show any significant difference in the mean durations of these periods (Table 3.1).

Longevity of the female moths was inversely related to temperature (Figure 3.1b). Female *S. frugiperda* moths lived significantly longer at 18 °C compared to 22, 26, 30 and 32 °C ($F_{4, 120} = 80.3$; $P < 0.001$) (Table 3.1). There was, however, no significant difference in female longevity at 22 and 26 °C and also at 30 and 32 °C respectively, with longevity at 30 and 32 °C, being the shortest (Table 3.1). The number of days in which no eggs were laid during the overall oviposition period, did not differ significantly between the respective temperatures ($F_{4, 120} = 3.2$; $P < 0.02$) (Table 3.1). The mean number of eggs laid per day did, however, differed significantly ($F_{4, 116} = 6.2$; $P < 0.001$), with the fewest eggs laid at 18 °C. There was no significant difference in daily fecundity at 22, 26, 30 and 32 °C (Table 3.1). The maximum ($F_{4, 120} = 8.3$; $P < 0.0001$), as well as the minimum number of eggs laid per day ($F_{4, 116} = 4.2$; $P < 0.01$), differed significantly at the respective temperatures. The highest number of eggs laid per day was at a constant temperature of 22 °C. However, there was no significant difference in the maximum number of eggs laid per day at 18, 26, 30 and 32 °C (Table 3.1). The lowest number of eggs laid per day was at 30 °C and this number differed significantly from the lowest minimum at 22 °C (Table 3.1). There was also a significant difference in the number of egg batches laid by females at the different temperatures ($F_{4, 120} = 4.9$; $P < 0.01$). Significantly more egg batches were laid at 22 °C compared to 30 and 32 °C (Table 3.1).

## 3.5 Discussion

The reproductive parameters of *S. frugiperda* female moths were significantly affected by temperature. The pre-oviposition period of female moths was the longest, approximately six days, at 18 °C and on average less than four days at temperatures between 22 and 30 °C. Females had an oviposition period that ranged between 4 and 17 days. This is in accordance with the findings of Luginbill (1928), who reported a pre-oviposition period of 3 to 4 days, as well as with Habib *et al.* (1982) and Tisdale and Sappington (2001) who reported *Spodoptera* species to have an overall relatively short pre-oviposition period. This indicates that adults reach sexual maturity and mate shortly after emergence. In this study *Spodoptera frugiperda* females laid eggs at all temperature regimes, namely 18, 22, 26, 30 and 32 °C. Longevity and oviposition periods of females shortened with increasing temperatures. This was expected since the longevity and oviposition periods of insects in general decrease with an increase in temperature (Aksit *et al.,* 2007). Barfield and Ashley (1987) also reported longevity of *S. frugiperda* moths to decrease with increasing temperatures. In addition, Aksit *et al.* (2007) also reported an association between female moth longevity and oviposition period in terms of the temperatures at which the larvae were kept. The fecundity and longevity of adults from larvae that fed and developed on host plants with a low nutritional value under unfavourable temperature conditions, are also adversely affected (Combs & Valerio, 1980; Pencoe & Martin, 1981).

Longevity of *S. frugiperda* moths was reported by Luginbill (1928) to range between 6 and 23 days, depending on temperature and food sources, with an average of 10 days. Longevity of adult females in this study varied between 11.8, 11.0 and 8.3 days, at 22, 26 and 30 °C respectively. Longevity determined in this study at 18 and 32 °C was 16.6 and 7.4 days, respectively, whilst Milano *et al.* (2008) reported 20.7 and 6.4 days at 18 and 35 °C respectively. Longevity in both these studies was therefore shorter than the adult longevity reported by Barfield and Ashley (1987), which were 20.5, 17.0 and 12.9 days for larvae reared on maize in the reproductive stage and 16.8, 14.5 and 11.9 days for larvae reared on the late vegetative stage maize at 21, 25 and 30 °C respectively. Longevity of female moths when larvae were fed with maize tissue from plants in their early vegetative stages was 20.3, 19.0 and 11.9 days at the respective above-mentioned temperatures (Barfield & Ashley, 1987). Longevity was inversely related to temperature, with a very high percentage of female moths that died at a constant temperature of 32 °C without laying any eggs. Barfield and Ashley (1987) also reported longevity of *S. frugiperda* moths to decrease with increasing temperatures. Moths kept at 21 °C survived the longest compared to those kept at 25 and 30

°C (Barfield & Ashley, 1987). These authors concluded that longevity of adults also depended on diet and temperature. The difference in results between this study and that of Barfield and Ashley (1987) may possibly be explained by the difference in larval diets. Barfield and Ashley (1987) reared the larvae on maize tissue in the early and late vegetative stages, as well as on maize in the reproductive stage. Larvae were reared on the kernels of sweetcorn in this study, but moth longevity was markedly shorter than that reported by Barfield and Ashley (1987) for moths from larvae that were fed on maize plants in the reproductive stage.

