



Oviposition and Feeding Preferences of the Groundnut Leaf Miner *Aproaerema modicella* (Syn. *Bilobata subsecivella*) (Lepidoptera: Gelechiidae): Current Knowledge and Research Gaps: A Review

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ABSTRACT

The groundnut leaf miner (GLM), *Aproaerema modicella* (syn. *Bilobata subsecivella*) (Lepidoptera: Gelechiidae) is a significant pest of groundnut (*Arachis hypogaea*) and soya bean (*Glycine max*) in Africa and Asia. First recorded in Africa in 1998, GLM has rapidly expanded its range, causing yield losses of up to 100% in severe infestations and posing a growing threat to food security. While research has explored its bio-ecology and management, key aspects of its oviposition behaviour and feeding preferences, particularly the influence of chemical cues and structural traits, remain poorly understood. Understanding these traits is crucial for predicting host plant susceptibility, improving Integrated Pest Management (IPM) strategies and developing resistant cultivars. This review synthesises current knowledge on the oviposition site selection, host plant preference and feeding behaviour of GLM. It highlights critical research gaps and a potential mismatch between female oviposition choice and subsequent larval performance, underscoring the complexity of host suitability. Future research should investigate the underlying mechanisms of host preference and validate findings under diverse agro-ecological conditions.

Key words: *Aproaerema modicella*, *Bilobata subsecivella*, Feeding behaviour, Host plant selection, Integrated pest management, Oviposition preference.

The groundnut leaf miner, *Aproaerema modicella* (syn. *Bilobata subsecivella*) (Lepidoptera: Gelechiidae), is a significant pest of groundnut (*Arachis hypogaea* L.) and soybean (*Glycine max* L.), particularly in Africa and Asia. Originally confined to Asia, GLM was first recorded in Africa in 1998, where it has since spread across multiple countries, including Uganda, Malawi, Kenya, Mozambique, the Democratic Republic of Congo and South Africa (Kenis and Cugala, 2006; Buthelezi *et al.*, 2012). The pest is known by different names across continents: *Bilobata subsecivella* in Africa, *Aproaerema modicella* in Asia and *Aproaerema simplexella* in Australia.

The larval stage of GLM causes the most severe damage, mining leaf tissues and reducing the photosynthetic leaf area by up to 30% (Kenis and Cugala, 2006). This reduction in assimilate production adversely impacts pod filling and overall crop yield, posing a substantial threat to food security in affected regions (Shanower *et al.*, 1993). Infestation levels vary, but in severe cases, losses can be catastrophic, requiring extensive pest management interventions (Du Plessis, 2011).

Groundnut and soybean are economically and nutritionally important crops, serving as key protein sources, income-generating commodities and contributors to soil fertility through nitrogen fixation (Chabi *et al.*, 2021). Among the groundnut cultivars evaluated, K-4, K-1563 and TCGS-341 were found to be susceptible to GLM infestation (Saheb *et al.*, 2015). Soybean cultivars, Namsay 4M, Maksoy 1N,

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Maksoy 2N and Maksoy 4N were classified as moderately susceptible to GLM infestation in a study conducted by Namara (2015). Despite the pest's economic significance, research on its oviposition preferences and feeding behaviour remains limited, particularly in African agroecosystems. A better understanding of these biological traits is crucial for predicting infestation patterns and improving pest management strategies.

This review consolidates available knowledge on the oviposition and feeding behaviour of GLM, incorporating insights from related Gelechiidae species where data are lacking. Additionally, it highlights key research gaps and

proposes future research directions to enhance IPM strategies.

Economic importance of GLM

Groundnut leaf miner infestations are associated with substantial yield losses in groundnut and soybean production across India and Africa (Ibanda *et al.*, 2018). High larval populations result in extensive leaf mining and defoliation, drastically reducing the plant's ability to photosynthesise and, consequently, its productivity. Yield losses vary depending on infestation severity, but in some cases, complete (100%) crop loss has been reported, particularly in South Africa, Mozambique and Uganda (Buthelezi *et al.*, 2013; Ibanda *et al.*, 2018).

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.

Distribution of GLM

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 in South Africa occurred during the 1999-2000 growing season, after which the pest established itself in all major groundnut-producing regions (Du Plessis, 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.

Taxonomy of GLM

Aproaerema modicella 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).

Bio-ecology of GLM

Life cycle

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.*, 1993; 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, 2012). Under optimal field conditions, eggs hatch within three to four days, but at lower temperatures, the incubation period extends to six to eight days (Buthelezi, 2015; Namara *et al.*, 2024).

