Host suitability of poaceous and broad leaf plants for Fall armyworm (*Spodoptera frugiperda*) (Lepidoptera: Noctuidae)

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Dissertation accepted in fulfilment of the requirements for the degree *Master of Science in Environmental Sciences with Integrated Pest Management* at the North-West University

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Graduation October 2020
26060868

DECLARATION BY THE CANDIDATE

I, HANRICKE VAN STADEN, declare that the work presented in this MSc thesis is my own work, that it is not been submitted for ay degree or examination at any other University and that all the sources I have used or cited have been acknowledged by the complete reference.

Signature.. Date 06/05/2020

DECLARATION AND APPROVAL BY SUPERVISORS

We declare that the work presented in this thesis was carried out by the candidate under our supervision and we approve this submission.

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ACKNOWLEDGEMENTS

This dissertation would not have been possible without the help and support of so many people whom I cherish in life.

> I thank our God Almighty for the ability, strength, wisdom and opportunity to undertake and accomplish this research study. All glory to Him.

I would like to thank Prof. Johnnie van den Berg for all his guidance and support. His passion for entomology and crop protection inspired me to pursue my studies in this field. Thank you for the opportunity to have done research on this interesting project. I would not be where I am, without all his guidance.

Prof. Hannalene du Plessis, thank you for all your advice and understanding throughout this journey. I appreciate all the help and patience with the statistics. Thank you for always making time in your own busy schedule to guide and help me. I am truly grateful.

> I would also like to thank fellow students who helped me with my research practical. Thank you Nini for spending countless hours with me during my practical experiments and rearing of insects. To Carla, I am appreciative for all the assistance when I needed it.
>
> Special thanks to my parents and sister Miandi whom I dearly love, for all their love and support. Your motivation and patience enabled me to stay positive. Thank you for all sacrifices to make it possible for me to study, I will always be thankful.
>
> To my boyfriend Arno, for all his encouragement and love he has given me to finish this project. I am blessed with you in my life.

ABSTRACT

Spodoptera frugiperda is native to the Americas but invaded the African continent in 2016, causing damage to maize and sorghum. Reports from literature indicate that larvae of *S. frugiperda* can feed on 353 different host plant species belonging to 76 plant families, indicating that it is highly polyphagous. Several strategies such as chemical control, host plant resistance, biological control and cultural control can be implemented in an Integrated Pest Management (IPM) system to manage *S. frugiperda* populations*.* Chemical control (mainly synthetic insecticidal sprays) and genetically modified crops (mainly Bt maize) are the primary tools used to manage *S. frugiperda.* However, alternative methods to insecticidal sprays and genetically modified crops are essential for subsistence farmers in Africa to control *S. frugiperda* in a more cost-effective and sustainable manner. These control methods can include cultural control practices such as intercropping and crop rotation. It is necessary to identify crop and non-crop hosts that are cultivated in Africa on which *S. frugiperda* larvae can survive and complete their lifecycles. Through this, crops that can serve as ''bridging'' crops for *S. frugiperda* during off seasons when no maize is cultivated, can be identified and classified as having a high or low risk of suffering infestation and damage. Also, pest management strategies can be developed if poor larval hosts can be identified and used as trap crops. The aim of this study was to evaluate the host suitability of 22 poaceous and broad leaf plant species that are potential hosts of this pest, and which are cultivated in South Africa, for development of *S. frugiperda* larvae. *Spodoptera frugiperda* larvae were reared in petri dishes under laboratory conditions on tissue of the different plant species and their life history parameters were recorded. Results showed that the Poaceae species were more suitable larval host plants compared to broad leaf plant species. Maize, oat, forage sorghum and grain sorghum were the most suitable poaceous hosts for *S. frugiperda.* Development of larvae reared on maize was the optimum, compared to the other poaceous and broad leaf species. The superior performance of larvae on maize and sorghum may indicate that larvae used in this study were from the maize strain of *S. frugiperda*. However, there is a possibility that some larvae may be interstrain hybrids since larvae reared on rice also performed very well. *Spodoptera frugiperda* is composed of two morphologically indistinguishable strains, namely the rice strain and the maize strain, and recent reports showed the presence of an interstrain hybrid in in Africa. Brachiaria grass, Panicum grass, as well as Napier and Vetiver grass have the potential to be used as trap crops in a push-pull system to control *S. frugiperda*. The broad leaf species evaluated in this study, especially Indian mustard, woolly pod vetch and pumpkin, can possibly be used in habitat management strategies (e.g. crop rotation, trap cropping and intercropping systems) to reduce the extent of *S. frugiperda* infestation of maize. Oat was the only winter crop identified as a high-risk crop which can serve as a bridging crop for *S. frugiperda* during off seasons when no maize is cultivated in South Africa. However, although some winter-crops could be regarded as suitable hosts, temperature will ultimately determine if *S. frugiperda* larvae can overwinter in a particular area. Other winter crops such as wheat, cultivated radish and Japanese radish was identified as low-risk crops to sustain *S. frugiperda* during winter months.

Keywords: broad leaf plants, larval development, Poaceae, push-pull system*.*

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Chapter 1: Literature review and aims of study

1.1 Importance of crops

Global food insecurity is growing due to an increase in the world population (FAO, 2018). It is expected that the world population will grow from nearly 7.6 billion people in 2017 to an estimate of 10 billion by 2050 (United Nations, 2017; FAO, 2018). Around 795 million people in 2018 suffered from hunger and over two billion people exhibited micronutrient deficiencies (FAO, 2018). Food insecurity and malnutrition remain a problem in many developing countries, especially in Africa and Asia (Sibhatu and Qaim, 2017). It is estimated that the African population will double over the next 33 years (United Nations, 2017). In Africa, 98% of farmers are subsistence farmers (FAO, 2017) producing crops for themselves, mainly for food and to sustain their families (Tadele, 2017). The main yield limiting factors for these farmers are poor soil fertility, drought, insect pests, diseases and weeds (Tadele, 2017).

The lepidopteran stemborers, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) (Van den Berg *et al.,* 1993; Kfir *et al.,* 2002; Calatayud *et al*., 2014) and *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) (Seshu, 1998; Kfir *et al.,* 2002), has been considered as the most damaging insect pests of maize and sorghum in Africa. In East Africa, *B*. *fusca* and *C*. *partellus* was identified as the dominant pest species (Asmare *et al*. 2014). Recently, another lepidopterous pest, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), invaded the African contient causing major damage to maize and sorghum (Stokstad, 2017), becoming the most important maize pest on the continent. This pest invaded Africa in 2016 and since then spread throughout the African continent (Goergen *et al*., 2016; Day *et al*., 2017; Rwomushana *et al.*, 2018). In Africa, *S. frugiperda* prefers mainly maize which is a staple food for many African people (Rwomushana *et al,* 2018). Thus, *S. frugiperda* poses a threat to livelihoods, food security and nutrition for families of African subsistence farmers (Rwomushana *et al,* 2018). In South Africa, *S. frugiperda* feeds primarily on maize, the most important food crop (Du Plessis, 2013). However, during off season when no maize is cultivated, other crops might serve as bridging crops for *S. frugiperda* (Montezano *et al.,* 2018). Furthermore, if a host shift occurs in this species, and it starts to attack other crops and forage grasses, which is the case in the USA (Hardke *et al.,* 2015) and Brazil (Favetti *et al.,* 2017; Montezano *et al.,* 2018), its pest status in South Africa will become much higher.

1.2. Distribution of *Spodoptera frugiperda*

Spodoptera frugiperda is a migratory insect pest native to tropical and subtropical regions of the western hemisphere, from the United States to Argentina in South America (Capinera, 1999). *Spodoptera frugiperda* infestations in the Unites States is mostly ascribed to migrating populations that overwinter in southern Texas and southern Florida where temperatures are higher, and where this pest can overwinter since they are susceptible to cold and freezing temperatures (Luginbill, 1928; Nagoshi *et al*., 2012; Nagoshi *et al.,* 2017a). During summer months, *S. frugiperda* moths are able to migrate to warmer areas, northwards to Canada, across the Unites States and southwards to Argentina and Chile in South America (Figure 1.1) (Johnson, 1987; Nagoshi *et al.,* 2017b). *Spodoptera frugiperda* is able to migrate thousands of kilometres during seasonal migrations, and therefore also pose a threat to crops cultivated in temperate regions (Early *et al.,* 2018).

1.2.1. *Spodoptera frugiperda* spreading to Africa

The first record of *S. frugiperda* in Africa was in 2016 and within a short time it spread to more than 44 African countries (Figure 1.1) (Goergen *et al*., 2016; Tindo *et al*., 2016; Day *et al.,* 2017; Nagoshi *et al*., 2017b; Cock *et al.,* 2017; Nagoshi *et al*., 2018; Rwomushana *et al*., 2018; Jacobs *et al.,* 2018; Prasanna *et al.,* 2018; Uzayisenga *et al*., 2018; CABI, 2019). This pest was first detected in Central and Western Africa and since then it has spread to almost all sub-Saharan African countries, except for Lesotho, Djibouti and Eritrea (Goergen *et al*., 2016; FAO, 2018; Rwomushana *et al.,* 2018). The *S. frugiperda* individuals that invaded Africa most likely originated from Florida or the Caribbean region (Nagoshi *et al*., 2017b; Nagoshi *et al*., 2018) but explanations of how this pest invaded Africa is speculative (Nagoshi, 2019). *Spodoptera frugiperda* prefers maize in Africa, causing significant damage compared to other crops (Rwomushana *et al.*, 2018). A study by Jacobs *et al.* (2018) indicated the presence of *S. frugiperda* in several provinces in South Africa, namely Limpopo, Mpumalanga, North West and Gauteng.

1.2.2. *Spodoptera frugiperda* spreading to Asia, Australia and European countries

Spodoptera frugiperda has recently been detected in Australia (Dupe, 2020) and Asia where it causes extensive damage to maize (Deole and Paul, 2018; Sharanabasappa *et al.,* 2018; Sisodiya *et al.,* 2018). The first detection of *S. frugiperda* in Australia was in March 2020 in Kununurra located in Western Australia (Dupe, 2020). The first confirmed report of *S. frugiperda* in Asia was in maize fields in Karnataka State in India and since then it has spread to other Asian countries (Figure 1.1) (CABI, 2019; Sharanabasappa *et al.,* 2018). *Spodoptera frugiperda* populations from India and Africa both originated from the same source in the Americas (Nagoshi *et al*., 2017b; Nagoshi *et al*., 2018). An explanation of how this pest might have arrived in India can be due to natural migrations between Africa and India, which have for example been reported for other insect species such as dragonflies (Hobson *et al*., 2012). The Globe Skimmer dragonfly (*Pantala flavescens*) (Fabricius) (Odonata: Libellulidae) undergoes seasonal migrations of 3500 kilometres between eastern Africa and India by using high altitude winds (Hobson *et al*., 2012). Therefore, Nagoshi *et al.* (2019) presumed that there might be a regular interaction between the African and Indian *S. frugiperda* populations. Although, considering the behaviour of *S. frugiperda*, it usually flies a few hundred kilometres during a single flight their ability to fly over the Arabian Sea is doubted.

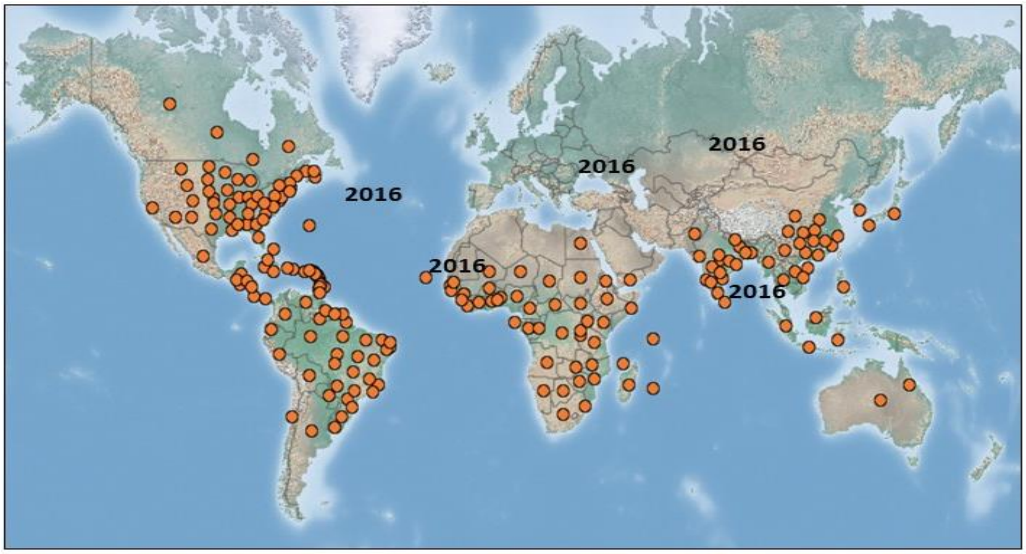


Figure 1.1: World map of the distribution of *Spodoptera frugiperda* (CABI, 2020).

1.3. Lifecycle and biology of *Spodoptera frugiperda*

The lifecycle of *S. frugiperda* takes approximately 30 days to be completed in warmer temperatures (summer months with daily temperatures of 28 °C) and 60 to 90 days at cooler temperatures (spring, autumn and winter months) (Sparks, 1979; Capinera, 1999; Du Plessis *et al.,* 2018).

1.3.1. Eggs

Spodoptera frugiperda eggs are dome shaped with a flattened bases and rounded at the top (Capinera, 1999; Shylesha *et al.,* 2018). An egg is approximately 0.4 mm in diameter and 0.3 mm in height (Capinera, 1999; Shylesha *et al.,* 2018). When eggs are freshly laid, it is white to light green in colour, turning brown to black before hatching, after two to three days (Hardke *et al.*, 2015; Shylesha *et al.,* 2018). Female moths lay eggs in clusters (Sparks, 1979) ranging between 150 to 200 per egg batch (Du Plessis *et al.,* 2018). The total egg production of a female moth during her two to three-week lifetime ranges between six to 10 egg batches, with a total of between 1500 and 2000 eggs (Figure 1.2) (Capinera, 1999). Eggs are usually deposited in a single layer attached to plant foliage, but sometimes in layers (Capinera, 1999; Shylesha *et al.,* 2018). Eggs are usually deposited on the underside of leaves when *S. frugiperda* population densities are low, but when densities are high, eggs are deposited all over the plant or objects such as sheds, window panes and flags (Sparks, 1979). The female moth covers the egg batches with greyish scales, giving it a furry appearance (Figure 1.2) (Capinera, 1999; Hardke *et al.*, 2015). Eggs hatch within 2-4 days if the mean temperature is between 21-27 °C (Sparks, 1979).

Figure 1.2: (a) Egg batch of *Spodoptera frugiperda* on a maize leaf (Photo: H. van Staden).

1.3.2. Larvae

The larval stage consists of six larval instars (Sparks, 1979; Capinera, 1999; Shylesha *et al.,* 2018). The total duration of the larval stage ranges between 14 and 30 days depending on the temperature and the plant species consumed (Ali *et al.,* 1990; Capinera, 1999; Da Silva *et al.,* 2017; Deole and Paul, 2018). A first-instar larva (L1) is greenish in colour with a black head, 1.7 mm long and a head capsule width of 0.35 mm (Capinera, 1999; Shylesha *et al.,* 2018). When a L2 moults into a third-instar larva (L3) the lateral white lines and a brownish dorsal surface appear (Capinera, 1999). A L3 is 6.4 mm in length and the head capsule width is 0.75 mm. The fourth-instar larva (L4), fifth-instar larva (L5) and sixth-instar larva (L6) are 10.0, 17.2, and 34.2 mm in length, respectively, with head capsule widths of 1.3, 2.0, and 2.6 mm, respectively (Capinera, 1999). L4 to L6 have a red to brown heads, brownish bodies and white lateral and subdorsal lines (Figure 1.3) (Capinera, 1999; Shylesha *et al.,* 2018). Mature larvae can be identified by the distinct white inverted "Y" on their front of the head, a set of four dark large spots forming a square on the upper surface of the second to last segment of the body, three yellow stripes on the back and a black and yellow stripe on the sides (Figure 1.3) (Capinera, 1999).