Fecundity usually increases as temperature increases, between a lower and upper threshold, up to the optimal point (Milonas & Savopoulou-Soultani, 2000). During this study, most eggs were laid at the medium temperatures of 18, 22 and 26 °C, indicating the optimum temperature range for oviposition to be between 18 and 26 °C. The duration of pre-oviposition, oviposition and post-oviposition periods at 22 and 26 °C were similar, but fecundity was much higher at 22 °C. The latter temperature can therefore be concluded to be the optimal temperature for oviposition.

The night temperatures are much lower compared to day temperatures during summer in South Africa. This optimum temperature determined for oviposition will therefore have practical significance. The negative impact of high constant temperatures of 30 and 32 °C on *S. frugiperda* female moths was evident from the shorter life span and reduced fecundity. Fertility of eggs was, however, not affected at any of the respective temperatures. All eggs were fertile, and hatched. This was in accordance with the findings of Luginbill (1928), who reported *S. frugiperda* to be highly fecund with 100% fertility. The mean fecundity per female determined in this study at 26 °C (641 eggs) and 32 °C (493 eggs), was much lower than the fecundity of *S. frugiperda* on maize in the reproductive stage which was reported as 1510 eggs at 21 °C, 2019 eggs at 25 °C and 1086 eggs at 30 °C (Barfield & Ashley, 1987). The latter authors also reported the mean fecundity of *S. frugiperda* feeding on maize in the late vegetative stage as 1929 eggs at 21 °C; 2080 eggs at 25 °C and 1337 eggs at 30 °C, respectively. The lowest number of eggs was laid at 35 °C with 443 eggs followed by 761.7 eggs at 15 °C (Barfield & Ashley, 1987). Milano *et al.* (2008) reported 1571 eggs laid at 25 °C, 1500 eggs at 20 °C and 1327 at 30 °C. The present study indicated the fecundity at the different temperatures as follows: 18 °C (716.7 eggs); 22° C (979.2 eggs); 26 °C (641.2 eggs); 30 °C (493.2 eggs) and 32 °C (224.4 eggs).

Barfield and Ashley (1987) concluded that maize growth stage at the time of larval feeding, affects fecundity and longevity of *S. frugiperda*. Host-specific information on adult fecundity and longevity is therefore important for understanding the population dynamics of a species.

Longevity and fecundity of populations can also differ between geographical locations (Castro & Pitre, 1988). *Spodoptera frugiperda* populations that were collected in Mississippi and Honduras followed by rearing on similar maize plant diets at 26 ± 3 °C and a 14L: 10D photoperiod differed in their fecundity and longevity (Castro & Pitre, 1988). These differences in fecundity and longevity indicated that the populations had different biological characteristics (Castro & Pitre, 1988). This also reflects the biotype phenomenon as explained by Qiu *et al.* (2009) using *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) that biotypes differ in aspects such as pesticide resistance, plant specialization and reproduction It can, therefore also be possible that the lower fecundity and longevity of the population studied in South Africa differed biologically from the populations studied by Barfield and Ashley (1987) in Gainesville, Florida, USA.

The number of egg batches laid by *S. frugiperda* females varies between field and laboratory conditions (Luginbill, 1928). This author reported an average of 6.7 egg batches per female over her entire lifespan, while Vickery (1929) reported 1782 eggs in 13 egg batches. It is therefore clear that the number of egg batches varies considerably, since up to 20 egg batches per female was laid in the current study.

Temperature was also observed to have an effect on mating of *S. frugiperda*. Simmons and Marti (1992) reported that only occasional mating takes place under laboratory conditions at a temperature of 10 °C. If mating is affected, the population dynamics of *S. frugiperda* is also affected (Simmons, 1993). Not only does larval diet impact on longevity and fecundity of *S. frugiperda* moths, but also adult diet. Sugar or honey solutions improved fecundity of *S. frugiperd*a moths (Luginbill, 1928). Simmons and Lynch (1990) reported more than double the number of eggs laid by females fed with honey (2375 eggs) compared to female moths provided with water only (1120 eggs). Their oviposition periods also more than doubled with the provision of honey when compared to water only, *viz*. 8.6 days vs. 4.1 days (Simmons & Lynch, 1990). *Spodoptera frugiperda* moths that feed on a honey solution were also reported to live longer, *viz*. 12.9 days, compared to female moths fed with water only, which only lived for 8 days (Simmons & Lynch, 1990).

