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New occurrence of corn and rice strains of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Bali and Lesser Sunda (Indonesia): Genetic diversity, distribution, and damage

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Abstract. *Yudha IKW, Supartha IW, Susila IW, Sudiarta P, Wijaya IN, Wiradana PA. 2024. New occurrence of corn and rice strains of* Spodoptera frugiperda *(Lepidoptera: Noctuidae) in Bali and Lesser Sunda (Indonesia): Genetic diversity, distribution, and damage. Biodiversitas 25: 1890-1900.* *Spodoptera frugiperda* is an invasive pest with rapid proliferation and is responsible for reducing corn productivity in several regions in Indonesia, including Bali and Lesser Sunda in Indonesia. Therefore, this study aimed to determine the geographic distribution, genetic diversity, and specific genes of *S. frugiperda* as well as assess its attacks in Bali and Lesser Sunda (NTB and NTT) regions. The study procedures were carried out using field surveys, followed by molecular identification to determine the genetic diversity of *S. frugiperda* with the COI locus. A total of 150 infected corn plants were sampled using the diagonal sampling method, with a unit size of 5 m × 5 m. The distribution data obtained were then analyzed using the QGIS application and SPSS 22 for statistical analysis. The geographic distribution results showed that *S. frugiperda* was evenly distributed in the provinces of Bali and Lesser Sunda, with the observation of 2 strains, namely corn and rice. Corn strain was more specifically found in the Karangasem, Flores, Lombok Highlands, and Timor areas, while rice strain occured in the Jembrana, Sumbawa, Sumba, Flores, and Lombok lowland areas. In addition, a total of 12 specific nucleotide bases from *S. frugiperda* gene were found in Bali, NTB, and NTT regions. The findings also showed that the haplotype network of Bali, NTB, and NTT populations was effectively isolated from other locations and was in the process of genetic divergence. The 3-year invasion of *S. frugiperda* in Indonesian territory was reported to have experienced a process of genetic population development. Lombok Island had the highest average plant damage at 54.63%, which was not significantly different from the value of Sumbawa, Bali, and Sumba at 47.79%, 42.65%, and 40.72%, respectively. On the other hand, the lowest plant damage level in Timor at 20.95%, followed by Flores (at 30.38%).

Keywords: COI, genetic variation, invasive pest, *Spodoptera frugiperda*

INTRODUCTION

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is a polyphagous pest originating from the American continent. This pest has been reported to affect 353 plant species belonging to 76 plant families and prefers to attack plants with high economic value, such as corn, sorghum, rice, millet, and sugar cane (Montezano et al. 2018; Srikanth et al. 2018; Venkateswarlu et al. 2018; Chormule et al. 2019). In addition, *S. frugiperda* has the ability to quickly cause damage to various plants, leading to a decrease in nutritional value (Prasanna et al. 2018). Several studies have also shown its quick transmission, spreading from its origin in America to various areas worldwide, including the eastern regions, such as Africa to Asia (Georgen et al. 2016; Firake and Behere 2020). Reports regarding the incidence of attacks and losses caused by this pest on corn crops in Africa and Europe range from 8.3 to 20.6 million tonnes per year, with an economic loss value of US$ 2.5-6.2 billion per year (CABI 2019; FAO and CABI 2019).

In Asia, the presence of *S. frugiperda* was first reported in India in 2018 (Ganiger et al. 2018) and damaged corn crops (Firake and Behere 2020). Since then, this pest has spread throughout Indonesia. In March 2019, it was discovered on corn plants in West Sumatra (Herlinda et al. 2022) and later found to be attacking corn plants in various regions, including West Java (Maharani et al. 2019), East Java (Megasari and Khoiri 2021), East Kalimantan (Andini and Triyuliana 2023), and Kulon Progo Regency, Yogyakarta (Putra et al. 2024). Additionally, *S. frugiperda* was reported to attack corn plants in the Bali Province region until the end of 2019 (Supartha et al. 2021a), and in East Flores District, East Nusa Tenggara Province in 2020 (Mukkun et al. 2021).

According to previous studies, *S. frugiperda* larvae typically feed on the stems, leaves, and reproductive parts of their host plants (Midega et al. 2018). A recent report also revealed that changes in its population depend on the nutrition and characteristics of host plants, which influences population growth (Subedi et al. 2023). In addition, demographic studies have been reported to play an important role in population dynamics and pest status in the field (Huang et al. 2018; Sunari et al. 2023). Although *S. frugiperda* prefers corn plants as the main host, other plants can be suitable hosts in their absence (Altaf et al. 2022; Supartha et al. 2023).

In line with previous reports, there are 2 strains of *S. frugiperda* in the world, namely Corn (C) and Rice strains (R) (Unbehend et al. 2013, 2014). Corn strains typically prefer corn and sorghum, while rice strains have a preference for pastures, such as rice (Dumas et al. 2015; Nagoshi and Meagher 2022). In addition, the genetic diversity of *S. frugiperda* in Indonesia was first reported by Sartiami et al. (2020), who stated that strains found in Banten were only rice strains. In Lampung, *S. frugiperda* found in corn plants were confirmed to be rice strains (Lestari et al. 2020), while corn and rice strains were collected from corn production centers in West Sumatra (Nelly et al. 2021). Herlinda et al. (2022) also found both strains in the South Sumatra area. The existence of 2 different strains of COI (COI-CSh4 and COI-RS) and 1 strain of Tpi (Tpi-C) has been reported in Bogor (Fahmi et al. 2023). The potential spread of *S. frugiperda* corn and rice strain in Indonesia poses a significant risk to corn and rice plants as well as other important crops. Despite the potential risk, information regarding strains and genetic diversity of *S. frugiperda* in Indonesia is still very limited, particularly from Bali and Lesser. Therefore, there is an urgent need for comprehensive data on the genetic diversity of *S. frugiperda* in Bali and the Lesser Sunda. The data can serve as a basis for controlling this pest and complement information regarding *S. frugiperda* strains in Indonesia.

