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A Noctuid Moth *Spodoptera Litura* Pertaining to Global Distribution, Crop Losses, Nutritional Needs, Preferred Host Interactive Effects and Anti-Herbivore Defences Evolve

Hamzah, A. A.

Faculty of Applied Sciences, Universiti Teknologi MARA, Perak Branch, Tapah Campus

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ABSTRACT

Spodoptera litura is a sporadically serious insect pest, being an extremely polyphagous and wide-ranging species. To date, this insect pest is well justified in terms of its polyphagousity on many economically important crops, thus necessitating the need to find effective action strategies to combat the threats of infestations and spreads, as delays can lead to considerable economic losses. Developing effective management strategies can be included to find potent insecticides that are safer for the user and consumer, besides control problem due to the problem of resistance development to several synthetic insecticides. The wider the range of potential candidates, the higher the likelihood of finding top performers as an alternative method to control *S. litura* infestations, especially on agricultural lands and reduce chemical pesticide over-reliance. This review addresses a brief discussion about a polyphagous lepidopteran, *S. litura* recovering the global extent of invasion, the damage it causes and host plant preferences. In the following objective is to explore feeding behaviours and the nutritional composition of a preferred host plant that required for *S. litura* to grow and develop. This review focus also related to identify and describe the role of plant-derived secondary metabolites that could exert toxic effects to *S. litura* and possibly decipher a serious polyphagous herbivore its uniquely different and crucial strategy types evolved to deal with anti-herbivore defence of host plants. In conducting the literature survey or finding published information for this review, various scientific resources were relied on such as PudMed, ScienceDirect, ResearchGate and Google Scholar. The keywords used for collecting literature were global distribution, economic losses, plant secondary metabolites and defence mechanisms related to *S. litura*. The chronological period in which the papers were published was not considered during the literature survey and review writing process because the primary focus was on selecting noteworthy works for the topics covered. The occurrence and economic importance of this insect vary from region to region, but commonly found in the Asia-Pacific region and has caused some specific problematic pest population reports in Europe and the United States (US). Different populations of *S. litura* may demonstrate differences in feeding preference and width of the host range to complete their development but are considered significant for a better chance to survive with wild plants, weeds, shade trees, ornamental, agricultural and horticultural crops as hosts. Looking to the mode of damage, this insect pest emergence is observed to be associated with food availability and climatic conditions during its larval stages and consumption rate varies depending on the instar. Severe damages sometimes can extend to the whole plant dies in field conditions. It is noted that the nutritional difference of the plant hosts significantly induce divergence to the growth performance, reproduction, feeding behaviour, as well as adult oviposition. In association with continuous usage of synthetic pesticides contributing in adverse effects such as pollution, health hazards and loss of biodiversity, while adoption of botanical pesticides leads to a healthy environment and sustainable agriculture. Based on this, the extensive range of chemical variations or notably amazing chemical diversity found in plants offers a wide selection of chemicals that have potential uses as botanical insecticides. Several plant families have been reported to contain plants with bioactive compounds or secondary metabolites effective against *S. litura*, including *Asteraceae*, *Fabaceae*, *Meliaceae* and others which were rich in flavonoids, alkaloids and terpenoids. As opposed to many secondary metabolites found in plants against herbivores, the insect pest used different mechanisms to resist these toxins or induce defence responses, such as releasing secretory proteins from salivary glands, detoxifying enzyme activities and highly sensitive olfactory sensory systems. Significantly, this review highlights the recent scenarios that explore the global habitats for *S. litura*, global agricultural impacts due to the damage it causes to various crops, food utilisation and the effects of host plant nutrients on the growth and development of *S. litura*, the effectiveness of botanical insecticides derived from plant extracts containing a wide variety of defensive secondary metabolites in response to the insect herbivory; and lastly, strategies used by the insect pest that have been utilised to overcome its host plants' diverse chemical defences.

Keywords: *Spodoptera litura*, polyphagousity, plant-derived secondary metabolites, botanical insecticides, olfactory sensory systems

INTRODUCTION

In Japan, *Spodoptera litura* is called 'night thief' because it tends to feed voraciously on a wide variety of plants by the night-active last instar larvae to avoid predators that hunt during the daytime such as from a group of birds (Zhang *et al*., 2021; Shivankar *et al*., 2008). Its native habitats spread across the globe and it has become one of the most pestiferous insects found worldwide. Exacerbating the longstanding challenges to control the insect pest, owing in part to adaptations of different plants around the world, resistance to insecticides, the extraordinary ability for detoxification and tolerance to many plant secondary metabolites, a great expansion of its detoxification gene families and gustatory receptor genes, long-distance migration contributed to the expansion of its territories and developed genomic uniformity in Asia, high fecundity and so forth (Zhang *et al*., 2021; Lin *et al*., 2019; Tong *et al*., 2004) that could cause so palpably loss to agricultural production.

