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Optimizing extraction timing and characterizing the sex pheromone profile of the fall armyworm (*Spodoptera frugiperda*) in Indonesia

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Abstract. *Subagyo VNO, Yuniawati R, Hidayat P, Dadang, Widyanto H, Samudra IM. 2026. Optimizing extraction timing and characterizing the sex pheromone profile of the fall armyworm (*Spodoptera frugiperda*) in Indonesia. Biodiversitas 27 (2): d270238. https://doi.org/10.13057/biodiv/d270238.* The fall armyworm (*Spodoptera frugiperda*) threatens maize production in Indonesia, highlighting the need for pheromone tools tuned to local populations. We defined an operational extraction window and quantified the gland pheromone profile of Indonesian FAW females as a baseline for lure development. Virgin females from nine populations were sampled across age (1-4 days) and time after scotophase onset (2-6 hours). Pheromone glands were extracted in hexane and analyzed by GC-FID for three acetate components (Z7-12:OAc, Z9-14:OAc, Z11-16:OAc). In total, 130 extract vials (286 females pooled at 1-3 per vial) were analyzed; the vial was treated as the experimental unit and amounts were expressed as ng per gland. Total pheromone yield showed a consistent mid-scotophase ridge (generally 3-6 hours after lights-off), most apparent in 2-3-day-old females. A linear mixed model on log10(Total_ng) with Population as a random intercept detected a significant Age×Hour interaction (LRT χ^2: 19.176, df: 10, p: 0.0381). Cells were ranked by mean Total_ng while prioritizing replication (n_vials ≥3) and population coverage; the selected global window was 3 days old and 5 h after scotophase onset. Within this window, composition was consistently Z9-major (mean±SD: 80.18±13.61% Z9-14:OAc; 16.15±13.44% Z11-16:OAc; 3.67±5.31% Z7-12:OAc; n: 28 vials). These results provide a reproducible extraction standard and a locally derived reference blend (≈80:16:4) for subsequent behavioral assays and multi-site field validation.

Keywords: Blend ratio, GC-FID, pheromone gland, semiochemical, *Spodoptera frugiperda*

INTRODUCTION

Native to tropical and subtropical Americas, the fall armyworm (FAW), *Spodoptera frugiperda* (Lepidoptera: Noctuidae), is a polyphagous invasive pest and a major global threat to maize (*Zea mays*) (Muthukumar and Kennedy 2021; Fiteni et al. 2022; Keerthi et al. 2023). After emerging in West and Central Africa in 2016 (Goergen et al. 2016), FAW spread rapidly across Africa and into Asia by 2018 (Jing et al. 2020; Tay et al. 2022), and was first detected in Indonesia in 2019 (Maharani et al. 2019; Trisyono et al. 2019). Early outbreaks in Lampung approached 100% plant attack, but surveillance showed moderate to severe damage, peaking at 52.78% in 2020 (Trisyono et al. 2019; Asfiya et al. 2020).

Synthetic insecticides remain the mainstay of FAW control (Muthukumar and Kennedy 2021). However, prolonged application has selected for resistance across several chemical classes, including pyrethroids, organophosphates, and carbamates (Yu et al. 2003). The diamide chlorantraniliprole has shown strong efficacy in Indonesian laboratory and field studies, yet long-term sustainability is threatened by resistance mutations reported in several regions (Bird et al. 2022). In addition, indiscriminate insecticide use can harm natural enemies and pose risks to human health and the environment, underscoring the need for Integrated Pest Management (IPM) strategies that are selective, effective, and environmentally sustainable (Tawakkal et al. 2021; Keerthi et al. 2023).

Sustainable IPM uses non-toxic, highly specific sex pheromones for monitoring, mass trapping, and mating disruption (Unbehend et al. 2013; Rizvi et al. 2021). FAW female pheromone blends contain long-chain unsaturated acetates, dominated by (Z)-9-tetradecenyl (Z9-14:OAc) and minor components like (Z)-7-dodecenyl (Z7-12:OAc) and (Z)-11-hexadecenyl (Z11-16:OAc) (Jiang et al. 2022; Tabata et al. 2023). Because pheromone tools must match emissions of the target population to be effective (Muthukumar and Kennedy 2021), intraspecific geographic diversity in pheromone composition (pheromonal dialects) can reduce the efficacy of blends developed for distant populations (Sisay et al. 2024). Across regions, reported ratios vary substantially: although Z9-14:OAc is typically dominant, its proportion can range from ~88-99.6%, with corresponding shifts in Z11-16:OAc and Z7-12:OAc (Andrade et al. 2000; Haenniger et al. 2020; Wakamura et al. 2021; Wang et al. 2022). Such heterogeneity emphasizes the need to quantify local chemotypes under standardized sampling conditions. Two non-morphological, host-associated strains, the corn (C) and rice (R) strains, can also differ in

pheromone component ratios (Unbehend et al. 2013; Nagoshi and Meagher 2022; Sisay et al. 2024).

