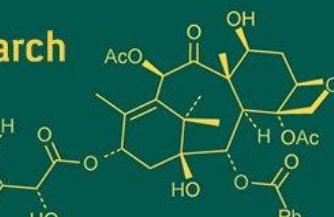
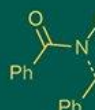


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Phenotypic plasticity of *Spodoptera frugiperda* (J. E. Smith) and *Spodoptera litura* (Hubner) raised on different hosts and seasons: A case study on age-dependent larval colour polymorphism

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Abstract

Larval colour polymorphism is an important adaptive trait in polyphagous insects, yet information on the combined effects of host plants and seasonal conditions on colour expression remains limited. The present study investigated phenotypic plasticity in larval colouration of *Spodoptera frugiperda* and *Spodoptera litura* reared on maize and castor during winter and spring under laboratory conditions. Larval colour was recorded from the first to the sixth instar. Both species exhibited progressive melanization with advancing larval age. Winter-reared larvae consistently developed darker pigmentation than spring-reared larvae, while castor-fed larvae showed greater melanization than maize-fed larvae, particularly during later instars. Despite marked variation in body colour, key diagnostic morphological characters remained stable across hosts and seasons, confirming environmentally induced phenotypic plasticity rather than genetic differentiation. The findings demonstrate that larval colouration is regulated by developmental stage, host quality and seasonal environment, reflecting adaptive responses that enhance thermoregulation, camouflage and ecological fitness in these economically important agricultural pests.

Keywords: Phenotypic plasticity, *Spodoptera frugiperda*, *Spodoptera litura*

Introduction

The genus *Spodoptera* includes several economically important, destructive agricultural pests. Among them, fall armyworm, *Spodoptera frugiperda* (J. E. Smith), and tobacco cutworm, *Spodoptera litura* (Hubner), are two closely related major polyphagous pests belonging to the family Noctuidae under the order Lepidoptera (EPPO, 2015; Goergen *et al.*, 2016; Pogue, 2002) [10, 11, 25]. *Spodoptera frugiperda* is an invasive pest in India and started infesting maize in 2018 (Sharanabasappa *et al.*, 2018) [28]. It was also noticed to infest maize in West Bengal in the latter part of 2018 (Dhar *et al.*, 2019) [9]. In contrast, *Spodoptera litura* is an indigenous pest to the Indian sub-continent (Herrero *et al.*, 2016) [13]. However, both pests are distributed worldwide (Bragard *et al.*, 2019; CABI, 2022; EPPO, 2015; Goergen *et al.*, 2016; Kartakis *et al.*, 2025; Pogue, 2002; Song *et al.*, 2024) [2, 3, 10, 11, 16, 25, 31]. They have a wide host range of over 350 plant species, including cereals, vegetables, and cash crops, contributing to their rapid spread and establishment (Kenis *et al.*, 2022; Montezano *et al.*, 2018; Qin *et al.*, 2004) [17, 21, 26]. They cause significant economic losses in a wide range of crops such as maize, soybean, cotton, and beans (Demis and Jemal, 2025; Kalinge *et al.*, 2024; Makgoba *et al.*, 2021; Nagoshi *et al.*, 2022; Pogue, 2002; Thakur *et al.*, 2024; Usman *et al.*, 2024) [8, 15, 20, 22, 25, 33, 36].

Both species undergo complete metamorphosis (holometabolous development) consisting of egg, larval, pupal, and adult stages (Chapman, 2013; Triplehorn and Johnson, 2005) [6, 35]. Although they share similarities, distinct morphological traits allow developmental differentiation, especially in the larval and adult stages (EPPO, 2015; Pogue, 2002) [10, 25]. Tobacco cutworm and fall armyworm exhibit phenotypic plasticity through distinct colour morphs in the larval stage.

Larval colouration shifts with age, population density, host species, and environmental factors such as temperature and seasons (Higo *et al.*, 2022; Tojo, 1991; Wen *et al.*, 2025) [14, 34, 37].

Such phenotypic plasticity through different colour morphs serves as more than just a morphological trait; it is a valuable indicator of pest population status and offers practical applications across multiple IPM components. Body colour can serve as an intuitive "indicator light" for assessing population density and outbreak risk, aiding early warning and decision-making.