MATERIALS AND METHODS

Sampling of larvae *S. frugiperda*

Spodoptera frugiperda larvae sampling was carried out in the provinces of Bali, West Nusa Tenggara (NTB), and East Nusa Tenggara (NTT), Indonesia (Figure 1, Table 1). The geographic distribution pattern of *S. frugiperda* in the Bali-Nusa Tenggara region was performed using a survey method by recording each coordinate point of the sampling location that had been determined. In addition, the selection of sampling locations was conducted on several islands in the Bali, NTB, and NTT regions. Environmental parameters, including temperature, humidity, and location altitude were also documented. Data distribution was visualized using Arc-GIS tools and combined with ArcGIS 10.2 software.

Molecular identifications for *Spodoptera frugiperda*

DNA extraction

DNA extraction was carried out based on the method proposed by Lestari et al. (2020) with several modifications. *S. frugiperda* larvae preserved in 70% alcohol solution were taken and dried on a tissue for 30 min. Subsequently, the caterpillars were soaked in hot water (85°C) for 30 min until the samples turned slightly whitish. A total of 2 abdominal segments were then cut and inserted into a 1.5 µL tube, followed by adding 5 µL Proteinase K and complete crushing.

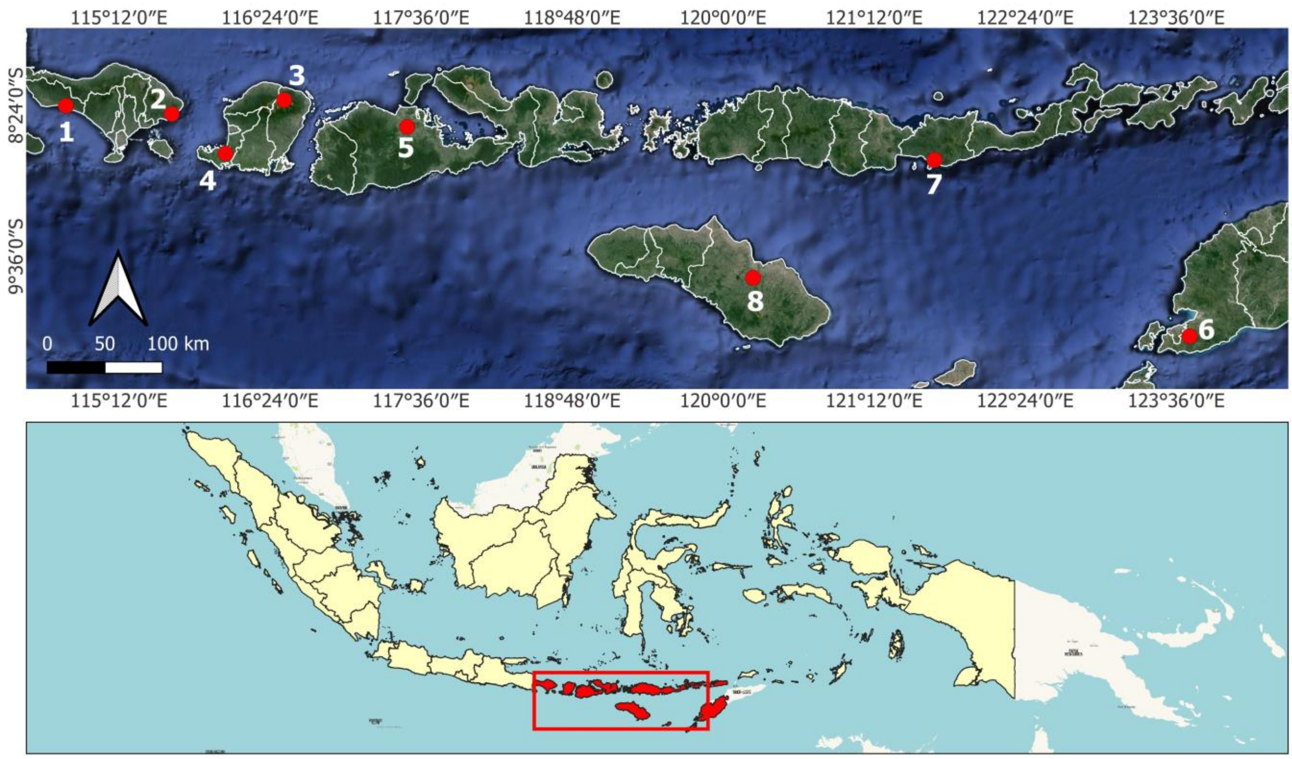

Figure 1. Geographic distribution of *S. frugiperda* in Bali, NTB, and NTT regions of Indonesia. Note: 1. Jembrana, Bali, 2. Karangasem, Bali, 3. Sembalun, Lombok, 4. Sekotong, Lombok, 5. Sumbawa, 6. Timor, 7. Flores, 8. Sumba

Table 1. Sampling locations in Bali, West Nusa Tenggara (NTB), and East Nusa Tenggara (NTT), Indonesia