It is predicted that more than 2,000 plant species from 189 families contain many bioactive secondary metabolites that are present in plant organs such as leaves, stems, roots and flowers, known to have insecticidal properties (Sharma *et al*., 2012; Isman, 2006; Rao *et al*., 2005). This is tremendously fruitful as an alternative method to currently use chemical insecticides against *S. litura*. The principal plant metabolites that impart such activity include flavonoids (Aboshi *et al*., 2018), terpenoids (Liu *et al*., 2021), alkaloids (Sun *et al*., 2012), acetogenins (Leatemia & Isman, 2004) and phenolics (Gautam *et al*., 2021). Even though plant metabolites can be used to deter or harm insect pests including *S. litura* larvae but undermined by exhibiting antiherbivory strategies related to the ability to detoxify and sequester toxic compounds in their diet using detoxifying enzymes such as cytochromes P450, carboxyl/cholinesterases, glutathione S-transferases (GST) and transporters such as ATP-binding cassette (ABC) transporters in insecticide resistance development (Hilliou *et al*., 2021).

Field resistance of *S. litura* to many chemical insecticides (Tong *et al*., 2004) caused further studies to be done in the future to understand its life cycle, feeding habits and habitat preferences, which help in identifying vulnerable stages for control and understanding how the insect pest interacts with its environment. Knowing which crops are susceptible to *S. litura* infestation helps in targeting control efforts as well, thus preventing economic losses. Furthermore, identifying factors influencing population growth and spread such as temperature, humidity and food availability, helps in predicting outbreaks and implementing timely control measures. Lastly, studying the mechanisms by which *S. litura* develops resistance (e.g., metabolic detoxification, target-site mutations and intestinal bacterial resistance) are important for developing new control strategies that bypass their resistance mechanisms.

Global Distribution and Economic Damages

Spodoptera litura (Fabricius) (Lepidoptera: Noctuidae) is one of the world's most destructive pests to many agricultural crops in the Asian tropics. Global distribution ranges cover tropical and temperate Asia, Australasia and the Pacific Islands (Kranz *et al*., 1977). This pest is a transboundary or highly migratory insect capable to spread across the world due to its natural distribution capacity that could migrate over long distances during adulthood to non-indigenous areas and nocturnal habits, which facilitating dispersion and oviposition on different hosts (Tojo *et al*., 2013). Tu *et al*. (2009) reported that the flight activity for this insect pest during the 72-hour tethered flight assay for male and female *S. litura*, respectively could fly for an average duration of 19.6 hours and 24.0 hours, and at a mean distance of 83.3 km and 105.4 km, which proven its great potential to undertake long-distance migratory flights. Thus, the long-distance dispersal of the insect pest could contribute to gene flow, evolutionary potential; and the spread of resistance genes at a regional and large spatial scale (Hu *et al.*, 2023). Next, accidental introduction through international trade, for example, eggs or larvae may be observed on planting materials, cut flowers, or vegetables; or pupal stages residing in soil can be important sources to transfer the pest outside of its native distributional range. Generally, *S. litura* has a relatively long duration of the pupal stage, therefore it could travel long distances unless are crushed or destroyed. For instance, some sporadic outbreaks of the pest in glasshouses have been reported in the United Kingdom (UK) and Germany after the discovery of *S. litura* in association with aquatic plants imported from Indonesia and Singapore (Aitkenhead *et al*., 1974; EPPO, 2004; EPPO, 2010). Likewise, all interception records of *S. litura* in United States (U.S.) ports of entry on commodities entering the US were found on orchids (*Dendrobium*, *Oncidium)* which originated from Thailand and made more than 85% cases in many years, as notified by Gilligan & Passoa (2014). Global distribution of habitats for *S. litura* has been detected in 52 infected countries as reported by Bragard *et al*. (2019). Amongst them, Bangladesh, China, India, Japan, Laos, Malaysia and Taiwan have been invaded with the most widespread population of *S. litura.*

In crop production, this significant pest species has been reported to cause serious damage by larval feeding preference upon many economically important crops worldwide with profound reductions in both yield quantity and quality (Bragard *et al.*, 2019). Severe infestation by this destructive insect pest could impair agricultural production and subsequently threaten the global food supply. Leafworm *Spodoptera litura* has been shown to be resistant to a wide range of insecticides which led to sporadic and the onset of an outbreak unpredictably; hence the consequences often devastating (Ahmad *et al*., 2007). To date, there are not much studies available online assessing the substantial economic losses caused by *S. litura* attacks to numerous agro-economic crops in Southeast Asia. In Malaysia, there are three prominent or publicly available articles reporting *S. litura* population attacking commercial crops. Firstly, Mamat & soon (1982) stated that one of the major pests faced by tobacco growers in Kelantan and Trengganu was *S. litura*, which heavily infested in farms where chemical insecticides were not applied. In a subsequent case, outbreak proportions in plantation nurseries of *Acacia mangium* due to *S. litura* attacks in Peninsular Malaysia have been highlighted by Intachat & Kirton (1997) and expected to be higher based on the number of pest species, as an intensive survey was not conducted. The folivorous insect also has been reported to cause the most serious in terms of degree of damage on young banana cultivar Pisang Mas (1–2 months after planting) in planted fields at Synergy Farm, Pulau Pinang, Malaysia, which percentage of plants infested and killed by the infestation more than 50% (Okolle *et al*., 2006). Furthermore, the moth also be found on other host crops, but damage speculated to be minimal or without further comprehensive investigation on its effects (Hamzah & Norsyazwina, 2020).