*Spodoptera frugiperda* is a tropical pest (Luginbill, 1928). The effect of temperature on development and reproduction of *S. frugiperda* should therefore be taken into account when an IPM strategy is developed for its control, since it can be useful in predicting pest outbreaks and it provides information on population dynamics. This is especially important in South Africa where the areas which is suitable for survival during the winter months are limited. Temperature plays an important role in regulating the phenology, seasonal abundance and

geographical distribution of species (Bale *et al.,* 2002). Future studies based on the effect of the fluctuating daily temperature on *S. frugiperda* development and reproduction should be conducted. Short-term exposure to high or low temperatures may affect reproduction and survival success differently than that determined during this study at constant temperatures.

## 3.6 References


Aksit, T., Cakmak, I. & Ozer, G. 2007. Effect of temperature and photoperiod on development and fecundity of an acarophagous ladybird beetle, *Stethorus gilvifrons. Phytoparasitica* 35(4): 357-366.

Andrewartha, H.G. 1952. Diapause in relation to the ecology of insects. *Biological Reviews of the Cambridge Philosophical Society* 27: 50-107.

Andrewartha, H.G. & Birch, L.C. 1954. The distribution and abundance of animals. - Chicago University Press. Chicago.

Atkinson, D. 1994. Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research* 25: 1-58.

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.

Barfield, C.S. & Ashley, T.R. 1987. Effects of corn phenology and temperature on the life cycle of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Florida Entomologist* 70: 110-116.

Castro, M.T. & Pitre, H.N. 1988. Development of fall armyworm, *Spodoptera frugiperda,* from Honduras and Mississippi on sorghum or corn in the laboratory. *The Florida Entomologist* 71: 49-56.

Combs, R.L. & Valerio, J.R. 1980. Biology of the fall armyworm on four varieties of Bermudagrass when held at constant temperatures. *Environmental Entomology* 9: 393-396.

Coulson, T., Mace, G.M., Hudson, E. & Possingham, H. 2001. The use and abuse of population viability analysis. *Trends in Ecology Evolution* 16(5): 219-221.

Danks, H.V. 1994. Diversity and integration of life-cycle controls in insects. In: Danks HV (ed.) *Insect Life-Cycle Polymorphism: Theory, Evolution and Ecological Consequences for Seasonality and Diapause Control*. Kluwer Academic Publishers, Dordrechrt, Series Entomologica 52: 5-40.

Davidson, J. 1944. On the relationship between temperature and rate of development of insects at constant temperatures. *Journal of Animal Ecology* 13: 26-38.

Engelmann, F. 1970. Factors that affect egg production and fecundity. In: Engelmann, F. (Ed.). *The Physiology of Insects Reproduction.* Pergamon Press, Oxford, UK. pp. 107-142.

Ernsting, G. & Isaaks, J.A. 1997. Effects of temperature and season on egg size, hatchling size and adult size in *Notiophilus biguttatus. Ecological Entomology* 22: 32-40.

Fernandes, F.S., Ramalho, F.S., Godoy, W.A.C., Pachú, J.K.S., Nascimento, R.B., Malaquias, J.B. & Zanuncio, J.C. 2013. Within plant distribution and dynamics of *Hyadaphis foeniculi* (Hemiptera: Aphididae) in field fennel intercropped with naturally colored cotton. *Florida Entomologist* 96: 92-103.

Habib, M.E.M., Paleari, L.M. & Amaral, M.E.C. 1982. Effect of three larval diets on the development of the armyworm, *Spodoptera latifascia* (Walker, 1856) (Noctuidae, Lepidoptera). *Revista Brasileira de Zoologia* 1: 177-182.

Hauptfleisch, K., Yonow, T., Kriticos, D.J. & Ota, N. 2014. *Busseola fusca*. HarvestChoice Pest Geography. St. Paul, MN: InSTePP-HarvestChoice. 6 p.

Ims, R.A. & Steen, H. 1990. Geographical synchrony in microtine population cycles: a theoretical evaluation of the role of nomadic avian predators. *Oikos* 57: 381-387.

IPCC (Intergovernmental Panel on Climate Change). 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.

Ju, R.T., Wang, F. & Li, B. 2011. Effects of temperature on the development and population growth of the sycamore lace bug, *Corythucha ciliata. Journal of Insect Science* 11:16.

Kim, D.S. & Lee, J.H. 2003. Oviposition model of *Carposina sasakii* (Lepidoptera: Carposinidae). *Ecological Modelling* 162: 145-153.