Location	District	Sub-district	Altitude (m asl.)	Coordinate point
Bali	Badung	Abiansemal	187	8°32'11.0"S 115°13'24.0"E
		Plaga	965	8°18'22.0"S 115°13'50.0"E
	Bangli	Kintamani	1253	8°14'31.0"S 115°16'31.0"E
	Buleleng	Gerokgak	57	8°10'56.0"S 115°45'49.0"E
		Kubutambahan	1328	8°13'15.0"S 115°13'20.0"E
	Denpasar	Sanur	18	8°39'28.0"S 115°15'24.0"E
	Gianyar	Blahbatuh	89	8°35'23.0"S 115°18'13.0"E
	Jembrana	Mendoyo	54	8°24'03.0"S 114°46'48.0"E
		Melaya	45	8°14'54.0"S 114°28'36.0"E
	Klungkung	Klungkung	79	8°33'35.0"S 115°23'58.0"E
	Karangasem	Karangasem	77	8°27'55.0"S 115°37'15.0"E
		Sidemen	219	8°30'43.0"S 115°25'14.0"E
	Tabanan	Marga	331	8°27'44.0"S 115°09'51.0"E
		Selemadeg	143	8°31'21.0"S 115°02'45.0"E
Lombok	West Lombok	Labu Api	27	8°38'52.0"S 116°06'56.0"E
		Narmada, Peresak	43	8°35'31.0"S 116°14'14.0"E
		Sekotong	15	8°46'47.0"S 116°02'52.0"E
		Narmada	179	8°35'38.0"S 116°13'54.0"E
	East Lombok	Terara	329	8°38'25.0"S 116°24'25.0"E
		Pringgabaya	5	8°38'18.0"S 116°25'18.0"E
		Selong	94	8°22'48.0"S 116°41'47.0"E
		Jerowaru	161	8°46'41.0"S 116°02'53.0"E
	Middle Lombok	Batukliang	383	8°37'20.0"S 116°19'41.0"E
		Mertak Pujut	12	8°53'20.0"S 116°20'41.0"E
	North Lombok	Pemenang	9	8°24'11.0"S 116°06'30.0"E
		Kayangan	21	8°16'00.0"S 116°14'55.0"E
		Karang bajo bayan	34	8°15'35.0"S 116°25'34.0"E
		Sembalun	998	8°21'15.0"S 116°30'48.0"E
Sumbawa	Sumbawa Besar	Serading	65	8°34'06.0"S 117°29'28.0"E
		Plampang	58	8°44'06.0"S 117°44'08.0"E
		Rhee	32	8°25'43.0"S 117°14'03.0"E
		Buwer	19	8°27'24.0"S 117°02'43.0"E
	Sumbawa Barat	Taliwang	13	8°50'04.0"S 116°49'09.0"E
		Seteluk	47	8°39'33.0"S 116°51'01.0"E
		Poto Tano	41	8°35'27.0"S 116°50'30.0"E
Sumba	Sumba Barat Daya	Wewewa	463	9°29'36.0"S 119°13'12.0"E
	Sumba barat daya	Wewewa Tengah	425	9°30'46.0"S 119°16'10.0"E
	Sumba Timur	Cambera	38	9°40'27.0"S 119°18'09.0"E
Timor	Kupang	Taebenu	319	10°13'56.0"S 123°42'27.0"E
		Sulamu	28	10°01'05.0"S 123°44'53.0"E
		Kupang Timur	20	10°06'38.0"S 123°49'08.0"E
	Belu	Atambua	332	9°06'03.0"S 124°53'33.0"E
	Malaka	Laenmanen	342	9°21'58.0"S 124°49'24.0"E
	Timor Tengah Utara	Insana	466	9°25'35.0"S 124°44'37.0"E
Flores	Ende	Ndona	25	8°50'43.0"S 121°40'48.0"E
		Ende Timur	43	8°49'42.0"S 121°40'35.0"E
		Lokoboko	55	8°49'55.0"S 121°40'49.0"E

After being crushed, 300 L of TNES buffer was added (Tris HCl 1 M (pH 7.5), NaCl 5 M, EDTA 0.5 M, ddH2O, and 20% SDS), and the samples were homogenized and incubated at 60°C for 3 h. A total of 85µL of 5 M NaCl was added and then shaken by hand for 15 s, followed by centrifugation for 10 min at 14,000 rpm. During the procedures, 400 µL of supernatant was taken, placed into a new tube, and added with Isopropanol. Approximately 60% of the taken volume of supernatant was placed in a -40°C freezer for 20 min and centrifuged for 5 min at 14,000 rpm. The supernatant was then discarded, followed by the addition of 500 µL of cold 70% alcohol and centrifugation for 5 min at 14,000 rpm. In addition, the supernatant obtained was discarded again, dried at room temperature for 24 hours (one night), and added with 20 µL buffer TE (1st Base, Malaysia). The DNA suspension was stored at -4°C before being used for further analysis. The centrifugation process in this study was carried out using Microspin12 (Biosan, Latvia).

DNA amplification

DNA amplification was performed to amplify the Cytochrome Oxidase Subunit I (COI) region using LCO 1490 (Forward 5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO 2198 (Reverse 5'-TAAACTTCAGGGTGACCAAAAAATCA-3') primers (Folmer et al. 1994. PCR was carried out using a Sensoquest Thermal Cycler Machine (Germany) with a total volume of 25 mL consisting of 1 mL DNA, 12.5 mL master mix (2x MyTaq HS Red Mix, Bioline, USA), 1 mL of each primer LCO 1490 and HCO 2198, with a concentration of 10 M and 9.5 mL of sterile distilled water. In addition, PCR was conducted in stages, namely 1 cycle initiation at 95°C for 5 min, followed by 30 cycles consisting of denaturation at 95°C for 1 min, annealing at 54°C for 1 min, extension at 72°C for 1 min, and 1 elongation cycle at 72°C for 5 min. The results obtained were then electrophoresed using a 0.5% agarose gel suspension that had been given 1 mL of ethidium bromide (ETBr; 10 mg/mL, per 20 mL agarose) at 55 V for 70 min. The findings were then visualized using a DigiDoc UV transilluminator (UVP, USA).

Sequencing and data analysis of sequencing results

The PCR results were sent to 1st Base Malaysia for the sequencing process. In addition, the sequencing results were analyzed using the Bio Edit ver. 7.2.6 for windows. The findings of the analysis were then submitted to the Basic Local Alignment Search Tool (BLAST) (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to determine their possible identity. The phylogeny tree was created using the Mega 7 for Windows program with the maximum Likelihood method (1000X bootstrap; Tamura-Nei model). The reference strains used in this study were obtained from NCBI (https://www.ncbi.nlm.nih.gov/).

Observation of *Spodoptera frugiperda* in maize fields

Damage by Spodoptera frugiperda

The observations of *S. frugiperda* attacks were carried out from the lowlands to the highlands in Bali, NTT, and NTB Province. From each location, the sample land was taken with an area of 10 are-1 ha per location, and the age of the selected maize ranged from 1 to 6 weeks, following the criteria proposed by Lestari et al. (2020). The observation of attacks was carried out directly using a scouting system. In addition, the scouting system was chosen because the survey area was large and located in several locations (Kuate et al. 2019), and the protocol followed the guidelines of Prasanna et al. (2018). The field scouting was performed to calculate the percentage of infested plants or incidence of damage as well as to estimate the intensity of attack by *S. frugiperda* larvae (Kuate et al. 2019). The maize fields were scouted using a diagonal ''X'' pattern approach, and the total samples observed were 50 plants (10 consecutive plants at five different spots along the diagonal ''X'' transect) (Supartha et al. 2021b). Damage to the plants was distinguished by the severity of pinholes, shot-holes, lesions, tattering, and dead hearts. The percentage of severity or attack intensity was calculated using a rating scale for scoring damage severity on whorl-stage plants (Kuate et al. 2019) and calculated with scale Davis (Davis and Williams 1992).