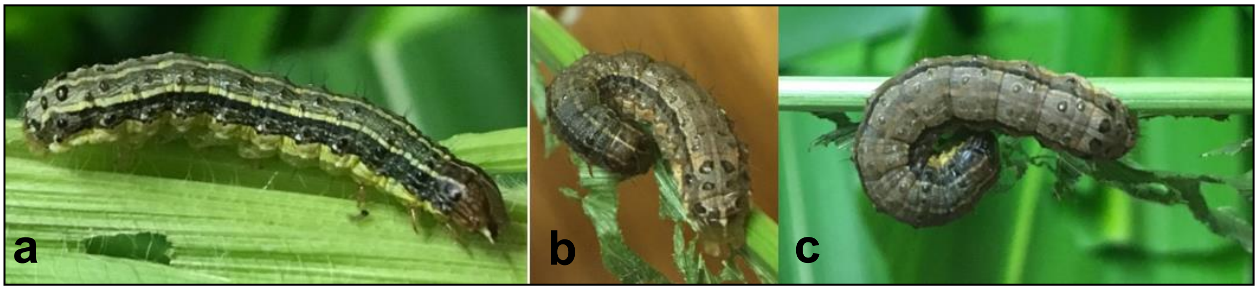


Figure 1.3: (a-c) Fourth and fith-instar larvae of *Spodoptera frugiperda* (Photo by H. van Staden).

1.3.3. Pupa

The pupal stage can take between seven to 37 days to complete, depending on the temperature and other environmental conditions (Sparks, 1979). Furthermore, Capinera (1999) reported that pupal duration ranges from eight to nine days at warm temperatures, whereas at cooler temperatures it ranges between 20 and 30 days. Pupation takes place in a cocoon constructed by the larva by tying loose soil particles together with silk

(Capinera, 1999). The pupa is usually found in the soil (Sparks, 1979), two to eight cm deep. Pupae are rarely found in the stalks of maize plants (Capinera, 1999; Shylesha *et al.,* 2018). The pupa is 14 to 18 mm long and approximately 4.5 mm wide (Figure 1.4) (Capinera, 1999; Shylesha *et al.,* 2018). The specific characteristics of the different sexes of *S. frugiperda* pupae has not yet been described, but male and female pupa can be identified using the generalized description of pupae by Butt and Cantu (1962). The genital aperture of females, visible as a black line, are located on the fourth segment while the genital aperture of males, which is visible as a kidney-shaped bump, are located on the fifth segment when counting from the wing cases (Figure 1.5).

Figure 1.4*: Spodoptera frugiperda* pupa (Hardke *et al.,* 2015).

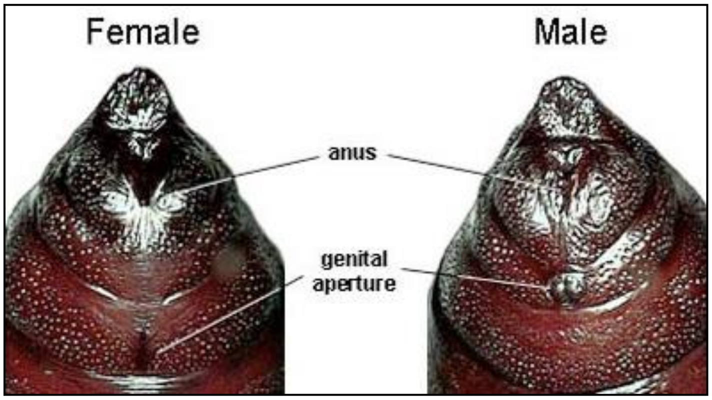


Figure 1.5: The posterior ends of female and male pupae of *Spodoptera frugiperda* (Caruthers, 2005).

1.3.4. Moth

The longevity of moths is between seven and 21 days with an average of 10 days (Capinera, 1999). Moths have a wingspan of 32 to 40 mm, with front wings dark brown and rear wings grey to white. A slight sexual dimorphism is visible, e.g. the forewing of male moths is shaded brown and grey with white spots, while the forewings of females is uniform brown to grey (Figure 1.6) (Capinera, 1999). Adults are nocturnal (Sparks, 1979), emerge at night and during their pre-oviposition period (1 day long), fly long distances of up to 100 km per night, before mating and laying eggs (Capinera, 1999; Maiga, 2017). Adults are most active during warm and humid evenings. Females lay most of their eggs during the first five days after emergence, but oviposition and egg laying can occur for up to three weeks (Capinera, 1999). Female moths usually lay their eggs on the inner side of maize whorls and on the abaxial leaf surface (Shylesha *et al.,* 2018).

Figure 1.6: Female (left) and male (right) moths of *Spodoptera frugiperda* (Photo by H. van Staden).

1.4. Host plants and strains of *Spodoptera frugiperda*

Spodoptera frugiperda is a polyphagous pest posing a threat to many commercial crops such as maize, cotton and soybean. The pest is however considered to be most important on maize and sorghum (Pogue, 2002; Nagoshi, 2009). A recent study showed that *S. frugiperda* larvae can feed on 353 different host plant species belonging to 76 plant families (Montezano *et al.,* 2018). The polyphagous nature of this pest might be an important survival strategy (Lee *et al*., 2003), for example, dispersing neonate larvae have a better chance to come in contact with a suitable host plant (Rojas *et al*., 2018) and it is able to migrate and feed on less preferred host plants when more preferred hosts are not available in the area (Johnson, 1987). Poaceae (106 taxa), Asteraceae (31 taxa) and Fabaceae (31 taxa) are the three plant families with the highest number of taxa serving as hosts for *S. frugiperda* (Montezano, 2018). The main hosts favoured by *S. frugiperda* are maize, rice and sorghum, all belonging to the grass family (Poaceae).

Spodoptera frugiperda is composed of two strains, namely the rice strain and the maize strain (Meagher and Nagoshi, 2004; Dumas *et al.*, 2015; Da Silva *et al.*, 2017). These strains are morphologically indistinguishable (Nagoshi, 2010; Dumas *et al.*, 2015). However, these strains differ according to their physiology and behaviour (Nagoshi, 2010; Meagher, 2011; Dumas *et al.*, 2015). The maize strain larvae preferentially feed on maize, cotton and sorghum, whereas the rice strain preferentially feeds on rice, numerous pasture, turf grasses, lucerne and millet (Pashley *et al.,* 1987; Meagher and Nagoshi, 2004; Prowell *et al.,* 2004; Ríos-Díez and Saldamando-Benjumea, 2011; Juárez *et al*., 2014; Dumas, 2015; Murúa *et al.,* 2015; Cock *et al.,* 2017; Nagoshi *et al.,* 2017b; Nagoshi *et al.,* 2018; Otim *et al.,* 2018; Kalleshwaraswamy *et al*., 2019). Although both strains are adapted to different host plants, with some overlap, these differential host preferences may be the most distinguishable characteristic between the two strains (Dumas, 2015; Groot *et al*., 2010; Meagher, 2011).

Several studies reported that these two strains can cross and hybridize (Levy *et al.,* 2002; Saldamando and Vélez-Arango, 2010; Nagoshi *et al.,* 2018; Nagoshi *et al.*, 2019). However, the behaviour of interstrain hybrids are currently not well understood (Nagoshi, 2010; Nagoshi; 2019). So far, interstrain hybrids were found in maize and sorghum fields in Africa, and it therefore seems as if these hybrids prefer host plants that are also preferred by moths of the maize strain (Nagoshi, 2019).

Strain-specific molecular markers are usually used to differentiate strains from each other (Nagoshi, 2010; Meagher *et al.*, 2011; Dumas *et al.*, 2015; Nagoshi *et al.,* 2018; Nagoshi *et al.*, 2019). The coding region of the mitochondrial cytochrome-oxidase subunit I (*COI*) gene and the sex-linked triosephosphate isomerase (*Tpi*) gene are used to distinguish between the two strains and interstrain hybrids (Nagoshi, 2010; Nagoshi *et al.,* 2018; Nagoshi *et al.*, 2019). Several studies have been conducted to determine the strain composition of *S. frugiperda* in Africa, but it is still unclear whether the maize strain, rice strain and or interstrain hybrids dominate (Nagoshi *et al*., 2019). However, Kuate *et al.* (2019) reported that both the maize strain and rice strain were present in all regions of Cameroon. Furthermore, Jacobs *et al*. (2018) identified that both the maize strain and the rice strain were present in various sites collected in the Limpopo, Mpumalanga, North

West and Gauteng provinces in South Africa. Studies using the *COI* marker, indicated that both strains are present in Africa, predominated by the rice strain (Goergen *et al*., 2016; Cock *et al*., 2017; Nagoshi *et al.,* 2017; Nagoshi *et al.,* 2018; Otim *et al.,* 2018; Srinivasan *et al.,* 2018). However, studies using the *Tpi* marker, indicated that the maize strain predominates (Nagoshi *et al.,* 2017; Nagoshi *et al.,* 2018). Consequently, hybridization between strains could explain the observed discrepancies in strain identifications observed in Africa (*COI* and *Tpi*) (Nagoshi, 2010). Furthermore, surveys from multiple locations in Africa showed that *S. frugiperda* populations are dominated by maize strain and interstrain hybrids (Nagoshi, 2019). It seems that rice strain of *S. frugiperda* is rare or absent in Africa (Nagoshi, 2019). Thus, host plants preferred by the rice strain may be at low risk of *S. frugiperda* infestation in Africa (Nagoshi, 2019).

1.5. Damage and economic importance of *Spodoptera frugiperda*

Brazil is the third largest maize producer in the world after United States and China (Shylesha *et al.,* 2018). Maize production in Brazil is threatened by *S. frugiperda* which was reported as the most important maize pest in that country, causing annual losses of up to 400 million US dollars, and up to 34% grain yield loss (Cock *et al.,* 2017). The annual cost of control of this pest in Brazil is estimated at approximately 600 million US dollars (Shylesha *et al.,* 2018). It was estimated that *S. frugiperda* infestations in Africa would result in yield losses of 8.3 million to 20.6 million tons of maize, to the value of three billion US dollar per annum if no control methods were initiated (Shylesha *et al.,* 2018; Nagoshi *et al.,* 2018). An estimated 20 to 50% yield loss could be experienced in Africa due to *S. frugiperda* damage to maize (Early *et al.,* 2018). Estimated losses of 22 to 67% in Ghana and Zambia, 32% in Ethiopia and 47% in Kenya was indicated by Day *et al*. (2017) and Kumela *et al.* (2018). Yield losses of 15 to 73% can occur if 55 to 100% of maize plants are infested with *S. frugiperda* (Hruska and Gould, 1997). Another lepidopteran pest, *B. fusca*, caused major maize yield losses in monocropped fields (Kfir *et al.,* 2002).

General *S. frugiperda* larval damage symptoms are external feeding on the ears, leaves and stems, internal feeding of the ear and growing point, and, in some cases, stems of seedlings are severed at the base (CABI, 2019). The damage *S. frugiperda* cause to maize plants varies depending on the developmental stage of the plant at the time of infestation (Table 1.1) (Morril and Greene, 1973).

Table 1.1: Symptoms of *Spodoptera frugiperda* larval damage to maize plant parts attacked at different developmental stages.

Plant growth stage	Plant part attacked	Symptom or damage
Seedling	Whorl	Numerous holes in whorl with yellow-brown larval frass inside (CABI, 2019).
	Growing point	Dead heart (CABI, 2019).
	Stem	Larvae can cut seedlings at the stem base (Du Plessis *et al.,* 2018).
Mature plant	Whorl	Windowed whorl leaves, holes in whorl leaves with yellow-brown larval frass inside (Figure 1.7-a,b,c) (CABI, 2019).
	Leaves	Skeletonized leaves (Figure 1.7-d) (CABI, 2019).
	Ear	Damaged kernels (CABI, 2019).

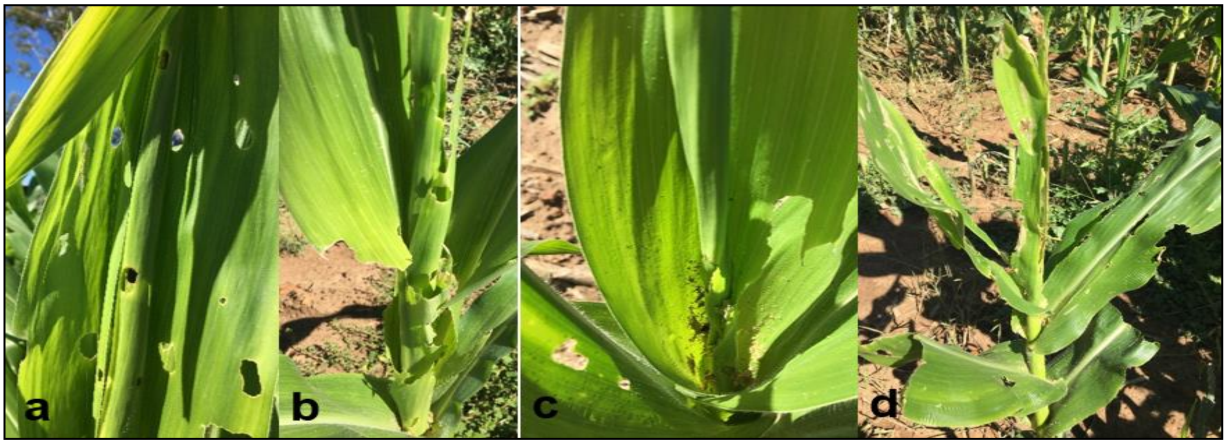


Figure 1.7*:* Typical damage symptoms caused by *Spodoptera frugiperda* larval feeding on maize plants. (a,b,c) Holes in maize whorl leaves with larval frass inside, (d) Skeletonized maize leaves (Photos by H. van Staden).

1.6. Control of Spodoptera frugiperda

It is challenging to control *S. frugiperda* due to their polyphagous nature (Da Silva *et al.*, 2017). The presence of other host crops in close proximity increases the likelihood of pest migration between crops because different host plants are cultivated in different seasons throughout the year (Da Silva *et al.*, 2017). If not well managed, S. *frugiperda* can have many generations per year, for example, in the United States there is evidence that *S. frugiperda* has up to six generations per year (Luginbill, 1928). There are several Integrated Pest Management (IPM) strategies that can be used to manage *S. frugiperda* and significant results have been achieved with chemical control, host plant resistance, biological control and cultural control (Assefa and Avalew, 2019). In America, chemical control, specifically synthetic insecticide sprays, and genetically modified Bt maize, are the primary management tools for this pest (Rwomushana *et al.,* 2018).

1.6.1. Chemical control

Chemical control is an effective method to control a wide range of insect pests, including *S. frugiperda* (Belay *et al.*, 2012; Johansen, 2017). Insecticides have different modes of action (MoA) which is the way whereby insecticides affect the insect at a specific target site (IRAC, 2017). However, the improper use of insecticides can lead to *S. frugiperda* building up resistance to the active ingredient of the insecticide (Johansen, 2017).

IRAC (2017) defined insect resistance as “a heritable change in the sensitivity of a pest population that is reflected in the repeated failure of a product to achieve the expected level of control when used according to the label recommendation for that pest species”. Polyphagous pests such as *S. frugiperda* are much more likely to develop resistance compared to monophagous pests (FAO, 2012). There are numerous reports of *S. frugiperda* which already developed resistance to a range of synthetic insecticides (Yu *et al.,* 1991; Abrahams *et al.,* 2017). For example, *S. frugiperda* has developed resistance toMoA categories 1A (Carbamates), 1B (Organophosphates), and 3A (Pyrethroids-Pyrethrins) in the Americas (Abrahams *et al.,* 2017). Kumela *et al.* (2018) reported reduced pesticide efficacy against *S. frugiperda* in Kenya. However, efficacy may be influenced by many factors such as misuse (Kuate *et al.,* 2019), incorrect dose or incorrect pesticides sprayed (Baudron *et al.,* 2019). Other factors that influences the efficacy of chemical control are reduced insecticidal exposure, for example, as soon as *S. frugiperda* larvae hatch, they tend to move to the whorl of the plant, consequently reducing larval exposure to the insecticide which do not always reach the target site deep inside the plant whorl (Young, 1979).