Kolberg, I. 2013. The effect of temperature on trophic Interactions. Unpublished PhD thesis. University of Uppsala, Sweden.

Krebs, R.A. & Loeschke, V. 1994. Effects of exposure to short-term heat stress on fitness components in *Drosophila melanogaster. Journal of Evolutionary Biology* 7: 39-49.

Kroschel, J., Sporleder, M., Tonnang, H.E.Z., Juarez, H., Carhuapoma, P., Gonzales, J.C. & Simon, R. 2013. Predicting climate-change-caused changes in global temperature on potato tuber moth *Phthorimaea operculella* (Zeller) distribution and abundance using phenology modeling and GIS mapping. *Agricultural and Forest Meteorology* 15: 228-241.

Lee, J.H. & Elliott, N.C. 1998. Comparison of developmental responses to temperature in *Aphelinus asychis* (Walker) from two different geographic regions. *Southwestern Entomologist* 23: 77-82.

Liu, S.S., Zhang, G.M. & Zhu, J. 1995. Influence of temperature variations on rate of development in insects: analysis of case studies from entomological literature. *Annals of the Entomological Society of America* 88: 107-119.

Luginbill, P. 1928. The Fall Army Worm. USDA *Technical Bulletin*. 34. 92p.

Milano, P., Berti Filho, E., Parra, J.R.P. & Cônsoli, F.L. 2008. Influência da temperatura na frequência de cópula de *Anticarsia gemmatalis* (Hübner) e Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae). *Neotropical Entomology* 37: 528–535.

Milonas, P.G. & Savopoulou-Soultani, M. 2000. Development, survivorship, and reproduction of *Adoxophyes orana* (Lepidoptera: Tortricidae) at constant temperatures. *Annals of the Entomological Society of America* 93: 96-102.

Pencoe, N.L. & Martin, P.B. 1981. Development and reproduction of fall armyworms on several wild grasses. *Environmental Entomology* 10: 999-1002.

Qiu, B., Chen, Y., Liu, L., Peng, W., Li, x., Ahmed, M.Z., Mathur, V., Du, Y. & Ren, S. 2009. Identification of three major *Bemisia tabaci* biotypes in China based on morphological and DNA polymorphisms. *Progress in Natural Science* 19: 713-718.

Ratte, H.T. 1985. Temperature and insect development. In: Environmental Physiology and Biochemistry of Insects. Hoffmann, K.H. (ed) Berlin, Heidelberg, New York, Tokyo: Springer Verlag. pp. 33-66.

Shahout, H.A., Xu, J.X., Yao, X.M. & Jia, Q.D. 2011. Influence and mechanism of different host plants on the growth, development and, fecundity of reproductive system of common cutworm *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae). *Asian Journal of Agricultural Science* 3(4): 291-300.

Simmons, A.M. & Lynch, R.E. 1990. Egg production and adult longevity of S*podoptera frugiperda, Helicoverpa zea* (Lepidoptera: Noctuidae), and *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae) on selected adult diets. *Florida Entomologist* 73(4): 666-671.

Simmons, A.M. & Marti, Jr., O.G. 1992. Mating by the fall armyworm (Lepidoptera: Noctuidae): frequency, duration, and effect of temperature. *Environmental Entomology* 21: 371-375.

Simmons, A.M. 1993. Effects of constant and fluctuating temperatures and humidities on the survival of *Spodoptera frugiperda* pupae (Lepidoptera: Noctuidae). *Florida Entomologist* 76(2): 333-340.

Solomon, M.E. 1951. Control of humidity with potassium hydroxide, sulphuric acid or other solutions. *Bulletin of Entomological Research* 42: 543-554.

Son, Y. & Lewis, E.E. 2005. Modelling temperature-dependent development and survival of *Otiorhynchus sulcatus* (Coleoptera: Curculionidae). *Agricultural and Forest Entomology* 7(3): 201-209.

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.

StatSoft, Inc. 2013. STATISTICA (data analysis software system), version 12. www.statsoft.com.

Tisdale, R.A. & Sappington, T.W. 2001. Realized and potential fecundity, egg fertility, and longevity of laboratory-reared female beet armyworm (Lepidoptera: Noctuidae) under different adult diet regimes. *Annals of the Entomological Society of America* 94: 415-419.

Vickery, L.A. 1929. Studies on the fall army worm in the Gulf coast district of Texas. USDA *Technical Bulletin* 138: 64.

