Cape Peninsula
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Oviposition and feeding preferences of the groundnut leaf miner (*Bilobata subsecivella*, Lepidoptera: Gelechiidae) on selected host plants under controlled environmental conditions

by

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DECLARATION

I, Muhle Pretty Ndimande, declare that the contents of this dissertation/thesis represent my own unaided work, and that the dissertation/thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

Signed **Date**

ABSTRACT

The groundnut leaf miner (GLM), *Bilobata subsecivella*, is a highly destructive pest of legume crops, particularly groundnut (*Arachis hypogaea*) and soybean (*Glycine max*), but it also infests wild species such as hairy indigo (*Indigofera hirsuta*). However, little is known about how its behavioural preferences influence its spatial distribution and population dynamics. Such information is crucial for informing effective pest control measures, especially within the framework of Integrated Pest Management (IPM), which emphasises ecological understanding as the foundation for sustainable control strategies. This study compared infestation levels of GLM on groundnut, soybean, and hairy indigo; evaluated female GLM oviposition preferences among these three plants; and determined the preferred host plant for GLM larval feeding, using non-choice, two-choice, and three-choice assays. Results showed that all three host plants were suitable hosts for GLM feeding, though the intensity and mining patterns varied. Groundnut displayed broader blotch mines, hairy indigo had primarily linear mines, and soybean displayed intermediate characteristics.

Oviposition trials revealed that soybean was the most preferred host for egg laying; however, it did not support successful larval development due to early defoliation. In contrast, groundnut was the most suitable host for infestation and larval performance. Hairy indigo, though least preferred for oviposition, supported larval development and was the only host on which adult emergence occurred in the second infestation trial. These findings highlight a significant mismatch between oviposition preference and larval performance, underscoring the importance of considering both host selection and developmental success when evaluating host suitability. The observed differences in feeding, oviposition and infestation patterns suggest that host plant suitability is strongly influenced by chemical, structural, and defensive traits. Future research should focus on identifying the specific cues driving oviposition and feeding intensity, as this knowledge could guide sustainable management strategies for GLM in legume cropping systems.

Key words: GLM, infestation, larval feeding, preferred host, oviposition

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LIST OF ACRONYMS

CPUT	Cape Peninsula University of Technology
GLM	Groundnut leaf miner
NRF	National Research Fund
CRF	Consolidated Research Fund
IPM	Integrated Pest management
ha	Hectares
VOC	Volatile Organic Compound
DDT	Dichloro-Diphenyl-Trichloroethane
EC	Emulsifiable Concentration
SC	Suspension Concentration
g/L	Grams per Liter
WSP	Water Soluble Powder
ml/L	Millilitre per Liter
SADAFF	South African Department of Agriculture Forestry and Fisheries
FAO	Food and Agriculture organisations of the United Nations
GSS	Glucosinolates sulfatase
%	Percentage
NS	Not Significant

CHAPTER ONE

INTRODUCTION AND BACKGROUND

1.1 Introduction

Legume crops such as groundnut (*Arachis hypogaea* L.) and soybean (*Glycine max* (L.) Merr.) are among the most important oil seed crops cultivated in tropical and subtropical regions particularly by the resource poor farmers for human consumption (Okello *et al.,* 2010; Murithi, 2019). These crops play a critical role in food and nutritional security due to their rich content of dietary proteins, carbohydrates, fibre, vitamins, and essential minerals, all of which contribute significantly to human health and well-being (Verma *et al.,* 2023). In Africa, groundnut is predominantly cultivated by the smallholder farmers as a cash crop (Janila *et al.,* 2013), while soybean serves as a major source of high-quality protein for both human and livestock consumption. Moreover, soybean is widely used as a key ingredient in the formulation of infant foods (Tukamuhabwa and Oloka, 2016). Despite their nutritional and economic importance, these legume crops are highly susceptible to a wide range of diseases and insect pest infestations, which constrain their productivity and sustainability (Ngiru and Mwongera, 2023).

One of the major insect pests threatening the production of leguminous crops such as groundnut and soybean is the groundnut leaf miner (GLM) (*Bilobata subsecivella*, Lepidoptera: Gelechiidae). Historically, GLM was confined to the Asian continent, where it is considered one of the most destructive pests of both groundnut and soybean (Shanower *et al.,* 1993a). In India, it causes severe damage to groundnut during both the rainy and post-rainy seasons, and it also affects groundnut and soybean across South and Southeast Asia. This pest is classified as oligophagous, with feeding preference limited to leguminous host plants (Shanower *et al.,* 1993a). Under rainfed conditions in India, GLM is regarded as the most significant insect pest of groundnut (Naresh *et al.,* 2017).

In Africa, GLM was first reported in Uganda in 1998 (Epeiru, 2004), and its presence has since been confirmed in several other African countries, including Malawi, Uganda, Kenya, Mozambique, Democratic Republic of Congo, and South Africa (Kenis and Cugala, 2006). In South Africa, the first reported outbreak occurred in the Northern Cape Province during the 1999–2000 cropping season. Remarkably, within that single season, the pest spread rapidly across the entire groundnut production region of the country (Du Plessis *et al.,* 2011). The aggressive spread and infestation of GLM pose a significant threat to the productivity of groundnut and soybean, and by extension, to food and nutritional security across the African continent.

The larvae of GLM represents the most destructive phase of its life cycle in both soybean and groundnut production (Namara, 2015). Larval feeding significantly reduces leaf area, with losses ranging from 34.8 to 179.3 cm^2 per plant (Islam *et al.,*1983). This damage is particularly detrimental as it reduces the plant's photosynthetic capacity by approximately 30% (Shanower *et al.,* 1993b). The resulting decline in photosynthetically active leaf area directly impacts the amount of assimilates available to developing pods during the pod filling stage, ultimately compromising yield potential (Shanower *et al.,*1993b).

Infested groundnut leaves typically exhibit mines on both the upper and lower epidermal surfaces. The larvae initiate feeding as first instars within the leaf epidermis, progressing into the mesophyll tissue to create serpentine mines between the two epidermal layers (Buthelezi, 2015). As the larvae grow, these mines expand from their initial serpentine form to larger blotch-like structures (Chanthy *et al.,* 2010; Buthelezi, 2015). Upon reaching a size too large for the mines, the larvae migrate to the leaf surface where they manipulate the foliage by folding individual leaves or webbing together multiple leaflets using silk to create sheltered feeding sites (Buthelezi, 2015). This behaviour results in leaf browning, curling, and eventual defoliation (Kenis and Cugala, 2006).

In groundnut, infestations by GLM typically begin during the flowering stage; however, the specific physiological or ecological factors that render the crop more susceptible at this stage remain unclear (Buthelezi *et al.,* 2013). Studies investigating oviposition and feeding preferences in other Lepidopteran pests, such as the diamondback moth (*Plutella xylostella*), offer insights that may inform research on GLM. For instance, Newman (2014) investigated the oviposition behaviour of *P xylostella* on six

Brassicaceae host plant species and concluded that host selection is influenced by a variety of factors, including host plant suitability, availability of shelter, and interspecific competition. The study also found that specific chemical compounds such as glucosinolates and saponins, although toxic to many herbivorous insects, were tolerated and metabolised by *P. xylostella*, albeit with negative effects on larval and pupal development. Despite these findings in related species, there is currently a lack of empirical research on the oviposition and feeding preferences of GLM. Understanding these behavioural traits is essential, as it would provide valuable insights into the pest's ecology and inform the development of targeted and sustainable pest management strategies.

1.2. Problem statement and justification

The GLM is a highly destructive pest that infests a range of leguminous crops including groundnut, soybean, and wild leguminous hosts such as hairy indigo (Buthelezi *et al.,* 2013). Larval feeding and mining on host plant leaves result in substantial reductions in the photosynthetically active leaf area, thereby diminishing the translocation of assimilates to developing pods during the critical pod filling stage (Shanower *et al.,* 1993). This physiological impairment ultimately translates into substantial yield losses. Groundnut and soybean are vital legume crops grown across Africa for both human consumption and livestock feed. These crops are particularly important for resource-poor smallholder farmers, who rely on them for food security and income generation. Alarmingly, yield losses of up to 100% due to GLM infestation have been documented in soybean in various countries, including India, South Africa, Uganda, and Mozambique (Buthelezi *et al.,* 2021). As such, GLM represents a growing threat, not only to the production of these crops, but also to food security.

Despite its economic importance, there is limited scientific understanding of the bio-ecology of GLM, particularly with respect to its oviposition and feeding preferences. Moreover, little is known about how these behavioural preferences influence its spatial distribution and population dynamics. Such information is crucial for informing effective pest control measures, especially within the framework of Integrated Pest Management (IPM), which emphasizes ecological understanding as the foundation for sustainable control strategies. This study, therefore, seeks to contribute essential knowledge on the oviposition and feeding behaviour of GLM, which will inform the development of context-appropriate and sustainable management practices.

1.3 Study aim

The aim of this study was to investigate the infestation levels, oviposition and feeding preferences of GLM on selected host plant species under controlled environmental conditions.

1.4 Study objectives

- To evaluate the oviposition preferences of female GLM on groundnut, soybean and hairy indigo.
- To determine the preferred host plant for GLM larval feeding among groundnut, soybean and hairy indigo.
- To compare GLM infestation levels on groundnut, soybean and hairy indigo.

1.5 Hypothesis

- Oviposition and feeding preferences of GLM vary in response to the availability of different host plant species.
- GLM exhibits a preference for soybean for both oviposition and larval feeding.
- Host plant species significantly influence the population dynamics of GLM.

1.6 Thesis Outline

This thesis consists of Six Chapters. Chapter One provides the background and introduction of the study. Chapter Two outlines the literature review of the study. Chapter Three is the general materials and methods used, which is followed by Chapter Four and Chapter Five of results and discussions. Chapter Six provides the conclusions and recommendations of the study.

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CHAPTER TWO

LITERATURE REVIEW

2.1 Introduction

Understanding the biology and behaviour of agricultural pests is an important aspect for developing sustainable and precise pest management strategies. This chapter presents a comprehensive review of the literature on the groundnut leaf miner (GLM), a major pest of groundnut and soybean in Asia and, more recently, in Africa. Originally restricted to the Asian continent, GLM was first recorded in Africa in 1998 and has since been reported in several countries including Uganda, Kenya, Malawi, Mozambique, the Democratic Republic of Congo, and South Africa (Kenis and Cugala, 2006; Buthelezi *et al.,* 2021). Despite regional variations in nomenclature, being referred to as *Aproaerema modicella* in Asia *Aproaerema simplexella* in Australia and *Bilobata subsecivella* in Africa, the species is universally acknowledged for its significant impact on legume production.

The larval stage of GLM causes the most damaging effects by mining leaf tissues and reducing photosynthetic area by up to 30%, thereby limiting assimilate production and compromising pod filling and crop yield (Shanower *et al.,*1993b). Groundnut and soybean are not only important sources of dietary protein and household income but also contribute to soil fertility through biological nitrogen fixation, reducing the need for chemical fertilizers (Savadogo *et al.,* 2017; Chianu *et al.,* 2018). Given their importance, protecting these crops from GLM infestation is crucial for food security and economic resilience in affected regions.

This literature review aims to consolidate current knowledge on the oviposition and feeding behaviour of GLM, with a focus on host plant interactions, environmental influences, and life cycle dynamics. Given the limited species-specific research available, the review incorporates findings from closely related lepidopteran species to provide comparative insights and highlight areas where information is lacking. These biological traits are central to understanding the pest’s population dynamics and predicting outbreak potential, both of which are critical for designing targeted IPM strategies. The review is organised around key thematic areas aligned with the objectives of this study. It begins by examining the biology and host range of GLM, detailing its geographical distribution, preferred host crops, and its status as an agricultural pest. The section on oviposition behaviour synthesises current knowledge on host selection cues, egg-laying preferences, and their broader ecological implications. This is followed by feeding preferences and infestation, focusing on larval feeding patterns, the susceptibility of different crops, and the physiological effects of infestation on host plants. The review also explores environmental influences, with particular emphasis on the role of abiotic factors in shaping the behaviour and population dynamics of the pest. Finally, the review discusses recent technological advancements in pest monitoring, highlighting tools such as the Bio-Leaf app that enhance the precision of foliar damage quantification and support scalable, accurate assessments of pest incidence.

2.2 Importance of Groundnut, Soybean, and Hairy Indigo in Agriculture

2.2.1 Groundnut

Groundnut, commonly referred to as peanut, is an annual leguminous crop belonging to the family Fabaceae. It is extensively cultivated across tropical and subtropical regions due to its agronomic versatility and high economic value (Singh *et al.,* 2013). The plant typically exhibits a prostrate to erect growth habit, with a hairy stem that branches profusely from the base (Savitha *et al.,* 2012). The foliage is composed of pinnately compound leaves with two pairs of oblong leaflets, which are a dark green in colour and exhibit a smooth, glossy texture (Singh *et al.,* 2013). Flowering generally commences 30-40 days after sowing (Ramanatha Rao, 1988). The flowers typically grow on short peduncles emerging from the leaf axils (Savitha *et al.,* 2012). According to Perez-Vichy *et al.* (2019), following successful fertilisation, the flowers give rise to the fruit, which is in a pod, each pod typically contains two to four seeds, which are rich in carbohydrates, proteins and oils, making groundnut an important source for food.

Groundnut is an important self-pollinating annual legume cultivated on over 24 million hectares (ha) globally for its high protein content and the extraction of edible oil (Buthelezi, 2015). It is a nutrient dense crop, rich in essential vitamins, minerals, healthy fats, and proteins, all of which are key dietary components, particularly in resource-limited settings and developing countries (Sharma *et al.,* 2010). Economically, groundnut support the livelihoods of millions of smallholder farmers and contributes to foreign exchange earnings through international trade and export (FAO, 2020). It is used in several sectors to make confections, peanut butter, and oil (Smith and Jones, 2015). Moreover, as a leguminous crop, groundnut improves soil fertility through biological nitrogen fixation, thereby enriching the soil with nitrogen and benefitting subsequent crops in the rotation cycle (Nigam, 2000). The Northwest, Free State, and Northern Cape provinces are the main groundnut producing regions in South Africa. The Northwest province accounts for approximately 40% of national production, followed by the Free State with around 25%, the Northern Cape with about 20%, and Limpopo and Mpumalanga collectively contributing roughly 15% (SADAFF, 2021; Grain SA, 2020).

Groundnut production is hindered by several constraints, most notably diseases and insect pests. Among these, the GLM poses a significant threat, with infestations capable of causing yield losses of up to 100% (Buthelezi *et al.,* 2013; Ibanda *et al.,* 2018). In the absence of natural enemies, severe outbreaks may result in total crop failure (Wightman and Ranga Rao 1993; Buthelezi, 2015). These challenges are further compounded by limited access to high-quality seed, pesticides and fertilisers, which restrict farmers' ability to manage pests effectively and mitigate associated yield losses (SADAFF, 2021).

2.2.2 Soybean

Soybean is an annual herbaceous legume belonging to the family of Fabaceae, cultivated primarily for its protein and oil-rich seeds, which serve a wide array of nutritional, industrial, and agricultural purposes (Namara, 2015). The plant is characterised by a strong taproot system capable of penetrating up to two meters deep (Müller *et al.,* 2020). In addition, this plant has extensive lateral roots spread across the topsoil, improving its ability to absorb water and nutrients (Boerma and Specht, 2004). The soybean stem is typically erect and covered with fine trichomes (hairs), which may offer protection against insect herbivory and environmental stressors. Plant height varies considerably, ranging from 20 to 200 cm, depending on the genotype and environmental factors (Ghosh and Bandyopadhyay, 2019). The soybean plant has trifoliate leaves, which have three leaflets on each leaf. These leaflets have smooth or slightly serrated borders, and they are oval to lanceolate. They usually measure 6 to 15 cm. Although the colour of the leaves varies depending on the type and growing environment, they are typically green (Shurtleff and Aoyagi, 2009).

The flowers are arranged in racemes with each flower having a yellow or white corolla; the fruit is a pod, flat and hairy with seeds being yellow and green (Ghosh and Bandyopadhyay, 2019). It requires a warm and humid climate with a minimum temperature being 10°C, and sensitive to photoperiods (Namara *et al.,* 2019). The growth period for this crop is 90-110 days, flowering period of 15-30 days and seed development, and the period for pod filling and seed development is 30-70 days (Namara *et al.,* 2019). Soybean seeds have a diameter of 5 to 11 mm and are spherical to ellipsoid. They are available in a range of colours, such as yellow, green, brown, black, or mixtures of these. The two large cotyledons on the smooth seed coat provide as the main nutritional supply for the budding seedling (Shurtleff and Aoyagi, 2009). Soybean plants exhibit two distinct growth habits: determinate varieties grow to a specific size and initiate flowering synchronously, whereas indeterminate varieties continue vegetative growth while producing flowers over an extended period (Boerma and Specht, 2004). Soybean is predominantly self-pollinating, with flowers containing both male and female reproductive organs, allowing most fertilization to occur within the same flower (Boerma & Specht, 2004). Although cross-pollination is generally low (1–5%), pollinators such as honeybees and bumblebees can facilitate it, potentially improving pod set and seed yield (Singh *et al.,* 2018). Environmental factors like temperature, humidity, and photoperiod also influence flower opening and pollen viability, affecting the efficiency of both self- and cross-pollination (Namara *et al.,* 2019).