Despite severe FAW impacts in Indonesia, a standardized pheromone-gland extraction protocol and a quantitative baseline of local pheromone composition are not yet available, limiting the development of locally adapted lures. Accurate definition of local blend composition requires strict, standardized sampling because pheromone production varies with female age and hours after scotophase onset (Schöfl et al. 2009; Ramya et al. 2024). Without standardized timing, comparisons across studies become difficult and may yield blends that perform sub-optimally when transferred across regions. Therefore, we focused sampling within 2-6 hours after scotophase onset and 1-4-day-old virgin females, a biologically relevant window consistent with circadian regulation of calling and pheromone biosynthesis in noctuid moths (Cardé and Haynes 2004; Schöfl et al. 2009; Levi-Zada and Byers 2021; Ramya et al. 2024).

Here, we optimize pheromone-gland extraction across female age (1-4 d) and hours after scotophase onset (2-6 h) and characterize the quantitative gland profile of Indonesian FAW females as a basis for locally adapted lure development. Specifically, we identify a standardized, high-yield extraction window and quantify Z7-12:OAc, Z9-14:OAc, and Z11-16:OAc across nine Indonesian populations to establish reproducible chemical baseline for subsequent behavioral testing and multi-site field validation.

MATERIALS AND METHODS

Insect collection and rearing

FAW larvae were collected from nine maize fields across Java and Sumatra between June 2023 and December 2024, sampling locations are shown in Figure 1. Larvae were collected predominantly from farmer maize fields planted with commercial hybrid cultivars, and sampling targeted the vegetative whorl stage (approximately V3-V10) when larvae were actively feeding in the whorl.

Colonies were maintained at the Cikeumeuh insect-rearing laboratory, Bogor, West Java, Indonesia under 29±1°C, 65±5% RH, and a 12L:12D photoperiod. Rearing followed Sianturi et al. (2022): early instars were kept in plastic containers (30×20×7 cm) and fed baby corn; late instars were transferred to containers with sawdust for pupation. Pupae were placed in jars (15 cm diameter) lined with filter paper, covered with gauze, and provided with a 10% honey solution. To ensure virginity, pupae were sexed and held individually until emergence. For chemical analyses, females were obtained only from early laboratory generations (F_2-F_3), and no later generations were used in this study.