Chemical control is an important aspect of *S. frugiperda* control in Africa. In Ghana and Zambia, for example, large volumes of insecticides have been used against this pest, even though cultural control methods are also used (Tambo *et al.,* 2019). Tambo *et al.* (2019) reported that 51% of farmers in Ghana and 49% in Zambia made use of insecticides to control *S. frugiperda*. It is important to advise farmers in Africa on the appropriate use of insecticides, for example on dosages, timing of applications, and insect resistance management strategies to delay the evolution of resistance in *S. frugiperda* (Kuate *et al.,* 2019).

1.6.2. Host plant resistance

Painter (1951) defined plant resistance as heritable characteristics enabling a plant to suppress the ultimate degree of damage done by the insect. Plant resistance is a mechanism of the plant to protect itself against attacking insects (Peshin and Zhang, 2014).

Huesing and English (2004) mentioned that pest resistant plant varieties such as *Bacillus thuringiensis* (Bt) maize, developed through plant breeding, can also be used to manage *S. frugiperda*. Bt crops are crops that have been genetically modified to produce Cry endotoxins in every cell of the plant to protect the crop from pests such as *S. frugiperda* (Strizhov *et al.,* 1996). This protein is effective against various crop pests, but most importantly against lepidopteran larvae (Hellmich and Hellmich, 2012). There are various Cry toxins categorised according to their spectrum of activity (Hellmich and Hellmich; 2012). Cry1 and Cry2 are the major Cry proteins for lepidopteran maize pests and Cry3 for coleopteran maize pests (Hellmich and Hellmich, 2012). Crops can be genetically modified to produce these specific Cry toxins by inserting the gene into the specific crop genome (Strizhov *et al.,* 1996). In some cases, multiple Cry toxins are inserted into the genome of the crop, thereby providing resistance to multiple insect pest species (Hellmich and Hellmich, 2012). Transgenic maize hybrids expressing Bt proteins such as Cry1F, Cry1Ab, and Cry1A.105 + Cry2Ab2 proteins have proven to be effective to control *S. frugiperda* populations in the USA and Canada (Buntin *et al*., 2004; Siebert *et al.,* 2012; Storer *et al.,* 2012; Reay-Jones *et al*., 2016) and MON89034 maize in South Africa (Botha *et al.,* 2019). However, long term cultivation and poor resistance management strategies may lead to insect pests evolving resistance (Xiao and Wu, 2019). Reports of *S. frugiperda* resistance to Bt maize has been reported in Argentina, Brazil, Puerto Rico, and the south-eastern mainland of the USA (Prasanna *et al.*, 2018). In South Africa, Botha *et al*. (2019) reported high levels of survival of *S. frugiperda* on Cry1Ab maize and that alleles with resistance against the pyramid varieties that produce both the Cry1.105A and Cry2Ab2 proteins, were present.

1.6.3. Biological control

In the natural environment*,* biotic factors (e.g. predators, parasites, pathogens and food availability) and abiotic factors (climate) regulate *S. frugiperda* population numbers (Cruz *et al.,* 2018). However, when a species invades new geographical areas, abiotic and biotic factors that normally regulate their population numbers in their native region are absent, leading to pest outbreaks such as that observed for *S. frugiperda,* in Africa (Cruz *et al.,* 2018). To control invasive pest outbreaks, the most effective and long-term approach is biological control. Biological control is the use of a pest's natural enemies like predators, parasitoids and entomopathogens from the native region of the pest to reduce pest population numbers in the invaded areas, by means of human intervention (Peshin and Zhang, 2014; Kenis *et al.,* 2019). Biological control is a more economical and environmentally sustainable management strategy with which to manage invasive pests, than the use of synthetic insecticides (Kenis *et al.,* 2019) which are in some cases frequently and improperly used (Agboyi *et al.,* 2020).

Natural enemies (predators, parasitoids and pathogens) all differ in the way they kill pests. For predators, pests serve as prey (Cruz *et al.,* 2018). There are insect predators attacking multiple life stages of *S. frugiperda,* for example the family Coccinellidae, Dermaptera, and hemipteran insects such as *Podisus* and *Orius* (Cruz *et al.,* 2018). Parasitoids are intimately associated with certain of the life stages of a pest (Cruz *et al.,* 2018), consuming resources from the pest to reach maturity and ultimately killing its host. For example, insects from the genus, *Trichogramma* and *Telenomus* parasitise *S. frugiperda* eggs (Cruz *et al.,* 2018). Entomopathogens used to reduce *S. frugiperda* population numbers are bacteria (e.g. Bt), viruses (e.g. *S. frugiperda* multiple nucleopolyhedrovirus (SfMNPV)), fungi (e.g. *Beauveria bassiana* and *Metarhizium* *anisopliae*) and protozoans infect *S. frugiperda* causing a disease in this pest (Cruz *et al.,* 2018). Examples of natural enemies of *S. frugiperda* in North and South America are listed in Table 1.2. A viral pathogen, nucleopolyhedrovirus (SpexNPV), has been evaluated to control *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae) (Grzywacz *et al.,* 2008; Escasa *et al.,* 2019) and can perhaps in future be applied for the biological control of *S. frugiperda.* Sisay *et al.* (2018) identified 52 indigenous parasitoid species from the families Diptera and Hymenoptera in Africa with established interactions with *S. frugiperda* and these parasitoid species can possibly be used in biological control programmes to supress pest numbers. The dominant parasitoids were identified as *Cotesia icipe* (Fernandez-Triana and Fiaboe) (Hymenoptera: Braconidae) in Ethopia, *Palexorista zonata* (Curran) (Diptera: Tachinidae) in Kenya and *Charops ater* (Szépligeti) (Hymenoptera: Ichneumonidae) and *Coccygidium luteum* (Brullé) (Hymenoptera: Braconidae) in both Tanzania and Kenya (Sisay *et al.,* 2018). Furthermore, an egg parasitoid, *Telenomus remus* (Nixon) (Hymenoptera: Scelionidae), has been identified as a promising biological agent to control *S. frugiperda* in the African countries where their presence has been confirmed such as in Benin, Côte d'Ivoire, Kenya, Niger and South Africa (Kenis *et al*., 2019).

In the study of Agboyi *et al.* (2020) native parasitoids and parasites have been identified in two West African countries, namely Ghana and Benin, that can serve as biological agents to control *S. frugiperda* in a more sustainable manner than the use of insecticides. Ten species that parasitizes *S. frugiperda* were identified in Ghana and Benin with *Chelonus bifoveolatus* (Szépligeti) (Hympenoptera: Braconidae), an egg-larval parasitoid, and *Coccygidum luteum* (De Saussure) (Hymenoptera: Braconidae), a larval parasitoid, being the most abundant (Agboyi *et al.,* 2020). It is important to implement conservation biological control to enhance the effectiveness of natural enemies by increasing their abundance (Landis *et al.,* 2000; Amala and Shivalingaswamy, 2018; Harrison *et al.,* 2019). Conservation practices such as conserving trees and field borders such as bushes and flowers serve as an extra food source and provides shelter to natural enemies (Landis *et al.,* 2000; Nafiu *et al.,* 2014; Amala and Shivalingaswamy, 2018). Thus, conservation biological control is a useful tool in IPM to help sustain and enhance the biological control of pests (Nafiu *et al.,* 2014*;* Amala and Shivalingaswamy, 2018).

Table 1.2: Natural enemies of *Spodoptera frugiperda* in North and South America.

Natural enemy		Country	References
Order	Species name		
Hymenoptera	*Rogas vaughani*	Mexico	(Ruíz-Nájera *et al*., 2007)
	R. laphygmae		
	Chelonus insularis		
Diptera	*Archytas marmoratus*		
	Lespesia archippivora		
	Archytas spp.		
Hymenoptera	*Aleiodes laphygmae*	Honduras	(Wyckhuys and O'Neil, 2006)
	Campoletis sonorensis		
Hymenoptera	*Cotesia marginiventris*	USA	(Meagher *et al.,* 2016)
	Chelonus texanus)		
	Chelonus insularis		
Diptera	*Archytas marmoratus*		

1.6.4. Cultural control

Cultural control is a long-term strategy and preventative measure whereby the environment of the pest is altered so that it becomes unfavourable and difficult for them to colonise, survive and reproduce (Hill, 1987)

Examples of cultural control practices are intercropping, crop rotation, weeding, application of fertilizer or manure, sanitation practices, pheromone traps (Kendra, 2016; Abrahams *et al*., 2017; Harrison *et al.,* 2019) and adjusting planting dates (Dara *et al.,* 2019). These practices can be applied to suppress *S. frugiperda* numbers.

Kumela *et al.* (2018) reported that 14% of farmers in Ethiopia and 39% in Kenya make use of cultural control methods, for example, maize intercropping and by physically killing pest larvae in their crop fields (Abate *et al.,* 2000). Crop rotation is an effective cultural control method to suppress pest numbers whereby a series of dissimilar crops are cultivated on the same field in consecutive planting seasons (Bullock, 1992; Brankatschk and Finkbeiner, 2015). Crop rotation reduces insect pest numbers by interrupting their reproductive cycles, thereby lowering the build-up of pest numbers over time (Dara *et al.,* 2019). However, the highly polyphagous nature of *S. frugiperda* makes it difficult to incorporate crop rotation as a control strategy to disrupt the lifecycle of this pest. Other advantages of crop rotation include improved soil fertility and suppression of pests, diseases and weeds (Saddiq *et al.,* 2017). Behavioural manipulation practices such as intercropping of plants that deter pests, or non-hosts and trap crops (Pretty and Bharucha 2015, Nielsen *et al.,* 2016) are part of the cultural control methods used to suppress pest numbers in crop fields. Also, intercropping enhances predation and parasitism of insect pests as a result of habitat diversification and the positive effect it has on beneficial insects (Khan *et al.,* 1997).

Another cultural control method, the push-pull strategy, is a method used to manage insect pests (Khan and Pickett, 2008). In the push-pull strategy a repellent crop (push) that is intercropped with the main crop, repels pest insects away from the main crop and attracts them to a trap crop (pull) (Khan and Pickett, 2008; Van den Berg, 2006a). A successful trap crop needs to be preferred over the main crop by the insect pest for the biggest part of the growing season (Hokkanen, 1991). Dead-end crops are plants that are unsuitable for insect pests to survive on, thereby preventing future dispersal to the main crop (Shelton and Badenez-Perez, 2006; Cook *et al*., 2007).

A successful example of a push-pull strategy is in East Africa where Napier grass (*Pennisetum purpureum*) is used as a trap crop for the stem borers *B. fusca* and *C. partellus* (Khan *et al.,* 2001; Van den Berg *et al.,* 2001; Van den Berg, 2003; Khan and Pickett, 2008; Van den Berg, 2006a). Although Napier grass is highly attractive for stem borer moths for oviposition, larval survival on Napier grass is poor (Midega *et al.,* 2005; Van den Berg, 2006a). This strategy therefore results in control of the stem borer infestation in maize fields (Midega *et al.,* 2005). Observations done in maize fields surrounded by Napier grass showed a lower incidence of pests than in maize monocrops (Van den Berg, 2006a).

The climate-adapted push-pull strategy developed by Midega *et al.* (2018) consists of maize intercropped with Greenleaf desmodium (*Desmodium intortum*), used as the push component, and *Brachiaria* cv Mulato II, a drought tolerant grass variety (pull) planted around the maize field (Figure 1.8) (Midega *et al.,* 2018). The data showed 97% less *S. frugiperda* infestation on maize and higher maize grain yields in the climate-adapted push-pull plot compared to the maize mono plots (Midega *et al.,* 2018). Thus, a push-pull strategy can be effective to control *S. frugiperda.*

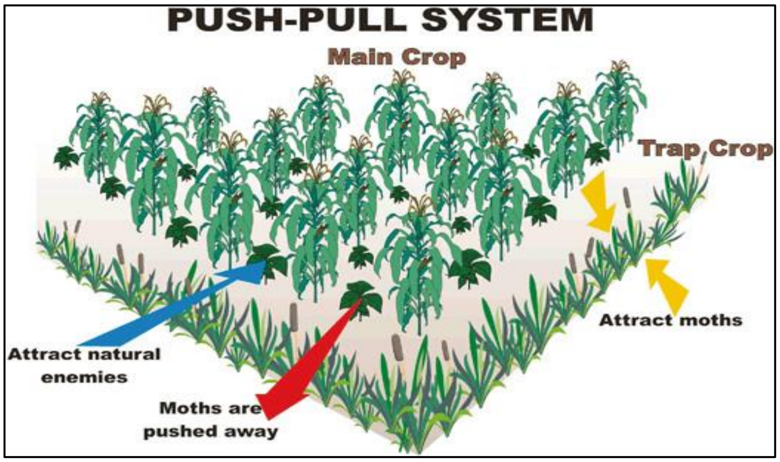


Figure 1.8*:* Diagrammatic presentation of push–pull strategy for insect pest management (Courtesy of Johnnie van den Berg, North-West University, South Africa).

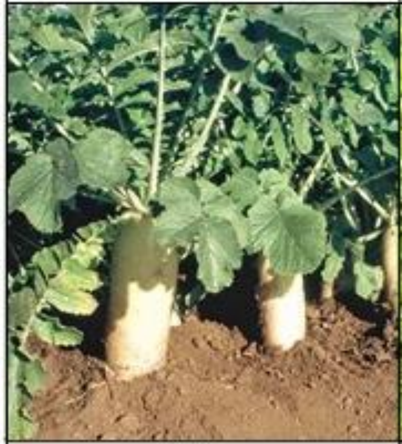
It is important to understand the biology and behaviour of *S. frugiperda* (Montezano *et al.,* 2018). *Spodoptera frugiperda* is capable of feeding on both poaceous and broad-leaf crops as well as weed species (Montezano *et al.,* 2018). This wide host range enables them to feed and survive on other plant species during non-cropping seasons, leading to continuous generations. Therefore, it is important that possible host plants that surround crop fields throughout the year be identified since these may serve as seasonal bridging crops for *S. frugiperda.*

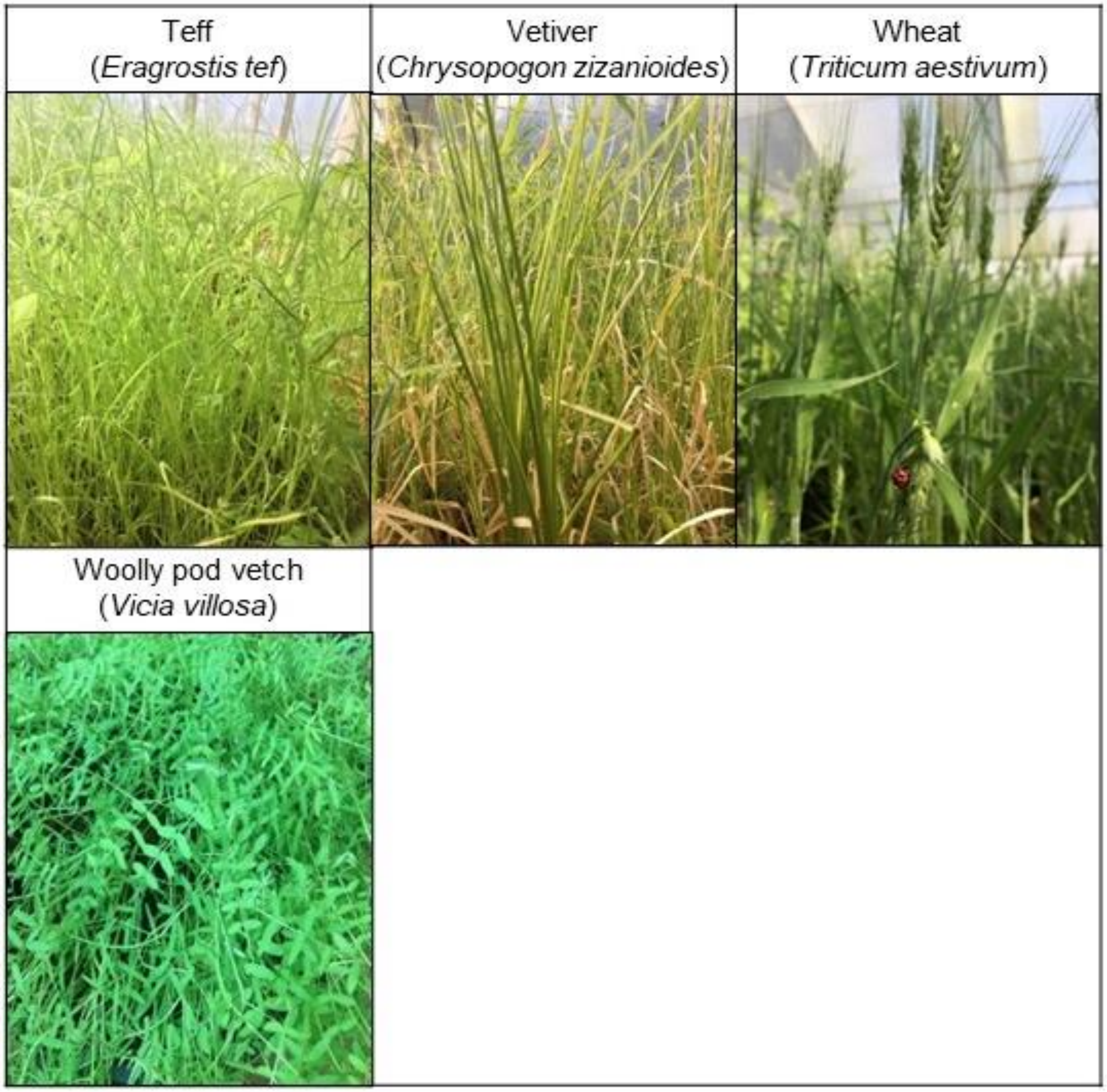
1.7. Potential bridging crops cultivated in South Africa

Several other crop species are planted as part of crop rotation systems or as cover and winter crops, as well as in conservation agriculture systems with maize in South Africa (Du Plessis, 2013). Since several of these crop species have been listed as host plants of *S. frugiperda* (Montezano *et al.,* 2018), their host suitability needs to be assessed.