Soybean is believed to have originated in Southeastern China between 4000-5000 years ago (Namara, 2015). It is widely cultivated globally (Li *et al.,* 2018). Soybeans play a significant role in global economy because of their wide range of uses in industrial goods, animal feed, and food (Voora *et al.,* 2024). Soybeans are an essential component of the food business, serving as a primary source of protein and oil (Hartman *et al.,* 2011). They are processed into a variety of products, including edible oil, soy milk, and which satisfy the dietary needs of millions of people globally (Hartman *et al.,* 2011).

Furthermore, soybean meal is an essential component of feeds for both cattle and poultry because it offers a high-quality source of protein that promotes the sustainability and productivity of the agricultural industry (Masuda and Goldsmith, 2009). The crop plays an important economic role in the manufacturing of infant formula, offering a necessary substitute for infants who are allergic to the proteins found in cow's milk or who are lactose intolerant (Merritt and Jenks, 2004). Soy-based infant formula is made from soy protein isolates, which undergo processing to eliminate sugars and other ingredients, so leaving them appropriate for babies with certain dietary requirements (Merritt and Jenks, 2004). Soybean is considered as a source of income for farmers and a non-traditional export crop in Uganda (Namara, 2015). Furthermore, it enhances soil characteristics through leaf shedding, conservation of water, and the enrichment of nitrogen via biological nitrogen fixation, which can mitigate insect accumulation when incorporated into crop rotations (Namara, 2015).

2.2.3 Hairy Indigo

Hairy indigo is a leguminous plant with numerous applications in agriculture and a major economic impact since it enhances soil health. This species is particularly valued in South Africa for its contributions to environmentally friendly farming methods and its flexibility in growing environments (Peters *et al.,* 2003). According to the FAO (2013), hairy indigo is an herbaceous legume that is widely distributed inAustralia, tropical Asia, the Indian subcontinent, and Africa. It is currently naturalised in many regions of the world, including the Americas, after being extensively introduced as a cover crop and fodder plant. Given its extensive adaptation to many soil types, it has the potential to both compete with and out-compete the local flora. Hairy indigo is a free-seeding annual that can swiftly spread and naturalize in appropriate settings without the need for special Rhizobium needs (FAO, 2013).

The genus *Indigofera*, which includes hairy indigo is the largest within the family of Indigofereae and comprises over 700 species distributed across tropical and subtropical regions (Puy *et al.,* 2002). Hairy indigo grows upright and bushy, usually to a height of one to two meters. This perennial plant or herb grows well in tropical and subtropical climates. The plant grows best on well drained soils and is frequently found in disturbed areas, open forests, and grasslands, because of its sturdy growth habit, it's a useful species in agroforestry systems for cover crops and soil stabilization (Duke, 1981; Mullen *et al.,* 2003).

Morphologically, hairy indigo is characterized by its hairy stems and leaves, from which it derives its specific epithet. The leaves are pinnately compound, typically comprising 5 to 13 leaflets that are oblong to lanceolate, each measuring 2 to 6 cm (Mullen *et al.,* 2003). The leaflets have entire margins and are covered with fine hairs, giving them a soft texture. The stems and branches are also densely pubescent, contributing to the plant's overall hirsute appearance (Polhill, 1990; Smith, 1994).

Despite flowers being produced all year round, they are abundant in the wet season. Insects, especially bees, pollinate the flowers because they are drawn to their bright colours and nectar (Verdcourt, 1979; Polhill, 1990). Hairy indigo reproduces by both vegetative and seed methods. Small, cylindrical pods, measuring between 2 and 4 cm in length and heavily hairy, are produced by the plant. The smooth, kidney-shaped seeds are found in numerous pods. Dehiscence, in which ripe pods split open to release the seeds, is the main method of seed distribution (Mullen and colleagues, 2003).

In South Africa, hairy indigo commonly grows in the provinces of KwaZulu-Natal, Limpopo, and Mpumalanga (Smith, 1994; Van Wyk and Gericke, 2000).The high temperatures and well-drained soils found in these regions are ideal for the plant's growth, hairy indigo is a good option for farmers looking for low-maintenance, resilient crops because of its adaptability to a variety of environmental conditions (Smith, 1994; Van Wyk and Gericke, 2000). According to Cook *et al.* (2005), hairy Indigo is considered both a wild and cultivated genus, depending on the species and intended use with good adaptability and the plant is a great source of feed for animals because of its high protein content and palatability, especially in the dry season when other forage resources are limited.

These include the Central Bushveld, Lowveld, Mopane Bioregions, Drakensberg Foothill, Coastal Region, Savanna Group, and Northern Mist belt (Malan, 2005). This quality is essential for preserving the health and productivity of cattle, which supports the agricultural economy in areas where livestock production is the primary source of income (Mullen *et al.,* 2003). Its rapid regeneration following grazing or cutting also guarantees a steady and sustainable supply of fodder (Malan, 2005). Enhancement of soil and prevention of erosion are two other important benefits for hairy indigo. As a legume with a symbiotic relationship with Rhizobium bacteria, it can fix atmospheric nitrogen, enriching the soil with essential nutrients and reducing the need for synthetic fertilizers (Graham and Vance, 2003). Crop rotation and inter-cropping systems depend on this nitrogen-fixing ability since it improves soil fertility and fosters the growth of succeeding crops (Graham and Vance, 2003). Additionally, the plant's wide root system aids in stabilizing the soil and halting erosion, especially on soils that are sloped or degraded (Duke, 1981). Hairy indigo plays an important role in the regional economy and traditional medicine. Different plant components are utilized as folk remedies in different parts of South Africa to treat wounds, skin diseases, and stomach problems. These ethnobotanical uses highlight plant's cultural value and provide communities who gather and sell therapeutic herbs with an additional source of income (Smith, 1994).

2.3 Biology and Ecology of GLM

2.3.1 Taxonomy and identification

Bilobata subsecivella (Zeller, 1852) belongs to the order Lepidoptera and the family Gelechiidae. It is known by different names across its geographic distribution: *Bilobata subsecivella* in Africa, *Aproaerema modicella* in Asia, and *Aproaerema simplexella* in Australia. Taxonomic classification of GLM has undergone several revisions, with various synonyms historically assigned to the species. Based on the consultations with the Lepidopteran expert Dr K. Sattler from the Natural History Museum (Sattler, 2015, pers. comm.) and supported by DNA and morphological analyses (Bailey 2007; Van der Walt *et al.* 2008; Buthelezi *et al.* 2012), the African, Indian, and Australian populations are proposed for classification as follows:
Bilobata Vári, 1986

Biloba Janse, 1954, nom. praeocc.

Bilobata subsecivella (Zeller, 1852)

Gelechia (Brachmia) subsecivella Zeller, 1852

Gelechia simplexella Walker, 1864, syn. nov.

Xystophora modicella Deventer, 1904, syn. rev. (Synonymized with *G. (B.) subsecivella* by Meyrick, 1925: 111 but subsequently recalled from synonymy).

Anacampsis simplicella Meyrick, 1904 (An unjustified emendation of *G. simplexella* Walker).

Anacampsis nerteria Meyrick, 1906 (Synonymized with *G.* (*B.*) *subsecivella* by Meyrick, 1925: 111).

2.3.2 Lifecycle and developmental stages

The life cycle of GLM consists of four distinct developmental stages: egg, larva, pupa, and adult, with the duration of each stage influenced by environmental conditions such as temperature and humidity (Shanower *et al.,*1993b; Buthelezi, 2015). The adult female lays eggs on the undersides of host plant leaflets, stems, and petioles, with fecundity ranging between 87 and 473 eggs per female, depending on environmental conditions (Kenis and Cugala, 2006; Buthelezi, 2015). Under optimal field conditions, eggs hatch within three to four days, but at lower temperatures, the incubation period ranges from six to eight days (Namara, 2015; Buthelezi, 2015).

Upon hatching, GLM larvae mine the leaf tissues, consuming mesophyll cells between the upper and lower epidermis. This stage, which causes the most significant damage to host plants, lasts between nine to 28 days, depending on temperature and humidity (Kenis and Cugala, 2006). Pupation occurs within the webbed leaflets of the host plant and is completed within three to 10 days under room temperature conditions, requiring an accumulated 72-degree days (Shanower *et al.,* 1993b; Buthelezi, 2015). The emergence of adults marks the completion of the cycle, which may take between 15 and 28 days in warm climates but can extend to 37 to 45 days in cooler environments. Under extreme conditions, where temperatures drop to 15°C, the life cycle may be prolonged up to 80 days, with lower egg production and reduced larval survival (Ranga Rao and Rameshwar Rao, 2013). In India it has been noted that the longevity of female moth is 17 days with an oviposition period of 11 days, while the longevity for males 2–7 (Kapadia *et al.* 1982).

The number of generations per growing season varies with climate and geographical location. In India, GLM is reported to complete between two and seven generations annually, while in South Africa, two generations occur per season, with each lasting 28 to 30 days (Buthelezi *et al.,* 2017; 2021). The pest's ability to complete multiple generations per season contributes to its high reproductive potential and rapid population buildup in favourable environments, making it a persistent threat to legume production.

2.3.3 Geographic distribution and spread

Groundnut leaf miner is geographically distributed across South and Southeast of Asia, Africa, and Australia, with its range expanding in recent decades. In Asia, the pest is prevalent in India, Pakistan, China, the Philippines, Indonesia, and Sri Lanka (Kenis and Cugala, 2006). In India, it has been recorded in multiple states, including Andhra Pradesh, Gujarat, Karnataka, Madhya Pradesh, Maharashtra, Odisha, Punjab, Rajasthan, Tamil Nadu, and West Bengal (Nandhini *et al.,* 2024). In Africa, GLM was first reported in Uganda in 1998, and has since spread to Malawi, Kenya, Mozambique, the Democratic Republic of Congo, and South Africa (Kenis and Cugala, 2006; Buthelezi *et al.,* 2021). The first detection of GLM in South Africa occurred during the 1999–2000 growing season, after which the pest established itself in all major groundnut-producing regions (Du Plessis *et al.,* 2011).

In Australia, GLM has been reported in Western Australia, the Northern Territory, Queensland, New South Wales, Victoria, Tasmania, South Australia, and Norfolk Islands. It has also been reported in New Zealand (Buthelezi *et al.,* 2021). Its continued expansion across multiple continents highlights its high dispersal potential and adaptability to diverse agroecological zones, necessitating comprehensive surveillance and management strategies.

2.4 Damage Caused by GLM

The larval stage of GLM is the most destructive, as the larvae mine leaf tissues, significantly reducing photosynthetic efficiency and overall plant productivity. Early instars create narrow, serpentine mines between the epidermal layers, which later develop into larger blotches as the larvae grow and consume more leaf tissue (Okello *et al.,* 2016). As the larvae mature, they transition to external feeding, where they fold individual leaflets or web multiple leaves together with silk, forming shelters that protect them from predators and environmental stressors (Buthelezi *et al.,* 2021).

The characteristic injury symptoms of GLM infestations include distorted, blotched leaves with visible mining trails, webbed or folded leaflets, and in severe cases, early leaf senescence and defoliation. This reduction in the photosynthetically active leaf area may result in up to a 30% decline in photosynthetic capacity, ultimately affecting biomass accumulation, pod development, and overall yield (Shanower *et al.,* 1993a). Groundnut and soybean crops are particularly vulnerable towards the flowering stage, with severe infestations leading to stunted growth, reduced pod set, and economic yield losses (Shanower *et al.,* 1993b).

In extreme cases, where GLM populations reach outbreak levels, yield losses can be as high as 100%, as observed in some regions of South Africa, Mozambique, and Uganda (Buthelezi *et al.,* 2013; Ibanda *et al.,* 2018). The severity of damage is influenced by seasonal variations, crop growth stage and pest population density. Infestations are often more pronounced in crops under drought stress, as water-deficient plants tend to be more susceptible to GLM attack. Additionally, early in the cropping season, injury is generally localised to the leaf margins, whereas later in the season, entire leaves may become necrotic, dry, and defoliated, exacerbating yield losses (Murithi *et al.,* 2019).

2.5 Host Plants

Groundnut leaf miner exhibits a strong preference for plants within the Fabaceae family. In both India and Africa, the pest predominantly targets groundnut and soybean, which are highly susceptible due to their nutritional profile and chemical composition (Buthelezi *et al.,* 2021; Table 1). In addition to these cultivated legumes, wild Fabaceae species also serve as alternate hosts, providing a reservoir for the pest during off seasons. In Australia, although groundnut is cultivated, no infestations have been reported on the crop, whereas soybean experiences only occasional and minimal pest infestations. The selection of these host plants is likely influenced by their inherent nutritional quality and the balance of defensive compounds, which collectively render Fabaceae crops particularly favourable for GLM development.

Table 2.1: Host plants of GLM compiled from literature across its geographic range

Host plants family	Host plants	References
Leguminosae	*Arachis hypogea, Glycine max, Medicago sativa*	Shanower *et al.,*1993 Van der walt, 2007 Buthelezi *et al.,* 2013
	Vigna radiata, Phaseolus aureus, Psolarea corylifolia	Shanower *et al.,*1993
	Cajanus sativa, Indigofera hirsute	Shanower *et al.,*1993 Buthelezi *et al.,* 2013
	Hibiscus sp, Senna occidentalis, Indigofera astragalina, Crotalaria Vasculosa	Van der walt, 2007
	Desmodium tortuosum, Glycine wightii,	Buthelezi *et al.,* 2013
	Vigna umbellate, Phaseolus calcaratus, Glycine soja, Trifolium alexandeium, Teramnus labialis, Lablab purpureus, Rhynchosia minima	Shanower *et al.,*1993
Rubiaceae	*Boreria hispida*	Shanower *et al.,*1993
Convolvulaceae	*Ipomoea sinerisis*	Buthelezi *et al.,* 2013 Van der walt, 2007
	Ipomea wightii	Buthelezi *et al.,* 2013
Malvaceae	*Malvastrum coromandelianum, Pavonia burchelli*	Buthelezi *et al.,* 2013
Asteraceae	*Acanthospermum hispida*	Buthelezi *et al.,* 2013
Lamiaceae	*Ocinum canum*	Buthelezi *et al.,* 2013
Capparaceae	*Cleome monophylla*	Van der walt, 2007
Pedaliaceae	*Sesamum aluium*	Van der walt, 2007
Tiliaceae	*Corchonis tridens*	Van der walt, 2007

2.6 Host Plant Selection in Lepidoptera Moths

2.6.1 Mechanisms of host selection

Behavioural adaptations further refine feeding preferences on host plants. Larvae often exhibit selective host plant consumption based on a combination of nutritional value and reduced defensive barriers. Many Lepidoptera species specialize in feeding on young leaves or flowers, which typically offer higher nutritional quality and lower levels of chemical defences (Krenn, 2010). To avoid predation, larvae may feed on the undersides of leaves or construct protective shelters using silk. In GLM, larvae initially mine within the leaf tissue and, as they grow, bind leaflets together with silk to form shelters that not only facilitate feeding but also provide protection during subsequent developmental stages (Okello *et al.,* 2016).

Plants produce an array of secondary metabolites including alkaloids, terpenoids, glucosinolates, and phenolics that can either stimulate or deter feeding depending on the herbivore's capacity to detoxify these compounds (Bezerra *et al.,* 2021). Specialist species, such as *Pieris brassicae*, preferentially feed on glucosinolate-rich hosts like mustard and cabbage due to their evolved detoxification mechanisms (Shakour *et al.,* 2022). Conversely, generalist feeders may be deterred by high tannin levels or other toxic compounds that reduce palatability and hinder digestion (Wari *et al.,* 2022). Additionally, herbivory itself can trigger plants to bolster their defences through increased jasmonic acid production, which in turn reduces nutritional quality (Shikano *et al.,* 2018). While the precise impact of these chemical defences on GLM feeding behaviour remains to be fully determined, its strong association with Fabaceae crops suggests that it is well adapted to the chemical profiles of its preferred hosts.

The surface texture of a plant influences feeding by affecting the ease of chewing and digestion (Zhang *et al.,* 2021). Smooth or soft leaves typically facilitate larval feeding, whereas rough, hairy, or waxy surfaces often due to dense trichomes or thick cuticles can create mechanical barriers and may secrete compounds that deter feeding (Coapio *et al.,* 2018; Kaur *et al.,* 2022; Prasad, 2022). Although specific data of feeding and oviposition on different host plants regarding GLM are limited, observations of 100% infestation on smooth-leaved Fabaceae crops, such as soybean and groundnut, indicate that leaf texture is an important factor in host selection for infestation (Buthelezi *et al.,* 2021). Nutrient availability is a critical factor influencing feeding preferences of the GLM. Lepidoptera larvae require essential nutrients including nitrogen, carbohydrates, and water for rapid growth and development (Silva *et al.,* 2018). Plants with higher nutrient content generally offer a more suitable feeding environment, while those with lower nutrient levels or elevated defensive compounds tend to be less preferred (Silva *et al.,* 2018). The strong preference of GLM for nitrogen-fixing Fabaceae crops further supports the hypothesis that nutrient availability is a key determinant in feeding behaviour.