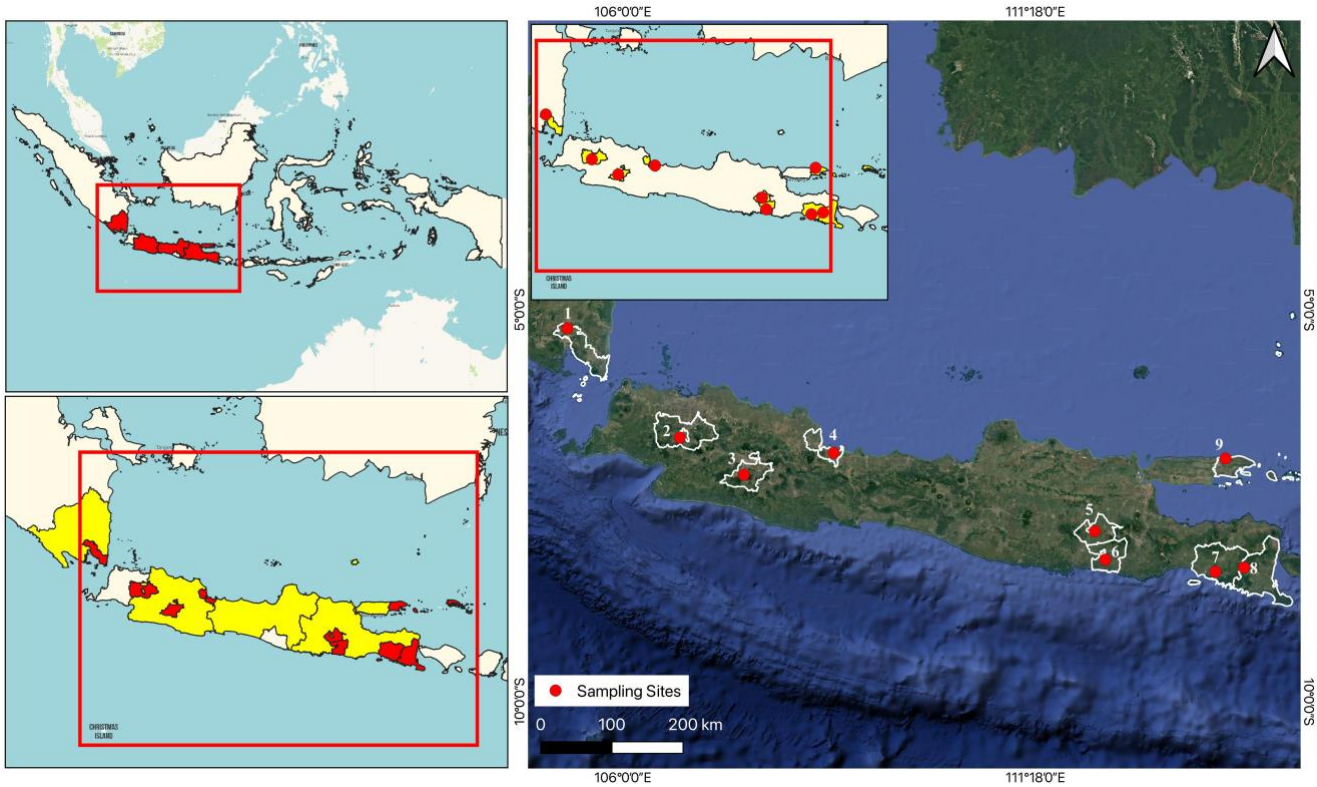

Figure 1. Sampling locations of *Spodoptera frugiperda* on maize in Java and Sumatra, Indonesia. Points indicate the nine source populations used for chemical analyses: 1. South Lampung (5°14′13.0″S, 105°17′15.3″E), 2. Bogor (6°37′50.5″S, 106°43′49.5″E), 3. Bandung (7°06′16.7″S, 107°33′18.3″E), 4. Cirebon (6°49′28.3″S, 108°42′34.2″E), 5. Kediri (7°49′25.2″S, 112°03′49.4″E), 6. Blitar (8°11′17.0″S, 112°11′52.0″E), 7. Jember (8°20′31.7″S, 113°36′46.8″E), 8. Banyuwangi (8°17′16.1″S, 113°58′49.9″E), 9. Sumenep (6°53′50.0″S, 113°44′31.0″E)

Pheromone gland extraction

Female age (1-4 days) was counted from adult emergence (day 0: emergence). Females used for pheromone extraction were maintained as virgins by sexing pupae (Deshmukh et al. 2021) and holding females individually after emergence, thereby preventing mating prior to gland dissection. After gentle cleaning of the abdominal tip, the terminal abdominal segment containing the sex pheromone gland was excised with fine scissors and immediately immersed in hexane containing 1000 ppm butylated hydroxytoluene (BHT). Solvent volume was standardized at 5 µL per pheromone gland, so vials containing 1-3 females received 5-15 µL depending on the number of females pooled per vial. All extractions were carried out in 1.5-mL glass vials in an air-conditioned laboratory at approximately 25±2°C and under low light to minimize degradation. Extraction time was defined as the soaking time after the gland was immersed in solvent and was fixed at 30 min for all samples, controlled with a digital timer; vials remained capped during this period. After 30 min, glands were removed with clean forceps, and extracts were immediately recapped and refrigerated at 4°C; GC-FID analysis was performed within 1-2 days. Solvent and BHT stocks were prepared in a single batch and used throughout the experiment to reduce variation among samples.

Each vial contained glands from 1-3 females, and amounts are reported as ng per gland by dividing vial totals by the number of glands (females) pooled. A total of 130 vials (GC-FID injections) were analyzed across all populations and sampling cells, representing 286 females pooled across vials. Because females pooled within a vial share the same extraction and GC-FID injection, they were not treated as independent replicates; therefore, the vial (one extract/injection) was considered the experimental unit for inferential analyses. Replication across the Age×Hour grid (number of vials/observations, total females contributing to each cell, and population coverage) is summarized in Table 1.