Table 1.3: Host plants and crops species cultivated as cover or forage crops in maize-based farming systems in South Africa.

Brachiaria/Palisade grass (*Brachiaria brizantha*)	Cowpea (*Vigna unguiculata*)	Cultivated oat (*Avena sativa*)
		
Cultivated radish (*Raphanus sativus*)	Panicum grass/ Guinea grass (*Panicum maximum*)	Forage sorghum (*Sorghum bicolor* ssp. *arundinaceum*)
		
Grain sorghum (*Sorghum bicolor* ssp. *bicolor*)	Groundnut (*Arachis hypogaea*)	Indian mustard (*Brassica juncea*)
		

Japanese radish (*Raphanus sativus* var. *longipinnatus*)	Kikuyu (*Pennisetum clandestinum*)	Lucerne/Alfalfa (*Medicago sativa*)
		
Maize (*Zea mays*)	Napier (*Pennisetum purpureum*)	Potato (*Solanum tuberosum*)
		
Pumpkin (*Cucurbita maxima*)	Rice (*Oryza sativa*)	Soybean (*Glycine max*)
		



The crop species listed in Table 1.3 which are reported as larval host plants for *S. frugiperda,* are also listed in Table 1.4 (Montezano *et al.,* 2018). There were no reports of Brachiaria, Indian mustard, Japanese radish, Napier, Panicum grass, teff, Vetiver and woolly pod vetch as larval host plants for *S. frugiperda.* Napier grass (Khan and Pickett, 2008; Van den Berg, 2006a; Finch and Collier, 2012).

Vetiver grass (Van den Berg *et al*., 2006b) and Brachiaria grass (Khan *et al*., 2016; Cheruiyot *et al.,* 2018) are successfully used as trap crops in maize fields for lepidopteran stemborers. Napier has already been described as a trap crop for *S. frugiperda* in a push-pull system in maize in Kenya. With the wide host plant range of *S. frugiperda* it is possible that Brachiaria, Indian mustard, Japanese radish, Panicum grass, teff and woolly pod vetch could serve as larval host plants. *Spodoptera frugiperda* feeds on five other *Brassica* species and varieties, such as rape, bore cole, broccoli, cabbage and field mustard, therefore, increasing the likelihood of Indian mustard also serving as a host plant. There is a high likelihood that Panicum Mombasa grass is also a larval host plant for *S. frugiperda*, because five other Panicum species, (*Panicum dichotomiflorum, Panicum laxum, Panicum miliaceum* and *Panicum virgatum*) has already been recorded as larval host plants (Luginbill, 1928; Montezano *et al.,* 2018). Japanese radish belongs to the same genus and species as cultivated radish, with only the variety that differs. It is therefore is highly likely that Japanese radish could serve as a larval host for *S. frugiperda,* since several reports of this pest on cultivated radish have been made (Biezanko *et al.,* 1974; Pastrana, 2004; Casmuz *et al.,* 2010; CABI, 2019). *Spodoptera frugiperda* larvae feed on a species belonging to the same genus as woolly pod vetch, the fava bean (*Vicia faba*), which makes woolly pod vetch a possible larval host plant (Biezanko *et al.,* 1974; Pastrana, 2004; Casmuz *et al.*, 2010).

Table 1.4: Crops listed as larval host plants for *Spodoptera frugiperda*. All these host plants were reported from the USA and South American countries, notabely Brazil.

Larval host plant species	References
Cowpea (*Vigna unguiculata*)	Luginbill (1928), Labrador (1969), Heppner (2007), Casmuz *et al.* (2010), CABI (2017)
Cultivated oat (*Avena sativa*)	Luginbill (1928), Silva *et al.* (1968), Labrador (1969), Biezanko *et al.* (1974), Pastrana (2004), Heppner (2007), Angulo *et al.* (2008), Casmuz *et al.* (2010), CABI (2017)
Cultivated radish (*Raphanus sativus*)	Biezanko *et al.* (1974), Pastrana (2004), Casmuz *et al.* (2010), CABI (2017)
Forage sorghum (*Sorghum bicolor* ssp. *arundinaceum*)	Boregas *et al.* (2013)
Grain sorghum (*Sorghum bicolor* ssp. *bicolor*)	Luginbill (1928), Bachini (1966), Silva *et al.* (1968), Labrador (1969), Biezanko *et al.* (1974), Pastrana (2004), Heppner (2007), Angulo *et al.* (2008), Vázquez-Moreno (2009), Casmuz *et al.* (2010), Silvie *et al.* (2010), CABI (2017)
Groundnut (*Arachis hypogaea*)	Luginbill (1928), Silva *et al.* (1968), Labrador (1969), Biezanko *et al.* (1974), Pastrana (2004), Heppner (2007), Angulo *et al.* (2008), Casmuz *et al.* (2010), CABI (2017)
Kikuyu grass (*Pennisetum clandestinum*)	Pastrana (2004), Casmuz *et al.* (2010), CABI (2019)
Lucerne/Alfalfa (*Medicago sativa*)	Luginbill (1928), Silva *et al.* (1968), Labrador (1969), Biezanko *et al.* (1974), Pastrana (2004), Heppner (2007), Angulo *et al.* (2008), Casmuz *et al.* (2010), CABI (2017)
Maize (*Zea mays*)	Luginbill (1928), Silva *et al.* (1968), Labrador (1969), Biezanko *et al.* (1974), Pastrana (2004), Heppner (2007), Angulo *et al.* (2008), Casmuz *et al.* (2010), CABI (2017)
Potato (*Solanum tuberosum*)	Luginbill (1928), Silva *et al.* (1968), Labrador (1969), Biezanko *et al.* (1974), Pastrana (2004), Heppner (2007), Angulo *et al.* (2008), Casmuz *et al.* (2010), CABI (2017)
Pumpkin (*Cucurbita maxima*)	Casmuz *et al.* (2010)
Rice (*Oryza sativa*)	Luginbill (1928), Silva *et al.* (1968), Labrador (1969), Biezanko *et al.* (1974), Pastrana (2004), Heppner (2007), Angulo *et al.* (2008), Casmuz *et al.* (2010), CABI (2017)
Soybean (*Glycine max*)	Luginbill (1928), Silva *et al.* (1968), Labrador (1969), Biezanko *et al.* (1974), Pastrana (2004), Heppner (2007), Angulo *et al.* (2008), Casmuz *et al.* (2010), CABI (2017)
Wheat (*Triticum aestivum*)	Silva *et al.* (1968), Labrador (1967), Pretto (1970), Heppner (2007), Angulo *et al.* (2008), CABI (2017)

1.8. Cover crops

The planting of cover crops is a practice that forms part of conservation agriculture (CA) (Dube *et al.,* 2014). SSSA (1997) defined cover crops as “close-growing crops that provide soil protection and soil improvement between periods of normal crop production or between trees in orchards and vines in vineyards”. Cover crops are largely grown in summer and winter between seasons when main-crops are not grown (Roberts *et al.,* 2018). During these off seasons the ground is left bare and exposed to weed growth and erosion (Roberts *et al.,* 2018). Thus, cover crops are grown to suppress weed growth and erosion as well as to improve soil quality (Roberts *et al.,* 2018). Cover crops are not grown for market purposes, but solely to improve physical, chemical, and biological properties of the soil and for grazing (Fageria *et al.*, 2009).

Cover crops can either be leguminous or non-leguminous (Fageria *et al.*, 2009; Roberts *et al.,* 2018; Sharma *et al.,* 2018). Legume cover crops such as alfalfa, vetch, cowpea and peanut formed a symbiotic relationship with bacterial colonies, *Rhizobium***,** in the root system which are able to fix atmospheric nitrogen (N) and convert it to the plant-available form, ammonium (NH4+), which is then available for plants (Smith *et al.,* 1987; Roberts *et al.,* 2018). This can reduce input costs for farmers as legume cover crops reduce the need for inorganic fertilizer application in following cropping season (Roberts *et al.,* 2018). Non-legume cover crops such as wheat are mainly used to reduce nitrate leaching and soil erosion (Fageria *et al.*, 2009; Sharma *et al.,* 2018).

Cover crops are also planted to control weeds, for example, in South Africa cover crops are annually planted to control weeds in vineyards and orchards (Fourie *et al.,* 2005; Fourie, 2010). Most of the cultivated soils in South Africa lack phosphorus (P), an essential nutrient (Dube *et al.,* 2014). In maize production it is the second most important nutrient after nitrogen (Dube *et al.,* 2014). However, if winter cover crops such as grazing vetch (*Vicia darsycarpa*) and oat are planted, decomposition of the residues of these crops increases the P and N contents of soil (Murungu *et al*., 2010).

There are many advantages associated with planting of cover crops. For example, their residues keep the soil cooler, they contribute to soil nutrient management, decayed cover crops enhance soil nutrients and reduction in soil erosion and nutrient leaching. Cover crops also provide potential forage harvest, enhance beneficial insect populations, disrupt disease and pest cycles, reduce weed growth and improve water infiltration and soil nitrogen content (Phatak and Dias-Perez, 2012; Roberts *et al.,* 2018). Disadvantages may include an increase in pest risk, reduction in soil moisture and additional costs for farmers to purchase and manage these crops (Murungu *et al*., 2010; Phatak and Dias-Perez, 2012; Roberts *et al.,* 2018).

1.9. Problem statement

The polyphagous behaviour of *S. frugiperda* provides both challenges and opportunities for its management. Non-crop plants can serve as bridging host species for *S. frugiperda* during off seasons when no maize is cultivated (Montezano *et al.,* 2018). Furthermore, the presence of cover crops in maize-based cropping systems could provide bridging hosts for *S. frugiperda* in these systems, thereby increasing its pest status. In South Africa, conservation agriculture as well as rotation of maize with other crops such as soybean is increasingly being practiced.

Since *S. frugiperda* is polyphagous, they can survive on many different host plant species during off-seasons, which may lead to a build-up of pest numbers and increased pest pressure (Montezano *et al.,* 2018). For example, it was detected in Brazil that *S. frugiperda* infested millet crops during off seasons when maize was not cultivated, and that pest numbers increased during off seasons (Favetti *et al.,* 2017). In the northern parts of North America, *S. frugiperda* larvae are exposed to freezing temperatures during winter months (Nagoshi *et al*., 2012; Nagoshi *et al.,* 2017a). This results in local extinction of this pest until new *S. frugiperda* migrations reach these regions again in the following maize cropping season (Nagoshi *et al*., 2012; Nagoshi *et al.,* 2017a). In Africa, *S. frugiperda* generations are continuous in areas where host plants are continuously available and temperature for survival is favourable (Du Plessis *et al.,* 2018; Early *et al.,* 2018). As a result, higher numbers of *S. frugiperda* occurs during relatively warm winter months, resulting in a build-up in pest populations.

There is currently a lack of information on *S. frugiperda* and its interaction with host plants which might serve as off-season hosts, and the role that cover crops may play in its ecology. Furthermore, certain non-crop hosts, if preferred by *S. frugiperda* moths for oviposition, may serve as trap or pull plant species in pest habitat management systems. While *S. frugiperda* is not a pest on crops such as soybean and forage grass species in Africa, this pest has the ability to infest and develop pest status on these plant species in its region of origin. For these reasons, plant species that are cultivated in Africa and on which *S. frugiperda* larvae can complete its life cycle, need to be identified to improve and innovate pest management strategies, and to assess the likelihood of this pest becoming important on crops other than maize and sorghum in Africa. The strain composition of *S. frugiperda* populations in Africa is unclear (Nagoshi *et al*., 2019) and it is unknown if this species has the same polyphagous host plant range as documented in the Western Hemisphere (Nagoshi *et al*., 2019).

1.10 Objectives

1.10.1 Main objective

The main objective of this study was to evaluate the suitability of various poaceous and broad leaf plant species for *S. frugiperda* larval developmentand fitness.

1.10.2 Specific objectives

i. to evaluate larval development (survival, duration), pupal duration period and pupal mass of *S. frugiperda* reared on different poaceous and broad leaf species.

ii. to determine the fitness (fertility) of *S. frugiperda* moths of which the larvae were reared on different poaceous and broad leaf plant species.

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Chapter 2: Suitability of selected poaceous host plants for development of *Spodoptera frugiperda* larvae.

Abstract

Spodoptera frugiperda (J.E. Smith) (Lepidoptera) is a highly polyphagous pest which damages crops such as maize, sorgum and rice, which all belong to the Poaceae. Allthough many poaceous plants have been reported as hosts of *S. frugiperda*, their suitability for larval development is not known. Moreover, while it is a pest on poaceous plants, some species such as Brachiaria grass are effectively used as a trap crop for its management. In this study, different poaceous species that are cultivated in maized-based agroecosystems in Africa were evaluated for their host suitability for larval development of *S. frugiperda*. The plant species were: maize, Brachiaria grass, oat, Panicum grass, forage sorghum, grain sorghum, kikuyu, Napier grass, rice, teff, Vetiver grass and wheat. Larvae were reared on plant tissue of these species under laboratory conditions and life history parameters were recorded. Larval survival was highest on maize (84%) followed by oat, forage sorghum, rice and grain sorghum, with a survival rate of higher than 70%. Only 22% and 11% of larvae survived on Brachiaria and Panicum respectively. This study is the first to report survival of *S. frugiperda* larvae on Panicum grass and teff (31%). Overall development period from egg hatch to adult emergence was significantly shorter in maize (23.0 days) compared to all other plant species. There was large variation in the fertility of moths of which larvae were reared on the different host plants and mean fertility per egg batch did not differ between host plants. No larvae survived on Napier and Vetiver grass, indicating that these grasses are potential dead-end trap crops in a push-pull system, provided moths prefer to lay eggs on these grasses.

Keywords: larval development, Poaceae, pest management, push-pull system, rice strain, trap crops, teff.