Damage to the plants was also scored by evaluating the severity of pinholes, shot-holes, lesions, tattering, and dead hearts. A rating scale from 1 to 5 was used for scoring damage severity on whorl-stage plants, namely 1) no damage, 2) 1-10% leaf damage or <5mm diameter or only the leaf cuticle destruction; 3) 11-25% leaf damage with the presence of chewed areas >5 mm, funnel leaves uninjured; 4) 26-50% leaf damage with the presence of chewed areas >1 cm, the funnel less severe; and 5) >50% leaf damage, plants stunting, and funnel damaged severely (Kuate et al. 2019).

Data analysis of *Spodoptera frugiperda* attack

Incidence and severity of *S. frugiperda* infestation were tested for normality using the Shapiro-Wilk test and for variance homogeneity by Levene's test. In addition, square root transformation was performed on homogenous variance to meet normality assumptions before being subjected to a one-way analysis of variance. Means were compared using Tukey's Honestly Significant Test (HSD), and back transformed means were presented after analysis. Infestation data was analyzed using SPSS V.23.

RESULTS AND DISCUSSION

Geographic distribution of *Spodotera frugiperda* in Bali, NTB, and NTT regions

The geographical distribution shown by *S. frugiperda* in this study was evenly distributed in the Bali and Lesser Sunda Provinces (NTB and NTT), as presented in Figure 1. After *S. frugiperda* invaded Indonesia in 2019 and was discovered in 2020 in Bali, until now, it has spread evenly and attacked farmers' corn plants, including on the islands of Bali, Lombok, Sumbawa, Sumba, Flores, and Timor (Supartha et al. 2021b; Pu'u and Mutiara 2023). This even distribution could be triggered by the types of host plants cultivated by farmers in each region, which is dominated by corn. Habitat heterogeneity and topographic variations also provided opportunities for insect pests to invade.

The distribution of *S. frugiperda* in corn plants in Indonesia was influenced by several factors, such as biotic and abiotic factors. Several biotic factors, such as the presence of host plants in the field, greatly determined the distribution process because corn plantations, which were the main host plants for *S. frugiperda*, were always present in the Bali, NTB, and NTT regions. Consequently, this pest's distribution and invasion process was typically very fast. The results revealed that abiotic factors, including the influence of climate, such as temperature, rainfall, and humidity, were very influential in the potential distribution of *S. frugiperda*. The main factor of the spreading of this pest in the field because *S. frugiperda* is highly polyphagous (Liu et al. 2023). It is also regarded as a "super pest" based on its inherent ability to survive in a wide range of habitats, its strong migration ability, high fecundity, rapid development of resistance to insecticides and its gluttonous characteristics (Wan et al. 2021).

The potential for invasion by *S. frugiperda* pest in this study was very high in all sampling locations in both Bali and Lesser Sunda Provinces, which still took into account the main host availability factor. Similar studies also reported that the presence of *S. frugiperda* was strongly influenced by environmental variables in various regions in China. These included West Gansu, eastern Qinghai, Shaanxi, most of Ningxia, and parts of Tibet. In addition, more than 60% of the ideal distribution for *S. frugiperda* in Western China was simulated using ArcGIS and MaxEnt software (Wang et al. 2020; Li et al. 2022). The even distribution of S. frugiperda reported in this study was due to the availability of host plants that could be used by this pest to continue reproducing. Corn was one of the agricultural commodities that farmers widely grew in the sampling area.

Genetic diversity of *Spodoptera frugiperda* in corn plants in Bali, NTB, and NTT regions

The results of DNA amplification using the COI gene primer from 8 sample isolates obtained from this study showed DNA bands with *S. frugiperda* species consistently showing a band pattern length of 683-697 bp (Figure 2).

The analysis results showed that 4 *S. frugiperda* sequences (Karangasem, Flores, Sembalun, and Timor) had 100% similarity with *S. frugiperda* sample from North Sulawesi, Indonesia (OQ891323.1). This group was then included in the corn sequence (corn strain). Meanwhile, the results of 4 sequences (Jembrana, Sumbawa, Sumba, Flores, and Sekotong) had 100% similarity with samples of *S. frugiperda* from India (MK105749.1 and MK105750.1.), which were included in rice sequence (rice strain). This was a new finding, considering that until now, there was limited information about *S. frugiperda* pest entering rice strains in Indonesia, particularly in Bali, NTB, and NTT (Table 2).

The study results outlined in the phylogenetic tree revealed that *S. frugiperda* sequences in Bali, NTB, and NTT had 2 groups (I and II). Group I consisted of 16 sequences, including 4 from study findings (Jembrana, Sekotong, Sumbawa, Sumba), and was included in rice strains. In addition, these samples had similarities with Indian (Acc. No. MK105749.1 and MK105750.1), Dominican (MK318297.1), Myanmar (MK713974.1), South Africa (MK493020.1), Pakistan (MT180097.1), Jamaica (MT881754.1), Mexico (ON038435.1), Kenya (MK492937.1), China (MK860942.1), India (OQ272110.1), and West Sumatra Indonesia sequences (MZ497026.1).

Group II consisted of 5 sequences and belonged to a clade that was very different from Group I. Furthermore, the 5 sequences included in group II were classified as corn strains. Group II sequences consisted of 4 sequences from study results (Karangasem, Flores, Sembalun, and Timor) and 1 sequence from North Sulawesi, Indonesia (OQ891323.1) (Figure 3).