Materials and Methods

Experimental site

The experiments were conducted at the laboratory of the Department of Agricultural Entomology, Uttar Banga Krishi Viswavidyalaya, Pundibari (26.404879°N Latitude, 89.386219°E Longitude and Altitude 18 meters mean sea level), Cooch Behar, West Bengal, India, to find out the phenotypic plasticity on colour variations into bacca caterpillar, *Spodoptera litura*, and fall armyworm, *Spodoptera frugiperda* at different larval stages. Both pest species were raised on maize and castor as hosts during the winter and spring months.

Insect sample collection and rearing

Insect samples, including larvae of the fall armyworm, *S. frugiperda* and *S. litura* were collected from the maize and cabbage fields of the instructional farm of the University, respectively.

The collected insect larvae were maintained on maize (*Zea mays* L.) and castor (*Ricinus communis* L.) leaves as a diet up to F-2 generations under laboratory conditions at normal ambient room temperature and relative humidity during both winter and spring months. The maize plants (Hybrid maize 91A21) were grown in both pots and fields without chemical application, and castor leaves were collected from the farm boundaries and used as hosts. The larvae were reared up to adult emergence.

Adults were maintained using a 10% honey solution soaked on cotton pads in a small watch glass (7.5 cm diameter) placed inside the jar, which was replaced daily until the moths died. The adult moths were allowed to deposit eggs on maize and castor leaves by keeping them separately at a 1:1 ratio in the oviposition jar (25 cm × 15 cm, 15 cm diameter), which was wrapped in black art paper (A1 size, 59 cm × 84 cm, 220 GSM). Maize and castor leaves were used as oviposition substrates. The jar's lid was covered with muslin. Eggs were collected and placed in separate jars (size: 15 cm × 10.5 cm) for hatching. The egg masses were observed at 12-hr intervals until the larvae hatched.

The newly emerged neonates (n = 28) were individually kept in small plastic jars (7.5 cm × 5.5 cm) filled with fresh maize leaves. The leaves were changed every 12-hr intervals, and the rearing jar was cleaned.

Neonates emerged from the eggs and were transferred to a small rearing plastic jar in specific host plants. Larvae were fed artificially on a natural diet of maize and castor (leaves up to the sixth instars) till cessation of feeding. During an experiment, observations were taken using the digital microscope Zoomstar III (Observation head inclined at 45°, rotatable at 360°, Eye piece with wide-field 10X paired, Magnification range 8X-50X, with a working distance of 115 mm).

Results and Discussion

Table 1 demonstrates that the larval colour of *Spodoptera frugiperda* exhibited pronounced phenotypic plasticity in response to both host plant and season, with the degree of pigmentation increasing progressively from the first to the sixth instar. Seasonal variation was evident throughout larval development, while host-induced differences became increasingly prominent in the middle and later instars.

During the first and second instars (Table 1), larvae remained predominantly light green irrespective of host plant, indicating that pigmentation is weakly expressed during the early stages of development. However, subtle differences were already apparent between treatments. Winter-reared larvae on castor exhibited a faint brownish or yellowish-green tint compared with maize-fed larvae. In contrast, spring larvae, particularly those reared on maize, appeared almost transparent or pale green. The persistence of a black head capsule and pinacula in all treatments indicates that these diagnostic structures remain stable despite changes in body colour. The limited variation during the early instars is expected because newly hatched larvae possess a thin and weakly sclerotized cuticle with minimal melanin deposition (Chapman, 2013) [6].

From the third instar onwards, colour variation became increasingly pronounced. Larvae reared during winter gradually changed from pale brownish green on maize to dark brownish green on castor, while spring larvae retained a comparatively lighter green to olive-green colouration. Simultaneously, longitudinal stripes, pinacula, setae, and the characteristic dorsal and dorso-lateral lines became clearly visible. The earlier appearance and greater contrast of these markings in winter and castor-fed larvae suggest enhanced cuticular melanization and pigmentation under these conditions. A similar age-dependent development of colour patterns has been reported by Pogue (2002) [25], who described progressive darkening and increasing prominence of longitudinal stripes in later instars of *S. frugiperda*.

In the later stage of larval development (fourth to sixth instars), the hosts and seasons had more pronounced effects on larval colour development (Fig 1). The fourth instar represented a transitional stage where host-mediated differences became more evident. Larvae reared on maize during winter developed a light brownish green body with conspicuous white dorsal and dorso-lateral stripes and distinct black spots on the penultimate abdominal segment. In contrast, castor-fed larvae developed heavy pigmentation ranging from dark brown to blackish brown with intense striping, although the abdominal spots were relatively smaller. Spring larvae remained considerably lighter, retaining greenish or light brown colouration.