2.1. Introduction

Spodoptera frugiperda (J.E. Smith) (Lepidoptera) is a polyphagous pest which have been reported to feed on 353 plant species (Montezano *et al.,* 2018). Sixty three percent of these reported larval host plants belong to the Poaceae (grass family) (Montezano *et al.,* 2018). Based on their preference for different host plant species, *S. frugiperda* is subdivided into two subpopulations, namely the maize strain and the rice strain (Nagoshi, 2019). The larvae and moths of these strains are however morphologically identical. The maize strain is more likely to occur on maize, sorghum and cotton, whereas the rice strain is typically found on rice, pasture grasses, turf grasses, lucerne and millet (Pashley *et al.,* 1987; Meagher and Nagoshi, 2004; Prowell *et al.,* 2004; Ríos-Díez and Saldamando-Benjumea, 2011; Juárez *et al*., 2014; Dumas, 2015; Murúa *et al.,* 2015; Cock *et al.,* 2017; Nagoshi *et al.,* 2017; Nagoshi *et al.,* 2018; Otim *et al.,* 2018; Kalleshwaraswamy *et al*., 2019). However, the maize strain is also able to feed on rice and the rice strain on maize (Saldamando and Vélez-arango, 2010). Furthermore, Lewter *et al.* (2006) stated that genetic differences occur between the maize strain and rice strain.

Spodoptera frugiperda invaded Africa in 2016 and there is genetic evidence that both the rice and corn strains are present in Africa (Cock *et al.,* 2017; Nagoshi *et al.,* 2017; Nagoshi *et al.,* 2018; Otim *et al.,* 2018). However, in Africa, damage by *S. frugiperda* has largely been recorded only on the preferred host plants of the maize strain, i.e. maize and sorghum (Stokstad, 2017). It seems that the maize strain and interstrain hybrids are predominant in Africa, including South Africa (Nagoshi, 2019). Behaviour of these interstrain hybrids are still not fully understood, but in Africa it appears that these hybrids are attracted to maize strain host plants, since African records of this pest has so far nearly exclusively been on maize and sorghum (Nagoshi, 2019).

Poaceous plant species such as Brachiaria and Napier grass are used in Africa in push-pull strategies to control stemborer species, particularly *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) and *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) (Khan *et al.,* 2001; Van den Berg *et al.,* 2001; Van den Berg, 2003; Cheruiyot *et al*., 2018; Khan *et al.,* 2006; Van den Berg, 2006a; Khan *et al*., 2007), and *S. frugiperda* (Midega *et al.,* 2018). In the Far East and China, where *S. frugiperda* also recently became a major pest of maize (Wu *et al*., 2019), and threatens rice production (Wang *et al*., 2020), Vetiver grass is used as trap crop for *C. partellus* (Lu *et al*., 2015; Lu *et al*., 2019), and may hold potential as trap crop for *S. frugiperda* as well.

It is important to assess the host status of different poaceous plant species that occur naturally or are cultivated in maize-based systems, for development of *S. frugiperda* larvae. This will enable identification of poaceous crop/plant species that may in future become hosts of this pest, and contribute to identification of plant species that can be used as dead-end trap crops in push-pull systems. The aim of this study was to evaluate a range of poaceous species that are cultivated in South Africa, for suitability as larval host plants of *S. frugiperda*. Specific objectives were to: 1) evaluate larval development (survival, larval duration), 2) pupal duration and pupal mass, and 3) to determine the fitness (fertility) of *S. frugiperda* moths of which larvae were reared on different poaceous plant species.

2.2. Materials and Methods

2.2.1. Cultivation of plants

The cultivar names of the 12 poaceous species used in this study are listed in Table 2.1. Plants were grown in 5 l pots in a greenhouse in the summer, fall and winter months (March to August) at ambient temperatures (Figure 2.1). Plants were regularly watered and fertilized with Nutrifeed when needed. No pesticides were applied onto the plants.

Table 2.1: Poaceous plant species evaluated for their suitability as hosts of *Spodoptera frugiperda* larvae.

Common name	Scientific name	Cultivar name
Brachiaria grass	*Brachiaria brizantha*	Marandu
Cultivated oat	*Avena sativa*	Pallinup
Panicum grass	*Panicum maximum*	Unknown
Forage sorghum	*Sorghum bicolor* ssp. *arundinaceum*	PAN 8909
Grain sorghum	*Sorghum bicolor* ssp. *bicolor*	AG Swift
Kikuyu	*Pennisetum clandestinum*	Whittet
Maize (control)	*Zea mays*	DKC 80-10
Napier	*Pennisetum purpureum*	Unknown
Rice	*Oryza sativa*	SAG-1012 short grain
Teff	*Eragrostis tef*	SA bruin
Vetiver	*Chrysopogon zizanioides*	Sunshine
Wheat	*Triticum aestivum*	Duzi

Figure 2.1: Example of plants grown in pots in a greenhouse (Photo by H. van Staden).

2.2.2. Mass rearing of *Spodoptera frugiperda*

Larvae were reared in an insect rearing chamber maintained at 28 ± 1 °C, RH 65 ± 5% and a 14L:10D photoperiod. Larvae were provided with maize leaf tissue every 2nd day until pupation. It is unknown whether the *S. frugiperda* colony used in this study were of the maize, rice or hybrid strain. The population used in this study was formed by mixing four other populations collected at Nelspruit (25°44'18.99"S, 30°99'34.38"E), Malelane, (25°59'40.7"S 31°66"23.7"E), Groblersdal (25°04'54.8"S, 29°23'56.5"E) and East London (33°03'14.00"S, 27°37'50.20"E), during January 2019 in South Africa. The larvae used in these experiments were from the F1, F2, F3, F4, F5 and F6 generation of this laboratory population.

2.2.3. Larval development

Laval development on the different host plant species was evaluated by conducting bioassays. Maize was included as the control treatment.

The experiment was replicated four times for each host plant species, with each replicate consisting of 20 larvae. Larvae were inoculated singly into petri dishes (12 cm diameter). Filter paper was placed in each petri dish and moistened with distilled water to prevent the plant material from desiccating (Figure 2.2). Larvae were supplied with fresh plant material on a daily basis until pupation (Figure 2.3). Larvae were kept in a rearing chamber at 28 ± 1 °C, RH 65 ± 5% and 14L:10D photoperiod.

The number of larvae that survived until pupation was recorded as well as the number of days in the pupal phase, sex and pupal mass. Sex was determined using the generalized description provided by Butt and Cantu (1962) and pupal mass was determined by means of an analytical balance.

The following life history parameters were used as indicators of the suitability of the different plant species as larval hosts, as suggested by Meagher *et al.* (2004): percentage survival, larval duration (number of days), pupal mass (grams), pupal duration (number of days) and the overall combined duration of the larval and pupal periods (number of days).

Figure 2.2: A 90 mm (diameter) plastic petri dish with filter paper placed inside, and a spray bottle filled with distilled water, used to rear *S. frugiperda larvae* on plant material.

Figure 2.3: A fifth-instar *S. frugiperda* larva in a petri dish with moist filter paper and fresh maize foliage (Photo by H. van Staden).

2.2.4. Ovipositional fitness

For each host plant, five moth pairs (male and female) (replicates) were put into plastic containers (12 cm diameter x 10 cm high) (Figure 2.4). The top of the container was covered with gauze and a rubber band to hold the gauze in place. A piece of plant material of the respective host plants were placed inside each container to serve as a stimulus for oviposition. A piece of cotton wool with a sucrose solution was placed inside the container as energy source for moths.

The containers were checked daily for the presence of eggs on the surfaces of objects incuding the plant material for the entire lifespan of the moth. Egg batches were collected and placed into small aerated plastic containers (52 mm high and 30 mm in diameter), which were kept in a glass desiccator (150 mm diameter) (Figure 2.5). The RH in the desiccator was maintained at 70 ± 5% using a potassium hydroxide solution according to the method of Solomon (1951). The desiccators were kept in the same rearing chamber as described above in the larval development experiment until neonates hatched from the eggs. The numbers of eggs per batch were not determined due to difficulties in doing this with the multi-layered batches and because handling of batches could injure eggs. Instead, the numbers of larvae that emerged were determined for each egg batch.

Figure 2.4: *Spodoptera frugiperda* moth pair inside a 12 cm diameter plastic container with Kikuyu grass foliage and sucrose solution (Photo by H. van Staden).

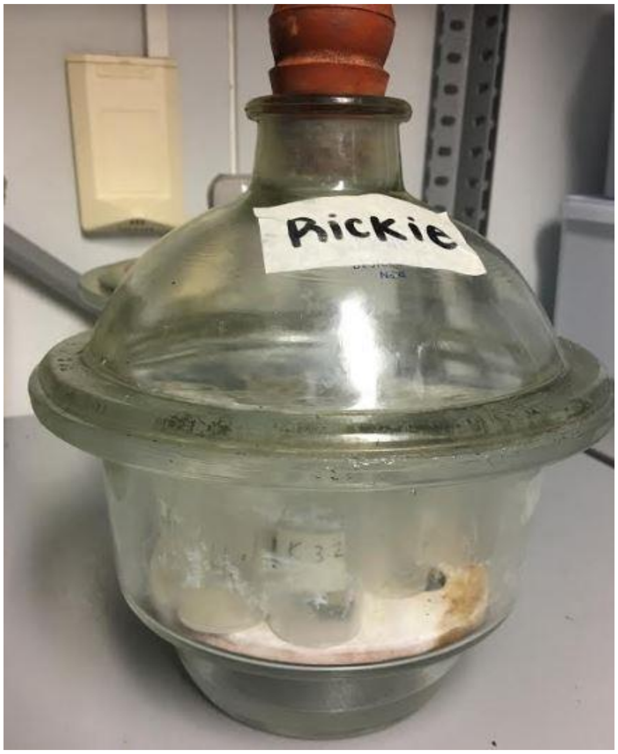

Figure 2.5: Desiccator filled with 46 g Potassium hydroxide dissolved in 100 ml water, to maintain the correct humidity for *S. frugiperda* eggs that were kept inside the smaller plastic containers (Photo by H. van Staden).

2.2.5. Data analysis

The response variable, survival, followed a binomial distribution since the only outcomes were either dead or alive. Data on survival were compared by means of binomial distribution tests. Bonferroni correction was used to adjust for multi means comparisons. Data on mean development times of larvae and pupae and mean pupal mass, were not homogenuous (Levene's test), and were analysed by means of Welch's ANOVAs followed by unequal Tukey post hoc tests. Data from moth pairs that did not produce eggs, were excluded from calculations and analysis of mean fertility. Data on mean fertility met the assumtions of normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test) and were analysed by means of oneway ANOVA, followed by an unequal Tukey post hoc test. All statistical analyses were done using Statistica Version 13.3 (TIBCO software Inc., 2017).

2.3. Results

2.3.1. Larval development

Larval survival was highest on maize (84.0%), while no larvae survived on Napier and Vetiver grass (Table 2.2). Significantly longer development times were recorded on wheat, kikuyu, teff, Brachiaria and Panicum grass (Table 2.2). There were, however, no significant difference in mean larval survival between maize, oat, forage sorghum, rice and grain sorghum. The mean percentage larval survival on Panicum grass (11.0%) was significantly lower than on maize, oat, forage sorghum, rice, grain sorghum, wheat, kikuyu- and teff grass, but larval survival on Brachiaria (22.0%) and Panicum grass did not differ significantly.

The duration of the larval development period ranged between 15.0 days on maize to 21.0 days on Brachiaria (Table 2.2). Larvae were able to develop and complete their development on all the poaceous species evaluated, except on Napier and Vetiver (Welch's $F_{9;123.47}$=92.55; P<0.001). The shortest larval development periods were recorded on maize (15.0 days) and oat (16.0 days), with no significant difference in development period of larvae between these crops. There were, however, also no significant difference in the mean development time of larvae reared on oat and grain sorghum (Table 2.2). Larval development time on rice, teff, wheat, kikuyu, Panicum grass and Brachiaria were significantly longer, compared to maize, oat and grain sorghum.

The mean mass of pupae from larvae that were reared on the respective plant species differed significantly (Welch's $F_{9;133.76}$=62.81; P<0.001). Pupae of larvae reared on maize and rice were heaviest (Table 2.2). The pupal mass of larvae reared on oat, forage sorghum, grain sorghum, wheat and kikuyu did not differ significantly. There was also no significant difference in pupal mass of larvae reared on oat, wheat, kikuyu, Panicum grass, teff and Brachiaria (Table 2.2).

The duration of the pupal period differed significantly (Welch's $F_{9;123.38}$=11.96; P<0.001) between the different treatments. The shortest pupal development period was recorded for those of which larvae fed on maize (8.0 days) and the longest for larvae that fed on teff (9.0 days) (Table 2.2). Pupal duration of larvae fed on maize, oat, wheat, Brachiaria and Panicum grass did, however, not differ significantly. There was also no significant difference in pupal development period from larvae fed on between oat, forage sorghum, grain sorghum, wheat, kikuju, teff, Brachiaria and Panicum grass.

The overall development period to completion of the pupal stage differed between the different host plants (Welch's $F_{9;123.12}$=99.55; P<0.001). Development period was significantly shorter on maize (23.0 days), followed by oat and grain sorghum, with no significant difference in development time on these two species. Significant slower development times were recorded on wheat, kikuju, teff, Brachiaria and Panicum grass (Table 2.2).

Table 2.2: Mean percentage survival, development time, pupal mass, pupal duration as well as larval and pupal duration of *Spodoptera frugiperda* reared on the respective poaceous species.

Crop	#Percentage survival	*Mean larval duration (days ± SE)	*Mean pupal mass (grams ± SE)	*Mean pupal duration (days ± SE)	*Mean overall development period (days ± SE)
Maize	84.0a	15.0 ± 0.1a	0.18 ± 0.00a	8.0 ± 0.4a	23.0 ± 0.1a
Oat	80.0a	16.0 ± 0.2ab	0.15 ± 0.00bc	8.5 ± 0.1b	24.5 ± 0.3b
Forage sorghum	78.0a	18.3 ± 0.2c	0.16 ± 0.00b	8.5 ± 0.1b	26.9 ± 0.3c
Rice	76.0a	18.9 ± 0.2cd	0.18 ± 0.00a	8.0 ± 0.1a	26.8 ± 0.3c
Grain sorghum	70.0ab	17.1 ± 0.2b	0.16 ± 0.00b	8.5 ± 0.1b	25.5 ± 0.2b
Wheat	44.0bc	20.1 ± 0.3de	0.15 ± 0.01bc	8.4 ± 0.1ab	28.4 ± 0.4d
Kikuyu	40.0c	20.3 ± 0.3de	0.15 ± 0.01bc	8.9 ± 0.1b	29.3 ± 0.3d
Teff	31.0c	19.7 ± 0.4cde	0.12 ± 0.01c	9.0± 0.2b	28.7 ± 0.4d
Brachiaria	22.0cd	21.4 ± 0.4e	0.11 ± 0.01c	8.3 ± 0.3ab	29.7 ± 0.9d
Panicum grass	11.0d	21.0 ± 0.6de	0.13 ± 0.01c	8.1 ± 0.3ab	29.1 ± 0.9d
Napier	0. e	-	-	-	-
Vetiver	0.0e	-	-	-	-

*Means within columns followed by the same letter, do not differ significantly at P<0.05. (#Bonferroni correction) (*Tukey's Unequal N HSD).

2.3.2. Ovipositional fitness

The mean fertility of moths ranged between 455 neonates that hatched from Brachiaria reared moths to 1045 neonates on maize (Figure 2.6). However, there were no significant differences between the mean fertility of eggs of moths of which larvae were reared on any of the plant species ($F_{8;49}$=1.93; P<0.001). Since larval survival was very low on Panicum grass, the numbers of moths that emerged were too low to get pairs of moths to mate and lay eggs.

