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Invasion of fall armyworm, (*Spodoptera frugiperda*, J E Smith) (Lepidoptera, Noctuidae) on onion in the maize–onion crop sequence from Maharashtra, India

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Introduction: Climate change affects geographical distribution of insect pests which poses threats to the environment, as well as agricultural productivity and production worldwide. *Spodoptera frugiperda* is commonly known as fall armyworm (FAW), a potential insect pest of monocot crops like maize, wheat, rice and sorghum globally. Among these, maize is the most preferred host crop while worldwide there are very few reports on onion being a host of fall armyworm.

Methods: The fall armyworm (FAW) was identified by examining the morphological characteristics of its immature and mature stages, as well as by analyzing the mitochondrial cytochrome oxidase 1 (COX1) gene. Further, the strain identity was confirmed through multiple sequence alignment with previously identified *S. frugiperda* strains from corn and rice. Also studied the biology and damage symptoms caused by FAW in onion crops.

Results: During our experiments, the incidence of FAW ranged from 5 to 20 percent in different plots. The highest incidence was observed in young crops (30–45 days after transplanting) that were sown in November 2020. The FAW larvae exhibited six instars, with a total larval duration of 22.2 \pm 0.37 days. The pest had multiple generations per year. The fully developed larvae formed earthen cocoons in the soil for pupation, with a pupal duration of 8.0 \pm 0.45 days. The male adults had a recorded longevity of 6.4 \pm 0.40days, while the female adults lived for approximately 9.2 \pm 0.37 days. The COX1 gene sequencing revealed its 100% similarity with *Spodoptera frugiperda* and the comparison of sequences among FAW infecting rice and maize by using multiple sequence alignment showed differences at 11 positions.

Discussion: The present study is the first report of FAW invasion in onion in India and provides basic ideas about FAW characteristics which will help to control this new invasive pest in onion. In tropical regions with multiple cropping system and seasons, it becomes very important to investigate invasive pests as well as its host range in order to forecast its potential damage and devise suitable control measures.

KEYWORDS

Allium cepa, cropping sequence, cytochrome oxidase 1, invasive pest, Spodoptera frugiperda

Introduction

The fall armyworm (FAW), scientifically known as Spodoptera frugiperda (J E Smith, 1797), is originally from tropical and subtropical regions in America. It is a notorious pest known for causing extensive damage to maize crops (Labatte, 1994; Goergen et al., 2016). This pest has a long history of outbreaks in the United States since its first occurrence in 1797 and has subsequently spread to over 40 nations in sub-Saharan Africa (Goergen et al., 2016; Cock et al., 2017; Nagoshi et al., 2018). In India, the presence of FAW was initially reported on maize in Karnataka in 2018 (Sharanabasappa et al., 2018a). Within a span of 1-3 years, this invasive insect rapidly spread throughout India (Ganiger et al., 2018; Mahadeva Swamy et al., 2018; Sharanabasappa et al., 2018a), other Asian and Oceania countries (Ma et al., 2019; Prasanna et al., 2021; Tambo et al., 2023). FAW is a long-distance, sporadic migrant pest whose adult moths are capable of flying several miles (Johnson, 1987; Westbrook et al., 2016; Early et al., 2018). Furthermore, factors contributing to its rapid expansion include increased transboundary movement of agricultural products, human activities, and climate change (Paini et al., 2016). Being a polyphagous pest, FAW can sustain its population even in the absence of its main host by feeding on cultivated and wild grasses (Favetti et al., 2017). Earlier studies have reported a wide host range (353 species) for FAW (Montezano et al., 2018). It inflicts significant damage to economically important crops such as rice, sorghum, sugarcane, pasture grasses, millet, cabbage, beet, tomato, potato, peanut, soybean, alfalfa, and cotton (Chapman et al., 2000; Pogue, 2002; CABI, 2022). In South Africa, FAW commonly infests maize, leading to yield losses of approximately 33 to 36%, resulting in substantial economic losses (De Groote et al., 2020; Abro et al., 2021).