The sampling design was informed by published evidence on circadian regulation of pheromone biosynthesis and calling in noctuid moths and by reported scotophase-associated variation in FAW and related species (Cardé and Haynes 2004; Schöfl et al. 2009; Levi-Zada and Byers 2021; Ramya et al. 2024). To capture a biologically relevant signaling period while reducing edge-of-night variability, we restricted gland extractions to an "early-night" window spanning 2-6 hours after scotophase onset. We further limited sampling to 1-4-day-old virgin females, corresponding to the early reproductive phase when calling activity and pheromone output are typically high in noctuid moths (Cardé and Haynes 2004; Schöfl et al. 2009; Levi-Zada and Byers 2021; Ramya et al. 2024).

Chemical analysis (GC-FID)

Pheromone extracts were analyzed on a Shimadzu GC-2010 Pro gas chromatograph equipped with a flame-ionization detector (FID) (Shimadzu, Japan). Separations were performed on a DB-WAX capillary column (30 m × 0.25 mm i.d., 0.25 µm film). The oven temperature program was 80°C for 3 min, then increased at 5°C min^{-1} to 200°C, followed by a 22-min hold. Injections (2 µL) were made in splitless mode (splitless time 1.0 min), with the injector set at 210°C and the FID detector at 200°C. Nitrogen (N_2) served as the carrier gas in constant-flow mode (1.23 mL min^{-1}). FID gas flows were set to 40 mL min^{-1} for H_2, 400 mL min^{-1} for air, and 30 mL min^{-1} for make-up N_2.

Compounds were identified by comparing GC retention times of peaks in extracts with those of synthetic standards of (Z)-7-dodecenyl acetate (Z7-12:OAc), (Z)-9-tetradecenyl acetate (Z9-14:OAc), and (Z)-11-hexadecenyl acetate (Z11-16:OAc). Standards for Z9-14:OAc and Z11-16:OAc were obtained from Shin-Etsu (Japan), whereas Z7-12:OAc was obtained from Sigma-Aldrich (USA). Quantification used a single-point external-standard approach based on a mixed standard solution containing the three acetates at 250 ppm each (≈250 µg mL^{-1} each). The mixed standard was injected under the same GC conditions (2 µL injection), and peak areas were recorded. For each extract, the amount of each component was calculated from the ratio of the sample peak area to the corresponding standard peak area multiplied by the standard mass per injection for that compound. Quantities were expressed as ng per gland by dividing vial totals by the number of glands extracted. Quantification relied solely on external standards; no internal standard was used.

Quality control. At the start of each GC-FID run, a solvent blank was injected followed by the mixed external standard to monitor contamination/carry-over and to verify retention-time stability and response consistency. One run typically comprised 3-5 sample injections. Replicate injections of the same extract were not routinely performed.

Data processing and statistical analysis

Experimental unit and data structure

Each GC-FID chromatogram corresponded to one extract vial containing pheromone glands from 1-3 females (pooled). Therefore, the vial/injection was treated as the experimental unit (N: 130 vials/observations). Amounts were expressed as ng per gland by dividing vial totals by the number of glands extracted (i.e., the number of females pooled in the vial).

Pheromone yield (total amount)

Total pheromone amount (Total_ng; ng per gland) was defined as the sum of Z7-12:OAc, Z9-14:OAc, and Z11-16:OAc. To test effects of female age and diel timing while accounting for among-population differences, we fitted a linear mixed model (LMM) with Age (1-4 days) and Hour (2-6 hours after scotophase onset) treated as categorical fixed effects, and Population as a random intercept:

$$\log10(\text{Total\_ng}) = \text{Age} \times \text{Hour} + (1 \mid \text{Population})$$

The response was analyzed on the log10 scale to stabilize variance and reduce right-skewness. Significance of fixed effects was assessed using likelihood ratio tests (LRTs) from single-term deletion of the model fitted by maximum likelihood (drop1, test: "Chisq"; lme4). Because the Age×Hour grid was unbalanced with some empty

combinations (rank-deficient fixed-effect design matrix), LRTs are reported only for estimable terms.

For interpretability, descriptive summaries (heatmaps and tables of means) are presented on the original ng per gland scale, whereas inferential tests are based on the log10-transformed response. Estimated marginal means (EMMs: estimated marginal means) for sampled Age×Hour combinations were obtained using emmeans with Kenward-Roger degrees of freedom; combinations with no observations were non-estimable (nonEst) and were not interpreted (Table 2). Fixed-effect estimates and model fit (marginal and conditional R^2) are provided in Table 3.