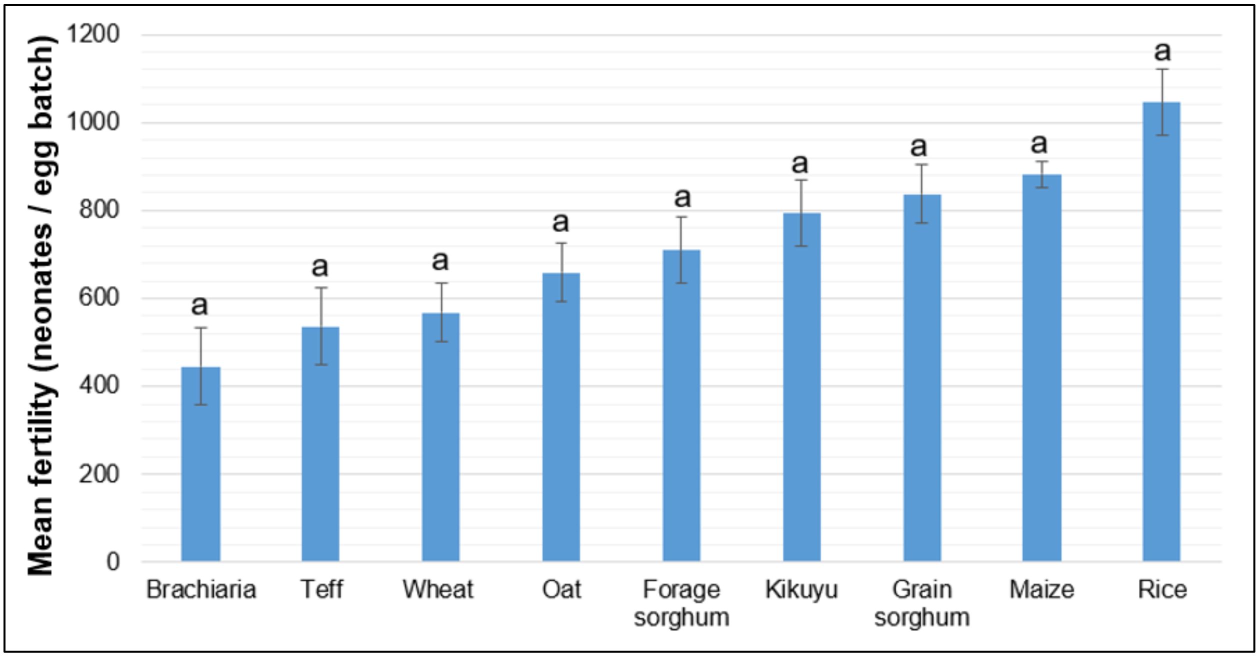

Figure 2.6: Mean fertility (number of neonates) of *Spodoptera frugiperda* moths of which larvae were reared on the respective poaceous species. Different letters above bars indicate significant differences (P < 0.001).

2.4. Discussion

The quantity and quality of a plant's nutrients consumed by larvae affect their survival, development time and mass (Shingleton *et al*., 2008; Güler *et al*., 2015). If *S. frugiperda* larvae consume plant tissue with optimum nutritional value, larval survival will be higher, development times shorter and larval and pupal mass will be higher. In this study, maize was used as control and, based on the above-mentioned life history parameters, it was identified as the most suitable host plant species for larval development of *S. frugiperda*.

Larvae reared on maize had the highest survival rate (84.0%), shortest larval duration (15.0 days) and shortest combined larval and pupal duration (23.0 days). In a study by Sá *et al*. (2009), the duration of the larval period of *S. frugiperda* on maize was also recorded as 15 days. Similar results have been found by Da Silva *et al*. (2017), also affirming maize as the most suitable host plant for the development of larvae. Da Silva *et al*. (2017), who reared *S. frugiperda* on maize, reported a pupal duration period of 8.5 days, and a combined larval and pupal duration of 21.4 days and pupal mass of 0.23 g, considerably higher than the pupal mass recorded in this study. Dias *et al.* (2016) also reported that larvae reared on maize had the highest survival rate (90%). In this study larvae took 15.0 days to complete their development on maize, which is comparable to the 16.7 days reported by Dias *et al.* (2016).

In this study, oat, forage sorghum and grain sorghum were also suitable larval host plant species for *S. frugiperda.* High larval survival was observed on oat (80.0%), forage sorghum (78%) and grain sorghum (70%) and did not differ significantly from maize. Also, in a laboratory study conducted by Dias *et al.* (2016), it was found that larvae reared on black oat and maize both had survival rates of higher than 80%. Dias *et al.* (2016) and Da Silva *et al*. (2017) both identified oat and maize as highly suitable hosts for the development of *S. frugiperda* larvae.

Survival rates of larvae that were reared on rice (76.0%) did not differ significantly from that on maize (84.0%) but the combined larval and pupal development time was slower on rice. *Spodoptera frugiperda* populations are composed of different host strains, i.e., the maize strain, rice strain and interstrain hybrids, distinguished from each other through molecular markers (*COI* and *Tpi* genes) and their host plant preferences (Pashley, 1988; Lu *et al.,* 1994; Nagoshi, 2010; Nagoshi, 2019, Nagoshi *et al.,* 2019). It is presumed that maize strain larvae favour maize, sorghum and cotton whereas the rice strain favours rice, pasture grasses, turf grasses, Bermuda grass, millet and lucerne (Pashley *et al.,* 1987; Meagher and Nagoshi, 2004; Prowell *et al.,* 2004; Ríos-Díez and Saldamando-Benjumea, 2011; Juárez *et al*., 2014; Dumas, 2015; Murúa *et al.,* 2015; Cock *et al.,* 2017; Nagoshi *et al.,* 2017; Nagoshi *et al.,* 2018; Otim *et al.,* 2018; Kalleshwaraswamy *et al*., 2019). The behaviour and host preferences of the interstrain hybrids are unknown, but it seems that they prefer hosts similar to the maize strain (Nagoshi, 2019). Larvae of the maize strain and interstrain hybrids will therefore presumably have a higher survival rate, shorter development time and higher mass when feeding on their preferred host plants. Taking the preference of *S. frugiperda* strains into consideration, it is not surprising that both maize and rice were good host plants for larvae in this study. This can possibly be ascribed to the polyphagous nature of this pest.

Unfortunately, the strain composition of larvae used in this study is not known. Nagoshi

(2019) confirmed the presence of maize strain and interstrain hybrids in Africa, including South Africa. A study by Jacobs *et al*. (2018) identified the presence of both the maize strain and the rice strain at various sites in the Limpopo, Mpumalanga, North West and Gauteng provinces in South Africa. Furthermore, the behaviour of interstrain hybrids are unclear and larval development of these hybrids on rice compared to maize is unknown. Therefore, it is possible that larvae or some of the larvae used in this study were interstrain hybrids which may explain why larval development of *S. frugiperda* larvae reared on rice was almost as good as on maize.

Twenty-two percent of larvae reared on Brachiaria survived, 31.0% on teff and 11.0% on Panicum grass, but no survival was recorded on Napier and Vetiver grass. This is in agreement with results form a study by Dias *et al.* (2016) who reported that larvae reared on Brachiaria had a lower larval survival (73.0%) and longer development time (18 days) compared to those reared on maize.

No reports of Napier grass, Panicum grass, teff and Vetiver grass as larval host plants for *S. frugiperda* has previously been made*.* Teff is the most important grain crop in Ethiopia (Stallknecht *et al.*, 1993). It has a short growing season and is utilized as a grain for both humans and livestock (Stallknecht *et al.*, 1993). In South Africa, teff is mainly cultivated as hay for feed because of its good nutritional qualities during the summer season (Truter *et al.,* 2016). Teff is becoming more popular worldwide for its soil conservation and the soil health benefits it provides in the rehabilitation of disturbed soils (Truter *et al.,* 2016). In this study, teff was identified as a poor larval host plant for *S. frugiperda.* Thus, teff is not a high-risk crop for *S. frugiperda* infestation in South Africa. However, in countries such as Ethiopia, where teff is planted as a staple crop and dominates the landscape, *S. frugiperda* may in future become an important pest on teff.

Panicum grass is a perennial grass species, native to Africa, and is grown in almost all tropical areas worldwide as forage crop (Aganga and Tshwenyane, 2004). It is widely distributed throughout South Africa and mainly cultivated for soil rehabilitation and fodder for animals utilized as hay feed and general grazing for cattle, sheep, goats, horses and game (Ackermann, 2019). The low survival and slow development of *S. frugiperda* larvae reared on Panicum grass showed that this pest poses a low threat to this crop in South Africa. It also has the characteristics to serve as a possible trap crop for *S. frugiperda*. Grasses such as Brachiaria and Napier have successfully been used as trap crops in push-pull systems in maize-based agro-ecosystems in Africa for control of stem borers as well as for *S. frugiperda*. Cheruiyot *et al*. (2018) recommended Brachiaria as a trap crop for *C. partellus* and in the studies by Van den Berg *et al.* (2003) and Van den Berg (2006a) it was concluded that Vetiver grass also has the potential as a trap crop to control this pest. Several studies confirmed the use of Napier grass as a trap crop for stem borers, for example, Van den Berg *et al.* (2001) reported that it is used by resource-poor farmers in South Africa and Khan *et al.* (2001), as well as Van den Berg *et al.* (2003) indicated that it is also used in many African countries. Both Van den Berg (2006b) and Khan *et al.* (2006) confirmed Napier as a trap crop for *C. partellus.* It was also reported that Napier has the potential as a trap crop to control *B. fusca* (Khan *et al*., 2007). Midega *et al*. (2018) pointed out a possible habitat management strategy to reduce *S. frugiperda* infestation in maize fields by combining a Brachiaria trap crop with Greenleaf desmodium as intercrop. The possibility of using Vetiver as a trap crop around paddy rice fields to suppress *C. partellus* numbers has also been suggested by Huq (2000). The low larval survival of *S. frugiperda* on Brachiaria, Napier and Vetiver make these plants ideal to serve as trap crops in a push-pull system. The reason for *S. frugiperda* larvae not surviving on Napier and Vetiver might be explained by the physiology and structure of leaves. Larvae are not able to eat the tough leaves of these plant species, as Van den Berg (2006b) reported structural differences between Napier and maize.

In this study, wheat and kikuyu was identified as average larval hosts for *S. frugiperda* with a survival rate of 44.0% and 40.0% respectively. Larval and pupal development time on wheat (28.4 days) and kikuyu (29.3 days) took longer compared to those on maize (23.0 days). Pupae of larvae that were reared on wheat and kikuyu were smaller than those from maize. Although Da Silva *et al*. (2017) reported that pupal mass of larvae reared on wheat and maize were similar, this was not the case in this study where pupal mass was significantly lower when wheat was provided as food to larvae.

Turf grasses, such as kikuyu, can be grown in different environments such as urban, agricultural fields and managed turf grass, for example golf courses and sod farms (Meagher and Nagoshi, 2004). Luginbill (1928) and Sparks (1979) pointed out that *S. frugiperda* causes substantial damage to turf grasses in the United States of America. Turf grass is known to be attacked by rice strain larvae (Kalleshwaraswamy *et al.,* 2019). Pashley *et al.* (1995) reported that maize strain and rice strain larvae both preferred maize over turfgrass. Taking into account that *S. frugiperda* larvae presumably have a better development on their preferred host plant, it can be inferred that larvae might have a slower development on turfgrass compared to on maize, similar to this study. Under laboratory conditions, development of larvae of both strains reared on rice and turf grass have been reported to be similar (McMichael and Prowell, 1999). However, in the field, only 3% of larvae that occur in rice and turf grass were identified as maize strain (McMichael and Prowell, 1999). It is not very likely that *S. frugiperda* will become a major pest on the wheat and kikuyu in South Africa, as larval mortality on this plant species is high (>50%) and larval and pupal duration periods are significantly longer compared to that on maize. However, this study shows that if *S. frugiperda* moths lay eggs on kikuyu grass, larvae will survive on this crop. A low number of larvae will survive and therefore pose a low threat to kikuyu fields. However, this pest can pose a serious threat to the diary industry, especially in the Eastern Cape in South Africa, where kikuyu is widely cultivated for grazing. If *S. frugiperda* moths lay their eggs on kikuyu and there are no other favourable hosts for this pest in the area, *S. frugiperda* will survive on kikuyu and over a few generations *S. frugiperda* may become a pest on this grass and pose a threat to the diary industry.

Even though fertility, determined as the mean number of neonates that hatched per egg batch, ranged between 445 for Brachiaria and 1045 for rice, there were no significant differences in fertility between the different treatments. In this study, the fertility of female moths of larvae reared on rice was, however, surprisingly high (883 neonates). This can be ascribed to the value of nutrition larvae consumed. Most of the lepidopteran species feed very little as adults and uses stored energy for reproduction (Colasurdo *et al*., 2009). Therefore, nutrients must be acquired by *S. frugiperda* larvae to survive, migrate and reproduce as adults (Colasurdo *et al*., 2009). Taking this into account, data from fitness cost of moths from larvae reared on the respective poaceous crops did not differ significantly, despite the variation in larval development data obtained from this study. To also account for natural variation in fertility of moths, the number of moth pairs, which serve as replications in fertility studies, should be increased. Rearing of FAW in masse on less suitable host plants to ensure a high number of pairs, is however challenging.

2.5. Conclusion

Based on the different life history parameters evaluated in this study, maize, oat, forage sorghum, rice and grain sorghum, were more suitable host planst to *S. frugiperda* larvae than wheat, kikuyu, teff and other grasses. The good performance of *S. frugiperda* on rice in this study, could indicate that most, or all larvae were from interstrain hybrids. It is presumed that larvae will have a better and faster larval development if feeding on their preferred hosts.

The low larval survival rate of *S. frugiperda* on Brachiaria and Panicum grass and no survival on Napier and Vetiver grass highlights the potential of these species as trap crops. However, this will only be the case if the female moths prefer to oviposit on these grasses. Wheat, kikuyu and teff are at low risk of infestation in South Africa as larval development on these crops were slow. However, if the preferred hosts of *S. frugiperda* are not available, this pest may switch to these alternative crops.

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Chapter 3: Suitability of selected broad leaf plants for development of *Spodoptera frugiperda* larvae.

Abstract

Athough *Spodoptera frugiperda* is primarily a pest of poaceous crops such as maize, sorghum and rice, it has a wide host plant range which includes numerous broad leaf plant species. Insecticide application and the cultivation of genetically modified crops are the two main strategies used for management of *S. frugiperda.* There is a need for cost-effective and accessible (e.g. crop rotation and intercropping) alternative control methods for this pest in Africa. The aim of this study was to evaluate suitability of different broad leaf plant species that are cultivated in South Africa as larval hosts for *S. frugiperd*. These plant species were: cowpea, Indian mustard, groundnut, lucern, potato, pumpkin, Japanese radish, soybean and woolly pod vetch. Maize, which is the preferred host of this pest, was included as control treatment. Larvae were reared on plant tissue of these species under laboratory conditions and life history parameters were recorded. All these broad leaf plant species were inferior hosts for larval development, compared to maize. All the broad leaf species evaluated for *S. frugiperda* larval development in this study have the potential to be used in crop rotation, trap cropping and intercropping systems to control this pest. However, the attractiveness of the above mentioned crops for *S. frugiperda* needs to be evaluated. Soybean was the most suitable host for larval development of *S. frugiperda*. This study is the first to report successful larval development on Japanese radish and woolly pod vetch, and, although very low (14%), also on Indian mustard.

Keywords: broad leaf plants, crop rotation, pest managememt, intercropping, soybean.

3.1. Introduction

Broad leaf crops such as cowpea, groundnut, potato and soybean are of global economic importance (CABI, 2020; Pogue, 2002). Although these crops have been reported as host plants of *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), little is known of the host status of these crops for this pest in Africa (Montezano *et al.,* 2018). The major damage caused by *S. frugiperda* to crops in Africa has largely been confined to maize and sorghum (Stokstad, 2017; Nagoshi, 2019). The host status of various plant species that are attacked in the western hemisphere, but which also occur in Africa where they are not attacked, is not fully understood (Montezano *et al.,* 2018).