In tropical country like India, where multiple cropping systems are prevalent, polyphagous pests can adapt quickly to new agroecosystems (Bortolotto et al., 2014). The "green bridge effect," which allows pests to persist even in the absence of their preferred hosts, contributes to frequent pest outbreaks in diverse agro-climates (Kennedy and Storer, 2000; Pedigo, 2002; Saeed et al., 2017). This phenomenon can elevate secondary polyphagous pests to the status of "key pests" with significant economic impact (Pedigo, 2002). In India, the incidence of FAW has been reported in crops such as maize (Sharanabasappa et al., 2018a), sugarcane (Srikanth et al., 2018; Chormule et al., 2019), paddy (Ali et al., 2018), ginger (Shankar and Adachi, 2019), bajra, sorghum (Venkateswarlu et al., 2018), cotton, johnson grass, sunflower (Bharadwaj et al., 2020), banana (Ragesh and Balan, 2020), and fodder grass, grain amaranth (Maruthadurai and Ramesh, 2019). Farmers in maizegrowing regions have resorted to using two rounds of insecticides to manage FAW (Deshmukh et al., 2021a). Despite frequent reports in maize and sugarcane-growing regions of Maharashtra, FAW had not been found infesting onions. However, the fact that most onion farmers use maize as a barrier crop to prevent the entry of adult thrips from nearby fields (Srinivas and Lawande, 2006), which can serve as the primary source of FAW infestation in onions, led us to suspect its occurrence in onions. Hence, we suspected its occurrence in onions, as farmers generally follow the maize-onion (Surve et al., 2019; Kawade et al., 2020) and sugarcane-onion cropping system (Kumar et al., 2014) in Maharashtra. Moreover, earlier reports have listed onions in the host list of S. frugiperda (Montezano et al., 2018; Luginbill, 1928; Andrews, 1988; Casmuz et al., 2010; Fernandes et al., 2012; Cokola et al., 2021). Since corn, sugarcane, and onions are three of its preferred host plants, it is anticipated that FAW will spread quickly in these areas and have a negative impact on the economy. As part of ongoing pest surveillance, efforts were focused on tracking of invasive pest species and its outbreaks, through regular monitoring of onion fields. In the coming years, FAW will undoubtedly be a major threat to onion production. Hence, much attention is required on the pest bio-ecology in onion ecosystem, scope of current IPM strategies and identification of safer insecticides to prevent yield losses. Therefore, the present study was undertaken to gain insights into the biology of insect pests and their preferred food sources, essential for developing durable and sustainable management strategies (Behmer, 2009).

Materials and methods

Sample collection and rearing

The experiment was conducted at ICAR-Directorate of Onion and Garlic Research (ICAR-DOGR), Pune, Maharashtra, India (N 18°84', E 73°88', and 553.8 m above sea level). The 45 days old onion seedlings were transplanted on the raised beds of 15 cm height and 120 cm width, by maintaining 10 cm plant to plant and 15 cm row to row distance. These beds were divided into different blocks measuring 1.2×5 m each, resulting in an area of 6 m². Each block contained 408 plants. The soil of experimental plots was sandy loam in texture with 32-35% clay, 40% sand, and 20% silt with 7.9 pH. Regular monitoring of the experimental plots, was conducted during Rabi (winter) 2020-21 season to record the incidence of invasive and emerging insect pests in onions, which revealed sporadic infestation of FAW. We recorded the pest occurrence in these blocks, specifically focusing on the damage symptoms caused by Spodoptera frugiperda. Pest infestation was recorded throughout the growing period in 10 blocks. The total number of plants in each block and the number of infested plants were counted in randomly selected blocks from one-acre onion field. The extent of infestation was determined by using the formula provided by Maruthadurai and Ramesh (2019).

 $Percent Infestation = \frac{Number of plants damaged}{Total number of plants observed} \times 100$

Live larvae from various locations were collected and reared in the laboratory under controlled conditions $(25 \pm 1^{\circ}C, 70 \pm 5^{\circ}N RH)$, and a photoperiod of 16:8 h light:dark) on a natural food source (maize leaves) for one generation. Subsequently, larvae from the next generation were reared on onion leaves and used for further studies. A few larvae were preserved in 95% ethanol for molecular identification. Voucher specimens are being maintained at the insect repository of the center with the voucher specimen number: DOGR Voucher 16, following standard procedures. (Yoshimoto, 1978).