The developmental stage of the host plant plays a crucial role in determining feeding preferences among Lepidoptera moths (Piyasaengthong *et al.,* 2016). Generally, younger plants or tissues such as young leaves and shoots are more attractive to larvae because they are softer, more nutritious, and contain lower concentrations of defensive chemicals (Piyasaengthong *et al.,* 2016; Jeong *et al.,* 2023). As plants mature, they tend to accumulate higher levels of lignin, cellulose, and other structural compounds, rendering the tissues tougher and more difficult for larvae to consume. In addition, mature plants often produce increased quantities of secondary metabolites as a defence mechanism against herbivory. Consequently, many Lepidoptera larvae exhibit a strong preference for feeding on younger, more tender plant tissues, where the balance between nutritional benefits and defensive barriers is more favoured (Jeong *et al.,* 2023). This preference underscores the importance of host plant age in influencing feeding behaviour and may explain why infestations are particularly severe when crops are at their early growth stages (Ode *et al.,* 2022).

2.6.2 Factors influencing oviposition and feeding preference of Lepidoptera moths

Groundnut leaf miner exhibits a strong infestation for plants within the Fabaceae family. In both India and Africa, the pest predominantly targets groundnut and soybean, which are highly susceptible (Buthelezi *et al.,* 2021), this may be due to their nutritional profile and chemical composition. In addition to these cultivated legumes, wild Fabaceae species also serve as alternate hosts, providing a reservoir for the pest during off seasons. In Australia, although groundnut is cultivated, no infestations have been reported on the crop, whereas soybean experiences only occasional and minimal pest occurrences. The selection of these host plants is likely influenced by their inherent nutritional quality and the balance of defensive compounds, which collectively render Fabaceae crops particularly favourable for GLM development (Crane *et al.,* 2022).

Host selection for oviposition and feeding behaviour are influenced by a combination of chemical cues, physical plant traits, and environmental conditions. Oviposition site selection is driven by volatile organic compounds (VOCs), secondary metabolites, and the presence of epicuticular waxes that guide females to specific host plants (Crane *et al.,* 2022; Staton *et al.,* 2023). Similarly, the texture of plant surfaces, trichome density, and nutritional quality determine larval feeding preferences. Younger leaves, with softer tissues and lower secondary metabolite concentrations, are often preferred (Wang *et al.,* 2023; Rupngam and Messiga, 2024). Additionally, behavioural adaptations play a crucial role in feeding ecology. Larvae initially mine within the leaf tissue and later transition to external feeding by webbing leaflets together, providing protection from predators and environmental stressors (Okello *et al.,* 2016). Feeding site preferences and host plant interactions collectively shape GLM impact on legume crops. Understanding these interactions is essential for developing targeted pest management strategies, including breeding for resistant cultivars, semio-chemical-based interventions, and precise timing of control measures.

2.6.2.1 Chemical cues

Chemical cues are fundamental in shaping the oviposition behaviour of female moths. Plants release a variety of chemical signals, including VOCs, which provide information regarding the nutritional quality and chemical defences of potential host plants (Crane *et al.,* 2022; Staton and Williams, 2023). Additionally, surface chemicals such as epicuticular waxes and trichome secretions are detected by sensory receptors on the antennae, tarsi, and ovipositors, guiding females to select sites that will favour larval development (Crane *et al.,* 2022). These chemical cues enable moths to avoid herbivore-damaged plants, which might indicate heightened competition or an increased presence of natural enemies (Graham *et al.,* 2024). For example, studies on *T. absoluta* revealed that approximately 50% of eggs were deposited on domesticated tomato plants, suggesting an evolutionary adaptation to host-specific compounds while also demonstrating the potential for oviposition on alternative hosts (Desneux *et al.,* 2011).

Herbivore-induced plant responses further modify host selection. Plants subjected to prior herbivory often increase jasmonic acid production and secondary metabolite concentrations, thereby reducing palatability and deterring further egg deposition (Shikano et al., 2018). Females frequently avoid damaged plants, likely to minimize competition and exposure to natural enemies (Hilker and Fatouros, 2015). Although the precise chemical drivers of GLM feeding remain under investigation, its strong association with Fabaceae crops suggests adaptation to their characteristic chemical profiles.

2.6.2.2 Physical characteristics and surface texture

The surface texture of a plant influences feeding by affecting the ease of chewing and digestion (Zhang *et al.,* 2021). Smooth or soft leaves typically facilitate larval feeding, whereas rough, hairy, or waxy surfaces often due to dense trichomes or thick cuticles can create mechanical barriers and may secrete compounds that deter feeding (Coapio *et al.,* 2018; Kaur *et al.,* 2022; Prasad, 2022). Although specific data regarding GLM are limited, observations of 100% infestation on smooth-leaved Fabaceae crops, such as soybean and groundnut, indicate that leaf texture is an important factor in host selection (Buthelezi *et al.,* 2021). These physical attributes, which may also indicate the plant's defensive strategies, lead females to avoid surfaces that are less conducive to offspring survival (Reisenman *et al.,* 2013).

2.6.2.3 Nutritional quality and plant age

Nutrient availability is a critical determinant of feeding preference and oviposition behaviour. Larvae require nitrogen, carbohydrates, and water for optimal growth and development (Silva *et al.,* 2018). Nitrogen-fixing Fabaceae crops therefore provide a favourable nutritional environment for GLM.

Plant age is closely linked to nutritional quality and defensive chemistry. Younger plants and tissues generally contain higher nitrogen and water content and lower concentrations of structural compounds such as lignin and cellulose, making them softer and more palatable (Wang *et al.,* 2023; Jeong *et al.,* 2023). Consequently, many

Lepidoptera species prefer to oviposit and feed on young leaves or early growth stages. In India and South Africa, GLM infestations often commence approximately 5–6 weeks after crop emergence, coinciding with flowering, suggesting that this growth stage offers an optimal balance between nutrient availability and manageable defence levels (Ranga Rao and Rameshwar Rao, 2013; Buthelezi *et al.,* 2013). However, some species may exploit older plants if they possess adaptations to overcome mature plant defences.

2.6.2.4 Egg deposition and feeding site selection

The specific location chosen for egg deposition and larval feeding significantly influences offspring survival. Females often lay eggs on the undersides of leaves, stems, or petioles, where they are protected from desiccation, rainfall, direct sunlight, and predators (Mutamiswa *et al.,* 2023). GLM predominantly deposits eggs on the undersides of leaves, stems, and petioles of groundnut and soybean (Shanower *et al.,* 1993a; Kenis and Cugala, 2006; Buthelezi *et al.,* 2021).

Feeding site selection further enhances larval survival. Leaf-mining species gain protection within leaf tissues, shielding themselves from predators and surface defences (Desneux *et al.,* 2010). GLM larvae initially mine between epidermal layers before transitioning to external feeding, binding leaflets together with silk to form protective shelters (Okello et al., 2016). This behavioural adaptation optimizes feeding efficiency while minimizing predation risk.

2.6.2.5 Feeding time and behavioural adaptations

Feeding time also contributes to larval success. Many Lepidoptera larvae are nocturnal feeders, reducing exposure to predators and limiting water loss during high daytime temperatures (New, 2023). Nocturnal feeding may also coincide with reduced plant defensive activity, thereby enhancing feeding efficiency (Šigutová *et al.,* 2023). Understanding these temporal feeding patterns is essential for optimizing pest monitoring and control strategies.

2.6.2.6 Abiotic and biotic factors

Environmental conditions indirectly shape oviposition and feeding behaviour. Temperature influences plant metabolism and secondary metabolite production, altering host palatability (Senior *et al.,* 2021). Moisture availability affects plant physiological status; well-watered plants typically provide higher nutritional value, whereas drought stress may increase defensive compound production (Nguyen *et al.,* 2024). Light and soil quality further influence plant morphology and nutrient profiles, thereby affecting host suitability (Lev-Yadun, 2021).

2.6.3 Comparative studies of feeding and oviposition preferences in other Lepidopterans

Lepidopteran pests pose considerable challenges to global agriculture due to their evolved capacities to overcome host plant defences through a combination of biochemical, physiological, and behavioural adaptations (Shylesha *et al.,* 2006). Among these, GLM is a key pest of economically significant leguminous crops, including groundnut, and soybean (Namara *et al.,* 2019). Although molecular studies on GLM are limited, its consistent success in infesting legumes that are rich in defensive compounds such as saponins and tannins strongly suggests the involvement of detoxification systems (Tamo *et al.,* 2003). *Plutella xylostella* (Diamondback moth), a specialist herbivore of cruciferous plants, presents one of the most well-documented cases of biochemical adaptation to plant chemical defences (Xiong *et al.,* 2022).

Crucifers defend themselves with glucosinolates, which upon plant tissue damage are hydrolysed by myrosinase into toxic isothiocyanates (Angelino *et al.,* 2015). To overcome this, diamondback moth has evolved glucosinolate sulfatas, which desulfate glucosinolates, thereby preventing their conversion into harmful compounds (Xiong *et al.,* 2022). The critical importance of this pathway was highlighted by Chen *et al*. (2022), who demonstrated that inhibition of Glucosinolates sulfatase (GSS) significantly reduces larval survival and performance on Brassica hosts.

Cotton bollworm *(Helicoverpa armigera)* a highly polyphagous pest, exhibits remarkable adaptive flexibility (Pearce *et al.,* 2017). It feeds on over 200 plant species, including legumes, cotton, and cereals, and counters host protease inhibitors by modulating the expression of its own digestive proteases (Singh *et al.,* 2020). Specifically, it upregulates serine peptidases to maintain digestive efficiency in inhibitor-rich environments. Velasquez-Vasconez *et al*. (2022) provided compelling evidence that this gene regulation is transgenerational, suggesting an epigenetic component that allows cotton bollworm offspring to better cope with dietary inhibitors encountered by previous generations. Such molecular plasticity contributes substantially to the pest’s persistence and adaptability across diverse agroecosystems. Similarly, tomato leaf miner, a major pest of tomato crops, utilizes both biochemical and behavioural adaptations (Pandey *et al.,* 2023). Solanaceae crops like tomato produce alkaloids and VOCs as part of their defence arsenal (Chen *et al.,* 2021). *Tuta absoluta* females have been found to use plant-emitted VOCs to locate and select suitable oviposition sites (Naselli *et al.,* 2017). Specifically, the moth tends to prefer host plants that emit VOC profiles associated with reduced or delayed defensive responses (Chen *et al.,* 2021).

These comparative insights highlight the diverse mechanisms by which lepidopteran pests avoid host plant defences. Whereas diamondback moth illustrates specialised biochemical detoxification, cotton bollworm and tomato leaf miner demonstrate generalist or behaviourally mediated strategies. Although knowledge on GLM remains limited, its capacity to succeed on chemically defended legumes recommends the connection of comparable biochemical pathways, emphasising the need for molecular and genomic investigations on this species

2.7 Role of Smartphone Technology in Monitoring Insect Feeding Behaviour

Smartphone technology has become a helpful tool in monitoring insect feeding behaviour, offering real-time data collection, precise damage analysis, and user-friendly interfaces (Mendes *et al.,* 2020). These advancements empower farmers, researchers, and agronomists to make informed decisions promptly, enhancing crop protection and management strategies. Modern smartphone applications utilize integrated cameras and sensors to capture high-resolution images of plant leaves directly in the field; these images are processed using advanced algorithms to detect and quantify insect-induced damage (Aziz *et al.,* 2025).

Applications like Bio-Leaf employ image processing techniques to assess foliar damage accurately by analysing the extent and pattern of leaf damage (Singh, 2022). These tools help in identifying specific pest infestations and evaluating the effectiveness of pest control measures (Machado *et al.,* 2016). Bio-Leaf App, developed by researchers from the Federal University of Mato Grosso do Sul and Dom Bosco Catholic University was introduced in 2016 as a free Android application. It enables users to measure foliar damage caused by insect herbivory by capturing or uploading leaf images. The app utilizes Otsu segmentation and Bezier curves to estimate defoliation percentages, even reconstructing damaged leaf borders for accurate analysis (Machado *et al.,* 2016). The Bio-Leaf mobile application has been effectively used to estimate foliar damage across a wide range of crops such cotton, potato, and sugarcane. It was initially confirmed on soybean (Amaral *et al.,* 2016).

2.8 Management Strategies for GLM

2.8.1 Chemical control

Chemical control remains an essential component of integrated pest management programs, although its use must be judicious to avoid environmental contamination and the development of resistance. Historically, dichloro-diphenyl-trichloroethane (DDT) was used to control GLM in India; however, due to its environmental and health hazards, it has been banned (Shanower *et al.,* 1993a). Presently, several insecticides are used against GLM in India, including formulations of deltamethrin (2.8% EC), lambda-cyhalothrin (5% EC), quinalphos (25% EC), buprofezin (25 SC at 1 ml/L), acephate (75 SP at 1 g/L), thiodicarb (75 WSP at 0.6 g/L), and thiamethoxam (25 WG at 0.2 g/L) (Pazhanisamy and Hariprasad, 2013; Muthu and Yogapriya, 2021). In South Africa and Mozambique, cypermethrin (20% EC at 2 ml/L) has been found effective in reducing infestations in groundnut and soybean crops (Buthelezi *et al.,* 2013). It is imperative that insecticide applications be timed according to economic threshold levels, ensuring that treatments are only applied when necessary to maximize control efficacy and minimize adverse environmental impacts (Hoidal and Koch, 2021). Economic threshold levels for GLM have been established primarily in India, where insecticide application is recommended when larval densities reach approximately 5–10 larvae per plant or when significant foliage damage occurs (Kenis and Cugala, 2006; Van der Walt *et al.,* 2008; Shanower *et al.,* 1993). Monitoring systems include field scouting and pheromone traps, with trap catches of approximately 10–12 moths per trap per day indicating potential economic damage (Kenis and Cugala, 2006). However, locally validated thresholds remain limited in many African regions, highlighting the need for region-specific monitoring and management strategies (Buthelezi and Zharare, 2025).

2.8.2 Biological control

Biological control strategies for GLM focus on the utilisation of natural enemies to suppress pest populations, thereby reducing the reliance on chemical interventions. In India, several predators including ground beetles (*Chlaenius* sp.), robber flies (Diptera: Asilidae), and lacewings (*Chrysoperla carnea*) have been observed preying on the larvae. Although these predators are generally polyphagous and may not always provide targeted control, their presence is an important component of the natural regulatory mechanism (Kenis and Cugala, 2006). Parasitoids have emerged as particularly promising agents for controlling GLM. In India, various parasitoids belonging to the families Braconidae and Eulophidae have been recorded, with some studies reporting parasitism rates exceeding 90% in certain areas (Kenis and Cugala, 2006; Murugasridevi *et al.,* 2022). In Africa, the parasitoid fauna associated with GLM is more diverse but generally exhibits lower parasitism rates. In Mozambique, parasitoid species from the families Braconidae, Ichneumonidae, Chalcididae, Eulophidae, and Bethylidae have been documented, with parasitism rates ranging from 0 to 23.2% (Kenis and Cugala, 2006). Furthermore, in South Africa, nine species of parasitic Hymenoptera have been recorded attacking GLM larvae, although their overall diversity and efficacy appear to be lower compared to their counterparts in India (Van der Walt, 2007). These findings underscore the need for further research to characterize the parasitoid communities in Africa and to evaluate their potential for classical biological control.

In addition to predators and parasitoids, several entomopathogens have demonstrated significant potential in suppressing GLM populations. Pathogens such as *Bacillus thuringiensis*, *Beauveria bassiana*, and *Metarhizium anisopliae* have been shown to cause considerable larval mortality, thereby reinforcing the role of biological control within integrated pest management programmes (Rajagopal *et al.,* 1988; Shanower *et al.,* 1992). Collectively, these biological control agents offer a sustainable alternative to chemical pesticides, and their strategic integration into IPM programs can significantly contribute to the long-term management of GLM.

2.8.3 Cultural and agronomic practices

Cultural control measures aim to modify the agroecosystem to disrupt the pest’s life cycle and reduce its populations. One effective approach is crop rotation, which involves alternating host and non-host crops to break the continuous availability of suitable oviposition and feeding sites. For example, rotating groundnut with non-host cereals such as maize and sorghum has significantly lowered GLM populations by limiting the availability of preferred host plants (Narayanamma *et al.,* 2013; Mohanty *et al.,* 2024). Irrigation is another critical cultural practice. Water-stressed groundnut plants tend to be more susceptible to infestation, whereas well-irrigated crops exhibit reduced pest pressure (Shanower *et al.,* 1995). In India, high rainfall has been correlated with lower populations of GLM, and experimental overhead irrigation designed to mimic natural rainfall has yielded positive results by reducing pest densities (Shanower *et al.,* 1995; Debele *et al.,* 2023; Kumar *et al.,* 2023).