These observations indicate that host plant quality and environmental temperature interact to regulate pigment deposition within the cuticle. Castor leaves contain defensive secondary metabolites, such as ricinine, which may stimulate physiological stress responses and, consequently, increase melanin synthesis. In contrast, maize provides a comparatively balanced nutritional environment, resulting in lighter pigmentation (Montezano *et al.*, 2018).

The greatest colour differentiation occurred during the fifth and sixth instars, when larvae attained maximum body size and cuticular development. Winter-reared larvae on maize became dark brown with a prominent inverted "Y"-shaped frontal suture, whereas castor-fed larvae developed an almost black body with highly contrasting longitudinal

stripes. During spring, larvae remained olive-green to dark brown with comparatively less intense pigmentation. The sixth instar showed the highest degree of melanization, particularly in castor-fed winter larvae, which developed a deep blackish-brown body with very prominent white stripes.

This progressive darkening reflects increasing cuticular sclerotization associated with larval maturation and environmental adaptation. Similar observations were reported by Sparks (1979) [32], who noted that late instars of *S. frugiperda* exhibit considerable variation in body colour while retaining stable diagnostic characters, such as the inverted "Y" mark on the head capsule.

Table 2 elucidated that *Spodoptera litura* exhibited pronounced phenotypic plasticity in larval colouration in response to host plant, season, and larval age. Progressive changes in body pigmentation and characteristic markings were observed from the first to the sixth instar, indicating that colour expression is developmentally regulated and strongly modified by environmental conditions. Overall, larvae reared during winter developed darker pigmentation than those reared during spring, while the host plant influenced the intensity and expression of characteristic colour patterns.

During the first instar, larvae were generally pale or almost transparent, irrespective of host plant, possessing a characteristic black head capsule and prothoracic shield. Winter larvae reared on maize appeared pale white with a greenish tinge, whereas castor-fed larvae were light green. Spring larvae remained almost transparent with either a whitish or greenish tinge. These observations suggest that pigmentation is minimal immediately after hatching because the cuticle is thin, weakly sclerotized, and contains little melanin. Similar descriptions of newly hatched *S. litura* larvae have been reported by Ahmad *et al.* (2013) [1] and Capinera (2017) [5], who noted that early instars are pale and gradually acquire pigmentation following successive molts.

In the second instar, the body became pale green with an orange head capsule, and amber-brown lateral spots appeared below the first abdominal segment. These spots subsequently increased in size and prominence with successive molts. Although both host plants produced similar colour patterns, winter larvae exhibited slightly greater pigmentation than spring larvae. The appearance of these lateral spots represents the onset of species-specific colour pattern formation associated with cuticular differentiation. Previous studies have likewise reported that abdominal markings become increasingly distinct after the second instar and constitute important diagnostic features of *S. litura* larvae (Ravishankar *et al.*, 2025) [27].

During the third instar, clear differences among treatments became evident. Winter larvae reared on maize developed a light blackish-green body, whereas castor-fed larvae appeared greyish green to yellowish green with brighter pigmentation than spring larvae. In all treatments, three characteristic longitudinal yellow lines (one dorsal and two lateral) became well developed. The emergence of these longitudinal stripes corresponds to increasing cuticular melanization and differentiation of epidermal pigments during larval growth. Similar ontogenetic development of longitudinal stripes has been described by CABI (2024) [4] and Capinera (2017) [5], who reported that the dorsal and lateral lines become progressively more conspicuous from the third instar onward.

The fourth instar (Fig 2) exhibited a marked increase in pigmentation. Winter larvae on maize became blackish green with a distinct reticulation pattern along the lateral body surface, whereas castor-fed larvae were greyish green but darker than those reared during spring. Spring larvae remained comparatively lighter, ranging from light brown on maize to greyish green on castor. The development of the reticulation pattern indicates progressive cuticular maturation and increased melanin deposition. This pigmentation enhancement during intermediate larval stages has been associated with increased cuticle thickness and improved protection against environmental stress (Nation, 2022) [23].

The greatest colour variation occurred during the fifth and sixth instars (Fig 2). Fifth-instar winter larvae on maize changed from blackish green to brownish black with a highly conspicuous reticulation pattern, while castor-fed larvae developed an even darker blackish brown body. Spring larvae remained comparatively lighter, although the reticulation pattern was still evident. In the sixth instar, winter larvae reared on maize attained a deep black body with characteristic black dorsal spots on the first and eighth abdominal segments. Castor-fed larvae remained greyish black with similar dorsal spots, whereas spring larvae developed blackish grey or dark brown colouration.