Identification of Spodoptera frugiperda

FAW has been identified using both morphological and molecular characters. Morphological characteristics of the immature stages (larvae) were identified based on the descriptions provided in (Passoa, 1991; Sharanabasappa et al., 2018a; Bajracharya et al., 2019). Meanwhile, adult moths that emerged from rearing were carefully pinned, and the preserved samples were sent to the Department of Entomology, Tamil Nadu Agricultural University, Coimbatore, for confirmation of the insect species. Adult moths, including male and female genitalia, were examined using keys (Brambila, 2009; EPPO, 2015; CABI, 2022). Different stages of the pest's life cycle, as well as its dissected mandibles and male and female genitalia, were photographed using the Leica S8 APO Stereozoom microscope, which has a built-in camera and a 100 mm macro lens. The damage symptoms were photographed using the Canon EOS 200D 24.2MP Digital SLR camera.

DNA isolation

The total genomic DNA was isolated from the larval samples using the DNeasy Blood and Tissue Kit (QIAGEN, Germany) following the manufacturer's protocol. The quality and quantity of the extracted DNA were assessed using a 1% agarose gel and a SmartSpec 3000 UV/Visible Spectrophotometer at 260 and 280 nm (Bio-Rad, Hercules, California, USA). The extracted DNA was stored at -20° C for further studies.

PCR amplification and sequencing

Molecular identification using diagnostic PCR was carried out using a universal primer set for the mitochondrial cytochrome oxidase 1 gene: LCO1490-F (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198-R (5'-TAAACTTCWGGRTGWCCAAARAATC-3') (Folmer et al., 1994). Approximately 10 µL of each amplicon was examined on a 1.5% agarose gel using gel electrophoresis to validate the amplification efficiency. The amplicons were later purified using the GeneJET PCR purification kit (Thermo Fisher Scientific) and processed for bi-directional amplicon sequencing using the highthroughput ABI3730 XI Sanger sequencing platform.

Biology of S. frugiperda

S. *frugiperda* larvae (n = 20) that hatched at roughly the same time were used to study the biology on onion leaves (Variety: Bhima Shakti) in each of the three (90 mm diameter) petri dishes. These petri dishes were kept in a Bio-Oxygen Demand incubator under controlled conditions ($25 \pm 1^{\circ}$ C, $70 \pm 5^{\circ}$ RH, and a 16:8 h [light: dark] photoperiod). Subsequently, the newly pupated FAWs were transferred to 5×10 cm plastic containers covered with black muslin cloth until adult emergence. For longevity and fecundity studies, adult FAWs were released into larger rearing cages (25×15 cm) with 10% honey solution as food source and paper towels to facilitate oviposition. The resulting egg masses were collected and stored in petri dishes for incubation. Both larvae and adults were observed to record the biological parameters such as larval duration, pupal duration, adult longevity, and total life cycle from egg to adult.

Data analysis

The gene sequence obtained was searched for homology using the BLAST+ program with the megaBLAST algorithm (Chen et al., 2015). The nucleotide sequences were aligned and analyzed using MEGA11 Software (Tamura et al., 2021). The phylogenetic tree was generated using the Neighbor-joining algorithm. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Maximum Composite Likelihood method (Tamura et al., 2004) and are in the units of the number of base substitutions per site.

Results

Biology and damage symptoms

At the ICAR-DOGR, the incidence of fall armyworm varied from 5 to 20 percent in various experimental plots, with the highest