Intercropping, the simultaneous cultivation of two or more crops, also plays a pivotal role by disrupting pest host-finding behaviour and promoting the presence of natural enemies. In India, intercropping groundnut with soybean (*Glycine max)*, sorghum (*Sorghum bicolor*), black gram (*Vigna mungo*), pigeon pea (*Cajanus cajan*), green gram (*Vigna radiata*), and pearl millet (*Pennisetum glaucum*) has been shown to substantially reduce infestation levels (Muthiah, 2000; Maitra *et al.,* 2021). Developing pest-resistant cultivars is an essential long-term strategy for managing GLM. An in-depth understanding of the pest's oviposition and feeding preferences is essential for the identification of key plant traits such as leaf surface texture, trichome density, and secondary metabolite profiles that deter infestation. Breeding programs can then focus on these characteristics to develop varieties that are less attractive or less suitable for pest development (Gelaye and Luo, 2024). Furthermore, targeting the growth stages most susceptible to infestation can result in cultivars that reduce the overall reliance on chemical controls, thereby contributing to more sustainable pest management.

2.8.4 Integrated Pest Management approaches

Understanding the oviposition and feeding preferences of GLM is crucial for devising targeted and effective pest management strategies. These biological traits directly influence population dynamics, infestation patterns, and host plant selection, thereby providing essential insights for optimizing chemical, biological, and cultural control methods within IPM frameworks.

2.8.4.1 Components and principles of IPM

A detailed knowledge of the preferred oviposition sites and feeding stages of GLM allows for the precise timing of control measures. For example, if the pest favours younger leaves for oviposition, insecticides or biological control agents can be applied when these tissues are most vulnerable, thus enhancing treatment efficacy. Targeting early larval stages before significant damage occurs maximizes the impact of interventions and reduces the overall pest population (Reddy *et al.,* 2020). Precision in application also minimizes off-target effects, ensuring that control measures are both cost-effective and environmentally sustainable.

Cultural control practices that disrupt the pest's life cycle are also enhanced by an in-depth understanding of its oviposition and feeding preferences. Adjusting planting dates to avoid peak oviposition periods can significantly reduce infestations, as late-planted groundnut crops are known to suffer higher pest pressure (Buthelezi *et al.,* 2013). Similarly, the use of irrigation to alleviate water stress not only improves plant health but also reduces pest populations by physically washing away eggs and early instar larvae. This practice may additionally promote the activity of entomopathogenic fungi, which naturally suppress GLM populations. Intercropping and crop rotation with non-host species further limit the availability of suitable hosts, thereby reducing pest abundance.

Integrating biological control measures into pest management programs is greatly enhanced by understanding the life cycle, oviposition timing, and feeding behaviour of GLM. The strategic release of natural enemies, such as parasitoids and predators, synchronized with the pest's most vulnerable stages, particularly early larval development, can significantly increase parasitism and predation rates (Reddy *et al.,* 2020). Knowledge of preferred oviposition sites also facilitates the targeted deployment of beneficial organisms, such as lacewings and ground beetles, while habitat manipulation can further conserve these natural enemies. Additionally, aligning irrigation practices with biopesticide applications, for example using *Beauveria bassiana*, can enhance pathogen-based control strategies.

A better understanding of the pest's behaviour in terms of oviposition and feeding preferences facilitates a reduction in reliance on broad-spectrum insecticides. By applying chemicals only during the most susceptible phases of the pest's life cycle and at a minimal rate, the frequency of treatments can be lowered, thereby mitigating the development of insecticide resistance (Kumar *et al.,* 2018). Additionally, this targeted approach reduces adverse impacts on beneficial insects and non-target organisms, ultimately enhancing environmental sustainability and reducing production costs an especially important consideration for smallholder farmers in regions affected by GLM.

2.8.4.2 Role of host plant selection knowledge in IPM

Pests can be controlled to minimize crop loss by taking advantage of their host plant preference. At every step of life cycle, insects exploit chemical information from their surroundings to find food, oviposition, and hibernation locations, to gather with conspecifics and sexual partners, as well as to stay away from unsafe conditions or inappropriate hosts and habitats (Agelopoulos *et al.,* 1999). According to Norris and Kogan (2000), most plant-arthropod interactions are mediated by the compounds that the plant produces. The key to using cultural management techniques, such as trap crops, is understanding the pests' preference for plant species. Trap crops are plant stands that are grown to attract insects away from the main crop to protect target crops from pest attack (Hokkanen, 1991).

Protection may be achieved either by preventing the pests from reaching the crop or by concentrating them in a certain part of the field where they can economically be destroyed (Hokkanen, 1991). It is important that the trap crop is more attractive to the pest than the main crop, at least at some critical time, but preferably over long periods (Hokkanen, 1991). If the trap crop is highly attractive for the pest and result in very low or no survival of the pest offspring, it may be termed a "dead-end" trap crop (Shelton and Badenes-Perez, 2006). The study of semio-chemicals and the interactions they mediate helps us understand how organisms behave, develop, and evolve (Agelopoulos *et al.,* 1999). Additionally, research supports the effective use of semio-chemicals as a substitute for the exclusive use of broad-spectrum toxicants in pest control (Agelopoulos *et al.,* 1999). Insect-attracting or insect-repelling semio-chemicals, as well as those that enhance or inhibit the action of other chemicals, may be used to directly control pests by disrupting mating, or by discouraging pests from food and oviposition sites (Agelopoulos *et al.,* 1999). Semio-chemicals can also be utilized to affect the behaviour of pests and their natural enemies because they are involved in multitrophic interactions (Agelopoulos *et al.,* 1999).

2.8.4.3 Need for eco-friendly and farmer-adapted solutions

The management of GLM, poses significant challenges, particularly in smallholder farming systems where groundnut is a major crop. Conventional pest control strategies have often relied heavily on chemical insecticides, which not only lead to environmental degradation and non-target effects but also promote pesticide resistance in pest populations (Sparks and Nauen, 2015). As such, there is an urgent need for eco-friendly, sustainable solutions that align with IPM principles. Integrated Pest Management emphasises the use of multiple, complementary approaches including cultural, biological, and mechanical controls to minimise pest pressure while reducing chemical dependency (Baker *et al.,* 2020). For GLM, such strategies may include intercropping, use of trap crops, timely sowing, and the conservation of natural enemies such as parasitoids and predators (Reddy *et al.,* 2020). These methods not only help regulate pest populations but also maintain agroecosystem health and resilience.

Moreover, it is critical that pest management strategies are adapted to the socio-economic realities of resource-limited farmers. The success of any IPM approach hinges on its applicability at the field level, ease of adoption, and cost-effectiveness (Rossi *et al.,* 2019). For example, introducing biological control agents, such as *Trichogramma* spp., can be a viable option when integrated with farmer-friendly monitoring tools like the Bio-Leaf app, which enables visual quantification of foliar damage (Machado *et al.,* 2016; Ballal, 2019). Additionally, participatory approaches that involve farmers in decision-making and training can improve awareness, early detection, and timely intervention, thereby increasing the long-term effectiveness of IPM strategies (Jules and Bharucha, 2015). Ultimately, eco-friendly and farmer-adapted IPM solutions for GLM offer a pathway toward sustainable groundnut production and improved livelihood outcomes for small-scale producers.

2.9 Research Gaps and Rationale for the Study

Groundnut Leaf Miner has emerged as a pest of increasing concern in legume-based cropping systems, yet critical gaps remain in the understanding of its bio-ecology. Existing literature has largely focused on its interaction with groundnut with limited consideration given to alternative host plants such as soybean and hairy indigo. This narrow focus hinders our ability to predict the pest's population dynamics across diverse agroecosystems. Furthermore, the oviposition behaviour of GLM remains poorly understood, particularly in relation to host plant traits that influence female preference. Similarly, detailed studies on larval feeding performance and development on different legume hosts are lacking, despite their importance for assessing the pest's ecological flexibility and potential impact. There is also a notable lack in research on how plant characteristics such as morphology, chemistry, or phenology affect host selection and larval success.

A comparative study of oviposition and feeding preferences across multiple host plants is therefore essential. Oviposition choice reflects the insect's perception of host suitability for reproduction, while larval performance provides insight into the actual nutritional and developmental value of the host. Understanding both preference and performance offers a comprehensive view of host utilization and helps identify plants that may either support pest build-up or limit population growth. Such findings can inform the selection of companion or intercrops, and guide breeding programs aimed at enhancing resistance or deterrent traits.

This research holds significant relevance for pest monitoring and sustainable management of GLM Insights into host preference and suitability which can enhance early detection efforts. Moreover, identifying the most vulnerable crops and growth stages allows for the strategic distribution of targeted interventions within IPM frameworks. In the long term, understanding the pest's host-use patterns contributes to ecologically based pest management strategies, such as the use of trap crops or host plants, and supports the development of sustainable environmental control practices that reduce reliance on chemical pesticides.

2.10 Recommendations for Future Research

To strengthen the understanding of oviposition and feeding preference of GLM and their implications for pest management, the following aspect should be prioritised:

- Identifying key semi-chemicals that influence oviposition site selection and feeding behaviour.
- Using RNA sequencing to identify genes linked to host plant recognition.
- Studying population genetics to detect potential host associated differentiation.
- Monitoring oviposition and feeding patterns under field conditions and in controlled environments across different seasons to assess seasonal variations.
- Conducting olfactometer or wind tunnel assays to assess attraction to plant volatiles.
- Adoption of technology including smartphone to enhance oviposition and feeding studies.

2.11 Summary

The review highlights the limited research on GLM, particularly its oviposition and feeding preferences in relation to host plant selection, environmental conditions, and life cycle dynamics. Due to the scarcity of species-specific studies, insights were drawn from related Lepidoptera moths, emphasising the need for further dedicated research to bridge the existing knowledge gaps. Expanding research on host plant interactions, behavioural ecology, and population genetics will enhance the understanding of GLM bio-ecology and population dynamics, thereby contributing to more precise and effective pest management strategies. Moreover, the integration of smartphone-based technologies in future studies, such as the use of the Bio-Leaf app, which offers a valuable tool for accurately scoring feeding damage in host crops by the GLM. These technologies can streamline data collection, improve real-time monitoring, and facilitate large-scale field assessments, ultimately supporting more data-driven decision-making in pest management programs. Considering these research gaps and technological advancements, the present study was designed to (i) compare infestation levels of GLM on groundnut, soybean, and hairy indigo; (ii) evaluate the oviposition preferences of female GLM on these host plants; and (iii) determine the preferred host plant for GLM larval feeding. The subsequent chapter outlines the methodology adopted to address these objectives, including experimental setup, data collection techniques, and analytical approaches.

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CHAPTER THREE

GENERAL MATERIALS AND METHODS

3.1 Study Site

The study was conducted in the greenhouse tunnel and laboratory for one year at the Cape Peninsula University of Technology (CPUT), Wellington Campus, situated in the Western Cape Province of South Africa (Coordinates: 33˚37’53’’S 19˚0’36’’E). The Wellington campus is situated in the Cape Winelands District of the Western Cape Province, and experiences a Mediterranean climate, characterised by hot, dry summers (November to March), with peak daytime temperatures often exceeding 30°C, and cool, wet winters (May to August), during which temperatures generally range between 5°C and 18°C (Goosen, 2014). Annual rainfall averages between 600 mm and 800 mm, mostly concentrated in winter months. Low humidity and high sunlight exposure, predominantly falling during the winter months. The region also experiences low relative humidity and high solar radiation levels during the growing season, conditions which significantly influence both plant development and pest population dynamics (Climate Data, 2025).

3.2 Cultivation and Management of Host Plants for Insect Rearing and Bioassays

Three host plant species were used in this study: groundnut (*Arachis hypogaea* L.), soybean (*Glycine max* L.), and hairy indigo (*Indigofera hirsute*). These plant species were selected based on their reported suitability as hosts for GLM. Groundnut was cultivated for both GLM rearing and experiments. Seeds of each plant species were sown in January 2025 inside a greenhouse tunnel located at the Wellington Campus, providing a semi-controlled environment conducive to year-round cultivation. The seeds were directly planted into pots containing a homogenised mixture of topsoil and compost to enhance nutrient availability, drainage and root aeration. To ensure experimental integrity, each plant species was grown in isolation to prevent cross-contamination and to maintain host specificity during insect rearing and bioassays.

Irrigation was adjusted according to seasonal temperature fluctuations. During the hot summer months, the plants were watered three times a week, while in the cooler winter season, irrigation frequency was reduced to twice a week to prevent waterlogging and minimise the risk of fungal infections. A balanced, water-soluble fertiliser (Nutri-feed) was applied weekly to sustain optimal vegetative growth and nutrient status. Plant health, soil moisture, and pest presence were routinely monitored. Weakened or dead plants were promptly replaced to maintain uniformity in plant growth stages across replicates. Although the greenhouse tunnel provided partial environmental protection, plant growth still varied seasonally.

During summer, all three plant species exhibited vigorous growth, characterised by lush foliage and healthy biomass suitable for bioassays. However, in winter, soybean plants demonstrated stunted growth and chlorosis, likely due to suboptimal temperature and light conditions affecting nutrient uptake. In contrast, groundnut and hairy indigo were more tolerant of winter conditions, although their growth rates were moderately reduced. These seasonal growth variations were considered when selecting host plants for GLM rearing and bioassay experiments to ensure consistency in plant quality and developmental stage.

3.3 Rearing of GLM

The initial population of GLM used to establish the laboratory colony was collected in March 2025 from naturally infested groundnut fields in Manguzi, KwaZulu-Natal, South Africa (coordinates: 27˚02’27.1’’S 32˚46’37.7’’E). Field-collected larvae were sorted according to instar stage and temporarily housed in paper bags, which were placed inside cushioned storage containers to minimise mechanical damage during transportation to the laboratory. Upon arrival at the CPUT’s entomology facility, the larvae were introduced into controlled rearing conditions the following day. Rearing was conducted in a climate-controlled growth chamber maintained at 30°C with a relative humidity range of 65–80%, relative humidity was measured using a smartphone-based device. It is important to note that irrigation may have contributed to variations in the recorded relative humidity levels within the growth chamber.

Infested leaf material from the field was replaced, and larvae were gently transferred onto fresh, pest-free groundnut plants to allow uninterrupted development. Under these controlled conditions, the complete life cycle of GLM was completed in approximately two weeks. Sex differentiation of both larvae and pupae was carried out using the diagnostic morphological markers described by Van der Walt *et al.* (2008). In larvae, males were distinguished by the presence of visible pink gonads located between the sixth and seventh abdominal segments, observable through the cuticle, while females lacked these structures. In pupae, sexing was performed under a light microscope following the same distinguishing characteristics.

Sexed individuals were separated into male and female groups to facilitate controlled mating. Larvae were continuously fed fresh groundnut leaf cuttings until pupation and were maintained until adult emergence. Emergent adult moths were paired in a one-to-one male-to-female ratio based on availability and placed in cylindrical rearing cages (46 cm × 56 cm) covered with fine insect-proof mesh. Each mating cage contained healthy, potted groundnut plants to serve as oviposition substrates. Adult moths were supplied with a 10% honey-water solution. To ensure colony stability and minimize the effects of field-related variability, three successive laboratory generations were reared under uniform conditions prior to initiating any experimental trials (infestation, oviposition, and feeding preference bioassays).

3.4 Experiment 1: Larval Feeding Preference Experiment

Feeding preference experiment was conducted in five different trials (22/03/2025-16/05/2025). Initial population obtained from Manguzi, was used to conduct trial one and trial two, with instar size from three to five. Trial three to trial five were conducted using third generation reared GLM population with instar size from three to four. Trial one and two included non-choice assay and three choice assays, while trial three- trial five included, non-choice assay, three choice assay and two choice assays. All third and fourth instar larvae were removed from infested groundnut leaves in the breeding cages to obtain the population required for the feeding experiment.

A total of 24 larvae were collected and placed in a large petri dish (145 mm × 20 mm), which was then kept inside a closed cage to prevent larval escape during the starvation period. The larvae were starved for three hours prior to the start of the experiment to enhance the feeding activity of GLM larvae (Chen and Ruberson, 2008). Fresh leaf cuttings from the host plants were prepared. Circular paper towels, cut to fit the size of the petri dishes, were placed at the bottom of each dish. All petri dishes were properly labelled. Following the starvation period, GLM larvae were introduced into the labelled petri dishes for feeding. The experiment included both choice and non-choice setups, each replicated four times. In each labelled petri dish (60 mm × 13 mm), and the petri dishes were sealed securely to prevent escape. All non-choice petri dishes were placed inside a small breeding cage (30 × 30 × 30 cm). For the choice experiment, five large petri dishes (145 mm × 20 mm) were used to accommodate all host plant leaves, regardless of size. These dishes were sealed and placed in large breeding cage (58 × 58 × 142cm) for the duration of 24 hours.

Data on larval feeding were collected at 24 hours to evaluate feeding behaviour and preferences. Bio-Leaf mobile application was used to calculate the leaf area and defoliation percentage digitally, providing a more accurate and non-destructive assessment of leaf surface available for feeding adopted from Mendez *et al.,* (2020). Additionally, photographs of both the upper and lower surfaces of each leaf were taken before and after feeding to document visible feeding symptoms.