Different strains (maize strain and rice strain) of *S. frugiperda*, with preference for different host plant species have been reported (Nagoshi, 2019). The maize strain is more likely to occur on maize and poaceous plants while the rice strain occurs mostly on rice, pasture grasses, turf grasses, lucerne and millet (Pashley *et al.,* 1987; Meagher and Nagoshi, 2004; Prowell *et al.,* 2004; Dumas, 2015; Murúa *et al.,* 2015; Cock *et al.,* 2017; Nagoshi *et al.,* 2017; Nagoshi *et al.,* 2018; Otim *et al.,* 2018; Kalleshwaraswamy *et al*., 2019). Nagoshi (2019) reported that the interstrain hybrids of *S. frugiperda*, which dominates throughout Africa, may in future behave differently in terms of host selection than the currently known behaviour of the maize and rice strains of this pest. The reports by Nagoshi *et al.* (2019) that the interstrain hybrid of *S. frugiperda* may in future attack other crops than maize and sorghum, together with the polyphagous nature of *S. frugiperda* makes it a serious threat to crop production in Africa. For example, *S. frugiperda* has progressively become a pest of broad leaf crops such as soybean, in areas where this crop is cultivated in rotation with maize in the Americas (Pitre and Hogg, 1983; Gouin *et al*., 2017). If this were to be the case in South Africa, crop production would be under serious threat, due to the importance of soybean and cover crops in the main grain production region of the country.

The polyphagous nature of *S. frugiperda* makes it difficult to control this pest (Da Silva *et al.,* 2017). Integrated pest management strategies based on biological control, chemical control, host plant resistance and cultural control have been developed against this pest (Assefa and Avalew, 2019). The main control methods used in the Americas are chemical control (e.g. synthetic insecticide sprays) and cultivation of genetically modified Bt maize (Rwomushana *et al.,* 2018). In the Western Hemisphere, these control methods are effective to control S. *frugiperda*, but in Africa these methods may not be sustainable since these control measures are not always available and often too expensive for subsistence farmers in Africa (FAO, 2018). Therefore, there is a need for alternative cost-effective strategies to control *S. frugiperda* in Africa (FAO, 2018). Other agro-ecological practices commonly used in pest management are crop rotation and intercropping (Abrahams *et al*., 2017; Harrison *et al.,* 2019). These practices can be used to control *S. frugiperda* and can be adapted and applied in Africa. Crop rotation is defined as a “system of growing different kinds of crops in recurrent succession on the same field” (Martin *et al*., 1976). Mousavi and Eskandari (2011) defined intercropping as “a multiple cropping system of two or more crops planted in a field during a growing season”. It is furthermore recommended that intercropping and rotation of crops with non-poaceous species such as legumes (e.g. cassava), which are known to repel *S. frugiperda* moths from the main crop, be done (FAO and CABI, 2019).

The aim of this study was to evaluate broad leaf species cultivated in South Africa for their suitability as larval hosts for *S. frugiperda.*

3.2. Materials and methods

Methods and data analyses used to evaluate the suitability of different broad leaf species as host for *S. frugiperda* development were largely similar to those described in Chapter 2.

3.2.1. Cultivation of plants

The cultivar names of the 12 broad leaf species used in this study are listed in Table 3.1. Since maize is the preferred host plant of *S. frugiperda* in Africa, maize was included as control treatment.

Table 3.1: Broad leaf plant species evaluated for their suitability as hosts for *Spodoptera frugiperda* larval development.

Common name	Cultivar name	Scientific name	Family
Japanese radish	Nooitgedacht	*Raphanus sativus* var. *longipinnatus*	Brassicaceae
Cultivated radish	Sparkler	*Raphanus sativus*	Brassicaceae
Indian mustard	Unknown	*Brassica juncea*	Brassicaceae
Groundnut	Opal	*Arachis hypogaea*	Fabaceae
Lucerne/Alfalfa	Aurora	*Medicago sativa*	Fabaceae
Cowpea	Betswit	*Vigna unguiculata*	Fabaceae
Soybean	DM 5953 RSF	*Glycine max*	Fabaceae
Woolly pod vetch	Capello	*Vicia villosa*	Fabaceae
Potato	Mondial	*Solanum tuberosum*	Solanaceae
Pumpkin	Flat White (Boer Ford)	*Cucurbita maxima*	Cucurbitaceae
Maize (control)	DKC 80-10	*Zea mays*	Poaceae

Figure 3.1: Example of plants grown in pots in a greenhouse.

3.2.2. Larval development

Larvae were reared on leaf tissue of the respective broad leaf species in petri dishes, fitted with filter paper, moistened with distilled water (Figure 3.2).

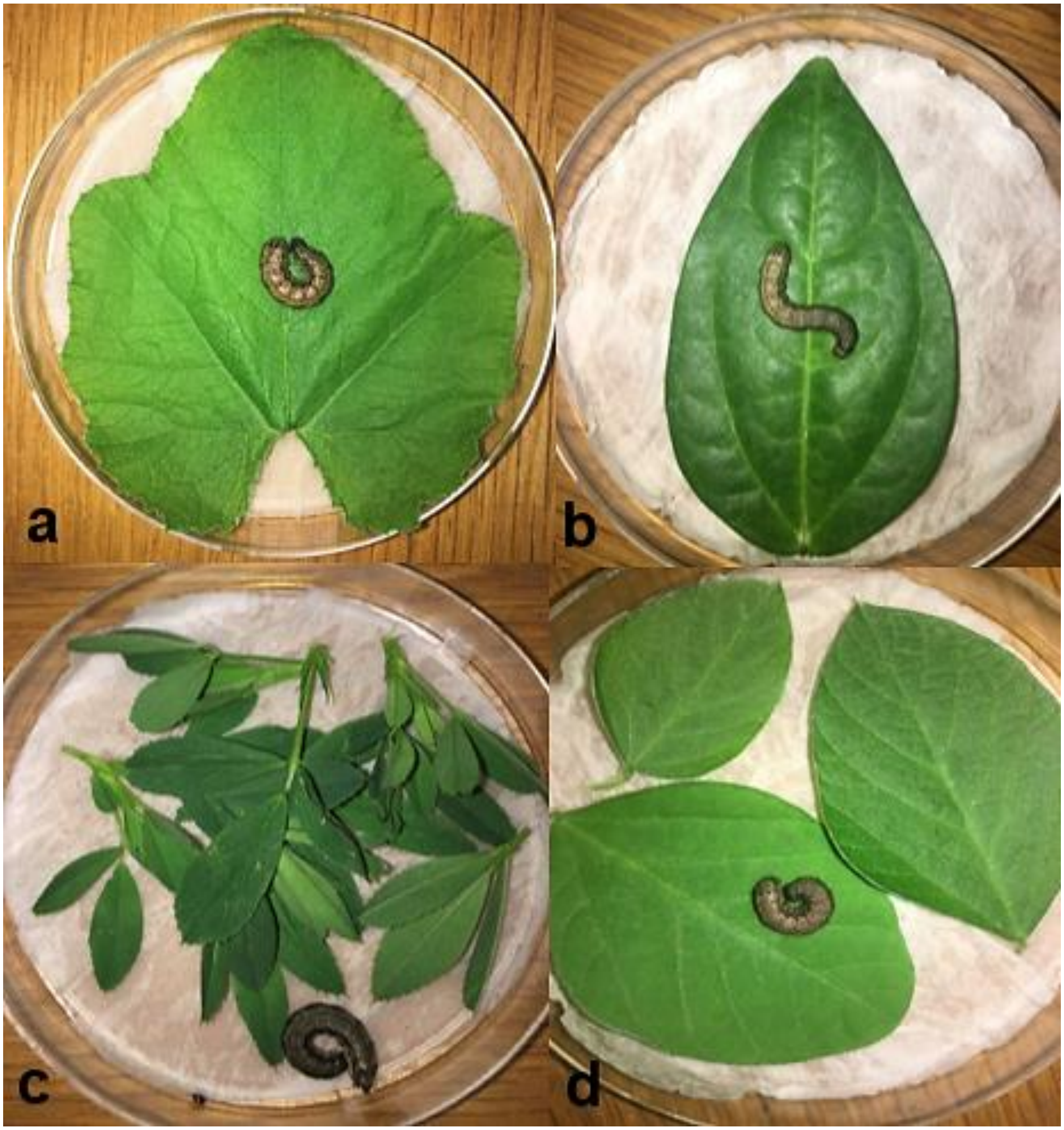

Figure 3.2: A fifth-instar *Spodoptera frugiperda* larva in a petri dish with moist filter paper and fresh foliage of a) pumpkin, b) cowpea, c) lucerne and d) soybean.

3.2.3. Ovipositional fitness

An example of a moth pair in a plastic container with maize foliage, sugar solution and cotton wool to determine their ovipositional fitness (number of neonates) is illustrated in Figure 3.3.

Figure 3.3: *Spodoptera frugiperda* moth pair inside a 12-cm diameter plastic container with maize foliage and sucrose solution (Photo by H. van Staden).

3.2.4. Data analysis

Data on survival were compared by means of binomial distribution tests. Bonferroni correction was used to adjust for multi means comparisons. Data on mean development times of larvae and pupae, mean pupal mass, and mean fertility were not homogenuous (Levene's test), and were analysed by means of Welch's ANOVAs followed by Tukey's unequal N HSD post-hoc test. Data from moth pairs which produced no eggs, were excluded from calculations and analysis of mean fertility. Mean fertility data were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test). The data met these assumtions and were analysed by means of oneway ANOVA followed by an unequal Tukey post hoc test. All statistical analyses were done using the Statistica Version 13.3 (TIBCO software Inc., 2017).

3.3. Results

3.3.1. Larval survival and development

The highest larval survival was on maize (84.0%) and the lowest (14%) on Indian mustard (Table 3.2). Significantly higher numbers of larvae survived on maize, soybean, cultivated radish, cowpea, Japanese radish and potato (Table 3.2). The percentage survival did, however, not differ significantly between soybean, cultivated radish, cowpea, Japanese radish, potato, lucerne, and groundnut. The lowest survival was recorded on pumpkin, woolly pod vetch and Indian mustard, with survival being significantly lower than that on most of the other crops (Table 3.2).

There were significant differences in development time of larvae reared on the respective broad leaf species ($F_{10173.92}$=310.11; P<0.001) (Table 3.2). Development time on maize was significantly shorter than on all the broad leaf crops (Table 3.2). The longest larval development times were recorded on woolly pod vetch, pumpkin, cowpea and it took the longest to complete their larval development on Indian mustard (22.4 – 24.4 days) (Table 3.2). Larval development time on groundnut and lucerne was significantly shorter, compared to cultivated radish, woolly pod vetch, pumpkin, cowpea and Indian mustard, but significantly longer than on maize and soybean.

There were significant differences in pupal mass of larvae reared on the different plant species ($F_{10;172.08}$=16.84; P<0.001). Pupal mass of larvae reared on maize was significantly higher compared to pupal mass of larvae that were reared on any of the broad leaf crops. The mass of pupae from larvae reared on soybean was significantly higher compared to pupae from larvae reared on any of the other broad leaf crops. There was, however, no significant difference in pupal mass of larvae reared on soybean, cultivated radish, cowpea, Japanese radish, potato, lucerne, and groundnut, lucerne, pumpkin, woolly pod vetch and Indian mustard (Table 3.2).

Mean pupal duration of larvae reared differed significantly ($F_{10;172.08}$=16.84; P<0.001) between plant species and ranged from 8.0 to 9.5 days (Table 3.2). The pupal duration on soybean was significantly longer compared to the other crops, followed by pupae from larvae that fed on cowpea. There were, however, no significant differences in the mean pupal duration of larvae reared on maize, potato, lucerne, Japanese radish, groundnut, pumpkin, woolly pod vetch, cultivated radish and Indian mustard (Table 3.2).

There were significant differences in mean overall duration of *S. frugiperda* larval and pupal periods on the respective broad leaf species ($F_{10;174.01}$=286.90; P<0.001) (Table 3.2). A significantly shorter overall duration of the larval and pupal period was recorded for larvae that were reared on maize (23.0 days), compared to between 27.2 and 32.5 days on the other plant species. The combined larval and pupal development period of larvae reared on soybean, groundnut and Lucerne was similar, while there was also no significant difference in this development period when larvae were reared on cowpea, Japanese radish, potato woolly pod vetch, pumpkin and Indian mustard.

Table 3.2: Mean percentage survival, development time, pupal mass, pupal duration as well as larval and pupal duration of *Spodoptera frugiperda* reared on the respective broad leaf species.

Crop	#Percentage survival	*Mean larval duration (days ± SE)	*Mean pupal mass (g ± SE)	*Mean pupal duration (days ± SE)	*Mean overall development period (days ± SE)
Maize	84.0a	15.0 ± 0.9a	0.18 ± 0.00a	8.0 ± 0.0a	23.0 ± 0.1a
Soybean	80.0ab	17.7 ± 0.2b	0.16 ± 0.00b	9.5 ± 0.1c	27.2 ± 0.2b
Cultivated radish	74.0abc	21.2 ± 0.2e	0.13 ± 0.00c	8.3 ± 0.1a	29.5 ± 0.3cd
Cowpea	67.0abcd	22.7 ± 0.2fg	0.14 ± 0.01c	8.5 ± 0.1b	31.2 ± 0.3e
Japanese radish	67.0abcd	22.0 ± 0.2def	0.12 ± 0.01c	8.2 ± 0.1a	30.2 ± 0.3cde
Potato	63.0abcd	21.9 ± 0.2def	0.16 ± 0.01b	8.1 ± 0.1a	29.9 ± 0.3de
Groundnut	60.0bcd	19.5 ± 0.3cd	0.14 ± 0.01c	8.2 ± 0.1a	27.7 ± 0.3b
Lucerne	56.0cd	19.6 ± 0.3cd	0.16 ± 0.01b	8.1 ± 0.1a	27.7 ± 0.3b
Pumpkin	41.0de	22.4 ± 0.3efg	0.13 ± 0.01c	8.3 ± 0.1a	30.7 ± 0.3cde
Woolly pod vetch	26.0ef	22.4 ± 0.4efg	0.14 ± 0.01c	8.3 ± 0.2a	30.7 ± 0.4cde
Indian mustard	14.05f	24.4 ± 0.5g	0.11 ± 0.01c	8.1 ± 0.2a	32.5 ± 0.6e

Means within columns followed by the same letter, do not differ significantly at P<0.05. (#Bonferroni correction) (*Tukey's Unequal N HSD).

3.3.2. Ovipositional fitness

The mean fertility of moths reared on the respective broad leaf species ranged from 388 neonates on potato to 955 neonates on soybean (Figure 3.4). There were no significant differences in mean fertility of *S. frugiperda* reared on any of the plant species ($F_{9;50}$ = 3.00; P<0.001). Fertility of moths from Indian mustard could not be determined since too few moths emerged to make mating pairs.

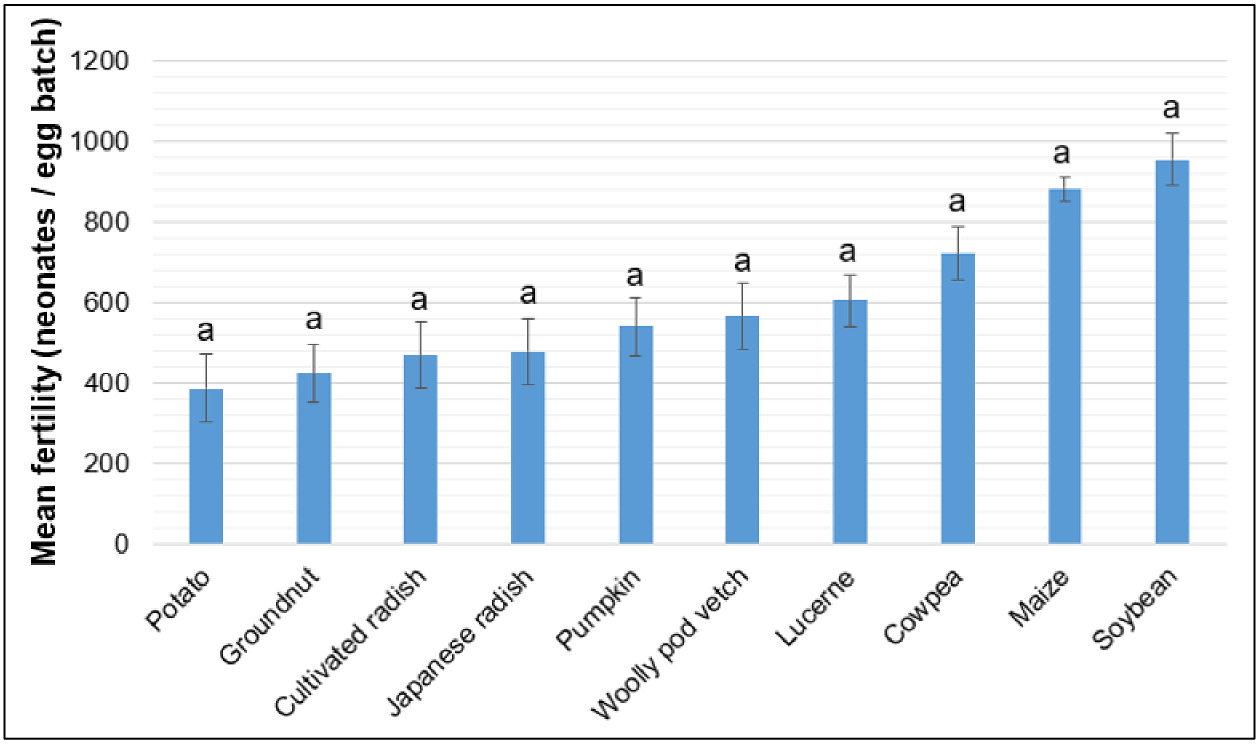

Figure 3.4: Mean fertility of *Spodoptera frugiperda* reared on the respective broad leaf species and maize. Different letters above bars indicate significant differences ($P < 0.001$).