The case in Indonesia demonstrated reduction of soybean productivity can be reached more than 63% due to the invasion of larval *S. litura* attacks on leaves in soybean cultivation (Rahayu *et al*., 2023). Moreover, a survey report by Crop and Horticultural Plant Protection Agency of Lampung Province, Indonesia from 2010 to 2019 in all corn-producing areas at Lampung has denoted that this destructive insect pest only caused a minor impact or less severely effected to the host plant (1 to ≤ 25% of plant damage) (Fitriana *et al*., 2021). In other Southeast Asian country whereby maize productivity constraints associated with *S.litura* attacks have been reported in Philippines even though this pest occurs less frequently but results in moderate-to-high yield losses (Gerpacio *et al*., 2004). In a similar infested country, the common cutworm, *S. litura* could cause heavy damaged to eggplants (Navasero & Navasero, 2003). On top of the economic impact cases of *S. litura* worldwide have been reported in India, which turned down the crop production planted in fields and greenhouses, respectively, such as sweet pepper, tomato, capsicum, cucumber and cabbage **(**Sabir & Singh, 2013**;** Vashisth *et al*., 2012).

Diet Breadth for *S. litura*

The preferences and host range of *S. litura* encompass a field crops grown for food and fibre, plantation and forestry crops, besides certain noxious weed species (EFSA PLH Panel [EFSA Panel on Plant Health]) *et al*., 2019; Sushilkumar & Ray, 2018). Lin *et al*. (2019) reported that the polyphagous pest fed nearly 289 species of plants, which comprising 109 families globally. Of that, 23 species of crops are notable from Malaysia (Hamzah & Norsyazwina, 2020). Figure 1 shows some examples of damaging plant in Malaysia caused by *S. litura* larvae gregariously eating patterns, frequently leaving the leaves completely destroyed. Divergent selection on host plants, which those economically important crops infested by *S. litura* in Asia included

Colocasia esculenta, cotton, flax, groundnuts, jute, lucerne, maize, rice, soybeans, tea, tobacco, vegetables (aubergines, *Brassica*, *Capsicum*, cucurbit vegetables, *Phaseolus*, potatoes, sweet potatoes, *Vign*a, etc.) (Natikar & Balikai, 2017). Besides, Mitra *et al*. (2021) reported that the tobacco caterpillar, *S. litura* could change or switch its host plant preferences in a similar mixed-crop field purposely to enhance larval digestion and metabolism in different ontogenic stages. The host switch as an advantageous behaviour for the insect pest that could shorten the development time and increase the eclosion success. In addition, the pest has been reported to cause multiple pest attack impacts or to form lepidopteran complexs with others substantial lepidopteran insect pest of crops (Hossain *et al*., 2021; Rahman *et al*., 2021; Aiswarya *et al*., 2018; Okolle *et al*., 2006). In terms of feeding preference, the effect of different parts of the plant host can be linked to the inconsistent growth and development speed performance of *S. litura* (Ye *et al*., 2022; Hu *et al*., 2020). Moreover, host plant preference during the larval stage also could develop behavioural isolation to *S. litura* in terms of mate choice and sexual isolation. Di *et al*. (2021) reported that female *S. litura* fed on an artificial diet preferred mates with males that were fed on the same diet and occasionally mated with males fed on natural hosts, which were tobacco or Chinese cabbage.

Phytonutrients and chemical plant defences

Plants are major dietary sources of macro- and micro-nutrients for insects, included *S. litura* that feed on varieties of host plant species, which differ with their quality of nutritional status (Ganguly *et al*., 2020; Shah *et al*., 2017). Those nutrients play important roles to support insect larval development, reproduction, fecundity and oviposition (Kang *et al*., 2021; Xue *et al*., 2010; Awmack & Leather, 2002). In previous study done by Vengateswari *et al*. (2020) revealed that host plant nutrients also could enhance immune defence mechanisms for the larvae of *S. litura* to eliminate the invading pathogenic bacteria such as *Bacillus thuringiensis* (Bt) infections. Besides, insects also could face great temporal and spatial variation in the quality of leaves that they were tend to eat. By different ways to overcome this obstacles, insects have evolved various intrinsic detoxification mechanisms, feeding behaviours, and/or limited food intake to a specific time of the season (Parry & McCullough, 2004). However, when plant-based and artificial diets have been compared in terms of the growth and development indices of *S. litura* such as larval and pupal growth index, demonstrably the total developmental index on the modified artificial diet could be higher than some important host plants preferred by *S. litura* (Ganguly *et al*., 2020). Nutrient requirement of *S. litura* from plant hosts also can be enhanced by the present of the potential functions of gut bacteria in *S. litura* larvae (Xia *et al*., 2020). These preliminary findings speculated that the gut microbiota of *S. litura* is important for feeding, digestion and utilisation of food. Moreover, the gut bacterial composition of *S. litura* can be varied when reared on different food supplies despite that most abundant in the same phylum Proteobacteria but belong at different family levels, such as Enterobacteriaceae when reared on taro leaves, followed by Pseudomonadaceae and Enterobacteriaceae on the artificial larval diet.