3.5 Experiment 2: Oviposition Preference Assay

The oviposition experiment was conducted under controlled laboratory conditions at a constant temperature of 30°C to determine whether female GLM moths exhibit a preference for specific host plants (22/05/2025- 31/05/2025). The host plants used in the experiment were first grown under uniform conditions in a greenhouse tunnel, from which the four most healthy individuals of each host plant species were selected. The experiment consisted of two types of bioassays: non-choice and choice. In the non-choice bioassays, individual potted plants, each with approximately equal leaf biomass were enclosed in insect-rearing nets measuring 46 cm × 56 cm.

Each host plant included a feeding container filled with a 10% honey-water solution and was clearly labelled according to the host plant and replicate. Each of the host plant enclosed in an insect net, one pair of 1–2-day-old male and female GLM moths were introduced and allowed to mate and oviposit over a period of three days. The choice bioassays followed the same basic procedure, but were conducted in larger insect-rearing net cages measuring 58 cm × 58 cm × 142 cm. In these setups, potted host plants of each species were arranged at 15 cm intervals to allow the moths the opportunity to choose between host options. Two pairs of moths were introduced into each of the six choice cages, with four replications and two validation trials conducted to ensure consistency and reliability of results.

The oviposition data were collected after 72 hours of daily observations. The number of eggs were counted on each leaf in a whole plant structure including petioles, stem and stem; to enhance visibility of eggs, smart phones magnifying lens was used to take zoomed pictures and manual counting of eggs was done.

3.6 Experiment 3: GLM Infestation Experiment (Overall Infestation in all Host Plants)

The experiment was conducted under both greenhouse and controlled environmental conditions to assess the infestation and reproductive behaviour of GLM on different host plants (26/05/2025-15/06/2025), and continuation of oviposition experiment. Host plants were grown and maintained in a greenhouse setting until they reached six weeks, corresponding to the appropriate growth stage for use in the assays. The experimental setup consisted of two approaches: a choice experiment and a non-choice experiment. In the choice experiment, three different host plants were used, each replicated four times. The trials were carried out in twelve breeding cages, each measuring 58 cm × 58 cm × 42 cm. Four adults GLM moths, with a sex ratio of 1 male to 1 female, were released into each cage with 1-2 days old. Additionally, a small container with 10% honey-water solution was placed inside each cage to prolong the insects' lifespan.

The moths were allowed to mate and reproduce freely within the cages. For the non-choice experiment, each of the three host plants was also replicated four times, totalling twelve pots, each enclosed with a virus-free mesh net. Inside each net-covered pot, a container with 10% honey-water solution was provided, and four adult moths (2 males and 2 females) were introduced and allowed to mate and reproduce for five days. This entire experimental design was arranged in a completely randomized block design to ensure consistency.

Infestation data was scored on day seven from the initial observation, the data for each trial was scored in three scouting intervals of 7 days, 14 days and 21 days.

3.7 Data Collection and Analysis

3.7.1 Larval feeding

Larval feeding behaviour GLM was observed and documented at 24 hours following larval placements on host plants. At each interval, detailed notes were taken on the location of feeding (adaxial vs. abaxial leaf surface) and the type of leaf damage. Attention was given to the mining patterns created by the larvae. Early instar larvae typically produced serpentine or narrow blotch mines that were distinct on each host plant. The extent of leaf area damage was assessed using the Bio-Leaf smartphone application, which enabled accurate, image-based quantification of feeding severity. This digital tool ensured consistency in scoring across samples and was supported by photographic documentation to enhance reliability and facilitate further analysis.

3.7.2 Female GLM oviposition

The oviposition preference of female GLM was assessed across all host plants by counting the number of eggs laid on at 72 hours, after the initial introduction of the moths. This time point was selected to ensure that the females had sufficient time for mating and subsequent oviposition. The number of eggs were counted on each leaf in a whole plant structure including petioles, stem; to enhance visibility of eggs, smart phones magnifying lens was used to take zoomed pictures and manual counting of eggs was done.

3.7.3 Groundnut leaf miner infestation level

First infestation was scored on day seven after the initial observation, and subsequent observations were conducted at 7-day intervals on days 14 and 21. During each scouting interval, the total number of leaves per host plant was recorded, followed by the number of infested leaves per plant and the number of mines present on the infested leaves. Host plants were also assessed to determine their ability to support the GLM population from oviposition through to adult emergence. In addition, GLM longevity was evaluated by recording the lifespan of emerged moths and provided with a 10% honey-water solution.

3.8 Data Analysis

All experimental data were subjected to statistical analysis using SPSS software (version 27). The number of eggs laid, number of leaves per plant, number of infested leaves and number of mines were compared across host plants. One-way analysis of variance (ANOVA) was used to test for statistically significant differences among means. Where significant differences were detected ($p < 0.05$), Least Significant Difference (LSD) test was applied for post hoc multiple comparison of treatment means. All the GLM longevity data were not subjected to statistical analysis due to limited replications. Instead, raw values were presented as recorded for each treatment and sex. Lifespan was expressed in days, counted from the time of adult emergence until death.

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CHAPTER FOUR

LARVAL FEEDING PREFERENCES OF THE GROUNDNUT LEAF MINER ON GROUNDNUT, SOYBEAN AND HAIRY INDIGO

Abstract

The groundnut leaf miner (GLM) (*Bilobata subsecivella*) is a major pest of legume crops, including cultivated species like groundnut and soybean, as well as wild species such hairy indigo. Understanding the feeding behaviour of GLM larvae on different host plants is crucial for developing effective integrated pest management strategies. The primary objective of the study was to determine the preferred host plant for GLM larval feeding among groundnut, soybean and hairy indigo. The feeding preferences of GLM larvae were assessed in five experimental trials using non-choice, two-choice and three-choice assays involving the three host plants. Results indicated that all host plants were preferred by GLM for feeding, although the extent of defoliation varied. Groundnut showed broader blotch formations, hairy indigo showed predominantly linear mines, while soybean displayed intermediate mines characteristics. These variations in feeding patterns suggest that while all host plants are suitable for feeding, the intensity of feeding is influenced by the structural and defensive characteristics of each host plant. Future research should focus on exploring the specific chemical and structural traits of these host plants that affect larval feeding intensity, which may provide insights for sustainable management of GLM.

Keywords: Groundnut leaf miner, host preference, larval feeding, legumes

4.1 Introduction

The groundnut leaf miner (GLM) is a major pest affecting legume crops such as groundnut (*Arachis hypogaea*) and soybean (*Glycine max*) (Okello *et al.,* 2010). The larval stage of this pest is known for causing considerable foliar damage, significantly reducing leaf area and compromising the photosynthetic capacity of the plant, ultimately limiting yield potential (Kenis and Cugala, 2006; Islam *et al.,*1983). Groundnut leaf miner is distributed across South and Southeast Asia, Africa and Australia, with its geographic range expanding in recent decades. In Asia, the pest is prevalent in India, Pakistan, China, the Philippines, Indonesia, and Sri Lanka and in Africa, GLM was first reported in Uganda in 1998 (Epeiru, 2004), and its presence has since been confirmed in several other African countries, including Malawi, Uganda, Kenya, Mozambique, Democratic Republic of Congo, and South Africa (Kenis and Cugala, 2006). (Kenis and Cugala, 2006). In South Africa, the first reported outbreak occurred in the Northern Cape Province during the 1999–2000 cropping season. Remarkably, within that single season, the pest spread rapidly across the entire groundnut production region of the country (Du Plessis *et al.,* 2011). The aggressive spread and high infestation of GLM pose a significant threat to groundnut and soybean, thereby posing broader implications for food and nutritional security across the African continent.

According to Shanower *et al*. (1993), newly hatched first-instar larvae of GLM feed by penetrating the epidermis to access the mesophyll. During the early instars, larvae typically create serpentine mines, which gradually expand into blotches as they develop. In later instars, larvae exit the mines and bind two leaflets together with silk to construct protective shelters (Buthelezi *et al.,* 2021). Larval feeding preference is largely influenced by the suitability of the host plant for growth and development (Okello *et al.,* 2016). This behaviour is a critical determinant of the pest's survival and performance on a given host crop.

Host selection and feeding behaviour in GLM are influenced by a combination of chemical cues, physical characteristics of the plant, and prevailing environmental conditions (Crane *et al.,* 2022). This chapter presents the results of a study conducted to evaluate the feeding preferences of GLM larvae on three leguminous host plants:

groundnut, soybean and hairy indigo. The objective of this study was to determine the preferred host plant for GLM larval feeding among groundnut, soybean and hairy indigo

4.2 Materials and Methods

4.2.1 The GLM specimens and host plant material for feeding trials

The feeding trials were conducted from 22 March to 16 May 2025. A total of five feeding trials were conducted to evaluate the feeding performance of GLM larvae. Three host plant species were used, namely groundnut, soybean, and hairy indigo. Details of their cultivation and management are provided in Chapter Three. In summary, all three host species were grown in greenhouse tunnels at the Wellington Campus. Groundnut was cultivated for both GLM rearing and feeding experiment, while soybean and hairy indigo were grown solely for experimental purposes. Leaves were collected at the 5-6 weeks after crop emergence, this stage was considered because it has been reported that literature that GLM infestation on groundnut starts from 5-6 weeks coinciding with the flowering stage (Buthelezi *et al.,* 2021). The insect population used in these trials originated from field-collected individuals in Manguzi, northern KwaZulu-Natal, and was maintained in a laboratory colony at the CPUT entomology facility, as described in Chapter Three.

The experimental design consisted of different host choice setups: non-choice (larvae restricted to one host plant), Two-choice (larvae offered two hosts plant simultaneously), and Three-choice (larvae given access to all three host plants at once). Trials One and Trial Two were conducted using only Non-choice and Three-choice setups, whereas Trials Three, Trial Four and Trial Five incorporated all three setups: Non-choice, Two-choice, and Three-choice. In Trial One and Trial Two, larvae from the original Manguzi field population were used, specifically instars three to four. In Trial Three, Trial Four and Trial Five, larvae were obtained from the third laboratory-reared generation, with third to fourth-instar larvae selected for testing. Each treatment was replicated four times to ensure reliability of the results.

4.3 Experimental Setup

Third- and fourth-instar larvae were removed from groundnut leaves in breeding cages to obtain the population required for the feeding experiment. A total of 24 larvae were collected and placed in a large Petri dish (145 mm × 20 mm), which was then kept inside a closed cage to prevent escape during a three-hour starvation period prior to the experiment (Salgado *et al.,* 2022). Fresh leaf cuttings from the host plants were prepared, and circular paper towels cut to fit the petri dishes were placed at the bottom to maintain leaf moisture. All dishes were clearly labelled.

One GLM larva was placed in the middle of each petri dish (60 mm × 13 mm), which were sealed and placed in small breeding cages (30 × 30 × 30 cm) to prevent escape. Following the starvation period, larvae were introduced into the labelled petri dishes with leaves for feeding. For the choice experiment, five large Petri dishes (145 mm × 20 mm) were used to accommodate leaves from all host plants regardless of size. One larva was introduced per dish, which was then sealed and placed in a large breeding cage for the duration of the feeding period (Figure 4.1). The experiment included both choice and non-choice setups, each replicated four times. For both experimental setups, each of the three host plants was replicated four times.

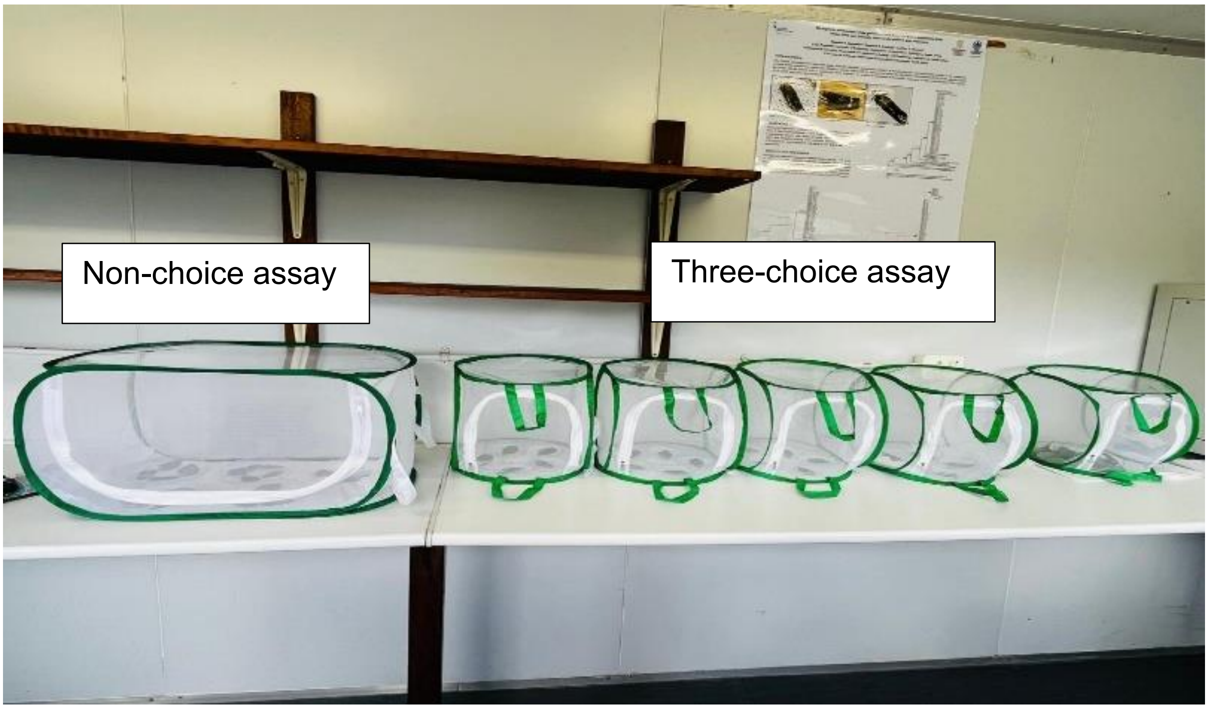

Figure 4.1: Experimental setup for the feeding experiment for both choice and non-choice.

4.4 Data Collection

Data on larval feeding were collected after 24 hours to evaluate feeding behaviour. Host plant leaves were carefully inspected for GLM feeding symptoms, including blotches, mines and feeding positions. Additionally, Bio-Leaf mobile application was used to measure leaf area and percentage defoliation digitally, providing a more accurate and non-destructive assessment of leaf surface available for feeding (Mendez *et al.* 2020). Photographs of both the upper and lower surfaces of each leaf were taken before and after feeding to document visible feeding symptoms.

4.5 Data Analysis

All data collected were subjected to analysis of variance using SPSS statistical software (version 27). Mean separation was done using the least significant difference (LSD) at 90% confidence level. Significant differences are presented in graphs and tables, with different letters indicating the highest and lowest significance levels, respectively. Means containing similar letters are not significantly different.

4.6 Results and Discussion

4.6.1 Larval feeding symptoms on host plants

The feeding patterns of GLM larvae varied across different host plants, indicate their potential to cause significant damage. As shown in Figure 4.2, larvae on hairy indigo fed primarily within the leaf tissue, creating narrow serpentine mines. On groundnut, feeding symptoms were serpentine mines and blotches on the upper of the leaves.
On soybean, the feeding pattern was like that observed on groundnut, although it was less distinct. Larvae penetrated the epidermis to reach the mesophyll tissue, with the damage appearing more visible on the lower surface of the leaf. These findings are consistent with Buthelezi *et al.* (2013), who also conducted research on the infestation of leguminous host plants including, groundnut, soybean, pigeon pea, lucerne and lablab. Soybean showed to be the most preferred host plant with highest infestation with serpentine mines and blotches as GLM larvae injury symptoms on groundnut and soybean.

Similarly, in the current feeding experiment, both soybean and groundnut supported significantly higher levels of leaf defoliation compared to hairy indigo, which recorded minimal feeding damage. The ability of GLM larvae to successfully progress through their instars across leguminous host plants indicates that while GLM larvae can feed on alternative hosts, soybean and groundnut provide higher nutritional quality that support larval growth and survival as shown in Figure 4.2. This suggests that both under field conditions and in controlled experiments, soybean and groundnut remain the most suitable and preferred hosts for GLM feeding.

Notable differences emerged in relation to the feeding results among the three host species. While hairy indigo sustained restricted, linear mines, groundnut exhibited broader blotch formation, suggesting a higher level of susceptibility. Soybean damage was intermediate, with webbing of the leaves and mines less visible but still present on the lower leaf surface. Such variation indicates that feeding location and intensity depend on the structural and defensive characteristics of each host plant.

The preference for groundnut and the distinct pattern of tissue consumption has practical implications for pest management as shown in Figure 4.2. These observations could inform strategies such as selecting resistant cultivars, as well as optimizing control measures to target critical larval stages before extensive blotching occurs. In GLM feeding, no specific studies have been reported in the literature apart from general descriptions of injury symptoms under infestation. Literature detailing these symptoms is more relevant to the infestation experiment, where progression of damage is measured.

Figure 4.2: GLM larval feeding symptoms on A (hairy indigo), B (groundnut) and C (soybean) at 24 hours duration after GLM larvae introduction.