FIGURE 1

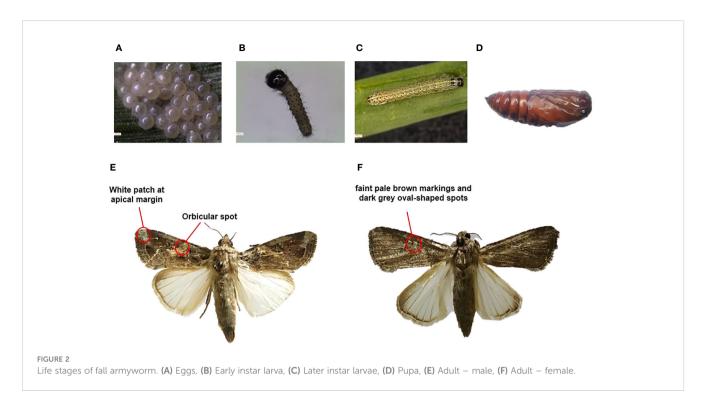
Fall armyworm damage symptoms on onion. (A) FAW feeding on onion leaves, (B) Foliar damage of leaves, (C) Scraping symptoms by early instar larvae.

incidence recorded in young crops (30-45 DAT) sown during November 2020. Early instars mostly scrape the leaf tissues, leaving the epidermal layer intact, whereas later instars cause extensive defoliation (Figure 1). It has four life cycle stages: egg, larva, pupa, and adult (Figures 2A-F). Like most Spodoptera spp, FAW females lay their eggs in overlapping clusters on the apex of tender leaves. These eggs are covered in protective hairs from the female's abdomen, giving them a distinctive cottony appearance. When reared on onion leaves, the egg incubation period was recorded as 4 ± 0.45 days. The neonate larvae quickly suspend themselves through silken threads to nearby onion plants after hatching from the eggs. There were six larval instars with a total larval duration of 22.2 \pm 0.37 days. Later, the fully grown larvae pupated and the pupal duration was recorded as 8.0 ± 0.45 days. The male and female longevity was recorded as 6.4 \pm 0.40 and 9.2 \pm 0.37 days, respectively. In contrast to those raised on onion leaves,

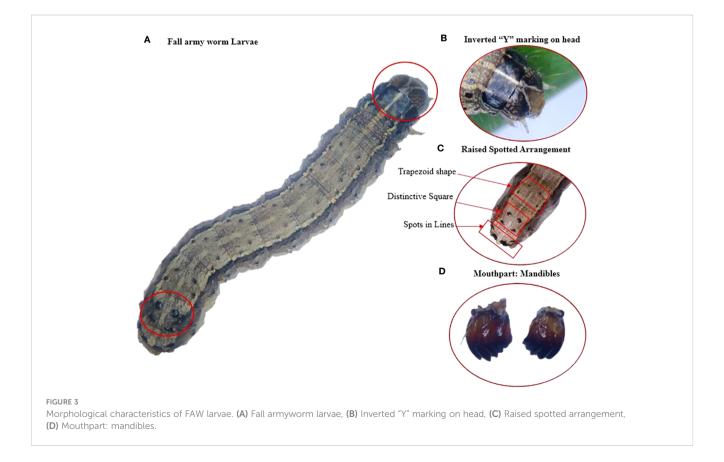
the larval duration in crops such as maize, millets, and grasses was 13 days, as reported earlier (Maruthadurai and Ramesh, 2019; Keerthi et al., 2021).

Morphological characterization

The eggs are creamy white in color with reticulate ribs (Figure 2A). The larva is a typical caterpillar with four pairs of prolegs in the 3rd to 6th abdominal segments and one pair in the final abdominal segment. The emerged young instar larvae are white in color and later turn greenish to dark brown with a black head (Figure 2B). Larvae can be easily identified by the presence of white longitudinal stripes on the dorsal surface and have prominent, hairy pinnacula on the body (Figure 2C). The head of the larva has a reticulate pattern, and the prothoracic plate is also



similar to the head. The ecdysial line on the head forms a "V" shape, and it continues with the mid-dorsal stripe of the prothoracic shield to form an inverted "Y"-shaped white marking (Figures 3A, B). The dorsal pinacula on the eighth and ninth abdominal segments are larger than the corresponding spiracles and pinacula on the other abdominal segments. On the eighth abdominal segment, pinnacula are arranged in a square pattern, and in a trapezoid pattern on the ninth (Figure 3C). The mandibles of the larva are serrated with conspicuous teeth (Figure 3D). The pupae are typical of Noctuidae, obtect type, with two spines on the cremaster (Figure 2D).