According to Lee (2010), the larval armyworm *S. litura* demonstrated behaviour and pysiological regulation of macro-nutrient intakes in different sexes. The study revealed that when *S. litura* was fed on two nutritionally complementary foods (a protein-rich diet and a carbohydrate-rich diet, respectively); females shown no difference in carbohydrate intake but regulated to a higher intake of protein than males, purposely to lay eggs. In contrast, males have a higher tendency to accumulate lipids in their body than carbohydrates they eat because they typically spread out in search of females during estrus, thus, lipid accumulation was thought to be an energy reservoir that helped males prepare for migration.

Plants synthesize a number of chemical compounds, commonly known as secondary metabolites to offset insect attacks but not engage in primary processes such as growth, reproduction, photosynthesis or protein production (War *et al*., 2012). Its number amounting to more than 2,140,000 have been discovered in the plant kingdom (examples include more than 12,000 alkaloids, 40,000 terpenoids and 8,000 phenyl propanoids (Al-Khayri *et al.*, 2023; Elshafie *et al*., 2023) and grouped into different classes such as alkaloids, terpenes, amines, glucosinolates, cyanogenic glucosides, quinones, phenolics, peptides and polyacetylenes (Jamwal *et al*., 2018). Many secondary metabolites demonstrate a number of different mechanisms to control pests (Divya *et al*., 2024, Ling *et al*., 2019; Kortbeek *et al*., 2018). Amongst all, isoprene-derived terpenoids have most often proven effective, followed by alkaloid and phenolic compounds (Boulogne *et al*., 2012). Meanwhile, a

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high amount of nitrogen content in plant tissue could boost the growth and development of insect pests (Biswas *et al*., 2013; Awmack & Leather, 2002).

In a different way upon anti-herbivore defence which is related to the rational applications of plant growth promoting rhizobacteria (PGPR) that could induce of systemic resistance to overcome insect infestations included *S. litura* attacks, concisely prevent the use of the agrochemicals besides enhance the plant growth and yield as well (Ling *et al*., 2022; Kousar *et al*., 2020; Bano & Muqarab, 2017). Example alleviated defenses stimulated by PGPR against a notorious leaf damaging pest on tomato leaves, *S. litura*, were raising in proline production, elevated activities of antioxidant enzymes, induction in the activities of protease and polyphenol oxidases, increased contents of phenolics, protein and chlorophyll (Bano & Muqarab, 2017). Further induced defence mechanisms by stimulating the expression levels of defence-related genes encoding allene oxide cyclase (AOC), allene oxide synthase (AOS), lipoxygenase D (LOXD) and proteinase inhibitor (PI-II) in tomato leaves (Ling *et al*., 2022). In a following study, Cortez Jr. *et al*. (2024) ascertained corn defence mechanisms against *S. litura* infestation. Their findings suggested that PGPR could enhance corn resistance to *S. litura* by feeding and oviposition deterrents for PGPFR-treated plants.

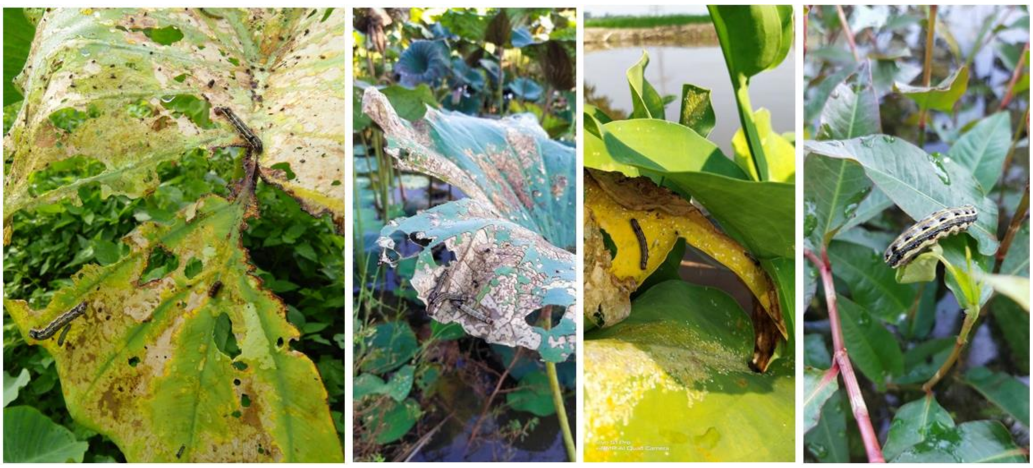

Figure 1: *S. litura* Fab. (Lepidoptera: Noctuidae) infesting four different wild plant species in Malaysia which are a) taro (*Colocasia esculenta*, b) pink lotus (*Nelumbo lucifera*), c) sawah flowering rush (*Limnocharis flava* [L.] Buchenau) and d) Unknown plant species.