4.6.2 Feeding Trial One and Trial Two: Non-choice and Three choice setups

The results from Trial One (Non-choice) and Trial Two (Three-choice) consistently demonstrated that GLM larvae are generalist feeders. In the non-choice assay, there were no statistically significant differences in defoliation among the three host plants (Tables 4.1 and 4.2). This indicates that when larvae were restricted to a single host, they fed equally on all three host plants, suggesting that they can utilise each species as a food source. Similarly, in the Three-choice experiment, where larvae were given simultaneous access to all three host plants, there were no statistically significant differences in defoliation (Tables 4.1 and 4.2). This finding further confirms that GLM larvae do not exhibit a clear feeding preference for a specific host when multiple options are available. The larvae fed on all three host plants, reinforcing their generalist feeding behaviour even when unconstrained which aligns with what Buthelezi *et al.* (2013), found on GLM host plant comparison study which reported that groundnut, soybean and hairy indigo were GLM host plants

However, in the Three-choice assays, the results for leaf area consumed were statistically different, which could be attributed to variations in host leaf size, structure, or palatability. This finding aligns with studies on *T. absoluta* larvae, which feed on all available hosts in non-choice setups, but exhibit clear preference patterns in choice assays (Archives and Blog, 2025). This suggests that feeding intensity reflects both host availability and suitability, indicating that GLM larvae can feed on multiple legumes if restricted. Consequently, cropping strategies such as monoculture or mixed cropping may influence infestation levels. For GLM feeding, no specific studies have been reported in the literature apart from general descriptions of injury symptoms under infestation.

Table 4.1: Effect of GLM larval feeding on groundnut, soybean and hairy indigo under non-choice and three-choice for Trial One.

	Non-choice		Three-choice	
Treatments	Leaf area	Defoliation %	Leaf area (cm^2)	Defoliation %
Groundnut	9.95 ± 3.24^a	0.82±1.45^a	5.92±4.30^b	0.73±0.81^a
Soybean	10.28 ± 1.21^a	0.15±0.12^a	10.63±1.20^a	0.03±0.65^a

Hairy indigo	10.17 ± 2.24^{a}	0.27±0.4^{a}	12.26±1.31^{a}	0.00±0.00^{a}
LSD	NS	NS	4.71±3.10	NS

Mean ± SE of leaf area(cm^{2}) defoliation percentage in non-choice and three choice combination. NS- stand for Not significant.

Table 4.2: Effect of GLM larval feeding on groundnut, soybean and hairy indigo under non-choice and three-choice for Trial Two.

	Non-choice		Three-choice	
Treatments	Leaf area	Defoliation %	Leaf area (cm^{2})	Defoliation %
Groundnut	10.07±1.16^{a}	0.17±0.11^{a}	12.25± 0.96^{a}	0.02± 0.04^{a}
Soybean	10.71±1.09^{a}	0.07±0.11^{a}	9.27± 0.80^{b}	0.04± 0.09^{a}
Hairy indigo	11.15±2.80^{a}	0.15±0.16^{a}	13.44±1.51^{a}	0.04± 0.09^{a}
LSD	NS	NS	2.98±0.16	NS

Mean ± SE of leaf area(cm^{2}) defoliation percentage in non-choice and three choice combination. NS-stand for Not significant.

4.6.3 Feeding Trial Three to Trial Five: Non-choice and Three-choice setups

In Trials Three, Four, and Five, GLM larvae were evaluated on three host plants: groundnut, soybean, and hairy indigo under both non-choice and three-choice conditions. Under non-choice conditions, larvae fed on all three host plants with no statistically significant differences in leaf area consumed across the three trials (Tables 4.3, 4.4 and 4.5). This indicates that when restricted to a single host, GLM larvae can feed and survive equally well on groundnut, soybean, and hairy indigo. In Trial Three, defoliation percentages were low and not statistically significant, while in trial four a significant difference was detected, with groundnut recording higher defoliation compared to soybean and hairy indigo (Table 4.3). In contrast, Trial Five again showed no significant differences, with defoliation remaining low across hosts. These findings suggest that GLM larvae can feed across all host plants, although minor differences in susceptibility may emerge due to factors like leaf structure or palatability.

Under choice conditions, the feeding responses were more variable. In Trial Three, significant differences in leaf area consumed were observed, with hairy indigo supporting the highest feeding, while groundnut and soybean recorded lower values (Table 4.3). The current study showed that GLM has a significant capacity to reduce leaf area through defoliation, which may negatively affect the available photosynthetic area. Shanower *et al.,* (1993) found that a reduction in the photosynthetically active leaf area can lead to a decline in photosynthetic capacity, ultimately affecting biomass accumulation. All feeding Trials were limited to 24 hours, which was too brief to capture advanced stages of infestation.

Table 4.3: Effect of larval feeding on groundnut, soybean and hairy indigo under non-choice and three-choice for Trial Three.

	Non-choice		Three-choice	
Treatments	Leaf area	Defoliation %	Leaf area	Defoliation %
Groundnut	9.82± 2.10^a	0.27± 0.44^a	8.58±1.31^b	0.23±0.39^a
Soybean	8.85± 1.52^a	0.41± 0.38^a	9.09±1.54^b	0.03±0.65^a
Hairy indigo	10.99± 3.16^a	0.25± 0.40^a	12.79±2.17^a	0.03±0.29^a
LSD	NS	NS	0.51±0.23	NS

Mean ± SE of leaf area(cm^2) defoliation percentage in non-choice and three choice combination. NS- stand for Not significant.

In contrast, Trial Four showed no significant differences in leaf area, only in defoliation (Table 4.4), While Trial Five showed no significant differences in either treatment. This variation across Trials suggests that while larvae may display emerging preferences under certain conditions, these preferences are not consistent and may be influenced by experimental factors such as plant condition and larval stage. These results are consistent with previous research on polyphagous Lepidoptera, such as *Spodoptera frugiperda* (Fall armyworm), where larvae readily feed on multiple hosts under restricted conditions, but may show fluctuating preferences when given choices (Volp *et al.,* 2022). The results have important implications for pest management. Since GLM larvae can feed on groundnut, soybean, and hairy indigo under both non-choice and choice conditions, this suggests that relying on monoculture of a single crop may not reduce the risk of infestation. Similarly, intercropping with other legumes such as soybean or hairy indigo may sustain GLM populations rather than acting as a repellent.

Overall, these findings highlight the adaptability of GLM larvae to diverse leguminous hosts and emphasize the need for pest management approaches that consider their ability to exploit multiple crops. All feeding trials were limited to 24 hours, which is too brief to capture advanced stages of infestation.

Table 4.4: Effect of larval feeding on groundnut, soybean and hairy indigo under three-choice for Trial Four.

Non-choice			Three choice	
Treatments	Leaf area	Defoliation %	Leaf area	Defoliation %
Groundnut	9.01± 1.12^{a}	0.33±0.22^{b}	9.90± 1.28^{a}	0.01± 0.03^{a}
Soybean	10.15±1.27^{a}	0.17±0.15^{ab}	9.18± 2.54^{a}	0.56± 1.07^{a}
Hairy indigo	14.39±2.66^{a}	0.18±0.21^{a}	9.71± 1.87^{a}	0.24± 0.24^{a}
LSD	NS	0.01±0.06	NS	NS

Mean ± SE of leaf area(cm^{2}) defoliation percentage in non-choice and three choice combination. NS- stand for Not significant.

Table 4.5: Effect of larval feeding on groundnut, soybean and hairy indigo under non-choice and three-choice for Trial Five.

Non-choice			Three choice	
Treatments	Leaf area	Defoliation %	Leaf area	Defoliation %
Groundnut	9.89 ± 1.70^{a}	0.23 ± 0.19^{a}	9.18 ± 2.06^{a}	0.10±0.16^{a}
Soybean	8.97 ± 2.42^{a}	0.51 ± 0.54^{a}	10.10 ± 2.44^{a}	0.13±0.17^{a}
Hairy indigo	10.26 ± 2.60^{a}	0.32 ± 0.51^{a}	10.88 ± 2.92^{a}	0.06±0.72^{a}
LSD	NS	NS	NS	NS

Mean ± SE of leaf area(cm^{2}) defoliation percentage in non-choice and three choice combination. NS- stand for Not significant.

4.6.4 Feeding Trial Three- Feeding Trial Five: Two-choice assay

Table 4.6 presents the average values of leaf area and defoliation percentage for feeding Trial Three-feeding Trial Five trial under Two-choice assays. Although statistical analysis was conducted, the results did not indicate whether the observed differences were statistically significant, because post hoc comparisons were not performed due to the limited number of replicates. Groundnut, in the groundnut–hairy indigo combination, recorded the highest mean leaf area (12.24 cm²), followed closely by hairy indigo in the same pairing, while soybean displayed the lowest mean leaf area in the soybean-hairy indigo combination. Even without statistical confirmation of significance, the trends are biologically meaningful because groundnut could be at higher risk of feeding damage, while hairy indigo may be less preferred. Defoliation percentages showed a different pattern. Groundnut in the groundnut–soybean combination, while maintaining relatively high leaf area, experienced the greatest feeding damage, with a defoliation percentage of 40% across the three trials. Soybean in the soybean–hairy indigo combination also showed elevated defoliation (37%). These patterns suggest that, even without confirmed statistical differences, groundnut was generally more susceptible to feeding, soybean was moderately affected, and hairy indigo was least preferred. It highlights the need for experiments with larger sample sizes more statistical approaches to confirm whether these observed differences are truly significant. This suggests pest management should prioritise groundnut protection, but further replicated trials are needed to verify the results.

Table 4.6: Effect of larval feeding on groundnut, soybean and hairy indigo under non-choice and three choices for Trial Three- Trial Five

Choice combination	Treatment	Leaf area	Defoliation %
Choice 1+2	Groundnut	11.05 ± 4.69	0.12 ±0.14
	Soybean	12.53 ± 2.40	0.03 ±0.06
Choice 1+3	Groundnut	12.86 ± 2.26	0.03 ± 0.06
	Hairy indigo	10.68 ± 1.02	0.01± 0.02
Choice 2+3	Soybean	9.37 ± 1.02	0.26 ± 0.16
	Hairy indigo	10.08 ± 2.63	0.06 ±0.13

The results were statistically analysed but post hoc analysis for results significance was not done.

4.7 Conclusion

The results showed that GLM larvae can feed on all three host plants tested. Under non-choice assay, larvae fed equally across hosts, which confirms that GLM larvae could be generalist feeders, while under choice, difference on the feeding behaviour was observed, with hairy indigo and groundnut having higher levels of leaf area consumption in certain trials. These findings directly address feeding preferences and host suitability, showing that while GLM larvae can utilize diverse legume hosts, their performance varies with host plant structure, leaf traits, and availability. The results have important implications for pest management, suggesting that reliance on either monoculture or intercropping with other legumes may not effectively limit GLM larvae feeding. Instead, management strategies should consider the adaptability of GLM to multiple host plants, emphasizing the need to integrate resistant cultivars, crop rotation, and targeted control of larval stages before extensive leaf damage occurs. Future research should investigate the chemical, nutritional, and structural traits of host plants that influence feeding behaviour, linking feeding intensity to physiological impacts such as photosynthesis, biomass, and yield loss will provide a more comprehensive understanding of GLM-host interactions and support the development of sustainable, integrated pest management strategies.

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CHAPTER 5

OVIPOSITION PREFERENCES AND THE RESULTING INFESTATION BY THE GROUNDNUT LEAF MINER ON GROUNDNUT, SOYBEAN AND HAIRY INDIGO

Abstract

The groundnut leaf miner (GLM) (*Bilobata subsecivella*) is a highly destructive pest of groundnut and soybean. This study investigated the oviposition preferences, infestation levels and adult GLM longevity among three different host plants: groundnut, soybean, and hairy indigo, using non-choice and three choice assays. The objectives were to compare GLM infestation levels on the three host plants and evaluate the oviposition preferences of female GLM. In the oviposition trials, both non-choice and three choices assays indicated that soybean was the most preferred host plant for egg-laying. However, soybean was not a suitable host for subsequent infestation and larval performance due to early defoliation. In contrast, groundnut was the most preferred host for infestation and successful larval performance across all trials. Hairy indigo was the least preferred host for oviposition, but was able to sustain larval development, and it was the only host plant on which adult GLM emerged, indicating successful development to the adult stage. The findings of this study revealed a mismatch between oviposition preference and larval performance for the GLM. This emphasises that host plant suitability is strongly influenced by the outcomes of infestation and larval success. Further research is needed to explore the chemical and structural cues of each host plant that drives oviposition and infestation levels.

Key words: Groundnut leaf miner, infestation, larval performance, longevity oviposition,

5.1 Introduction

The groundnut leaf miner (GLM) (*Bilobata subsecivella,* Lepidoptera: Gelechiidae) is a highly destructive pest of leguminous crops, notably groundnut (*Arachis hypogaea*) and soybean (*Glycine max)* and others across South and Southeast of Asia (Shanower *et al.,* 1993). In Africa, GLM was first reported in Uganda in 1998 (Epeiru, 2004), and its presence has since been confirmed in several other African countries, including Malawi, Uganda, Kenya, Mozambique, Democratic Republic of Congo, and South Africa (Kenis and Cugala, 2006). In South Africa, the first reported outbreak occurred in the Northern Cape Province during the 1999–2000 cropping season (Du Plessis *et al.,* 2011). Remarkably, within that single season, GLM spread rapidly across the entire groundnut production region of the country (Du Plessis *et al.,* 2011). The aggressive spread and infestation of GLM pose a significant threat to the productivity of groundnut and soybean, and by extension, to food and nutritional security across the African continent.

The GLM crop damage symptoms include distorted, blotched leaves with visible mining trails, webbed or folded leaflets, and in severe cases, early leaf senescence and defoliation. This reduction in the photosynthetically active leaf area may result in up to a 30% decline in photosynthetic capacity, ultimately affecting biomass accumulation, pod development, and overall yield (Shanower *et al.,* 1993b). Groundnut and soybean crops are particularly vulnerable to severe GLM infestation during critical growth stages, leading to stunted growth, reduced pod set, and economic yield losses (Shanower *et al.,* 1993b). The severity of damage is influenced by seasonal variations, crop growth stage and pest population density. Infestations are often more pronounced in crops may be subjected drought stress due to environmental conditions, as water-deficient plants tend to be more susceptible to GLM attack. Additionally, early in the cropping season, injury is generally localised to the leaf margins, whereas later in the season, entire leaves may become necrotic, dry, and defoliated, exacerbating yield losses (Murithi *et al.,* 2019). Groundnut leaf miner infestations are associated with substantial yield losses in groundnut and soybean production across India and Africa (Ibanda *et al.,* 2018). Yield losses vary depending on infestation severity, but in extreme cases, complete (100%) crop loss has been reported, particularly in South Africa, Mozambique, and Uganda (Ibanda *et al.,* 2018;

Buthelezi *et al.,* 2013). Beyond direct yield reductions, GLM infestations increase production costs by necessitating additional pest control measures and, in extreme cases, replanting. The economic impact extends to rural livelihoods, particularly for smallholder farmers who rely on groundnut and soybean as cash crops and dietary staples (Ibanda *et al.,* 2018). The pest's growing prevalence highlights the urgent need for sustainable, cost-effective control strategies to mitigate financial losses and maintain food security. The objectives of the study were to evaluate the oviposition preferences of female GLM on groundnut, soybean and hairy indigo and compare GLM infestation levels on these crops.

5.2 Materials and Methods

5.2.1 Study material

The research activity of oviposition and infestation trials were conducted from 22 May to 16 June 2025. The main population was collected in Manguzi and reared as mentioned in (Chapter Three). Oviposition and infestation experiment were conducted using third generation reared GLM. The first experiment conducted was oviposition with infestation experiment being the continuation of oviposition experiment, conducted at a laboratory at the 30˚C and humidity of 65- 80% (

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CHAPTER THREE). Larvae were sexed visually based on visible morphological characters observable with the naked eye, while pupae were examined under a stereomicroscope give specifics of focus) to distinguish males from females using genital and abdominal features, following Van der Walt *et al.* (2008), with representative images of male and female individuals from the current study population shown in Figure 5.1. Groundnut leaf miner larva and pupa were separated by sex, kept separately until adult moths emerged to be able to pair (male–female) prior to inoculation to ensure controlled and standardized infestations. Sexing of the GLM population was necessary prior the experiments to ensure controlled mating. All plants that were used for both experiments were grown and maintained at the greenhouse tunnel as mentioned in Chapter Three.