**Table 3.1:** Mean fecundity and longevity (± S.E.) of *Spodoptera frugiperda* moths at constant temperatures. Values in brackets represent minimum and maximum.

| Temp (± 1°C) | *n* | Total number of eggs laid | Pre-oviposition period (days) | Oviposition period (days) | Post-oviposition period (days) | Longevity of adults (days) | No. of days during which no eggs were laid | Mean number of eggs laid per day | Max no. of eggs laid per day | Min no. of eggs laid per day | Mean no. of egg batches per female |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 18 | 31 | 716.7 ± 52.6b (94 - 1186) | 5.9 ± 0.3a (4 - 10) | 8.0 ± 0.5a (2 - 15) | 1.8 ± 0.3a (0 - 6) | 16.6 ± 0.5a (13 - 22) | 0.9 ± 1.8a (0 - 4) | 90.4 ± 4.9a (47 - 148) | 240.0 ± 18.4a (71 - 468) | 15.3 ± 2.2a (1 - 38) | 18.4 ± 1.3ab (7 - 34) |
| 22 | 29 | 979.2 ± 57.1a (233 - 1674) | 3.3 ± 0.2b (2 - 8) | 6.5 ± 0.4ab (3 - 12) | 1.2 ± 0.1a (0 - 3) | 11.8 ± 0.2b (10 - 15) | 0.8 ± 0.2a (0 - 3) | 156.6 ± 9.1b (69 - 301) | 360.6 ± 20.1b (123 - 585) | 36.4 ± 9.6ab (4 - 253) | 20.3 ± 1.4a (6 - 37) |
| 26 | 25 | 641.2 ± 65.2bc (72 - 1438) | 3.5 ± 0.3b (2 - 9) | 5.0 ± 0.4bc (2 - 9) | 1.8 ± 0.3a (0 - 5) | 11.0 ± 0.5b (5 - 14) | 0.6 ± 0.2a (0 - 2) | 138.2 ± 16.7b (14 - 414) | 267.0 ± 24.1a (37 - 577) | 48.6 ± 16.0ab (1 - 398) | 16.6 ± 2.1ab (4 - 54) |
| 30 | 32 | 493.2 ± 51.4cd (96 - 1198) | 3.4 ± 0.2b (2 - 6) | 3.4 ± 0.2c (2 - 6) | 1.1 ± 0.1a (0 - 3) | 8.3 ± 0.2c (6 - 10) | 0.3 ± 0.1a (0 - 3) | 140.6 ± 12.0b (41 - 306) | 249.3 ± 20.0a (61 - 442) | 66.7 ± 10.0b (3 - 198) | 12.6 ±1.5b (3 - 46) |
| 32 | 8 | 224.4 ± 56.8d (39 - 584) | 4.4 ± 0.4ab (3 - 6) | 2.4 ± 0.6c (1 - 6) | 0.6 ± 0.3a (0 - 2) | 7.4 ± 0.5c (5 - 9) | 0 ± 0a (0) | [#]77.2 ± 10.6ab (47 - 97) | 151.0 ± 21.5a (39 - 225) | [#]9.5 ± 1.3ab (6 - 12) | 9.5 ±2.7b (3 - 26) |

Means in each column followed by the same letter are not significantly different (Tukey's Unequal N HSD, P = 0.05).

[#]The mean and minimum number of eggs laid per day at 32 °C was calculated for 4 females only. Number of eggs from the 4 females that oviposited for one day and died on the day of egg laying, was omitted. It was, however, used in the calculation of 'Maximum number of eggs laid per day'