Some metabolites from plants can inhibit the growth of *Spodoptera litura* larvae or kill them; for example quercetin negatively affected the mid-gut of *S. litura* from *Euphorbia hirta* L (Selin-Rani *et al*., 2016). Next, β-caryophyllene [(1*R*,4*E*,9*S*)-4,11,11-trimethyl-8-methylene bicyclo [7.2.0]undec-4-ene], a natural sesquiterpene was found as an essential oil in many plants like *Syzygium aromaticum*, *Piper nigrum* and *Cannabis sativa* revealing its insecticidal, genotoxic and cytotoxic potentials against *S. litura* (Mahajan *et al*., 2022). Meanwhile, Su *et al*. (2017) studied the effect of various flavonoids, lectins and phenyl *β*-D-glucoside on larval survival, weight and activities of digestive (total serine protease and trypsin); and detoxifying (esterase and glutathione-*S*-transferase) enzymes of *S. litura* larvae at 7 days after treatment through a diet incorporation assay, convincingly demonstrating various toxic effects against the larvae of targeted insect pest in a laboratory setting. Furthermore, the harmful effects on the growth and development of second instar larvae (6 days old) of *S. litura* using different phenolic compounds purified from the medicinally important plant, *Acacia nilotica*, which is rich in polyphenols and may provide proficient alternative ways to control the insect pest in the field have been reported by Gautam *et al*. (2021). Considerable evidences existed that a synergistic effect of secondary plant metabolites acted as a mixture of bioactive constituents or botanical insecticides derived from a mixture of leaf extracts of *Azadirachta indica* (neem), *Aglaia odorata*, and *Ageratum conyzoides* (in a ratio of 1:1:1) was effective in killing the third instar larvae *S. litura* through both oral and topical application techniques (Hoesin *et al*., 2023). However, the topical application has been found to be the most favoured method in inducing mortality due to a higher level of mortality rate and a lower median lethal time (LT_{50}) value. The death of *S. litura* larvae was predicted because of exposure to toxic properties of active compounds in the plant extract used. For example, the main active compounds in neem (commonly known as azadirachtins) associated to a group of complex tetranortriterpenoids which harboring potent insect growth regulators. On the other side, the leaves of *A. odorata* reportedly contain several chemical compounds that show insecticidal properties, including germacrene-D, benzyl benzoate, benzyl salicylate, coumarins and alkaloids (Giang & Son, 2016; Sugijanto & Dorra, 2016; Udebuani *et al*., 2015). Contrarily, essential oils were the main insecticidal compounds present in *A. conyzoides* that contained several bioactive compounds with insecticidal properties, such as limonene, p-cymene, γ-terpinene and α-pinene as described by Bayala *et al*. (2014). Other examples of compounds with entomotoxic properties derived from ethanolic extracts of *A. conyzoides* leaves are flavonoids, alkaloids and coumarins (Chahal *et al*., 2021).

The more likely potential candidate to exhibit deadly insecticidal properties against *S. litura* is natural coumarin. Coumarin is a phenolic compound that can be assimilated into a toxic compound and affects insect midgut (Rao *et al*., 2017). The entomotoxicant has been tested against *S.litura* through transcriptome- based toxicology analysis, resulting in significantly inhibited effects on the growth and development of *S. litura* larvae, specifically impaired detoxification enzymes and glycometabolism (Xia *et al*., 2023). Laterally, essential oils with insecticidal activity belong to *Thymus vulgaris* and *Satureia hortensis*, respectively, and could kill more than 90% of *S. litura* larvae as reported by Isman *et al.* (2001). Thymol and carvacrol are both monoterpenoid phenols in insecticidal oils were found to be the major components for both assessed plants, ultimately responsible for the death of the insect host. Some binary mixtures like trans-Anethole acted synergistically with thymol, citronellal and α-terpineol, respectively whereby they were efficacious to cause acute toxicity and feeding deterrence against *S. litura* (Hummerbrunner & Isman, 2001). In view of the complexity of insect-herbivore interactions, there is also the potential for plant secondary metabolites to play an essential role in mediating interaction between *S. litura* and its natural enemy for indirect defence. Such a citing report by Du *et al*. (2022) found that Chinese cabbage could emit specific volatile substances (limonene, linalool and hexadecane) to attract the parasitic wasp, *Microplitis similis* against *S. litura* larvae.

Another specialised metabolite with insecticidal activity against *S. litura* larvae with success is octacosane (Ponsankar *et al.*, 2016). The chemical compound was derived from *Couroupita guianensis* L. flower and showed high mortality against *S. litura* third instar larvae by damaging the gut epithelial layer and brush border membrane (BBM). A following study by Ponsakar *et al*. (2020) screened the antifeedant activity of the bioactive compound cucurbitacin E from *Citrullus colocynthis* L. Schrad (Cucurbitales: Cucurbitaceae) on different instar larvae of *S. litura*. The sublethal dose at 50 parts per million (ppm) displayed a high mortality rate in a dose-dependent way across all the instars. Besides, Vasantha-Srinivasan *et al.* (2016) evaluated larvicidal activity, inhibitors of the development and behavioural changes of *S. litura*, which were induced by the crude volatile oil belong to *Piper betle* leaves (Pb-CVO) in insecticidal bioassays. The study found that the Pb-CVO caused an acute mortality rate at concentrations of 1.0 and 1.5%, respectively, and its twenty constituents were significant inhibitors to the development and also caused behavioural changes of *S. litura* larvae. Likewise, a similar observed effect can be seen after *S. litura* larvae have ingested Db-Precocene I, a highly active bioactive compound from the grass *Desmosstachya bipinnata* (L.) Stapf. (Sundar *et al*., 2021). Alongside, Bis (2-ethylhexyl) phthalate (31.5%), a prominent active compound present in the methanolic leaf extract of *Swietenia mahagoni* Jacq. (Meliaceae) feasible as bio-rational plant product against the lepidopteran pest *S. litura* (Dinesh-Kumar *et al*., 2018).