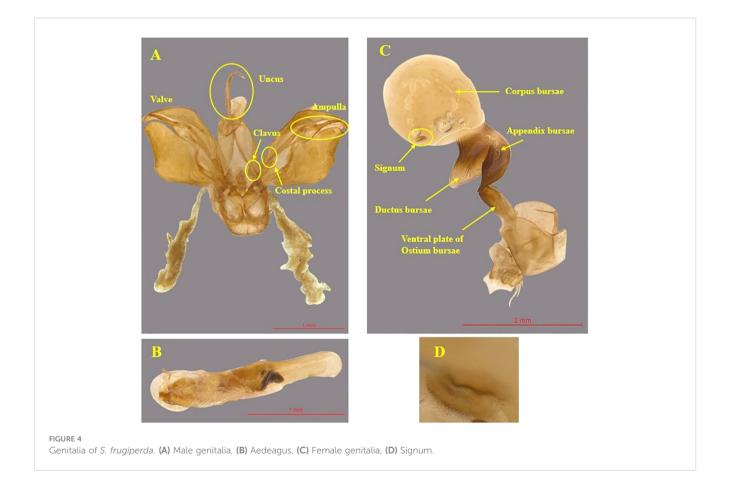
Adults of FAW exhibit sexual dimorphism (Figures 2E, F). The forewings of adult males are rusty brown to greyish brown with a triangular white patch close to the apical margin and some distinct markings in the center of the wing. Males have brown, oval, and oblique obicular spots. The reniform spots are obscure, only partially black-outlined, and have a small white marking in the shape of a sideways "V" in adult males. At the intersection of Median 3 and Cubitus A1 veins, a small conspicuous white spot is visible. The forewings of females are uniformly greyish brown in color, with faint pale brown markings and dark grey oval-shaped spots present along the outer margins. There is no reniform spot or white patch at the apical portion.

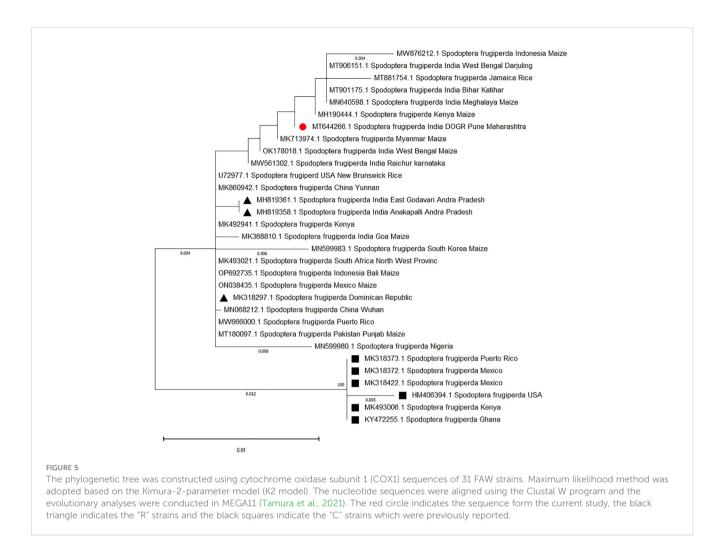
The male genitalia have broad, quadrate valvae, an uncus that is curved at the apical half, slender and pointed at the apex, and a slightly curved ampulla (Figure 4A). Similarly, the clavus is short; the costal process is narrow, elongated, straight, and inclined in the middle, with hairs on the tip. The coremata have a single lobe, and the aedeagus is well developed (Figure 4B). The hair mass associated with the female genitalia is also well developed. The ventral plate of the ostium bursa has a length less than twice its width, whereas the ventro-lateral ductus bursa is short and completely sclerotized. The appendix bursae is partially sclerotized, and the corpus bursae is bulbous with a length less than twice the width, having striate convolutions (Figure 4C). The signum is present in the basal half of the corpus bursae (Figure 4D).

Molecular characterization

Effective identification of the pest is needed for its efficient management, as similar species like *S. litura*, *S. exigua*, and *S. frugiperda* occur simultaneously in the onion fields. Morphological characteristics of these pests, as well as their damage symptoms on leaves, are similar, which results in misidentification with other noctuid species at early stages, especially during the 1st and 2nd instars. The lack of unambiguous keys to differentiate the adult females and immature stages makes it difficult to identify them. Therefore, DNA barcoding will complement morphometric analyses very well in order to distinguish between these *Spodoptera* species complexes.