Table 2. Genetic similarities of *Spodoptera frugiperda* collected from Bali, NTB, NTT Indonesia, and other countries including rice and corn line isolates

Seq	Similarity (%)										
	1	2	3	4	5	6	7	8	9	10	11
1	ID	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98	0.98	0.98
2	1.00	ID	1.00	1.00	1.00	0.98	0.98	0.98	0.98	0.98	0.98
3	1.00	1.00	ID	1.00	1.00	0.98	0.98	0.98	0.98	0.98	0.98
4	1.00	1.00	1.00	ID	1.00	0.98	0.98	0.98	0.98	0.98	0.98
5	1.00	1.00	1.00	100	ID	0.98	0.98	0.98	0.98	0.98	0.98
6	0.98	0.98	0.98	0.98	0.98	ID	1.00	1.00	1.00	1.00	1.00
7	0.98	0.98	0.98	0.98	0.98	1.00	ID	1.00	1.00	1.00	1.00
8	0.98	0.98	0.98	0.98	0.98	1.00	1.00	ID	1.00	1.00	1.00
9	0.98	0.98	0.98	0.98	0.98	1.00	1.00	1.00	ID	1.00	1.00
10	0.98	0.98	0.98	0.98	0.98	1.00	1.00	1.00	1.00	ID	1.00
11	0.98	0.98	0.98	0.98	0.98	1.00	1.00	1.00	1.00	1.00	ID

Description: Corn Strain: 1. *S. frugiperda*_Karangasem_Bali; 2. *S. frugiperda* Flores; 3. *S. frugiperda* Sembalun Lombok; 4. *S. frugiperda* Timor NTT; 5. *S. frugiperda* NorthSulawesi_Indonesia_OQ891323.1; Rice Strain: 6. *S. frugiperda* Sumbawa; 7. *S. frugiperda* Sumba; 8. *S. frugiperda* Sekotong Lombok; 9. *S. frugiperda* Jembrana Bali; 10. *S. frugiperda* India_RiceStrain_MK105749.1; 11. *S. frugiperda* India_RiceStrain_MK105750.1

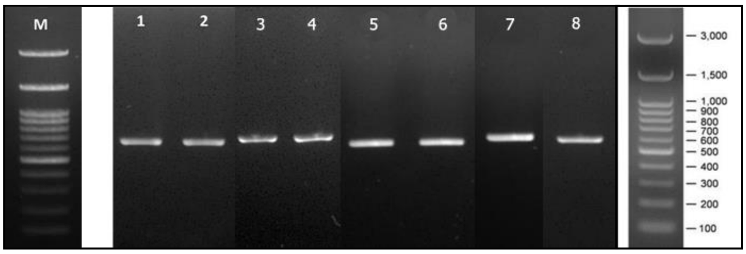

Figure 2. Results of DNA amplification of FAW isolates using mitochondrial COI primers. M: Marker, 1. Jembrana, 2. Karangasem, 3. Sembalun, 4. Sekotong, 5. Sumbawa, 6. Timor, 7. Flores, 8. Sumba

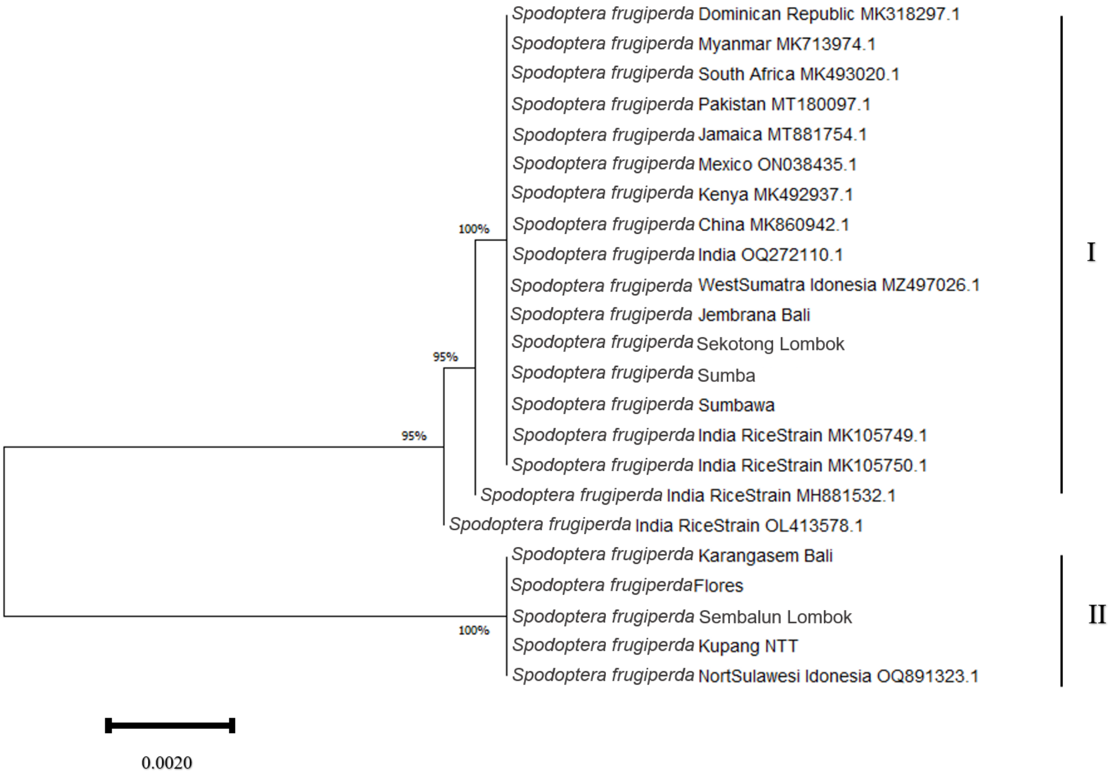

Figure 3. Phylogenetic tree based on the cytochrome oxidase I gene. Mitochondrial isolates of *Spodoptera frugiperda* collected from Bali, NTB, and NTT were divided into 2 groups (I and II). Group I is included in the "Paddy/Rice Strains" group, while Group II is a member of the "Corn/Corn Strains" clade

In this study, *S. frugiperda* has high genetic diversity which accordance with the previous study by Lestari et al. (2020), Nayyar et al. (2021), and Nelly et al. (2021). Genetic diversity refers to the level of biodiversity, which indicates the amount of genetic variation in a species. In addition, genetic variation and diversity were important for determining control strategies (Mahadeva-Swamy et al. 2018; Hoban et al. 2021) and monitoring the development of resistance (Omuut et al. 2023). Using Amplified Fragment Length Polymorphism (AFLP), Clark et al. (2007) revealed that the majority of genetic variability in 23 populations of *S. frugiperda* from Mexico, the United States, Puerto Rico, Brazil, and Argentina was within 1 population and not between populations. Partial COI gene sequence analysis showed the presence of haplotypes of rice lines (dominant) and corn lines, with a haplotype diversity of 0.382. Based on COI markers, pairwise difference distribution analysis, and neutrality tests showed that *S. frugiperda* population was experiencing expansion (Omuut et al. 2023). The potential for phenotypic plasticity to develop in maize lines that had native resistance to FAW leaf damage due to the strong influence of Genotype by Environment (GXE) interactions revealed the importance of conducting multi-year germplasm evaluations when screening maize germplasm for resistance to leaf damage by *S. frugiperda* (Liu et al. 2021). The findings of Acharya et al. (2021) showed that 92.6% of specimens collected from corn fields (25/27) were grouped with the COI rice line, while only 7.4% (Tan-3, Vie-3; 27/2) were clustered in the COI corn line. All COI rice line sequences (25 specimens) were 100% identical but were 98.33-98.48% similar to the two 99.85% COI corn line sequences (two specimens).