3.4. Discussion

The most suitable broad leaf host plant for larval development of *S. frugiperda* was soybean, on which larval survival and pupal mass were similar to that recorded on maize. Larval survival on cultivated radish was also similar to that on soybean and maize but the larval life cycle was significantly longer than on maize and pupae were significantly smaller. In Brazil, Da Silva *et al*. (2017) also reported that soybean was a good host for larvae of the maize strain of *S. frugiperda* but that its overall life cycle was longer and pupal mass lower, similar to what was recorded in this study. Furthermore, they observed pronounced preferences of 1st instar larvae for soybean and maize and no difference in survival of larvae on soybean and maize under laboratory conditions. Da Silva et al. (2017) furthermore reported that although pupal mass of larvae reared on soybean leaves was lower than on maize, fecundity of moths was similar when moths were evaluated in no-choice tests.

Similar results were found in other studies, for example *S. frugiperda* larvae reared on soybean compared to maize had a longer development time (Pitre and Hogg, 1983), lower pupal mass (Richter *et al.*, 2017) and lower survival rate (Pitre and Hogg, 1983; Richter *et al.*, 2017). In this study, larvae reared on soybean had a pupal period of 9.5 days, comparable to the 9.6 days reported by Da Silva *et al.* (2017). Overall duration of the life cycle of larvae and the pupal stage in this study was 27.2 days, compared to 26.2 days in the study of Da Silva *et al.* (2017). *Spodoptera frugiperda* has progressively become a pest of broad leaf crops such as soybean, in areas where soybean is cultivated in rotation with maize, even though this pest mainly prefers poaceous crops (Pitre and Hogg, 1983; Gouin *et al.*, 2017).

Although the survival of *S. frugiperda* larvae on cowpea was high, the overall development period was longer than on maize, soybean, groundnut and lucerne. Although this was largely due to an extended larval period on this crop, the pupal period was also significantly longer compared to all the other broad leaf crops in this study. Cowpea may therefore have the potential to suppress *S. frugiperda* numbers, due to comparatively lower survival and an increase in development time (Meagher *et al.*, 2004). Meagher *et al.* (2004) found that 51% of maize strain larvae reared on cowpea survived and that 68% of rice strain larvae survived on cowpea, comparable to the levels observed in this study. The development time of larvae reared on cowpea in the study was 22.7 days, which is comparable to the 23.3 days for the maize strain and 20.5 days for the rice strain, reported by Meagher *et al.* (2004). Thus, cowpea is a generally less suitable host plant for *S. frugiperda* larva, and could possibility supress pest numbers (Meagher *et al.*, 2004) as part of a crop rotation system in areas where this pest is endemic.

Groundnut was also identified as a less suitable host plant, although 60% of larvae survived to the pupal stage, pupal mass and duration time from neonate to adult was significantly longer (27.7 days) than on maize (23.0 days). *Spodoptera frugiperda* is only occasionally reported as a pest of groundnut, when preferred Poaceae crops are not available (Lynch *et al.*, 1981). Groundnut is not typically affected by *S. frugiperda*, but if high pest pressures occur in neighbouring fields, excess grass in groundnut fields is not present, or if no other suitable host plants are available, moths will lay eggs on groundnut plants (Campbell and Wynne, 1980).

For a plant species to be considered a host plant of an insect species, the plants should also be acceptable for oviposition by moths. Although oviposition was not evaluated in this study, no reports of Indian mustard, Japanese radish, and woolly pod vetch as larval host plants for *S. frugiperda* has previously been made. Larval survival observed in this study was relatively high on Japanese radish (67%), while only 26.0% survived on woolly pod vetch and 14.0% on Indian mustard.

Charleston and Kfir (2000) showed that another lepidopteran pest, diamondback moth (*Plutella xylostella*) (L.) (Lepidoptera: Plutellidae) had a low larval survival rate when reared on Indian mustard. They suggested the use Indian mustard as a trap crop, since despite low larval survival, moths preferred to oviposit on Indian mustard plants over the other Brassica species they evaluated (Charleston and Kfir, 2000). Cruz and Bamba (2001) also suggested Indian mustard as an effective trap crop for *P. xylostella.* Indian mustard may have the potential to serve as a trap crop for *S. frugiperda,* considering the low larval development results from this study. However, this will only be the case if *S. frugiperda* moths preferably oviposit on Indian mustard plants, over the main crop under field conditions. Eight Brassicaceae crop species, including cultivated radish, were previously reported as larval host plants for *S. frugiperda* (Montezano *et al*., 2018). However, results from this study showed that Japanese radish and Indian mustard should also be included in this list. Larvae that fed on these crops had a survival rate of above 60%, larval development time of 21.2 days and 22.0 days (cultivated radish and Japanese radish, respectively), low pupal mass of 0.13 g and 0.12 g (cultivated radish and Japanese radish, respectively) and combined larval and pupal development times of 29.5 days and 30.2 days (cultivated radish and Japanese radish, respectively). Both cultivated radish and Japanese radish can therefore be regarded as larval host plants on which poor to average performance of *S. frugiperda* can be expected.

In this study, larval survival of 63% was observed on potato, indicating average suitability for larval development. Although several sources report *S. frugiperda* larvae to feed on potato (Biezanko *et al.,* 1974; Angulo *et al*., 2008; Heppner, 2007; Casmuz *et al*., 2010), all of these were from South America and none indicated any field-level presence, injury or economic importance. The low fertility observed in this study together with the lack of reports on infestation of potato by *S. frugiperda* under field conditions, indicate that this crop is a poor host under natural conditions and that the risk of it being attacked is very low.

Lucerne is one of the host plant species of the rice strain of *S. frugiperda* (Juárez *et al*., 2014) and this pest can occur in significant numbers on this crop (Murúa *et al.,* 2009). It is assumed that only maize strain and interstrain hybrids are present and that rice strain is presumably rare or absent in Africa (Nagoshi, 2019). Lucerne crops in South Africa are therefore at low risk of *S. frugiperda* infestation if its preferred hosts are available. Casmuz *et al.* (2010) also reported that only when preferred hosts are not available, does *S. frugiperda* infest lucerne.

In this study, pumpkin was identified as a poor larval host for *S. frugiperda*. Larvae reared on pumpkin had a low survival (41.0%) and long larval and pupal duration of 30.7 days. Harrison *et al.* (2019) suggested an agro-ecological approach to suppress *S. frugiperda* numbers through intercropping of pumpkin with maize (Harrison *et al*., 2019). However, in a study conducted on 791 smallholder maize plots in Zimbabwe, Baudron *et al.* (2019) found higher *S. frugiperda* infestation levels on maize plants in fields where pumpkin was intercropped with maize. Baudron *et al.* (2019) ascribed this to pumpkin plants providing better shelter to moths during the day than maize-only fields, or possibly because pumpkin plants could facilitate easy migration of *S. frugiperda* larvae between maize plants.

Fitness cost of *S. frugiperda* was evaluated by means of fertility of moths from larvae reared on the respective broad leaf species evaluated in this study. Even though the fertility, determined by the number of neonates that hatched from egg batches, ranged from 388 on groundnut to 955 on soybean, fertility did not differ between the different host plant treatments. This is in agreement with observations made by Pitre and Hogg (1983) who reported that the number of eggs laid by moths of larvae that fed on maize and soybean did not differ significantly. Fertility, fecundity and survival rate of the adult stage of an insect is largely affected by the nutritional value of plant consumed by the larval stages of the species. A low nutritional value results in a lower survival rate, fecundity and fertility of the adult stage (Boggs, 2009). Taking this into account, all plants except Indian mustard, provided sufficient nutrition for this pest to reach adult stage, and produce fertile eggs. To also account for natural variation in fertility of moths, the number of moth pairs, which serve as replications in fertility studies, should be increased. Rearing of FAW in masse on less suitable host plants to ensure a high number of pairs, is however challenging.

3.5. Conclusion

Although soybean and cowpea can be considered good larval host plants for *S. frugiperda*, the large-scale absence of this pest from non-poaceous crops in Africa can possibly be explained by the host selection behaviour of the different strains that occur in the Americas and Africa. For a plant species to qualify as an appropriate host, the female moth has to select and lay her eggs on the specific plant. Since the larvae survived on nearly all the broad leaf plant species evaluated in this study, these could in future become hosts of *S. frugiperda* in Africa, if habitat management practices and long-term interaction between the pest and different crop species result in changes in the behaviour of the interstrain hybrids that occur on the continent. All the broad leaf species evaluated in this study, especially Indian mustard, woolly pod vetch and pumpkin, have potential for use in crop rotation and intercropping systems to interrupt the ecology of *S. frugiperda* in maize, provided moths also lay their eggs on these crops.

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Chapter 4: General discussion, conclusion and recommendation

4.1 General discussion and conclusion

Spodoptera frugiperda is a highly polyphagous pest of economic importance in Africa. Since it invaded the continent in 2016 (Goergen *et al.*, 2016), it caused major damage to maize (Rwomushana *et al.*, 2018). Since *S. frugiperda* does not undergo diapause, continuous generations occur throughout the year occur (Nagoshi *et al.,* 2009). Since *S. frugiperda* is a tropical pest that only invades non-tropical areas during summer months when climatic conditions are suitable, it is highly adapted to occur in many regions in Africa. However, cultivation of cover crops and winter crops that are hosts to this pest in South Africa could possibly provide bridging crops for this pest. This would increase its pest status in the country, especially in regions where the broad leaf crop species listed in Chapter 3, are abundant in maize-based agroecosystems. Continuous generations of *S. frugiperda* can occur in Africa where host plants are continuously available (du Plessis *et al*., 2018). Furthermore, in areas where temperatures do not decrease to below the minimum threshold temperatures for pest development, cover crops may provide *S. frugiperda* with continuous food throughout the winter months. This is however not yet the case and will in future be determined by whether or not the interstrain hybrids of *S. frugiperda* in South Africa start to infest non-poaceous crops. This can lead to a build-up in numbers, increasing year after year making it difficult to control *S. frugiperda* (Montezano *et al.,* 2018).

This study showed that Poaceae crops were more suitable hosts than broad leaf crops for the development of *S. frugiperda* larvae*.* Da Silva *et al.* (2017) also reported that poaceous crops was more adequate hosts for *S. frugiperda* larvae compared to broad leaf crops such as soybean. Maize, oat, forage sorghum and grain sorghum were shown to be the most suitable Poaceae hosts and since maize and sorghum are regarded as the preferred hosts of the maize strain, it is highly likely that larvae used in this study were that of the maize strain and/or the interstrain. Maize was by far the most suitable host plant for the development of *S. frugiperda* larvae. Nagoshi (2019) confirmed the presence of both maize strain and interstrain hybrids in Africa after many uncertainties about the strain composition of African *S. frugiperda*. So far, extensive damage by *S. frugiperda* has been recorded on only maize and sorghum in Africa, however, since the behaviour of interstrain hybrids are unknown (Nagoshi, 2019), many other crops cultivated in Africa are at risk of infestation.

The low survival rate and slow development of *S. frugiperda* larvae that fed on Brachiaria and Panicum grass and no survival on Napier and Vetiver indicated the potential of using these grass species in push-pull habitat management systems as trap crops to control this pest. In the only effective push-pull system currently known to successfully control *S.*

frugiperda in maize fields *Brachiaria* cv Mulato II grass is used as a ‘pull’ component or trap crop, and intercropped with Greenleaf desmodium (*Desmodium intortum*), to repel moths from the main crop (Midega *et al*., 2018).

Other habitat management strategies to control *S. frugiperda* are crop rotation and intercropping (Abrahams *et al*., 2017). It has been recommended to intercrop legumes with maize (FAO and CABI, 2019), since maize attracts *S. frugiperda* away from other crops, acting as a pull component, therefore lowering pest pressure in fields where legumes are the main crop. The FAO (2018) recommended intercropping and rotation of maize with non-host plants such as sunflower or beans (e.g. non-hosts or less preferred hosts) to reduce pest infestation in the main crop. Taking this into consideration, maize can be intercropped and rotated with leguminous broad leaf crops (e.g. cowpea, groundnut, lucerne, soybean and woolly pod vetch evaluated for their suitability as larval hosts for *S. frugiperda* in this study) and other non-host plants of *S. frugiperda*. This could lead to reduced invasion by this pest into the respective legume and non-hosts fields. The above-mentioned crops can be cultivated in rotation with crops favoured by *S. frugiperda* such as maize and sorghum that are more prone to be infested by this insect pest, hence to lower population numbers.

There are many winter crops that can possibly serve as bridging crops for *S. frugiperda* in South Africa, which holds the potential to increase its pest status. Favetti *et al.* (2017) reported that millet sustain *S. frugiperda* populations during off-seasons when no maize is cultivated in Brazil. From this study, oat is the only winter crop identified as a suitable bridging crop that could sustain *S. frugiperda* populations in areas in South Africa where winter temperatures allow for larval development. Other winter crops such as wheat, cultivated radish and Japanese radish were less suitable hosts for *S. frugiperda*. Larvae reared on cultivated radish and Japanese radish had a relatively high survival rate of more than 65%. However, larvae had an extended larval and pupal duration when they fed on wheat, cultivated radish and Japanese radish. Thus, cultivated radish and Japanese radish can sustain *S. frugiperda* populations in areas where no maize is cultivated during winter months where temperatures are above the minimum development threshold for this pest.

4.2. Future studies

Further studies should be conducted to elucidate the relationships between the different strains that occur in South Africa and the behaviour of the interstrain hybrid on the host plants evaluated in this study. Studies on the behaviour, specifically host preferences, of interstrain hybrids in Africa should be done in order to identify crops at risk for *S. frugiperda* infestation so that control measures to protect these crops can be developed. Future studies should address the identification of other crops or weed species that might serve as bridging species for *S. frugiperda* during winter months as well as the effect that feeding for more than one generation may have on pest survival and fertility. Future studies should include evaluation of the effect of larval host plant on *S. frugiperda* moth fertility, oviposition and host plant selection. This study serves as a preliminary study for the suitability of *S. frugiperda* reared on the selected poaceous and broad leaf species. Future studies should include a wider range of crop species such as barley, since the cultivation of barley is increasing in South Africa and considerable damage by *S. frugiperda* to barley have been reported in other countries such as Australia. It is also suggested that evaluations are done over two or more generations.

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Appendix A

Declaration of language editing

Language editing statement

To whom this may concern,

I, Prof. Johnnie Van den Berg, hereby declare that the thesis titled: “Host suitability of poaceous and broad leaf plants for Fall armyworm (*Spodoptera frugiperda*) (Lepidoptera: Noctuidae)” by Hanricke van Staden has been edited for language correctness and spelling by the supervisors. No changes were made to the academic content or structure of this work.

J van den Berg

4 May 2020

Prof. Johnnie Van den Berg　　　　Date