The mitochondrial COX1 gene was successfully amplified using the FAW samples obtained from the onion field, yielding an amplicon with the predicted size of 651 bp. The gene sequence obtained was submitted to the NCBI GenBank database with accession number MT644266. DNA barcodes from FAW specimens taken from onion plants in the Pune district were subjected to a BLASTn search, which revealed a 100% nucleotide sequence identity with *S. frugiperda* voucher specimens MN640598 in GenBank. A maximum likelihood phylogenetic analysis with bootstrap support (1000 replicates) using the MEGA11 program yielded a consensus tree with well-supported nodes (Figure 5), revealing two distinct clusters. One cluster consisted of 19.36% (6/31) of the "C"-strain of the FAW reported worldwide, while the





other cluster consisted of 80.64% (25/31) individuals from different regions, including the "R"-strains and the strain from the current study. This confirms that the strain under study is the "R"-Rice strain. Although R strains from India grouped together, there was a significant evolutionary distance between species, which may be due to their introduction from various geographical conditions and host plant adaptability.

Therefore, the strain from the present study was confirmed through multiple sequence alignment with previously identified *S. frugiperda* strains from corn and rice (MK318422.1 and MK318297.1, respectively). One sequence from each of the reference strains of the R and C strains was aligned with the strain under study. When the 'R' and 'C' strains of the Indian and global populations were analyzed, nucleotide variations between the 'R' strain and 'C' strain were found in 11 positions (48, 93, 147, 183, 234, 465, 540, 546, 576, 610, 639) (Table 1). Sequence alignment analysis indicates that the strain used in this study was indeed the "R" strain. Similar conclusions were observed in some previous works, despite the fact that they were reported at different locations (34, 79, 133, 169, 220, 451, 526, 532, 562, 596, 625). The variations in locations may be due to the variation in amplified sequence size (Mahadeva Swamy et al., 2018; Maruthadurai and Ramesh, 2019; Chormule et al., 2019; Dharmayanthi et al., 2022).

TABLE 1	Position wise nucleotide	variations in COX1 g	enes of S. frugi	erda in strain fror	m current study vs.	. previously reported Rice a	nd Corn strains.
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Strains	Nucleotide position										
Strains	48	93	147	183	234	465	540	546	576	610	639
MK318422.1 – S. frugiperda Mixico – Corn Strain	G	G	Т	Т	С	Т	Т	С	С	Т	Т
MK318297.1 – S. frugiperda Dominican Republic – Rice Strain	А	А	С	А	Т	С	С	Т	Т	С	А
MT644266.1 – S. <i>frugiperda</i> India DOGR Pune – Rice Strain	А	A	С	А	Т	С	С	Т	Т	С	А

Discussion

Plants with pest infestations produce a wide range of allelochemicals that affect the growth, survival, and reproduction of insects (Hoffmann-Campo et al., 2001; Piubelli et al., 2005; Silva et al., 2017). Crops like maize and related members of the grass family produce allelochemicals such as DIMBOA and MBOA, which affect the growth of several herbivores (Wouters et al., 2014). However, FAW larvae are able to overcome such physiological stressors due to the stereoselective reglucosylation (detoxification process) (Wouters et al., 2014). Furthermore, these crops are suitable hosts, with consideration given to ecological factors that influence host use (Veenstra et al., 1995; Silva et al., 2017). As FAW larvae exhibit a high level of cannibalism, they prefer to feed solitarily while hiding in the whorl region of the host crop. Additionally, this shields them from predators and chemical sprays (Sparks, 1979; Bernays and Graham, 1988; Prowell et al., 2004). This clearly indicates that maize and related grasses are more advantageous hosts for FAW growth. On the contrary, FAWs exhibited prolonged larval duration when reared on onion leaves, which might be due to some sulfur-containing secondary metabolites. These compounds could be responsible for inducing herbivore defenses and consequently leading to an increase in the duration of the larval stage (Ahmed et al., 2017). However, in the near future, FAW will be able to overcome the anti-nutritional factors in onions as they belong to the C4 plant family, similar to maize and other grasses. The adult morphological characteristics described here are comparable to those previously reported (Oliver and Chapin, 1981; EPPO, 2015; Ganiger et al., 2018; Sharanabasappa et al., 2018a; Sharanabasappa et al., 2018b; Shylesha et al., 2018; Bajracharya et al., 2019; Deshmukh et al., 2021b). The current study undoubtedly offers fundamental knowledge regarding the biology and external morphology of FAW on onions.