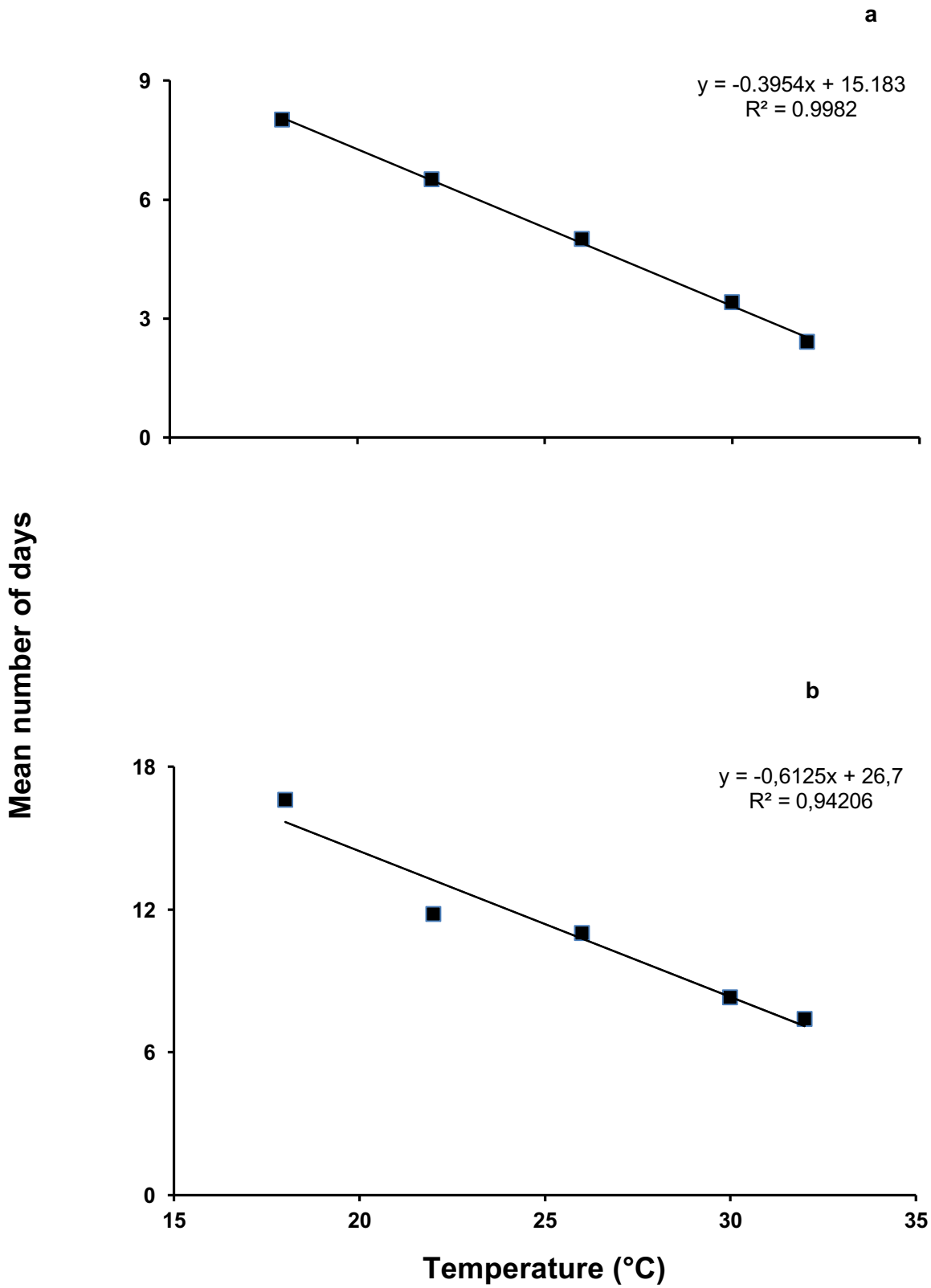



**Figure 3.1:** The relationship between temperature and a) duration of oviposition period, and b) female moth longevity.

# Chapter 4

## Conclusion

The Fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), is indigenous to the tropical and subtropical regions of the western hemisphere. It is ranked the second most destructive pest in the south eastern part of the United States (Sparks, 1986). It recently invaded Africa and it is expected to be a lasting threat to several important crops (Goergen *et al*., 2016). The biology, distribution and abundance of a pest is affected by the relationship between temperature and rate of development (Tobin *et al*., 2003). In this study the effect of temperature on the development of *S. frugiperda* was studied at five different temperature regimes, namely 18, 22, 26, 30 and 32 ± 1 °C. All eggs hatched at all the temperatures evaluated. Eggs developed slowly at 18 °C compared to the other temperatures and larval survival was low. It is, therefore concluded that continuous low temperatures, although above the lower thermal limit, will slow development down and may reduce population numbers as a result of high mortality indices. The optimal range for egg, larval and egg-to-adult development of *S. frugiperda* was between 26 and 32 °C, but development at 32 °C did not fit the linear model. Larval survival was also the highest between 26 and 30 °C and the optimum temperature was 30 °C, where the fastest development rate and lowest mortality was recorded. Pupal development time ranged between 7.82 and 30.68 days (32 - 18 °C), with a mean pupal development time of 17.06 days at 22 °C, and only 11.43 days at 26 °C. Development period of the egg-to-adult stage decreased from 71.3 at 18 °C to 20.2 days at 32 °C. Based on linear regression analyses of development rate at all temperatures, a minimum temperature threshold of 13.01 °C was calculated for egg development and 12.12 °C for larvae, 13.24 for pupae and 12.57 °C for egg-to-adult development. Degree-day requirements for *S. frugiperda* egg and larval development were determined at 35.72 ± 1.30 and 202.67 ± 4.45 °D respectively when larvae were reared on sweetcorn kernels. Pupae needed 147.06 °D for development and development of the life cycle (egg-to-adult), 391.01 ± 1.22.