Additional studies appraising on similar topic are catechin that isolated from the ethyl acetate crude stem extract of *Artocarpus lacucha* which could inflict the prominent toxicity effect against *S. litura* (24-hour 50% Lethal Dose value [LD50] of ~8.37 µg/larva) (Ruttanaphan *et al.*, 2023); gallic acid at lower concentrations had a deleterious impact to the growth of *S. litura* but minor effects against its larval parasitoid *Bracon hebetor* (Hymenoptera: Braconidae) (Punia *et al*., 2021); bioactive metabolites in *n*-hexane extracts of *Epaltes divaricata* (NH-EDx) showed significant mortality rate in a dose-dependent way across all the instars against the *A. aegypti* and *S. litura* larvae (Amala *et al*., 2021); the methanolic flower extract of *Nyctanthes arbor-tristis* (Mx-Na-t) containing 3-hydroxy-1,2-dimethyl-4(1H)-pyridone (3H-dp) and tyrosol (Ty-ol) showed higher toxicity effect to the third instar *S. litura* larvae (Divya *et al*., 2024); and the triterpenoid friedelin extracted from hexane extract of *Azima tetracantha* leaves showed highly effective larvicide against *S. litura* (Baskar *et al*., 2014). Without disregard other important plant secondary metabolites that responsible for various biological effects to *S. litura* related to the green-derived essential oils comprising of five major bio-active derivatives from *Sphaeranthus amaranthoides* (EO_Sa) which could activate toxicological responses against both third and fourth instar larvae of *S. litura* (Murfadunnisa *et al*., 2019); an essential oil blend from

Alpinia galanga Zingiberaceae (Zingiberales) rhizomes and *Ocimum basilicum* Lamiaceae (Lamiales) leaves was ideal to be implemented with due respect to provide a synergistic on mortality effects for cypermethrin resistance of *S. litura* (Ruttanaphan *et al*., 2019); chloroform crude extracts of chick weed *Ageratum conyzoides* (Linn.) as a promising source of compounds that could cause significant larval mortality rate against pest *S. litura* (Vasantha-Srinivasan *et al*., 2024); and the ethanolic leaf extracts of two fig tree species, *Ficus lyrata* and *Ficus auriculata;* consisting of 12 and 15 active compounds against *S. litura*, respectively yielded higher mortality rates (Vasantha-Srinivasan *et al*., 2023).

More such secondary metabolites against *S. litura* for example reported by Koul *et al*. (2013) that found the thymol (5-methyl-2-isopropylphenol) content in thyme oil was thought as a potential acute toxicant, oviposition deterrent, ovicide or feeding deterrent to *S. litura*. Next. ononitol monohydrate originated from the ethyl acetate extract of *Cassia tora* L. and showed significant antifeedant, larvicidal and pupicidal activities towards *S. litura* (Baskar & Ignacimuthu, 2012). Meanwhile, Huang *et al*. (2014) reported that the essential oil of *Pogostemon cablin* (Blanco) Benth could exert potent effects such as antifeedant, larvicidal, growth inhibitory and pupicidal activities against *S. litura*. Similar substantial antifeedant, larvicidal and pupicidal activities and least lethal concentration 50 (LC_{50}) values were observed for chloroform extract of *Ceasalpinea bonduc* (L.) Roxb seeds (Baskar *et al*., 2011a).The findings in a study by Jeyasankar *et al*. (2012) revealed the crude ethyl acetate seed extract of *S. pseudocapsicum* contained of triterpenoids, flovonoids, alkaloids and quinines that showed higher efficiency of antifeedant activity against *S. litura.* Besides, the crude root methanolic extract of *Aristolochia albida* also could demonstrate a strong level of antifeedant activity to *S. litura* (Lajide *et al*., 1993). Observing moderate larvicidal effects were recorded for the acetone, chloroform, ethyl acetate, hexane and methanol leaf extracts of *Ocimum canum*, *Ocimum sanctum* and *Rhinacanthus nasutus* against fourth instar larvae of *S. litura* after 24 hours of exposure (Kamaraj *et al*., 2008). Connected with that, dichloroethane (DCE) and methanol (Me) extracts of *Melia dubia* also could inhibit the growth in a dose-dependent manner to *S. litura* (Koul *et al*., 2000). Nevertheless, *Murraya koenigii* miraculin-like protein (MKMLP) was able to inhibit the trypsin-like activity and total protease activity of *S.litura* gut proteinases (SGP) by 81% and 48%, respectively, thus adversely affecting the growth and development of the insect pest (Gahloth *et al*., 2011). Baskar *et al*. (2011b) speculated that ethyl acetate and hexane leaf extracts of *Aristolochia tagala* Cham., respectively was able to produce higher feeding deterrence against *S. litura* at 5.0% final concentration. A deleterious effect on *S. litura* with regard to growth inhibition was reported by Jeyasankar *et al*. (2011) using a crystal compound (2,5-diacetoxy-2-benzyl-4,4,6,6-tetramethyl-1,3-cyclohexanedione) originated from the leaves of *Syzygium lineare*. A study on the influence of a trypsin inhibitor from *Archidendron ellipticum* (AeTI), which could inhibit the growth and serine digestive enzymes during larval development of *Spodoptera litura*, especially at early larval instars (1^{st} to 3^{rd}), has been reported by Bhattacharyya *et al*. (2007). Feeding deterrence was noticeable for the hexane extracts of *Vernonia cinerea* (73.44%); *Cassia fistula* (76.48%); and *Vernonia cinerea* (78.69%) after 24, 48 and 72 hours of exposure, respectively, due to the plant extracts providing an unpalatable taste to fresh castor leaf discs when fed by *S. litura* larvae in an antifeedant bioassay (Arivoli & Tennyson, 2020).