These findings indicate that maximum melanization occurs during the final larval instar, coinciding with completion of larval growth and cuticular sclerotization. Similar progressive darkening in mature *S. litura* larvae has been reported by Ahmad *et al.* (2013) [1] and Capinera (2017) [5], who described substantial colour polymorphism among late instars under different environmental conditions.

The consistently darker pigmentation observed during winter suggests that seasonal temperature strongly influences melanin biosynthesis in *S. frugiperda* and *S. litura*. It also indicates that temperature-dependent melanization is an important adaptive mechanism in both *S. frugiperda* and *S. litura*. Melanin enhances absorption of solar radiation, enabling larvae to maintain favourable body temperatures under cooler environmental conditions. Increased melanization is also associated with enhanced immune defense, greater cuticular hardness, and improved tolerance to environmental stress.

The phenomenon of thermal melanism has been extensively documented in insects, where individuals exposed to lower temperatures generally exhibit darker body pigmentation than those developing under warmer conditions (Clusella-Trullas *et al.*, 2007; Gunn, 1998; Solensky and Larkin, 2003) [7, 12, 30]. Therefore, the darker winter phenotype observed in the present study represents an adaptive response that improves physiological performance during cold conditions.

Host plants also played a significant role in regulating colour expression in many lepidopteran pests (Kesztheyli *et al.*, 2024; Liao *et al.*, 2025; Yamasaki *et al.*, 2009; Yoshida *et al.*, 2023) [18, 19, 38, 39]. Larvae reared on castor consistently exhibited greater melanization than those reared on maize, particularly during the later instars. This finding supports the hypothesis that host plant chemistry influences insect phenotype through nutritional and biochemical pathways. Castor contains ricinine, phenolic compounds, and other allelochemicals that may alter digestive physiology and induce oxidative stress, thereby increasing melanin synthesis as part of the insect's defense mechanism.

Comparable host-induced phenotypic plasticity has been reported in several polyphagous noctuid species, in which changes in host quality modify larval colour, growth rate, and developmental characteristics (Montezano *et al.*, 2018; Nylin and Gotthard, 1998; Simpson and Sword, 2008) [21, 24, 29].

The interaction between the host plant and season further enhanced phenotypic plasticity. Larvae reared on castor during winter generally developed the darkest phenotypes, whereas maize-fed larvae during spring remained relatively light. This phenomenon was more evident in *S. frugiperda*. This interaction indicates that it is a highly plastic trait rather than a genetically fixed character. Environmental cues act synergistically to regulate pigment production via endocrine and physiological pathways. Such plasticity provides adaptive advantages by improving camouflage, thermoregulation, and resistance to environmental stress, thereby increasing ecological fitness under diverse

environmental conditions. Darker larvae may absorb heat more efficiently and survive low-temperature stress, whereas lighter larvae reduce excessive heat absorption during spring and blend more effectively with green foliage, thereby improving crypsis against natural enemies.

Importantly, despite the extensive variation in body colour, diagnostic morphological characters remained unchanged. The inverted "Y"-shaped frontal suture, dorsal stripes, and arrangement of abdominal spots in *S. frugiperda* and longitudinal yellow stripes, reticulation pattern, and black dorsal spots on the first and eighth abdominal segments in *S. litura* were consistently present in all treatments, confirming that the observed variation represents environmentally induced phenotypic plasticity rather than genetic differentiation. This finding agrees with the comprehensive taxonomic revision of *Spodoptera* by Pogue (2002) [25], who emphasized that colour is highly variable and should not be used alone for species identification.

Table 1: Phenotypic plasticity on colour variation in *Spodoptera frugiperda* reared on two hosts during different seasons