Kroschel *et al.* (2013) emphasised the importance of predicting the potential geographic distribution and abundance of agricultural pests in that it could assist farmers to adapt to climate change by having enough pest management tools available to reduce crop losses. An increase in temperature can also cause an increased risk of invasion by migrant pests (Porter *et al.,* 1991, Memmott *et al.*, 2010; Parmesan, 2007). The number of generations that *S. frugiperda* can complete per year largely depends on the latitude

of specific habitats (Luginbill, 1928) and more generations are predicted in tropical regions where the conditions are more favourable and as such more constant (Sparks, 1979; Randall, 1986; Bale *et al.,* 2002). The above mentioned temperature thresholds were used and the number of generations that *S. frugiperda* can complete at different localities in southern Africa was estimated and a map was generated with CLIMEX (Sutherst & Maywald 1985; Kriticos *et al*., 2015) by using the "Wet Tropical" species template (Figure 4.1). The following temperature parameters were set: the lower temperature threshold at 12 °C; the lower optimal temperature at 25 °C; the upper optimal temperature at 30 °C; the upper temperature threshold at 39 °C and cold stress temperature threshold at 12 °C.

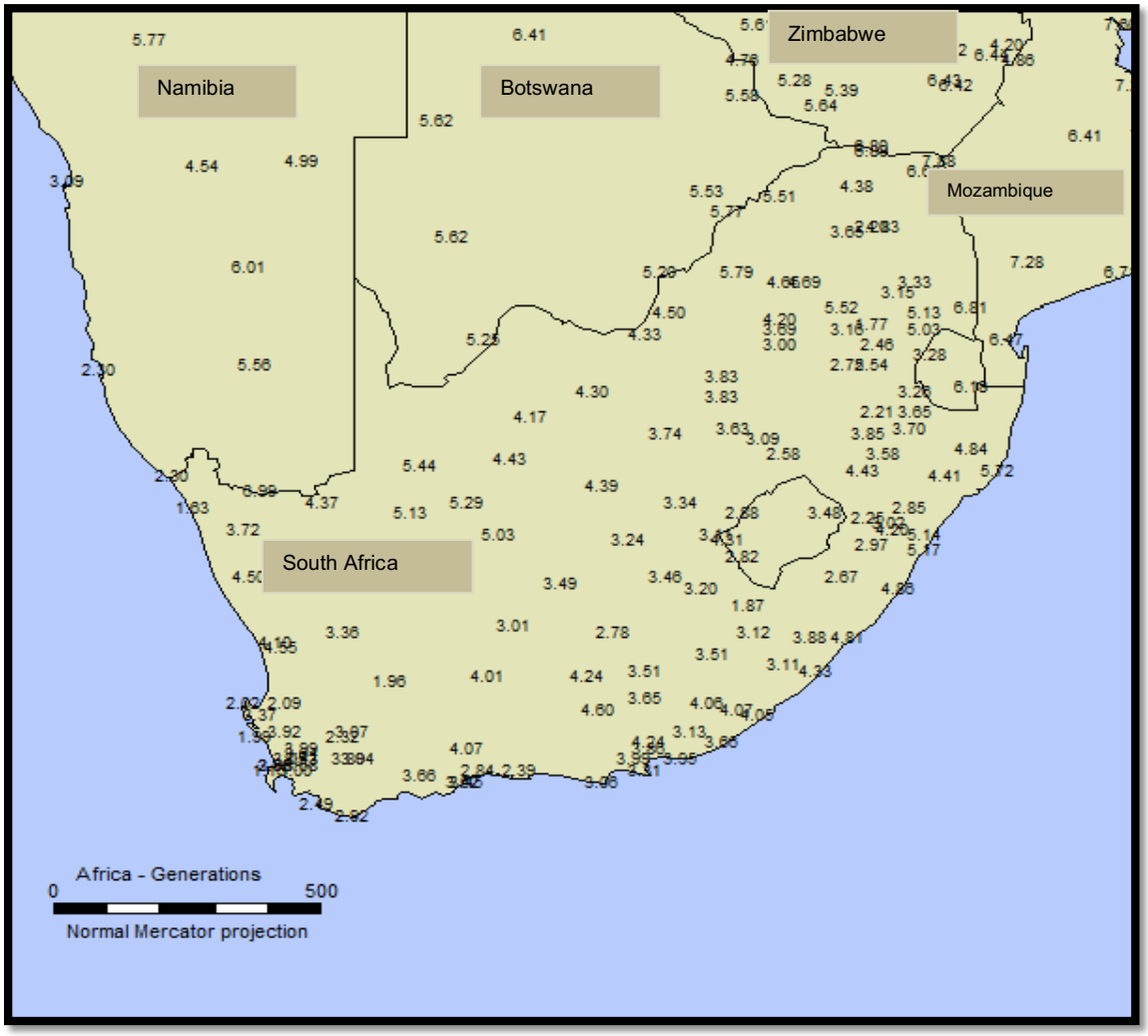



**Figure 4.1:** The estimated number of generations that *Spodoptera frugiperda* can complete at different localities in southern Africa.