The analysis results were that by aligning nucleotide bases and contigs from 8 samples in Bali, NTB, and NTT, then adding 2 references from rice strains in India, found 12 different nucleotide base loci. The 12 nucleotide bases had differences and were focused at the locus 22, 34, 79, 133, 169, 220, 451, 526, 532, 562, 596, and 625 (Table 3). The findings of the differences in the 12 nucleotide positions were loci 22 (CCCCCAAAAAA), 34 (GGGGGAAAAAA), 79 (GGGGGAAAAAA), 133 (TTTTTCCCCCCC), 169 (TTTTTAAAAAA), 220 (CCCCCTTTTTTT), 451 (TTTTTCCCCC), 526 (TTTTTCCCCCC), 532 (CCCCCTTTTTT), 562 (CCCCCTTTTTT), 596 (TTTTTCCCCCCC), and 625 (TTTTTAAAAAA). Genetic specifications of *S. frugiperda* were clearly shown in Table 2, where 12 nucleotide bases revealed the genetic diversity of each sample in the Bali, NTB, and NTT regions. However, it was important to note that there was a potential for the genetic plasticity possessed by *S. frugiperda* to expand and become more diverse.

Table 3. Genetic specifications and differences in *Spodoptera frugiperda* nucleotides from Bali, NTB, NTT and other locations

Isolate	Accession Number	Position of nucleotide difference											
		22	34	79	133	169	220	451	526	532	562	596	625
*S. frugiperda*_Karangasem_Bali	Bali	C	G	G	T	T	C	T	T	C	C	T	T
*S. frugiperda*_Flores	NTT	-	-	-	-	-	-	-	-	-	-	-	-
*S. frugiperda*_Sembalun_Lombok	NTB	-	-	-	-	-	-	-	-	-	-	-	-
*S. frugiperda*_Timor_NTT	NTT	-	-	-	-	-	-	-	-	-	-	-	-
*S. frugiperda*_NortSulawesi_Idonesia_	OQ891323.1	-	-	-	-	-	-	-	-	-	-	-	-
*S. frugiperda*_Sumbawa	NTB	A	A	A	C	A	T	C	C	T	T	C	A
*S. frugiperda*_ Sumba	NTT	A	A	A	C	A	T	C	C	T	T	C	A
*S. frugiperda*_Sekotong_Lombok	NTB	A	A	A	C	A	T	C	C	T	T	C	A
*S. frugiperda*_Jembrana_Bali	Bali	A	A	A	C	A	T	C	C	T	T	C	A
*S. frugiperda*_India_RiceStrain_	MK105749.1	A	A	A	C	A	T	C	C	T	T	C	A
*S. frugiperda*_India_RiceStrain_	MK105750.1	A	A	A	C	A	T	C	C	T	T	C	A

Note: Nucleotide length: 658 bp

This study revealed that genetic specifications using COI sequence analysis could detect differences between *S. frugiperda* obtained in Bali, NTT, and NTB compared to *S. frugiperda* from abroad. Furthermore, *S. frugiperda* isolates in Bali, NTT, and NTB also had 100% similarity to references from India, Dominican, Myanmar, South Africa, Pakistan, Jamaica, Mexico, Kenya, China, India, and West Sumatra Indonesia. The presence of the COI-RS strain in *S. frugiperda* individuals was influenced by crossing female and male corn lines (Nagoshi et al. 2019, 2020). The majority of *S. frugiperda* population in Indonesia consisted of the COI-RS Tpi-C strain (Dharmayanthi et al. 2022), similar to those in China, India, and Africa. This molecular detection approach can certainly be part of early detection of changes in strains of *S. frugiperda* so that we can understand its bioecology more comprehensively (host plant, reproductive behavior and degree of infection) as a pest control effort.

The spatial arrangement of subgroups of rice and corn strains (Rice Strain and Corn Strain) did not show a real relationship with the presence of rice and corn plantation areas. However, the sampling was almost entirely from corn fields, and the low presence of rice strain insects could indicate a certain degree of host specificity. The area where the insects were sampled was mostly corn, which could increase the number of corn-strain insects. The results showed that the corn area overlapped heavily with rice fields, thereby providing opportunities for interbreeding (Arias et al. 2019).

Haplotype network comparisons of COI variation

Network analysis was used to compare genetic variation in the COI gene of *S. frugiperda* in Bali, NTB, and NTT with genetic variation from 6 regional collection locations. The COI haplotypes identified from Bali had different sequences between Karangasem and Jembrana, while the haplotype models in Lombok also had different sequences between the highlands and lowlands. Haplotypes from Sumbawa had models that were very clearly separated from the region of origin. The Sumba haplotype model had unique specifications, with the Sumbawa *S. frugiperda* population group being separate from North Sumatra. The haplotype model in the Timor and Flores regions had almost the same grouping, with the same intersection as *S. frugiperda* from North Sumatra. The results revealed that all samples had a difference of 12 mutations between one haplotype and its most closely related variant (Figure 4). These findings indicated that the populations of Bali, NTB, and NTT were effectively isolated from other locations and were in the process of genetic divergence. This study provided the latest information that 3 years after the invasion of *S. frugiperda* in Indonesia, there had been a process of developing genetic populations of *S. frugiperda* in Bali, NTB, and NTT regions.

The genetic divergence of *S. frugiperda* was closely related to migration patterns between populations, the influence of climate suitability, plant availability, and corn planting patterns carried out by farmers in the field (Nagoshi et al. 2018, 2019, 2020). The lack of consistent clustering by host strain at the core genome level and the weak correlation between mitochondrial haplotypes suggested that there was some degree of hybridization (Schlum et al. 2021).