Stages of the pest	Winter		Spring	
	Maize	Castor	Maize	Castor
1 st instar larva	Light green in colour with black head capsule, the body covered with panicula	Pale green in colour with faint brownish tint, black head capsule, the body covered with panicula	Almost transparent, light green in colour with black head capsule, the body covered with panicula	Light green in colour with yellowish tint and black head capsule, the body covered with panicula
2 nd instar larva	Light green in colour with distinct dark head capsule	Yellowish green in colour with distinct dark head capsule	Almost transparent, light green in colour with distinct head capsule	Light green in colour with yellowish tint with distinct dark head capsule
3 rd instar larva	Pale brownish green in colour with prominent longitudinal stripes, pinacula and setae prominent, three pale to pale yellow lines, one dorsal, two dorso-laterals clearly visible	Dark brownish-green, longitudinal stripes more distinct, pinacula and setae prominent, three pale to pale yellow lines, one dorsal, two dorso-laterals first appear	Green to olive-green in colour with clear longitudinal stripes pinacula and setae prominent, three pale to pale yellow lines, one dorsal, two dorso-laterals clearly visible	Light brown with well-defined stripes, pinacula and setae prominent, three pale to pale yellow lines, one dorsal, two dorso-laterals first appear
4 th instar larva	Light brownish green in colour with conspicuous white dorsal and dorso-lateral stripes and prominent black dots in penultimate abdominal segment	Dark brown to blackish brown in colour with heavy pigmentation, conspicuous white dorsal and dorso-lateral stripes, and prominent black dots on the penultimate abdominal segment; these dots are smaller than those in maize-fed larvae.	Green to olive-green in colour with distinct stripes and prominent black dots in penultimate abdominal segment	Light brown in colour with prominent stripes and prominent black dots in penultimate abdominal segment but smaller than maize fed larvae
5 th instar larva	Dark brown in colour, inverted "Y" mark highly distinct	Nearly black with highly contrasting stripes and inverted "Y" mark	Olive green in colour with less intense pigmentation, inverted "Y" clearly visible	Dark brown with strong pigmentation and distinct markings
6 th instar larva	Dark brown to blackish brown with very distinct white longitudinal stripes	Deep blackish-brown, maximum melanization with very prominent markings	Greenish brown to dark olive, stripes visible but less contrasting	Dark brown to blackish-olive, darker than maize-fed larvae

Table 2: Phenotypic plasticity on larval colour variation in *Spodoptera litura* reared on two hosts during different seasons

Stages of the pest	Winter		Spring	
	Maize	Castor	Maize	Castor
1 st instar larva	Pale white with greenish tinge, black head capsule and prothoracic shield present	Light green in colour with black head capsule and prothoracic shield present	Almost transparent, whitish in colour with black head capsule and prothoracic shield present	Almost transparent with greenish tinge, black head capsule and prothoracic shield present
2 nd instar larva	Pale green in colour with orange head capsule, amber brown colour lateral spots developed right below at the first abdominal segments and gradually increase by later instars after each moult	Body is lighter in colour with amber brown colour lateral spots developed right below at the first abdominal segments and gradually increase by later instars after each moult.	Light green in colour with orange head capsule, amber brown colour lateral spots developed right below at the first abdominal segments and gradually increase by later instars after each moult.	Body is lighter in colour with amber brown colour lateral spots developed right below at the first abdominal segments and gradually increase by later instars after each moult.
3 rd instar larva	Light blackish green in colour with three longitudinal yellow lines: one dorsal and two laterals develop	Greyish green to yellowish green in colour- brighter than spring months with three longitudinal yellow lines: one dorsal and two laterals	Pale green in colour with three longitudinal yellow lines: one dorsal and two laterals develop	Pale greyish green to yellowish green in colour with three longitudinal yellow lines: one dorsal and two laterals
4 th instar larva	Blackish green in colour with a reticulation pattern on lateral side	Greyish green in colour- darker than spring months with a reticulation pattern on lateral side.	Light brown in colour with a reticulation pattern on lateral side.	Greyish green in colour with a reticulation pattern on lateral side.
5 th instar larva	Blackish green in colour to brownish black in colour with a reticulation pattern on lateral side more prominent	Blackish brown in colour- darker than spring months with a reticulation pattern on lateral side more prominent	Brown to blackish brown in colour with a reticulation pattern on lateral side more prominent	Blackish brown in colour with a reticulation pattern on lateral side more prominent
6 th instar larva	Deep black in colour, black dorsal spots present on first and eighth abdominal segments	Greyish black in colour, black dorsal spots present on first and eighth abdominal segments	Blackish grey in colour, black dorsal spots present on first and eighth abdominal segments	Dark brown in colour with blackish tinge, black dorsal spots present on first and eighth abdominal segments



Fig 1: Colour variations in *S. frugiperda* larvae on different developmental stages reared on maize and castor during winter and spring seasons (A: 4th instar-winter maize, B: 4th instar-spring maize, C: 4th instar-winter castor, D: 4th instar-spring castor, E: 5th instar-winter maize, F: 5th instar-spring maize, G: 5th instar-winter castor, H: 5th instar-spring castor, I: 6th instar-winter maize, J: 6th instar-spring maize, K: 6th instar-winter castor, L: 6th instar-spring castor)