Figure 4.1 shows the estimated number of *S. frugiperda* generations when the thermal limits determined in this study were applied. The maize producing area of South Africa extends north to the border of South Africa with Botswana. More than five generations per annum is estimated in that area. Maize is planted earlier towards the north and can therefore be infested earlier than maize crops in the central area of South Africa. A longer period of infestation will also take place as a result of climatic conditions which allow for more generations per season.

Temperature does not only influence the duration of each instar, but also the number of instars that the larvae go through before reaching the adult stage (Aguilon *et al.,* 2015). It is important to determine larval instars correctly for pest management strategies because the effectiveness of insecticides may differ between instars (Drooz, 1965). The head capsule widths of the six *S. frugiperda* instars ranged between 0.27 to 2.90 mm. This knowledge on head capsule size can provide for more accurate research on insecticide efficacy, since many insecticides are only registered for application against instars 1 to 3.

The effect of temperature on the reproductive parameters of *S. frugiperda* was also evaluated at 18, 22, 26, 30 and 32 °C, 70 ± 30 % RH and 14L: 10D photoperiod. These parameters were for the duration of the pre-oviposition, oviposition and post-oviposition periods, as well as the number of eggs laid and longevity of the moths. Fecundity and longevity of *S. frugiperda* moths were inversely related to temperature. The most eggs per female, as well as the maximum number of eggs laid per female, were at 22°C, which can be regarded as the optimum temperature for oviposition. Observations made during this study relates to the thermal requirements for each specific life stage under natural conditions. *Spodoptera frugiperda* moths lay their eggs at night, which may serve as an explanation for a medium temperature of 22 ° C as optimum temperature for oviposition. The optimum temperature for larval development was determined as 30 °C, but pupae develop at a temperature as high as 32 °C, which will enable successful development in spite of high soil temperatures. The thermal limits determined in this study are therefore explained by the tropical nature of the pest.

Future research should focus on using the threshold temperatures determined in this study in modelling in order to estimate and predict areas suitable for growth and to which *S. frugiperda* can migrate from its overwintering sites, as well as areas with suitable environmental conditions for persistent occurrence. These predictions should then be supported and verified by research under field conditions.

## 4.1 References


Aguilon, D.J.D., Medina, C.dR. & Velasco, L.R.I. 2015. Effects of larval rearing temperature and host plant condition on the development, survival, and coloration of African armyworm, *Spodoptera exempta* Walker (Lepidoptera: Noctuidae). *Journal of Environmental Science and Management* 18(1): 54-60.

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.

Drooz, A.T. 1965. Elm spanworm head capsule widths and instars. *Journal of Economic Entomology* 58: 629-631.

Goergen, G., Kumar, P.L., Sankung, S.B., Togola, A. & Tamo, M. 2016. First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in west and central Africa. *Plos one* 11(10): e0165632.

Kriticos, D.J., Maywald, G.F., Yonow, T., Zurcher, E.J., Herrmann, N.I. & Sutherst, R.W. 2015. *CLIMEX Version 4: Exploring the Effects of Climate on Plants, Animals and Diseases*. Canberra: CSIRO.

Kroschel, J., Sporleder, M., Tonnang, H.E.Z., Juarez, H., Carhuapoma, P., Gonzales, J.C., Simon, R. 2013. Predicting climate-change-caused changes in global temperature on potato tuber moth *Phthorimaea operculella* (Zeller) distribution and abundance using phenology modeling and GIS mapping. *Agricultural and Forest Meteorology* 15: 228–241.

Memmott, J., Carvell, C., Pywell, R.F. & Craze, P.G. 2010. The potential impact of global warming on the efficacy of field margins sown for the conservation of bumble-bees. *Philosophical Transactions Royal Society of London B Biological Science* 365(1549): 2071-2079.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phonological response to global warming. *Global Change Biology* 13:1860-1872.

Porter, J.H., Parry, M.L. & Carter, T.R. 1991. The potential effects of climatic change on agricultural insect pests. *Agricultural and Forest Meteorology* 57: 221-240.