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.*, 1993; 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 (Rao and Rameshwar, 2013).

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.*, 2021). The pest's ability to complete multiple generations per season contributes to its high reproductive potential and rapid population build-up in favourable environments, making it a persistent threat to legume production.

Crop injury symptoms

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 (Kenis and Cugala, 2006). Groundnut and soybean crops are particularly vulnerable during critical growth stages, with severe infestations leading to stunted growth, reduced pod set and economic yield losses (Shanower *et al.*, 1993). 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 grown 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).

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 [Table 1 adapted from (Buthelezi *et al.*, 2021)]. 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.

Environmental factors influencing GLM population dynamics

Environmental factors such as temperature, humidity and rainfall critically influence the population dynamics of GLM.

Table 1: Host plants of Groundnut leaf miner compiled from literature across its geographic range.

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

A. modicella = Indian groundnut leaf miner; *S. subsecivella*= African groundnut leaf miner.

Temperature, for instance, plays a fundamental role in determining the pest's developmental rate, reproductive capacity and overall survival (Shanower *et al.*, 1993). Studies in Asia have shown that optimal temperatures around 30°C significantly enhance egg production and larval survival, accelerating the life cycle and facilitating multiple generations within a season (Shanower *et al.*, 1993; Buthelezi *et al.*, 2021). Conversely, temperatures below 15°C result in reduced egg production and increased larval mortality. In South Africa, the pest reaches peak population levels during the hottest periods, when high temperatures in conjunction with other favorable conditions allow for rapid population build-up (Van der walt, 2007; Buthelezi *et al.*, 2017).

Humidity also exerts a significant influence on GLM populations. Low humidity typically supports higher infestation levels, as dry conditions promote faster development and may compromise the natural moisture-dependent defenses of host plants (Shanower *et al.*, 1995). In contrast, high humidity appears to suppress pest populations. In regions such as Uganda and South Africa, periods of higher atmospheric moisture are associated with decreased pest incidence, possibly due to enhanced pathogen activity or direct adverse effects on larval survival (Ibanda *et al.*, 2018; Buthelezi *et al.*, 2021).

Rainfall patterns further shape the dynamics of GLM populations by affecting both host plant health and the survival of early life stages. Heavy rainfall disrupts oviposition and increases larval mortality, as evidenced by reduced adult captures in pheromone traps during rainy periods in South Africa (Buthelezi *et al.*, 2017). Conversely, in India, pest populations often surge during dry seasons when moisture stress in host crops makes them more vulnerable to infestation (Shanower *et al.*, 1995). Continuous or excessive rainfall can also negatively impact egg and larval survival, thereby limiting the pest's population growth. Collectively, these interactions among temperature, humidity and rainfall underscore the complex environmental determinants of GLM population dynamics across diverse agro-ecological zones.

Control measures

Cultural control

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.*, 2013). 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). The strategy of using IPM practices such as deep ploughing and using soybean as the trap crop can effectively manage the GLM, which will result in reduced pest incidence and improvement of yield (Agurla *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, sorghum, black gram, pigeon pea, green gram and pearl millet has been shown to substantially reduce infestation levels (Muthiah, 2000; Maitra *et al.*, 2021).

Biological control

Biological control strategies for GLM focus on the utilization 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 Bethyridae 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 (Shanower *et al.*, 1992; Rajagopal *et al.*, 1998). 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.

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.*, 1993). 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).

Genetic plant resistance for GLM

In India, various groundnut breeding lines that are resistant to GLM have been released by ICRISAT, such as ICGV86031, ICGV86699, ICGV87359 and ICGV87940 (Reddy *et al.*, 2020; Buthelezi and Zharare, 2025). These genotypes could be used in breeding programs to develop more resistant groundnut lines in high risk regions (Buthelezi and Zharare, 2025). In soybean, there has been a recorded genotypic variation in resistance, with some breeding lines showing fewer infestation and leaf damage under field conditions, these are VI046160, VI046165 and VI046167 (Namara, 2015). These findings indicate that these breeding lines can be used in breeding programs which aims at developing soybean cultivars that has improved resistance towards the GLM (Ibanda *et al.*, 2018).

Host selection for oviposition and feeding

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). 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; Tao *et al.*, 2024). 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's impact on legume crops. Understanding these interactions is essential for developing targeted pest management strategies, including breeding for resistant cultivars, semi chemical-based interventions and precise timing of control measures.