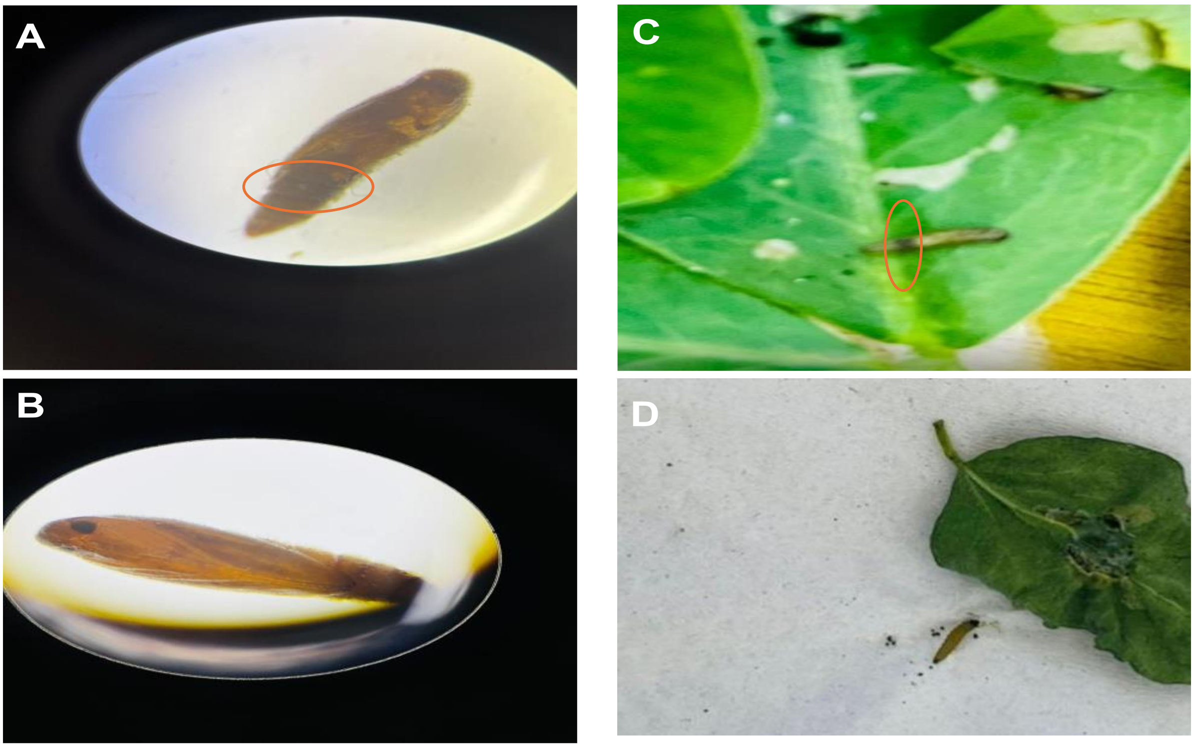

Figure 5.1. Distinguishing features of male and female GLM pupae and larvae. (A) male pupa, (B) female pupa, (C) male larvae, and (D) female larvae, illustrating distinct morphological differences between sexes and stages.

5.3 Experimental Setup

5.3.1 Oviposition experiment

The oviposition experiment had Two Trials which included Non-choice and Three choice assays as shown in Figure 5.2. Two sexed pairs of GLM adults (one male and one female per pair) were introduced into individual non-choice net cages (46 × 56 cm), each containing one of the three host plants. The setup was replicated four times under controlled conditions at 30 °C with a relative humidity of 65-80%. Under Three-choice assay, three pairs of sexed adults were introduced into the cage (58×58×142cm), where plants were spaced 15 cm apart. Daily observations started from the initial day of experiments until day three where eggs were observed in all host plants in each experimental assay. Adults were fed with a 10% honey water solution to prolong their lifespan and maintain normal reproductive activity, as recommended in previous studies of Lepidoptera (Harvey *et al.,* 2012; Pinheiro *et al.,* 2015).

Figure 5.2: Experimental setup for oviposition and infestation trials

5.3.2 Infestation experiment

Infestation experiment was carried out from continued observations of oviposition to monitor larval hatching, with the primary purpose of assessing host plant suitability and larval establishment for subsequent trials. The host plants used were groundnut, soybean, and hairy indigo, maintained under controlled cage environments as previously mentioned in Chapter Three. Daily observations were conducted to record the initial feeding symptoms, which appeared as small whitish dots on the adaxial surface of the leaves.

5.4 Collection of Data

5.4.1 GLM oviposition data

Oviposition daily observations were conducted with data were collected daily over a 72-hour period, but egg counts were conducted once at the end of the 72-hour interval. This approach minimised disturbance of the female GLM moths during active egg-laying and ensured an accurate, cumulative assessment of total oviposition. The primary parameter recorded was the number of eggs laid per plant, counted across all plant structures, including leaves, petioles, and stems, to fully characterize spatial oviposition behaviour. To enhance egg visibility, a smartphone magnifying lens was used to capture zoomed images, after which eggs were manually counted. Data were counted per leaf and added to make the total for the whole plant to aid visual identification. The use of a magnification-assisted approach was necessary to ensure accurate counts, given the small size of GLM eggs.

5.4.2 Infestation data

Infestation data were first recorded on day 7 from the start of the experiment, with subsequent scouting intervals at 14 and 21 days. At each interval, several parameters were assessed: the total number of leaves per plant, the number of infested leaves per plant, and the number of mines per plant. Infestation levels were assessed by visually inspecting each plant and recording the presence of characteristic leaf mines produced by GLM larvae.

These parameters were measured to evaluate host plant suitability, infestation intensity, and adult survival in all treatments. Observations were conducted manually on each plant, with careful visual inspection of leaves to count mines and assess infestation levels. In addition, the longevity of GLM adults was recorded per trial separately for each sex, with the average number of days per treatment calculated.

5.4.3 Longevity of the GLM adult

The data on adult GLM infested leaves were collected from all treatments in both Trial One and Trial Two of the infestation experiment. From each treatment, second to fifth instar larvae were removed, sexed, and reared on groundnut leaves according to their sex and treatment group. The number of larvae per treatment was counted and recorded, and observations continued until pupation. All pupae were then transferred from the groundnut leaves into separate closed cages according to their sex and treatment to allow adult emergence. Newly emerged adults were provided with a 10% honey–water solution, and their lifespan was monitored daily. Longevity was recorded separately for each sex and treatment from the first day of emergence of moths until all adults had died.

5.5 Data Analysis

All experimental data were subjected to statistical analysis using SPSS software (version 27). The number of eggs laid, number of leaves, number of infested leaves and number of mines were compared across host plants. One-way analysis of variance (ANOVA) was used to test for statistically significant differences among means. Where significant differences were detected ($p < 0.05$), Least Significant Difference (LSD) test was applied for post hoc multiple comparison of treatment means. All the GLM longevity data were not subjected to statistical analysis due to limited replications. Instead, raw values were presented as recorded for each treatment and sex. Lifespan was expressed in days, counted from the time of adult emergence until death.

5.6 Results and Discussion

5.6.1 Groundnut leaf miner oviposition on groundnut, soybean and hairy indigo

The oviposition patterns of female GLM moths were observed on groundnut, soybean, and hairy indigo until larval hatching. As shown in Figure 5.3, GLM females laid small, shiny eggs on the adaxial (upper) side of the leaves, stems and petioles across all the tested host plants. However, distinct differences in oviposition distribution were noted among the host plants. On soybean, most eggs were deposited on the leaf surface. In contrast, eggs were laid more evenly across all plant parts (leaf surface, stems, and petioles) on groundnut. On hairy indigo, eggs were predominantly laid on the leaf surface, but the leaf structure, specifically the presence of dense trichomes or hairs made them difficult to observe without the aid of a smartphone magnifier. According to Shanower *et al.* (1993a), GLM eggs are small, measuring less than 1.0 mm in length, and are typically deposited on the adaxial surface of leaves, stems, and petioles. In the present study, similar oviposition behaviour was recorded across all three host plants, with eggs consistently laid on the adaxial leaf surfaces as well as on stems and petioles, thereby confirming the patterns previously described in the literature.

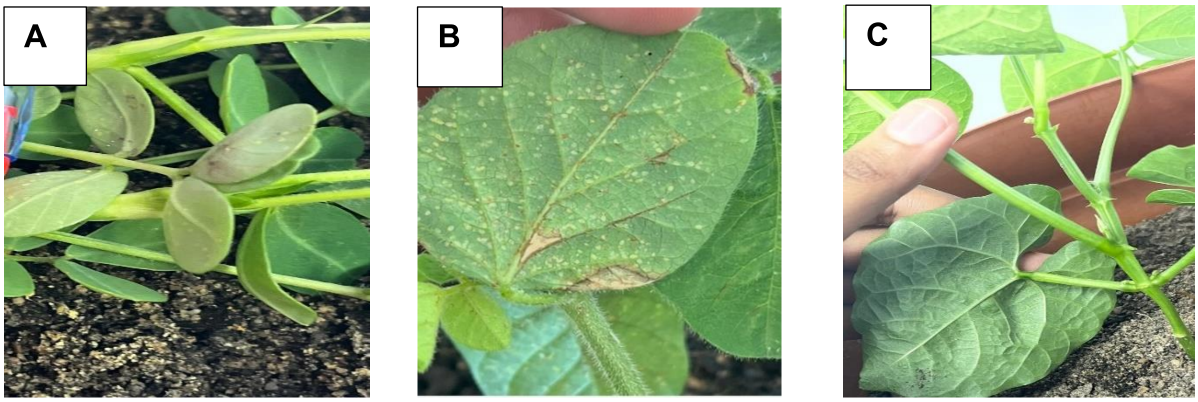

Figure 5.3: Egg deposition patterns of the GLM on each host plant, A (groundnut), B (soybean) and C (hairy indigo).

5.7 Number of Eggs Laid / Oviposition Per Host Plant

5.7.1 Trial One – Non-choice and Three-choice assays

In Trial One, female GLM adults were tested on the same three host plants. In the Non-choice assay the results were statistically significant among the three tested host plants (Figure 5.4). The highest number of eggs were observed in soybean, while the lowest was recorded in hairy indigo. These results suggests that soybean has attractive properties for oviposition compared to those of groundnut and hairy indigo. The Non-choice assay revealed that female GLM has the potential to oviposit in all tested host plants. However, the results demonstrated strong oviposition preference for soybean, even though the leaves could not support larval hatching which led to soybean leaves, yellowing and deteriorating, which means that oviposition preference does not necessarily correlate with larval performance (Figure 5.4). The study conducted by Can *et al.* (2024) on the oviposition preference of the *Spodoptera frugiperda,* showed that host plant suitability for larval development can vary significantly among the host plants, suggesting that *S. frugiperda* females may sometimes choose oviposition sites that are not suitable for offspring survival which correlate with female GLM oviposition behaviour.

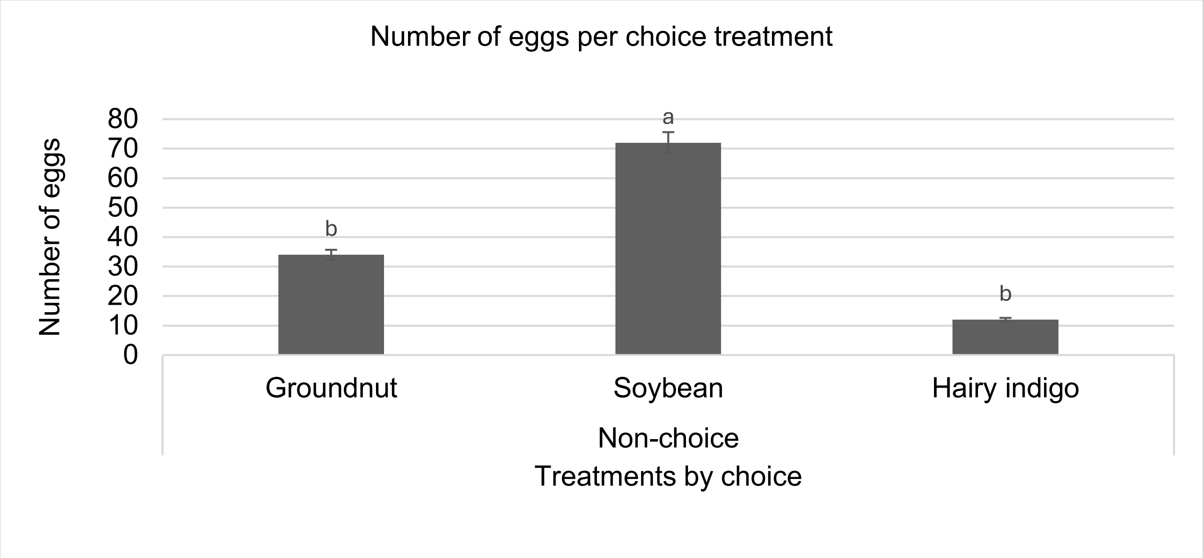

Figure 5.4: Number of eggs laid in non-choice assay, for groundnut, soybean and hairy indigo for Trial One.

Under Three-choice assays in which female GLM was exposed to three host plants simultaneously, the results were not statistically significant in egg laying among the three host plants (Table 5.1). This indicates that under Three-choice assay egg distribution was affected by underlying factors such as chemical cues and morphology of each host plant, Badenes-Pérez *et al.* (2005) studied *Plutella xylostella* and showed that oviposition was influenced by glucosinolate content in Brassicaceae. High concentrations attracted females to lay more eggs, confirming the role of host chemistry in egg distribution. This reinforces that under the choice assay, factors such as host plant chemistry will affect results outcomes will always be there.

Table 5.1: Number of eggs laid by female GLM adult on groundnut, soybean and hairy indigo, under Three-choice assay for Trial One

Treatment	Number of eggs
Groundnut	33.00±26.42^a
Soybean	47.50±36.15^a
Hairy indigo	12.25±5.80^a
LSD	NS

Egg laying preference of GLM on selected host plants under three-choice assay. NS-stand for Not significant.

5.7.2 Trial Two Non-choice and Three-choice assay.

In the Non-choice experiment, where female moths were restricted to a single host plant, a statistically significant difference in oviposition was observed among host plants. Soybean recorded the highest mean number of eggs, followed by groundnut, with hairy indigo receiving the lowest number of eggs (Figure 5.5). This indicates that even when confined to a single host, females preferred to lay eggs on soybean, though all three hosts were utilised.

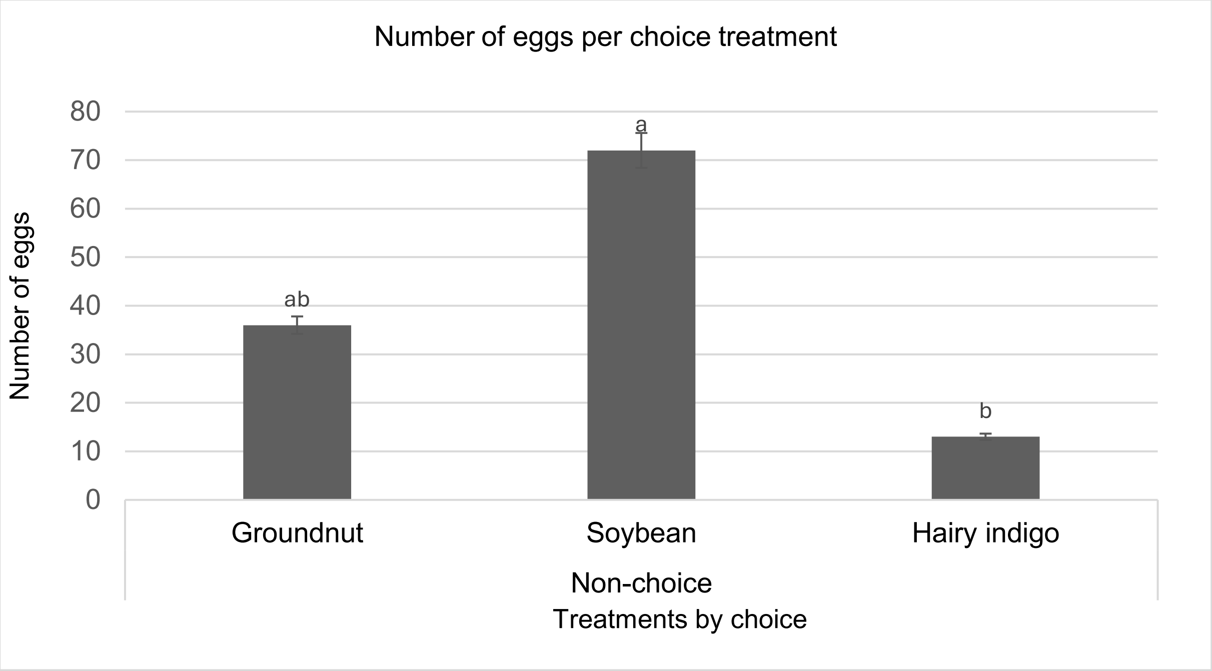

Figure 5.5: Number of eggs in non-choice assay, for groundnut, soybean and hairy indigo for Trial Two.

Similarly, the Three-choice experiment, where moths had access to all three hosts, showed significant differences in oviposition (Figure 5.6). Soybean again supported the highest number of eggs, while groundnut and hairy indigo received fewer eggs. While infestation occurred on all hosts, the oviposition intensity was clearly greatest on soybean. The consistent preference for soybean across both experimental setups suggests that it possesses qualities that make it a highly attractive host for egg-laying. The higher oviposition on soybean may be linked to specific leaf morphology, nutritional quality, or surface chemistry, which are known to influence host selection in

Lepidoptera moths. Lower oviposition on hairy indigo could reflect less suitable chemical cues or tougher leaf structure that deters females from depositing large numbers of eggs. These findings are consistent with earlier results shown in trial one showing that host preference of the GLM female moth is influenced by a host plant and surface characteristics. The results suggest that cropping strategies that include soybean are likely to be more susceptible to GLM infestation due to its higher attractiveness and suitability as an oviposition host. Groundnut, although moderately preferred, may still sustain economically relevant infestations, while hairy indigo may act as a less favourable host. These insights highlight the importance of considering host composition in agroecosystems when designing pest management control.