Remarkable (100%) antifeedant, larvicidal and pupicidal activities against *S. litura* were shown by the neem gum nano formulation (NGNF), a new pest control formulation using the aqueous extract of Neem gum (*Azadirachta indica*) (NGE) (Kamaraj *et al*., 2018). A similar finding was observed by Safder *et al*. (2022) when they examined the effectiveness of neem leaf extract (*A. indica*) against the second and third instar larvae of *S. litura*, respectively, and reported the mortality percentage received more than 70%, but under laboratory conditions. In addition to successful cases of secondary metabolites, several pure constituents from *Wedelia prostrata* essential oil, which are camphene (LC_{50} = 6.28 μg/ml), γ-elemene, (LC_{50} = 10.64 μg/ml), α-humulene (LC_{50} = 12.89 μg/ml) and (E,E)-α-farnesene (LC_{50} = 16.77 μg/ml) could highlight their promising insecticidal effect against larvae of *S. litura* (Benelli *et al*., 2018). Various solvents were implied to prepare crude extracts and obtained active fractions from *Argemone mexicana* L. (Papaveraceae) that could disrupt the growth and development of *S. litura*, particularly the least pupal weight, arrested pupation, nil fecundity, disturbed moulting, malformed moth and decreased adult life span (Malarvannan *et al*., 2008). An alternative bioefficacy of ethyl acetate extract of *Artemesia nilagrica* was studied by Raja *et al*. (2003) and observed notable amount of mortality activity against *S. litura*. Then, an anthraquinone aldehyde nordamnacanthal (1,3-dihydroxy-anthraquinone-2-al) found in the hexane extract of *Galium aparine* L. (bedstraw) and *Rubia akane* root powder, respectively has been recognised *in vitro* for its antifeedant propeties against *S. litura* (Morimoto *et al*., 2002). Even so, a study by Pavunraj *et al*. (2006) has shown that a 5% treatment of hexane extract of *Excoecaria agallocha* (L.) leaf extract resulted in significant antifeedant (73.08%), oviposition deterrent (83.71%) and ovicidal (65%) activities against *S. litura*. At a concentration of 0.05%, five plant extracts were tested against *S. litura*, consequently manifested diverse ovicidal activities with the highest in *Cleistanthus collinus* hexane (85.16%), followed by *Murraya koeingii* diethyl ether (83.60%), next *Aegle marmelos* ethyl acetate (76.14%), then hexane extracts of *Strychnos nuxvomica* (61.00%) and lastly *Vitex negundo* (52.02%) (Arivoli & Tennyson, 2013b). Afterwards, *Cinnamomum zeylanicum* hexane and *Ocimum americanum* ethyl acetate extracts exhibited more than 50% oviposition deterrent activity against *S. litura* at 1.0% concentration (Arivoli & Tennyson, 2013c).

The first trial report that notified the strong ovicidal and oviposition deterrent activities for *Atalanta monophyla* (L.) Correa crude leaf extract in hexane and included its active fraction against *S. litura* was reported by Baskar *et al*. (2012). Meanwhile, Pavunraj *et al*. (2012) revealed the ethyl acetate extract of *Alangium salviifolium* (L.F.) contained alkaloids, diterpenoids and saponins, which could exhibit profound larval mortality for the fourth instar larvae of *S. litura* under a laboratory setting. The same lead researcher (Pavunraj *et al*. (2011) explored the use of plant leaf extract of milkweed, *Pergularia daemia*, that possessed antifeedant activity against *S. litura*, typically the effect of crude leaf extract prepared in ethyl acetate has shown a convincing evidence of antifeedant activity (71.82%) at one percent concentration included its an active fraction known as 6-(4,7-hydroxy-heptyl) quinone with a similar effect on *S. litura* (68.31% at 2000 ppm). Despite that, five specific plant extract sources, which were prepared in different solvents at one percent concentration, respectively shown different acute feeding deterrent effect to *S. litura*, namely ethyl acetate extract of *Strychnos nuxvomica* (88.98%), hexane extracts of *Vitex negundo* (86.41%) and *Murraya koeingii* (81.46%), ethyl acetate extract of *Zanthoxylum limonella* (80.58%) and hexane extract of *Abrus precatorius* (78.61%) (Arivoli & Tennyson, 2013a). Then, the bio-efficacy of *Lippia javanica* as an antifeedant and larvicidal potential against the fourth instar larvae of *S. litura* at a 5% concentration has been confirmed in a study by Pavunraj *et al*. (2024), which both prepared in an ethyl acetate solvent. Among all, only one active fraction derived from *Melochia corchorifolia* leaf extract demonstrated significant antifeedant activity against *S.litura* either singly or in a co-formulated mixture with neem and karanj oil (Pavunraj *et al*., 2012).