Factors influencing host plant preference for oviposition in lepidoptera moths

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 (Wang *et al.*, 2023; Tao *et al.*, 2024). 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 *Tuta 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.*, 2012).

Host physical characteristics

Surface texture of the host plant

The surface texture of a plant is crucial because it directly affects the ease of egg attachment and subsequent larval movement. Moths generally prefer smooth or soft surfaces that facilitate egg deposition and promote larval feeding, whereas rough or hairy surfaces often due to dense trichomes or thick cuticles can hinder these processes and may even release deterrent substances (Coapio *et al.*, 2016; Benade, 2022; Prasad, 2022). 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).

Age of the host plant

Plant age is another critical determinant, as it often correlates with nutritional quality and physical condition. Younger plants typically have higher concentrations of essential nutrients like nitrogen and water, making them more attractive for oviposition because they support better larval growth (Wang *et al.*, 2023; Rupngam and Messiga, 2024). Consequently, female moths tend to prefer younger plants to minimize exposure to toxic compounds and maximize larval survival. However, in some cases, certain Lepidoptera may prefer older plants if their larvae have developed specific adaptations to overcome mature plant defences. In regions such as India and South Africa, infestations of GLM on groundnut have been recorded to commence approximately 5-6 weeks after crop emergence, coinciding with the flowering stage, which suggests that this growth stage provides an optimal balance of nutritional benefits and lower defensive compounds (Buthelezi *et al.*, 2013; Rao and Rameshwar, 2013).

Egg deposition site

The site of egg deposition on the host plant is another key factor influencing oviposition. Female moths typically select specific locations, such as the undersides of leaves, stems, or near the plant base, where eggs are better protected from predators, desiccation and environmental extremes like direct sunlight or rainfall (Mutamiswa *et al.*, 2023; Gonçalves *et al.*, 2024). Additionally, the structural characteristics of the plant and the availability of resources for larval development influence this choice. Females often avoid plants that show signs of previous herbivory, as these may indicate resource depletion or a higher risk of predation, thereby ensuring that eggs are laid on hosts that will maximize larval success (Hilker and Fatorous, 2015; Khallaf *et al.*, 2023). Studies have shown that GLM predominantly lays eggs on the undersides of leaves, stems and petioles of groundnut and soybean, strategies that contribute to higher offspring survival rates (Shanower *et al.*, 1993; Kenis and Cugala, 2006; Buthelezi *et al.*, 2021).

Abiotic factors

Abiotic factors, such as temperature, moisture availability, light and soil quality, also play critical roles in influencing oviposition. Temperature affects plant growth and chemical composition, thereby influencing the production of secondary metabolites that can alter host palatability (Senior *et al.*, 2021). Moisture availability influences the physiological state of the plant; well-hydrated plants generally have higher nutrient content and lower levels of defensive compounds, making them more attractive for egg-laying, whereas drought-stressed plants often produce higher levels of deterrents (Nguyen *et al.*, 2024; Seltzer *et al.*, 2024). Light availability can alter plant morphology, with larger, healthier leaves potentially offering better protection and food resources for larvae (Molleman *et al.*, 2020). Additionally, soil quality indirectly affects oviposition by determining the nutrient profile and defensive chemistry of the plant, with

nutrient-rich soils promoting more favourable conditions for larval development (Lev-Yadun *et al.*, 2021; Anttonen *et al.*, 2022).

Biotic factors

Biotic factors, including herbivore-induced plant defences, the presence of natural enemies and competition among herbivores, further refine oviposition choices. Plants that have experienced herbivory often activate chemical defences, such as the production of secondary metabolites and the release of VOCs, which can deter further egg deposition (Coapio *et al.*, 2016; Volp *et al.*, 2022). The presence of predators and parasitoids also influences oviposition, as females tend to avoid plants that are frequented by these natural enemies, thereby reducing the risk of larval predation or parasitism (Ogunfunmilayo *et al.*, 2021; Keerthi *et al.*, 2023). Moreover, high densities of herbivores on a plant can lead to resource competition, prompting females to select hosts with lower infestation levels to maximize larval survival (Can *et al.*, 2024).

Factors influencing feeding preference of lepidoptera moths

Chemical cues

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.

Host physical characteristics

Physical traits of host plants are critical determinants of larval feeding preferences.

Surface texture of the host plant

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.*, 2016; Prasad, 2022; Kaur *et al.*, 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).