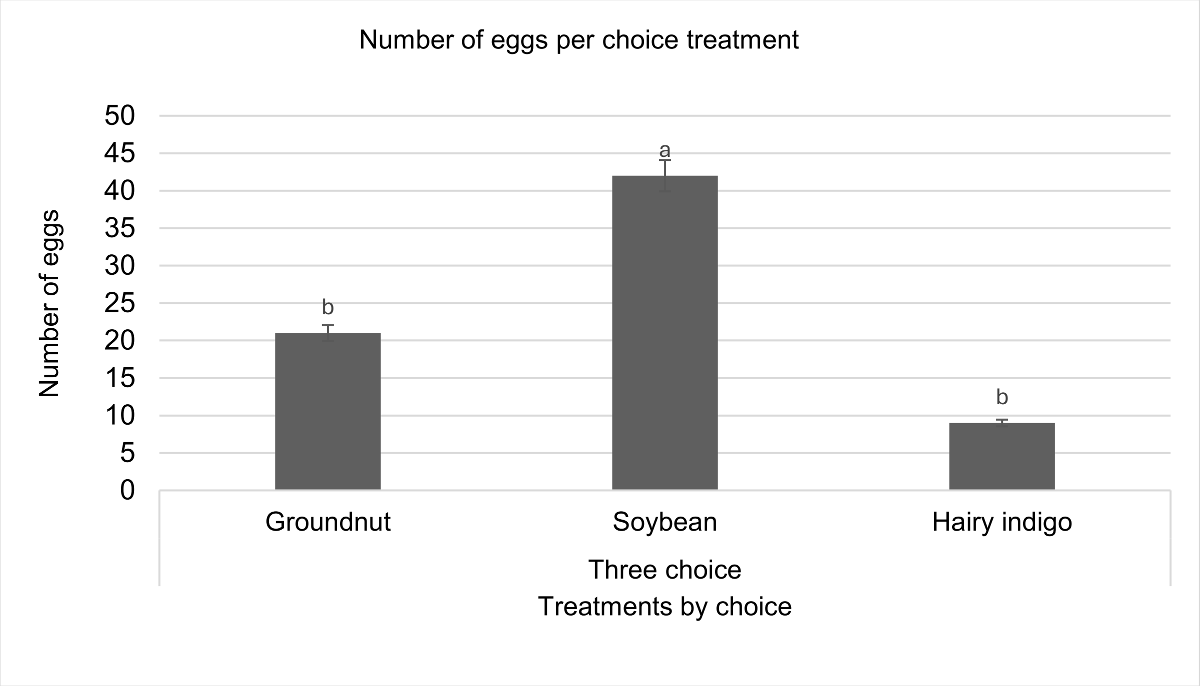

Figure 5.6: Number of eggs in three-choice assay, for groundnut, soybean and hairy indigo for Trial Two.

5.8 Groundnut leaf miner Infestation Symptoms

The infestation pattern of GLM varies across the host plants and highlights their potential damage to cause significant damage. As shown in Figure 5.7, the early symptoms were observed to be whitish small dots on groundnut and hairy indigo, while soybean had brown small dots which enlarge to bigger mines, later blotches. However soybean would deteriorate as the infestation advances, which shows that soybean may not be a suitable host for larval development. Groundnut and hairy indigo showed to be suitable hosts for support of larval development. This shows that female GLM lays eggs on the soybean because of the factors such as the leaf surface chemicals and texture which help in stimulation of oviposition. However, high egg laying does not guarantee that soybean is a suitable host for larval development. These findings are consistent with that of Liu *et al.,* (2012), who reported on the oviposition behaviour and larval success of *Helicorvepa armigera*, that oviposition behaviour and larval success can differ with host plants which highlights a mismatch scenario, where a lepidoptera moth lays loads of eggs in a host plant but the larval performance becomes low.

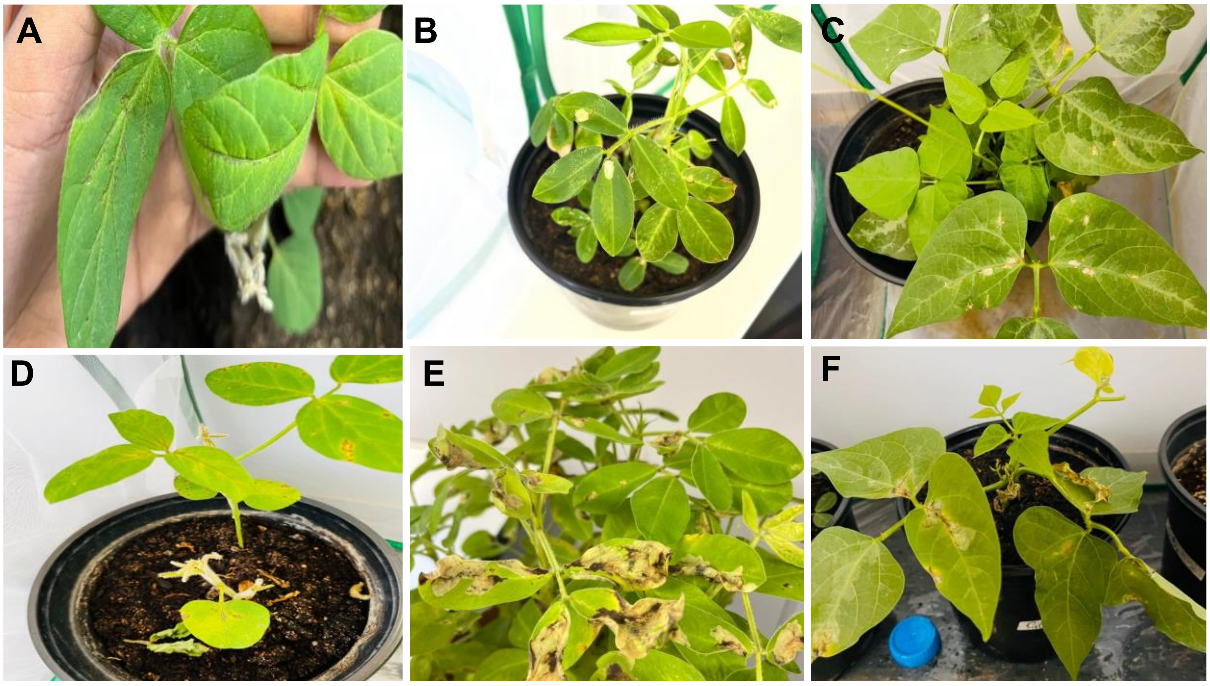

Figure 5.7: GLM infestation symptoms on A (early symptoms of soybean), B (early symptoms of groundnut), C (early symptoms of hairy indigo), D (severe symptoms of soybean), E (severe symptoms of groundnut) and F (severe symptoms of hairy indigo).

5.8.1 Infestation Trial One: Non-choice and Three-choice assays

In Trial One, GLM infestation was tested on three host plants: groundnut, soybean, and hairy indigo, conducted under both non-choice and three-choice assays. The objective was to assess infestation across the three different host plants. In the non-choice assay, the results were statistically significant (Table 5.2). This suggests that when female GLM moths were restricted to a single host plant (non-choice assay), eggs laid on groundnut had the highest hatch success compared to soybean and hairy indigo, indicating better larval performance on groundnut (Table 5.2). Although soybean was sometimes preferred for oviposition, larval survival was lower, highlighting a discrepancy between oviposition preference and larval performance. In the three-choice assay, where females were simultaneously exposed to all three host plants, the results were also statistically significant (Table 5.3). Groundnut again exhibited the highest levels of infestation, while soybean and hairy indigo had significantly lower infestation levels. These results indicate that groundnut is consistently the most suitable host for GLM larval development, regardless of oviposition preference.

Table 5.2: Effect of GLM infestation on groundnut, soybean and hairy indigo, under non-choice assay for Trial One.

Treatment	NL	NI	NM
Groundnut	97.00±37.06^{a}	11.92±8.46^{a}	19.92± 18.85^{a}
Soybean	20.00±3.62^{b}	3.17±1.95^{b}	5.25±3.52^{b}
Hairy indigo	7.50±1.57^{b}	3.50±1.17^{b}	12.00± 13.25^{ab}
LSD	12.50±2.05	0.33±0.78	6.75±9.73

Mean ± SE of NL (Number of leaves), NI (Number of infested leaves) and NM (Number of mines). NS- stand for Not significant.

Table 5.3: Effect of GLM infestation on groundnut, soybean and hairy indigo, under Three-choice assay for Trial One.

Treatment	NL	NI	NM
Groundnut	63.75± 21.36^{a}	17.25 ± 8.73^{a}	30.33 ± 22.2^{a}
Soybean	7.75 ± 4.75^{b}	5.42 ± 3.37^{b}	8.17 ± 10.12^{b}
Hairy indigo	10.75 ± 6.37^{b}	4.58 ± 3.12^{b}	7.42 ± 4.72^{b}
LSD	3.00±1.62	0.84±0.25	0.75±5.40

Mean ± SE of NL (Number of leaves), NI (Number of infested leaves) and NM (Number of mines). NS- stand for Not significant.

These results indicate that GLM larvae can infest multiple leguminous hosts when restricted or exposed to multiple host plants. However, the high infestation intensity on groundnut highlights its greater suitability as the host plant, which may be due to nutritional quality, leaf texture and lower levels of chemical defences compared to soybean and hairy indigo, which suggest further investigation is needed. Buthelezi *et al.* (2013) reported that soybean was the most preferred host, followed by groundnut. Infestation symptoms were also observed on hairy indigo adjacent to heavily infested groundnut and soybean crops, suggesting that hairy indigo may serve as an alternative host. However, it was not determined whether groundnut, soybean, and hairy indigo could support complete GLM development from oviposition to adult emergence. The present study demonstrates that all three host plants can support GLM populations through the full life cycle and are suitable for both oviposition and larval feeding. This reinforces the importance of the host suitability in determining infestation outcomes.

5.8.2 Infestation Trial Two: Non-choice and Three choice assays

In Trial Two, GLM infestation was assessed on three host plants: groundnut, soybean and hairy indigo under non-choice and three choice assays. Under non-choice assay, there was no significant difference observed for the number of infested leaves and the number of mines (Table 5.4), suggesting that all host plants were preferred and that all three host plants could support infestation. Under three-choice assay, when all three hosts were simultaneously available, the results also showed no significant differences in the infested leaves or mined leaves across all hosts, indicating that the GLM larvae population were able to feed and establish on all three host plants when given a choice (Table 5.5). These findings are consistent with a previous study on insect attraction versus plant stage on *Plutella xylostella* by Jaime Badenes-Pérez *et al.* (2014), which provides useful insight. Their study demonstrated that while *P. xylostella* females preferred to oviposit on young leaves, mature leaves failed to support successful larval development. Similarly, the present results reveal that initial infestation does not necessarily translate into sustained larval success. This highlights that oviposition preferences and infestation outcomes may not always align, reinforcing the need for further studies on how plant phenology influences host suitability.

Table 5.4: Effect of GLM infestation on groundnut, soybean and hairy indigo, under non-choice assay for Trial Two.

Treatment	NL	NI	NM
Groundnut	48.00 ± 10.47^a	4.58 ± 2.97^a	6.50 ± 4.95^a
Soybean	14.50 ± 1.57^b	4.17 ± 1.53^a	7.67 ± 3.03^a
Hairy indigo	9.75 ± 1.14^b	3.42 ± 2.87^a	11.42 ± 10.77^a
LSD	4.75±0.43	NS	NS

Mean ± SE of NL (Number of leaves), NI (Number of infested leaves) and NM (Number of mines). NS- stand for Not significant.

Table 5.5: Effect of GLM infestation on groundnut, soybean and hairy indigo, under Three-choice assay for Trial Two.

Treatment	NL	NI	NM
Groundnut	25.00± 8.39^a	4.58± 3.03^a	8.08± 5.32^a
Soybean	6.42± 1.51^b	5.08± 4.94^a	9.25± 6.66^a
Hairy indigo	10.50± 5.74^b	3.00± 1.86^a	7.50± 3.63^a
LSD	18.58±6.88	NS	NS

Mean ± SE of NL (Number of leaves), NI (Number of infested leaves) and NM (Number of mines). NS- stand for Not significant.

5.9 Longevity of the GLM Adult

In the current study, GLM longevity was monitored from the day of the emergence of the moths until the day they died. The moths were fed 10% honey water solution to prolong their lifespan. The GLM moths' longevity recorded was between 6-15 days whereas reports on studies undertaken in India indicated that the GLM adult lifespan varied from 2-17 (Kapadia *et al.,* 1982) and up to 13 days under field conditions (Madhumathi 1992). Furthermore, in those studies the moths were not fed honey but relied only on natural resources available in the field. These observations indicate that the lifespan of GLM does not rely on the feeding diet such as honey, but it may vary with the environmental conditions.

5.10 Conclusion

This study investigated the oviposition preferences, infestation across three host plants: groundnut, soybean, and hairy indigo and adult longevity of the GLM. Results showed that soybean is the most preferred host for oviposition under both non-choice and three-choice assays for both trials, while groundnut consistently supported the highest infestation levels and adult development. Hairy indigo was the least preferred for oviposition but supported some larval development and adult emergence, particularly in the second trial. These findings directly address the study objectives by demonstrating that oviposition preference does not always align with host suitability for larval survival. Soybean, while preferred for oviposition, failed to support successful larval development, whereas groundnut proved to be the most suitable host for infestation. Hairy indigo served as a secondary host with moderate infestation levels, but it was the only host plant to support longevity in Trial Two.

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CHAPTER SIX
CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

The GLM demonstrated significant ecological adaptability capable of feeding and reproducing across all three tested legume host plants: The study's results highlight a critical dissociation between host preference for oviposition and host suitability for offspring performance.

Feeding assays revealed that GLM larvae are generalist feeders when restricted to single hosts (Non-choice assays). This suggests a high capacity for persistence in mono-cropped environments. Under choice conditions, however, feeding patterns shifted, indicating that while generalist, larvae exhibit conditional preferences influenced by factors like host availability. Overall, while feeding varied, no single host was definitively avoided, reinforcing the idea that structural and chemical traits (e.g., leaf toughness, trichomes, or nutrient levels) mediate feeding intensity rather than outright deterrence.

Oviposition and infestation experiments established a clear hierarchy of host suitability and pest risk:

- Soybean was consistently the most preferred host for oviposition across all trials. However, this preference did not translate into larval success as it led to deterioration of soybean, as soybean proved largely unsuitable for larval performance and adult emergence.
- Groundnut emerged as the most suitable and vulnerable host, supporting the highest levels of larval performance, infestation, and adult emergence. This indicates that the actual pest risk for successful population growth is highest on groundnut.
- Hairy indigo functioned as a moderate or alternative host. It was the least preferred for oviposition but still supported moderate larval performance and adult emergence in some trials.

This study underscores the importance of separating behavioural preference from demographic outcome in pest management. While female GLM are strongly attracted to soybean for laying eggs, the high risk of economic damage remains on groundnut due to its superior capacity to support offspring success. These dynamics have direct implications for IPM in legume systems, emphasising the need for targeted strategies that consider both the initial oviposition attractant (soybean) and the ultimate host suitability (groundnut) to achieve sustainable control.

6.2 Recommendations

To strengthen the understanding of GLM feeding and oviposition preferences and their implications for pest management, the following areas of future research should be prioritised:

6.2.1 Expanding host range and chemical ecology

Future studies should focus on the underlying ecological and chemical mechanisms that govern GLM host selection and performance:

- Expand host scope: Broaden the investigation of feeding preferences to include additional host plants, such as other cultivated legumes and wild relatives, to fully map the GLM's feeding range.
- Analyse nutritional profiles: Conduct detailed analysis of the nutritional profiles of different host leaves, focusing on proteins, carbohydrates, and defensive secondary metabolites. This will provide critical insight into how plant chemistry directly influences larval performance and survival.
- Examine chemical cues: Isolate and identify plant volatiles and surface chemistry cues. This is essential for clarifying the mechanisms driving female oviposition behaviour, as chemical signalling is central to insect host selection.

6.2.2 Investigating behavioural dynamics and environmental context

Further research should explore how environmental factors, and temporal patterns influence GLM behaviour:

- Environmental effects on oviposition: Examine GLM female oviposition preference under varying environmental conditions, including temperature, humidity, and light intensity, to understand how climate factors mediate host choice.

- Temporal oviposition patterns: Investigate temporal patterns of oviposition, such as time of day, preferred leaf position (e.g., young versus mature), and the specific crop growth stage, to better characterize oviposition dynamics.

6.2.3 Field validation

- Long-term field studies: To validate the laboratory findings and ensure practical applicability, long-term infestation studies should be carried out under natural field conditions. This is crucial for translating controlled results into effective, real-world IPM strategies.