There is some flexibility in host-plant preference, as evidenced by the association between these morphocryptic strains and their hosts (Prowell et al., 2004; MaChado et al., 2008; Juárez et al., 2012). Despite having identical morphologies, these two strains have different host ranges, mating strategies, and pheromone compositions (Pashley, 1986; Pashley, 1988; Groot et al., 2008; Dumas et al., 2015). Studies from India suggests that the R strain has established itself on maize, sweet corn, and sorghum, while the C strain has been adapted to sugarcane (Mahadeva Swamy et al., 2018; Bhavani et al., 2019), thereby indicating the presence of both the strains of S. frugiperda in India. The current study confirmed that the strain reported feeding on the onion crop in India is the "R" Rice strain. The R strain is widely distributed on various host plants in Asia, America, and Africa, in contrast to the C strain, which dominates in Africa and America (Cano-Calle et al., 2015). The genetic diversity of the FAW population from the Indian subcontinent also revealed that, regardless of the host plant, the "R" strain predominates (Mahadeva Swamy et al., 2018; Maruthadurai and Ramesh, 2019; Acharya et al., 2021). Since these strains are sympatric and morphologically identical, conventional taxonomy is time-consuming and requires expertise. Usually, molecular techniques make it simple to distinguish between these strains (Lu et al., 1994; Lu and Adang, 1996). In Maharashtra, the typical crop rotation involves a maize-onion sequence. Maize is grown during the *kharif* (rainy) season, followed by onion cultivation in the rabi season (Surve et al., 2019 and Kawade et al., 2020). Besides the regular cropping pattern, most onion farmers in the region also plant maize as a protective barrier crop to deter adult thrips from neighboring fields, as suggested by Srinivas and Lawande (2006). However, it's important to recognize that this maize crop, acting as a protective barrier, can also inadvertently become a primary source of fall armyworm (FAW) infestation in the onion crop.

With the impact of climate change on the geographical distribution of insect pests, there are growing concerns about the threats they pose to the environment, agricultural productivity, and global food production. The FAW, being a highly polyphagous pest, has the ability to rapidly adapt to new agro-ecosystems with multiple cropping systems. This adaptation exacerbates the intensity of damage and leads to significant financial losses for farmers. The high dispersal ability, robust reproductive capacity, and the probable absence of diapause in tropical climates could expedite the expansion of its geographic range within both the host country and neighboring nations (Sharanabasappa et al., 2018a) In tropical regions with multiple cropping systems and seasons, it becomes very important to investigate invasive pests as well as their host range to forecast their potential damage and devise suitable control measures. Given that FAW has already been documented infesting maize and sugarcane, it is expected to invade onion crops, posing a substantial risk to onion production. In this study, we report the invasion of fall armyworm from maize to onion in Maharashtra, the largest producer of maize and onion in India. Furthermore, molecular-level characterization done in the present study would be helpful for early detection and diagnostic purposes. Despite causing negligible damage to onions, FAW has the potential to develop into a belligerent pest that poses a serious threat to onion production in the near future. Hence, proper monitoring needs to be done at periodic intervals to avoid economic loss in onions.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

SP: Conceptualization, Data curation, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. DS: Data curation, Formal Analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. CN: Data curation, Methodology, Validation, Writing – original draft. GG: Data curation, Formal Analysis, Validation, Visualization, Writing – original draft, Writing – review & editing. VK: Conceptualization, Formal Analysis, Resources, Supervision, Writing – review & editing. AG: Formal Analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. AT: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. VM: Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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