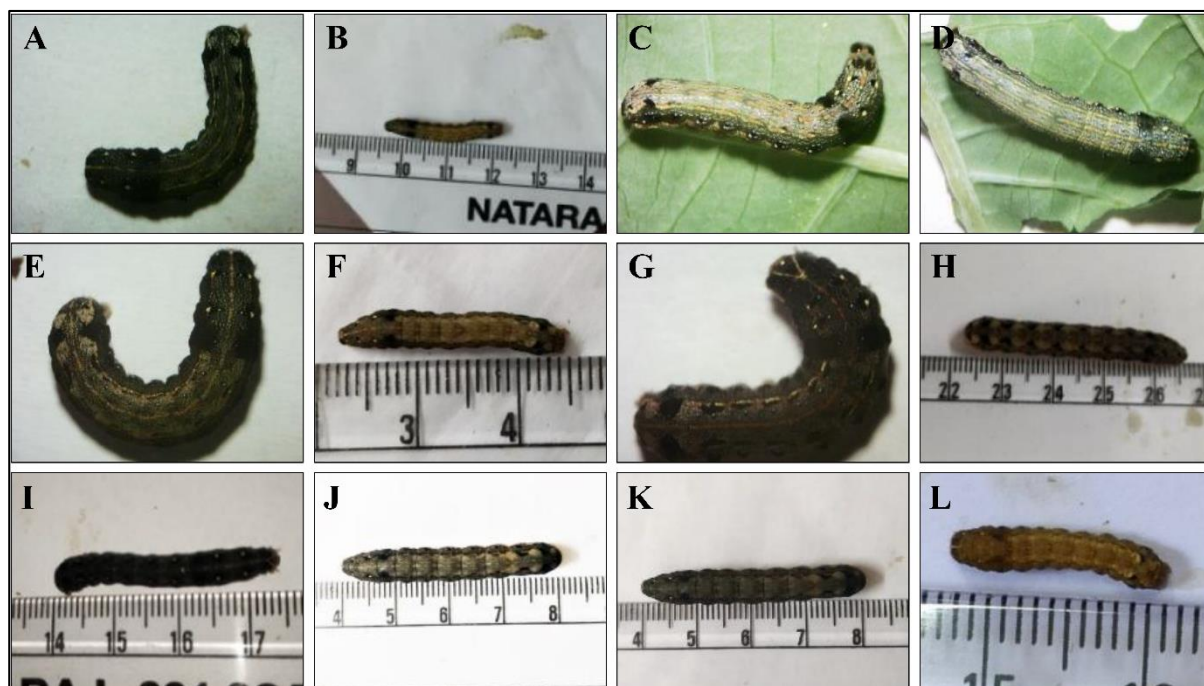


Fig 2: Colour variations in *S. litura* larvae on different developmental stages reared on maize and castor during winter and spring seasons (A: 4th instar-winter maize, B: 4th instar-spring maize, C: 4th instar-winter castor, D: 4th instar-spring castor, E: 5th instar-winter maize, F: 5th instar-spring maize, G: 5th instar-winter castor, H: 5th instar-spring castor, I: 6th instar-winter maize, J: 6th instar-spring maize, K: 6th instar-winter castor, L: 6th instar-spring castor)

Conclusion

Overall, the findings clearly demonstrate that larval colouration in *S. frugiperda* and *S. litura* is a highly plastic trait regulated by developmental stage, host plant quality, and seasonal environment. The progressive increase in melanization from the first to the sixth instar, coupled with darker pigmentation during winter and on castor, reflects adaptive physiological responses that enhance survival under varying ecological conditions. These results further emphasize the remarkable ecological adaptability of *S. frugiperda* and *S. litura*, which contribute to their success as wide spread polyphagous agricultural pests.