Damage characteristics of *Spodoptera frugiperda* on corn crops in Bali, NTB, and NTT

The damage characteristics of *S. frugiperda* were different from other armyworms and pest damage on corn plants. *S. frugiperda* pest had a characteristic attack, where it not only attacked the generative and vegetative vases, but also destroyed both vases of corn plants. Figure 5 shows eggs of *S. frugiperda* on the surface of corn plants (A). The vegetative phase of corn plants had typical attack characteristics, where this pest attacked the growing point of corn plants (B and C) until the leaves had holes (D), and produced a lot of feces resembling sawdust (E). In addition, it also attacked the stem (F), until the generative phase destroyed the flowers (G), and corn cobs (H, and I).

The results of the average plant damage presented on each island in Bali, NTB, and NTT regions are presented in Figure 6. The island of Lombok had the highest average plant damage at 54.63%. This was different but not significantly higher than the damage on Sumbawa, Bali, and Sumba, which were at of 47.79%, 42.65%, and 40.72%, respectively. Meanwhile, the damage in Flores was significantly lower at 30.38%, while Timor had the significantly lowest damage at 20.95%.

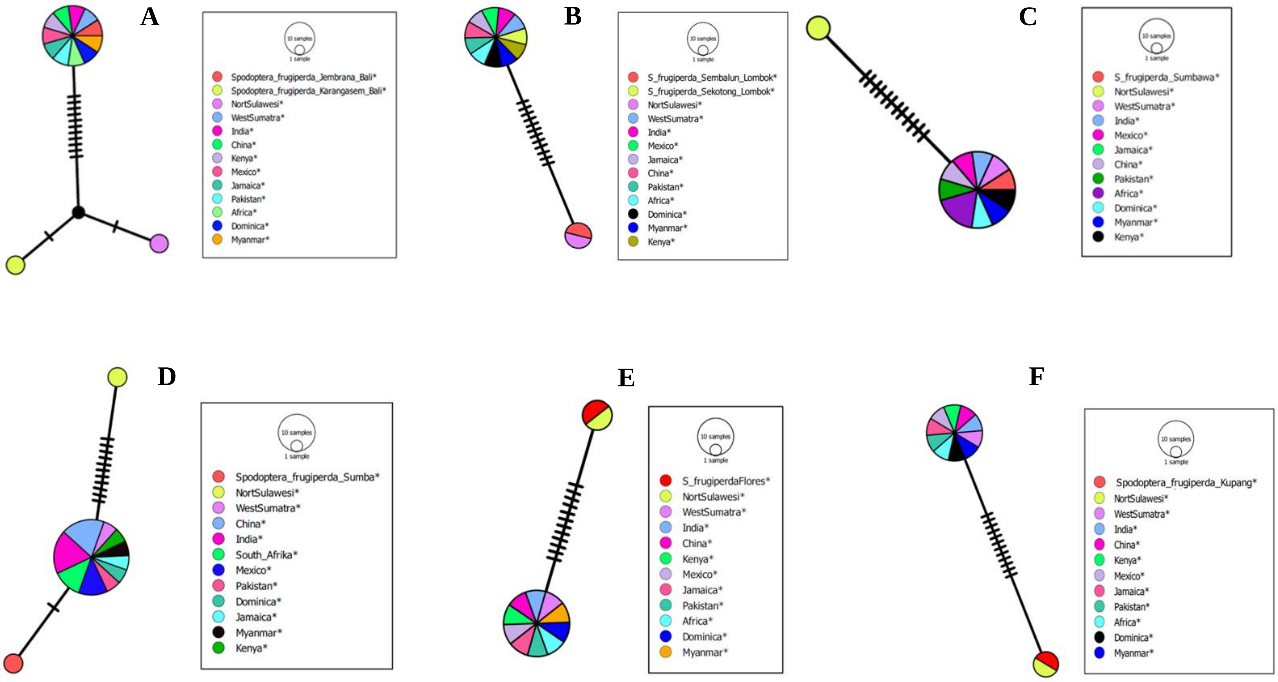

Figure 4. Haplotype network analysis using the COI gene segment which illustrates the genetic differences between haplotype found in Bali, NTB, and NTT. Kilometers in brackets indicate the distance from each sampling location. The area of the circle is proportional to the number of haplotype. Note: A: Bali, B: Lombok, C: Sumbawa, D: Sumba, E: Flores, F: Timor