Nutrient availability on the host plant

Nutrient availability is a critical factor influencing feeding preferences. Larvae require essential nutrients including nitrogen, carbohydrates and water for rapid growth and development (Silva *et al.*, 2017). 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 (da Silva *et al.*, 2023). The strong preference of GLM for nitrogen-fixing Fabaceae crops further supports the hypothesis that nutrient availability is a key determinant in feeding behaviour.

Growth stage of the host plant

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).

Behavioural adaptation in feeding preference of lepidoptera moths

Host plant selection

Behavioural adaptations further refine feeding preferences. 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 *et al.*, 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).

Feeding time

Feeding time is another adaptive trait influencing feeding preference. Many Lepidoptera larvae are nocturnal feeders,

a behaviour that reduces exposure to predators and minimizes water loss during high daytime temperatures (New, 2023). This nocturnal feeding strategy not only enhances feeding efficiency but also aligns with periods of lower plant defensive activity (New, 2023; Šigutova *et al.*, 2023).

Feeding site

The specific location on a host plant where feeding occurs can significantly impact larval success. For example, feeding within the leaf tissue, as observed in leaf-mining species, provides a protective refuge from predators and shields larvae from surface defences such as trichomes and waxy layers (Desneux *et al.*, 2012). In GLM, larvae initially mine between the epidermal layers and subsequently move to external feeding by binding leaflets together, thereby creating a continuous protected environment for development (Okello *et al.*, 2016).

Age of the host

Finally, the age of the host plant is a critical factor in feeding behaviour. Younger plants or tissues are generally more attractive to larvae because they offer softer, more nutritious material with lower levels of defensive compounds (Gómez Jiménez *et al.*, 2014). In contrast, older tissues may be tougher and more chemically fortified, reducing their suitability for larval consumption. Among Gelechiidae moths, such as *Tuta absoluta*, larvae have been observed to preferentially feed on young tomato leaves, an observation that parallels the feeding patterns of GLM on groundnut during the flowering stage, when the tissue is at its most tender and nutritious (Desneux *et al.*, 2012).

Interaction of host plants with beneficial microbes

In Lepidopteran moths, beneficial microorganisms such as arbuscular mycorrhizal fungi and plant growth-promoting rhizobacteria play a crucial role in modulating plant-insect interactions (Pineda *et al.*, 2010). These microorganisms modify host plant physiology, nutrient composition and the defence signalling pathways, thereby influencing herbivore performance and oviposition behaviour (Pangesti *et al.*, 2013). In several Lepidopteran moths, such as *T. absoluta*, microbial inoculation has been shown to enhance plant resistance or tolerance to larval feeding on tomato plants colonised by *Pseudomonas* spp., primarily through the modification of VOC and defensive metabolites (Gadhav *et al.*, 2016; Ibarra-Laclette *et al.*, 2024). The investigation on the beneficial microbe-host plant and GLM interactions remains unknown which provides evidence of research knowledge gap as microbial-mediated plant resistance could offer strategies for the sustainable management of GLM.

Management implications of understanding oviposition and feeding preferences of GLM

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 which, control strategies are adapted from (Buthelezi and Zharare, 2025).

Targeted control measures

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

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.

Integration of biological control

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 (Joshi and Patel, 2011).

Reduction in insecticide use

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, the frequency of treatments can be lowered, thereby mitigating the development of insecticide resistance

(Kumar *et al.*, 2023). 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.

Breeding resistant cultivars

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.

Recommendations for future research

Understanding the oviposition and feeding preferences of GLM is critical for improving integrated pest management. Future research should focus on identifying key semi chemicals such as volatile organic compounds that influence host selection, thereby enabling the development of semi chemical-based attractants or repellents (McCormick *et al.*, 2017). In addition, employing RNA sequencing to uncover genes involved in host plant recognition will shed light on the molecular mechanisms of host specificity and detoxification.

Research into population genetics is also needed to detect host-associated differentiation across various agro-ecological zones, which will help tailor region-specific management practices. Long-term monitoring of oviposition and feeding behaviours under both field and controlled conditions across seasons will further enhance predictive models of pest outbreaks and our overall understanding of GLM bio-ecology.

Finally, behavioural assays such as olfactometer and wind tunnel tests should be conducted to quantify the moth's responses to specific plant volatiles (McCormick *et al.*, 2017). Together, these focused research efforts will bridge critical knowledge gaps and support the development of precise, sustainable pest management strategies, ultimately reducing the economic impact of GLM on legume production.

CONCLUSION

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.

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