References

- Ahmad M, Ghaffar A, Rafiq M. Host plants of *Spodoptera litura* (Fabricius) (Noctuidae: Lepidoptera) in Pakistan. *Asian Journal of Agriculture and Biology*. 2013;1(1):23-28.
- Bragard C, Dehnen-Schmutz K, Di Serio F, Gonthier P, Jacques MA, Jaques Miret JA, *et al*. Pest categorization of *Spodoptera litura*. *EFSA Journal*. 2019;17(7):e05765. doi:10.2903/j.efsa.2019.5765.
- CABI. Invasive Species Compendium: *Spodoptera frugiperda* and *Spodoptera litura*. Wallingford: CAB International; 2022.
- CABI. Fall armyworm (*Spodoptera frugiperda*): CABI Invasive Species Compendium/Fall Armyworm Knowledge Bank. Wallingford: CAB International; 2024.
- Capinera JL. Fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Insecta: Lepidoptera: Noctuidae). Gainesville (FL): University of Florida IFAS; 2017. Available from: <http://edis.ifas.ufl.edu/in255>
- Chapman RF. The Insects: Structure and Function. 5th ed. Simpson SJ, Douglas AE, editors. Cambridge: Cambridge University Press; 2013.
- Clusella-Trullas S, Van Wyk JH, Spotila JR. Thermal melanism in ectotherms. *Journal of Thermal Biology*. 2007;32:235-245. doi:10.1016/j.jtherbio.2007.01.013.
- Demis E, Jemal A. Biology, distribution and management of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) in Ethiopia. *Indian Journal of Entomology*. 2025;87(1):199-207. doi:10.55446/IJE.2024.1980.
- Dhar T, Bhattacharya S, Chatterjee H, Senapati SK, Bhattacharya PM, Poddar P, *et al*. Occurrence of fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) on maize in West Bengal, India and its field life table studies. *Journal of Entomology and Zoology Studies*. 2019;7(4):869-875.
- EPPO. *Spodoptera littoralis*, *Spodoptera litura*, *Spodoptera frugiperda*. EPPO Bulletin. 2015;45(3):410-444.
- Goergen G, Kumar PL, Sankung SB, Togola A, Tamo M. First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), a new alien invasive pest in West and Central Africa. *PLoS One*. 2016;11(10):e0165632. doi:10.1371/journal.pone.0165632.
- Gunn A. The determination of larval phase coloration in the African armyworm, *Spodoptera exempta*, and its consequences for thermoregulation and protection from UV light. *Entomologia Experimentalis et Applicata*. 1998;86(2):125-133. doi:10.1046/j.1570-7458.1998.00273.x.
- Herrero S, Bel Y, Hernandez-Martinez P, Ferre J. Susceptibility, mechanisms of response and resistance to *Bacillus thuringiensis* toxins in *Spodoptera* spp. *Current Opinion in Insect Science*. 2016;15:89-96. doi:10.1016/j.cois.2016.04.006.
- Higo Y, Sasaki M, Amano T. Morphological characteristics to identify fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) from common