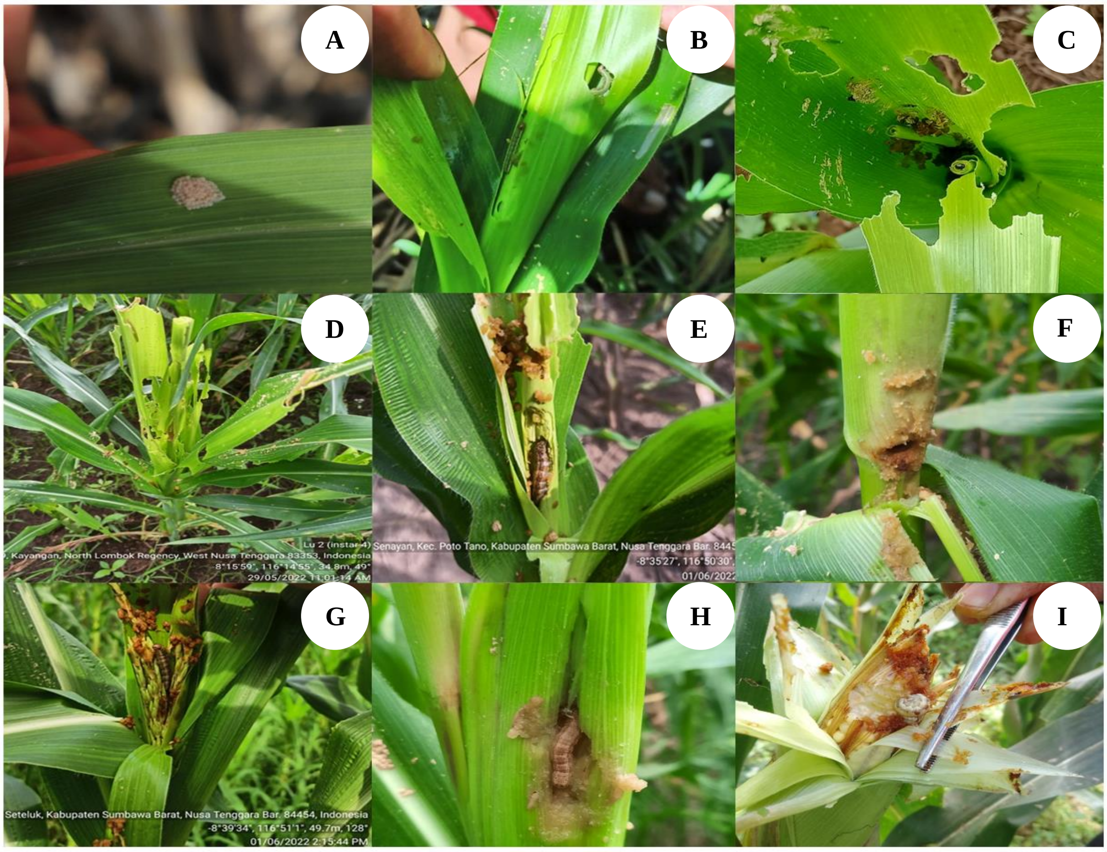

Figure 5. Symptoms of damage to *Spodoptera frugiperda* larvae on corn: A. A cluster of eggs on the leaf surface, B. 3rd instar larvae eat leaves, C. Advanced instar larvae eat leaf rings, D. Larvae attack 4-week old plants after planting, E. 4th instar larvae excrete frass droppings similar to sawdust, F. Symptoms of attack by larvae eating corn stalks, G. 5th instar larvae eating cornflowers, H. 5th instar larvae eating corn cobs, and I. 6th instar larvae eat the tips of corn cobs

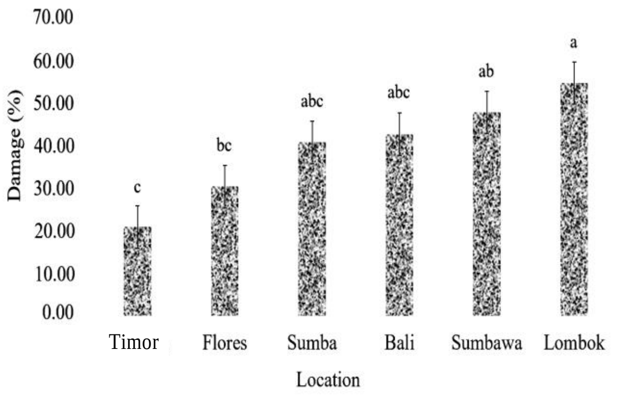

Figure 6. Average damage to corn plants due to attacks by *Spodoptera frugiperda* in Bali, NTB, and NTT. Means with letters are significantly different using the Tukey HSD test ($\alpha = 0.05$)

The attack symptoms shown by *S. frugiperda* larvae in this study had similar characteristics to those found in previous studies (Sartiami et al. 2020; Supartha et al. 2021a; Herlinda et al. 2022). In addition, the attack could begin with the larvae perforating the young leaves of the plant which were still curled up until the growing point of corn plants was cut.

The results of tracing the distribution of *S. frugiperda* are very dependent on the altitude of the location. This shows that *S. frugiperda* is able to adapt to highlands and lowlands and agricultural landscapes. The results of this study differ from the findings of Supartha et al. (2021b), that in highlands >5 meters above sea level, no symptoms of *S. frugiperda* attacks were found. Meanwhile, a high level of attacks occurred in the lowlands of Bali Province. The invasiveness of insect pests was greatly influenced by the size and quality of the host plants resulting from agricultural activities. Physical obstacles (mountains, rivers, and related environmental factors) and human agricultural activities could influence the structure and distribution of insect populations to varying degrees (Ali et al. 2021; Qiqi et al. 2022).

The development of *S. frugiperda* population on corn plants was strongly influenced by extrinsic and intrinsic factors. Extrinsic factors, such as environmental factors, included food adequacy, climate, space, competition, and natural enemies. Shu et al. (2021) and Supartha et al. (2021b) also stated that factors influencing growth, development, and population density were the availability of resources, such as food and living space, as well as the accessibility of resources and individual abilities in the process of distribution, distribution, and capacity to live looking for food and a mate. Intrinsic factors, such as high fertility and short life cycles, also greatly impacted insect pest populations (Bodlah et al. 2023).

The imago of *S. frugiperda* typically flies looking for a suitable place to lay eggs for larval development. *S. frugiperda* pest had a high dispersal capacity, allowing it to quickly spread to the host plants (Li et al. 2023). The reproductive development of *S. frugiperda* was more efficient in tropical and subtropical areas (Assefa and Ayalew 2019). The density of *S. frugiperda* depended on the preferred host plants because the nutritional content of the host was suitable for the growth and development of the insect (Nurkomar et al. 2023). Some Lepidoptera larvae preferred young plants over old plants (Qiu et al. 2023).

The spatial distribution shown by *S. frugiperda* in this study was evenly distributed in Bali and Lesser Sunda Provinces (West Nusa Tenggara and East Nusa Tenggara). *S. frugiperda* in corn plantations in Bali, NTB, and NTT regions had genetic diversity from rice and corn strains, where 4 sequences (Karangasem, Flores, Sembalun, and Timor) were included in corn strains. Meanwhile, the results of 4 sequences (Jembrana, Sumbawa, Sumba, Flores, and Sekotong) were included in rice strains. Specifications for 12 nucleotide bases of *S. frugiperda* gene were found at loci 22, 34, 79, 133, 169, 220, 451, 526, 532, 562, 596, and 625, which spread and attacked corn plants in Bali, NTB, and NTT. The characteristics of *S. frugiperda* attacks on corn plants in Bali, NTB, and NTT regions had their unique characteristics, namely attacking the generative and vegetative vases of corn plants. The intensity values and percentage of attacks varied on each island in Bali, NTB, and NTT. Implementation of integrated pest management, particularly through the use of natural enemies, changing host plant types, and application of botanical pesticides can be taken into account to control *S. frugiperda* attacks in Indonesia.

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