In a related study on the topic, the insect pest was susceptible to the methanol extract of *Sphaeranthus indicus*, which caused antifeedant activity and exhibited developmental deformities for larvae and pupae as well (Ignacimuthu *et al*., 2006). In addition to what precedes, an exploratory study done by Raja *et al*. (2005) discovered new bioactive compounds isolated from crude ethyl acetate extract of *Hyptis suaveolens* which showed positive results for both oviposition deterrent activity and antifeedant activity against *S. litura* after being tested at 1000 ppm and 2000 ppm concentrations, respectively. Eventually, the essential oil from *Lantana camara* could produce high larval and larval-pupal mortality,whereas *Curcuma* oil, the essential oil of *Curcuma longa* with insect growth regulator properties could cause adverse effects related to a high number of abnormal pupae and adults produced, respectively of *S. litura* (Javier *et al*., 2017).

Adaptations of *S. litura* to host plant secondary metabolites

Insect pests tolerate host plant secondary metabolites via different mechanisms such as detoxifying plant toxins, altering of the toxic compounds into favourable compounds for their growth and development, developing the choice of feeding on the basis of secondary metabolite concentration, quick engrossment and expulsion as faeces and the participation of symbiotic intestinal microbes in order to tackle the effect of toxic plant secondary metabolites (Afroz *et al.*, 2021; War *et al*., 2020). In the case of *S. litura*, behaviourally plastic host plants possesed by its larvae due to their ability to downregulate plant defence across different plants (Prajapati *et al*., 2020). Examples of adaptive mechanisms employed by *S. Litura* to downregulate plant defence by releasing oral secretions from salivary glands (such as labial salivary gland, ventral eversible gland and mandibular gland) known as effector proteins (Spitteller*et al*., 2004). Prajapati *et al*. (2020) reported that 267 out of 330 proteins were predicted as potential effector proteins from salivary glands of *S.litura*. Those effector proteins were identified in different families consisting of detoxifying enzymes (esterase, kazal-type serine protease inhibitors, metalloproteases and serine proteinase inhibitors), glucose oxidase, chemosensory proteins (odorant binding proteins and chemosensory proteins), calcium ion binding proteins (calumenin, calreticulin and armet), clip domain serine proteinase, lipases, phospholipases and peroxidase to mediate suppression of host plant defences. Among the effector proteins, employment of chemosensory proteins (CSPs) localised in chemoreceptive organs such as the apoprotein of *S. litura* CSP8 (SlCSP8) mainly expressed in the head of the *S. litura* larvae, especially the labrium can be used in identifying secondary metabolites in plants such as anthocyanins; and rhodojaponin III, a non-volatile secondary metabolite (Dong *et al*., 2024; Jia *et al*., 2021). Furthermore, findings in genomic studies of *S. litura* provide its genome information about the gene families encoding receptors for bitter or toxic substances and detoxification enzymes, such as cytochrome P450, carboxylesterase and glutathione-*S*-transferase, which massively expanded in this polyphagous species, facilitating its extraordinary ability to detect and detoxify many plant secondary metabolites (Cheng *et al*., 2017).

CONCLUSION

The current review delivers some specific problematic insect pest population reports on *S. litura*, which can be found in many countries, and is one of the major invasive insect pests globally. Its potential damages can affect crop production, economic returns for smallholder farmers and threaten global food security. Thus, comprehensive research efforts are required to understand its biology, behaviour and management strategies. Besides, the insect pest can adapt to many host plant species, which has caused the difficulty of effectively controlling it. Unveiling its feeding response, larval growth, development, survival and fecundity can be decreased on poor-quality host plants due to nutritional composition and/or secondary plant metabolites. Many published studies are available online on various plant extracts containing secondary metabolites that could provide promising effects in controlling *S. litura* larvae, such as repellent, antifeedant, larvicidal, ovicidal and pupicidal effects. Examples of plant secondary metabolites that are highly toxic to the insect pest include various alkaloids, flavonoids, phenolics, terpenes and terpenoids. Encountering the host plants' diverse defences against herbivory, the insect pest has evolved to deal with or suppress the plant host defensive responses, such as downregulating the production of plant secondary metabolites by releasing secretory proteins or oral secretions, also known as effector proteins from salivary glands, using various detoxifying enzymes, highly efficient olfactory systems and many more.

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