- polyphagous noctuid pests for all instar larvae in Japan. *Applied Entomology and Zoology*. 2022;57:263-274.
15. Kalinge PU, Shaila HM, Mallapur CP, Hanamaratti NG. Avoidable yield loss due to fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) in rabi sorghum. *Biological Forum-An International Journal*. 2024;16(3):224-226.
 16. Kartakis S, Horrocks KJ, Cingiz K, *et al.* Migration extent and potential economic impact of the fall armyworm in Europe. *Scientific Reports*. 2025;15:17405. doi:10.1038/s41598-025-02595-7.
 17. Kenis M, Benelli G, Biondi A, Calatayud PA, Day R, Desneux N, *et al.* Invasiveness, biology, ecology, and management of the fall armyworm, *Spodoptera frugiperda*. *Entomologia Generalis*. 2022;43(2):187-241.
 18. Keszthelyi S, Orsi-Gibicsar S, Pal-Fam F, Somfalvi-Toth K, Balog A. Colour polymorphism of cotton bollworm larvae as a function of the type of host plant providing its development. *Frontiers in Ecology and Evolution*. 2024;12:1376435. doi:10.3389/fevo.2024.1376435.
 19. Liao S, Mao X, Liu Y, Luo G, Wang J, Lin H, *et al.* Host-affected body coloration dynamics in *Perina nuda* larvae: a quantitative analysis of color variations and endogenous plant influences. *Insects*. 2025;16(7):728. doi:10.3390/insects16070728.
 20. Makgoba MC, Tshikhudo PP, Nnzeru LR, Makhado RA. Impact of fall armyworm (*Spodoptera frugiperda*) (J.E. Smith) on small-scale maize farmers and its control strategies in the Limpopo Province, South Africa. *Jamba: Journal of Disaster Risk Studies*. 2021;13(1):1016. doi:10.4102/jamba.v13i1.1016.
 21. Montezano DG, Specht A, Sosa-Gomez DR, Roque-Specht VF, Sousa-Silva JC, Paula-Moraes SV, *et al.* Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. *African Entomology*. 2018;26(2):286-300. doi:10.4001/003.026.0286.
 22. Nagoshi RN, Meagher RL. The *Spodoptera frugiperda* host strains: what they are and why they matter for understanding and controlling this global agricultural pest. *Journal of Economic Entomology*. 2022;115(6):1729-1743. doi:10.1093/jee/toac050.
 23. Nation JL. *Insect Physiology and Biochemistry*. 4th ed. Boca Raton (FL): CRC Press; 2022. doi:10.1201/9781003080616.
 24. Nylin S, Gotthard K. Plasticity in life-history traits. *Annual Review of Entomology*. 1998;43:63-83. doi:10.1146/annurev.ento.43.1.63.
 25. Pogue MG. A World Revision of the Genus *Spodoptera* Guenée (Lepidoptera: Noctuidae). *Memoirs of the American Entomological Society*. Vol. 43. Philadelphia: American Entomological Society; 2002.
 26. Qin HG, Ye ZX, Huang SJ, Ding SJ, Luo RH. The correlations of the different host plants with preference level, life duration and survival rate of *Spodoptera litura* Fab. *Chinese Journal of Eco-Agriculture*. 2004;12(2):40-42.
 27. Ravishankar BS, Thanuja A, Vanlalhmuliana H, Singh MK, Prasad S, Rachael C, *et al.* Studies on the biology of *Spodoptera litura* (Lepidoptera: Noctuidae) on artificial diet under laboratory conditions. *International Journal of Advanced Biochemistry Research*. 2025;9(12):717-721. doi:10.33545/26174693.2025.v9.i12i.7113.
 28. Sharanabasappa D, Kalleshwaraswamy CM, Asokan R, Mahadevaswamy HM, Maruthi MS, Pavithra HS, *et al.* First report of the fall armyworm, *Spodoptera frugiperda*, in India. *Pest Management in Horticultural Ecosystems*. 2018;24(1):23-29.
 29. Simpson SJ, Sword GA. Phase polyphenism in insects. *Current Biology*. 2008;18(17):R738-R744. doi:10.1016/j.cub.2008.06.030.
 30. Solensky MJ, Larkin E. Temperature-induced variation in larval coloration in *Danaus plexippus* (Lepidoptera: Nymphalidae). *Annals of the Entomological Society of America*. 2003;96(3):211-216. doi:10.1603/0013-8746(2003)096[0211:TVILCI]2.0.CO;2.
 31. Song Y, Cang X, He W, Zhang H, Wu K. Migration activity of *Spodoptera litura* (Lepidoptera: Noctuidae) between China and the South-Southeast Asian region. *Insects*. 2024;15:335. doi:10.3390/insects15050335.
 32. Sparks AN. A review of the biology of the fall armyworm. *Florida Entomologist*. 1979;62(2):82-87. doi:10.2307/3494083.
 33. Thakur N, Sharma A, Kaur S, Ahluwalia K, Sidhu A, Kumar S, *et al.* Insect pest *Spodoptera litura* (Fabricius) and its resistance against the chemical insecticides: a review. *Plant Science Today*. 2024. doi:10.14719/pst.3078.
 34. Tojo S. Variation in phase polymorphism in the common cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae). *Applied Entomology and Zoology*. 1991;26(4):571-578.
 35. Triplehorn CA, Johnson NF. *Borror and DeLong's Introduction to the Study of Insects*. 7th ed. Belmont (CA): Thomson Brooks/Cole; 2005.
 36. Usman MS, Adamu RS, Onu I, Kogi E, Musa N, Ahmed IA. Economic injury levels of fall armyworm (*Spodoptera frugiperda* Smith) at early-whorl vegetative growth stage of quality protein maize variety. *Journal of Agriculture and Environment*. 2024;20(1):253-264. doi:10.4314/jagrenv.v20i1.24.
 37. Wen L, Jin T, Luo X, Yuan H, Li J, Xu C, *et al.* The effect of population density on the phenotype, metabolic and immunological adaptations in the cuticle of *Spodoptera litura* larvae. *Pest Management Science*. 2025;81(6):2379-2393. doi:10.1002/ps.8635.
 38. Yamasaki A, Shimizu K, Fujisaki K. Effect of host plant part on larval body-color polymorphism in *Helicoverpa armigera* (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America*. 2009;102(1):76-84.
 39. Yoshida A, Yabu S, Otaki JM. The plastic larval body coloration of the pale grass blue butterfly *Zizeeria maha* (Lepidoptera: Lycaenidae) in response to host plant color: the maternal effect on crypsis. *Insects*. 2023;14(2):202. doi:10.3390/insects14020202.