Table 1. Global Age × Hour grid for total pheromone amount (Total_ng; ng per gland) in *Spodoptera frugiperda*: sample size (N: vials/injections), total females pooled, population coverage, and summary statistics (mean, SD, CV) per cell

Age (d)	Hour after scotophase onset (h)	N (vials/injections)	N (total females)	Population coverage (n)	Mean total (ng/gland)	Median total (ng/gland)	SD (ng)	CV
1	3	1	2	1	652.67	652.67	NA	NA
1	4	2	4	2	107.285	107.285	119.8192441	1.116831282
1	5	4	8	3	140.5025	109.56	126.2131352	0.898298145
1	6	2	5	2	55.375	55.375	31.21876439	0.563770012
2	2	3	8	2	55.08333333	46.18	16.50654517	0.299664965
2	3	7	14	5	100.1671429	69.32	102.961911	1.027901047
2	4	9	19	6	199.6722222	102.64	233.7882336	1.170860078
2	5	18	46	8	153.8155556	150.11	84.69164979	0.550605233
2	6	11	26	6	106.2709091	74.18	90.14547991	0.848261116
3	2	3	6	1	37.36	38.71	13.56547456	0.363101567
3	3	7	14	3	96.93285714	58.89	141.5953818	1.460757333
3	4	16	36	5	106.293125	71.405	106.0980112	0.99816438
3	5	28	59	7	170.6067857	106.26	233.4991431	1.368639249
3	6	8	19	4	211.39125	132.245	248.8574288	1.177236186
4	3	3	6	1	59.99	51.7	52.54775067	0.875941835
4	4	4	7	2	269.0975	270.575	90.05519914	0.334656395
4	5	3	6	2	352.06	101.15	479.4437002	1.361823838
4	6	1	1	1	273.39	273.39	NA	NA

Table 2. Estimated marginal means (EMMs: estimated marginal means) of total pheromone amount from the linear mixed model across sampled Age × Hour combinations for *Spodoptera frugiperda*

Hour after scotophase onset (h)	N (vials/injections)	N (total females)	Geometric mean (ng/gland)	Geometric mean lower (ng/gland)	Geometric mean upper (ng/gland)	EMMean (log10)	SE (log10)	Lower 95% CI (log10)	Upper 95% CI (log10)
2	0	0	NA	NA	NA	NA	NA	NA	NA
3	1	2	487.99	94.79	2512.31	2.688	0.363	1.977	3.4
4	2	4	86.28	26.74	278.42	1.936	0.26	1.427	2.445
5	4	8	81.95	34.36	195.5	1.914	0.193	1.536	2.291
6	2	5	66.74	21.04	211.71	1.824	0.256	1.323	2.326
2	3	8	79.89	29.77	214.42	1.903	0.219	1.474	2.331
3	7	14	45.19	22.33	91.48	1.655	0.156	1.349	1.961
4	9	19	123.45	67.86	224.58	2.092	0.133	1.832	2.351
5	18	46	137.58	86.18	219.63	2.139	0.104	1.935	2.342
6	11	26	78.25	47.06	130.12	1.893	0.113	1.673	2.114
2	3	6	37.45	13.55	103.55	1.573	0.225	1.132	2.015
3	7	14	48.62	23.69	99.8	1.687	0.159	1.374	1.999
4	16	36	85.1	53.31	135.86	1.93	0.104	1.727	2.133
5	28	59	110.92	72.65	169.34	2.045	0.094	1.861	2.229
6	8	19	176.53	95.46	326.43	2.247	0.136	1.98	2.514
2	0	0	NA	NA	NA	NA	NA	NA	NA
3	3	6	31.19	11.41	85.23	1.494	0.223	1.057	1.931
4	4	7	193.01	79.08	471.1	2.286	0.198	1.898	2.673
5	3	6	170.69	59.53	489.4	2.232	0.233	1.775	2.69
6	1	1	205.42	38.92	1084.16	2.313	0.369	1.59	3.035

Table 3. Fixed-effect estimates (estimate, SE, df, t, p, and 95% CI) and model fit for the linear mixed model of log10 total pheromone amount [log10(Total_ng)] in *Spodoptera frugiperda*

Term	Estimate	SE	df	t	p	Lower 95% CI	Upper 95% CI
(Intercept)	1.15	0.36	129.90	3.20	0.002	0.44	1.86
Age (2 d)	0.75	0.41	125.19	1.82	0.071	-0.07	1.57
Age (3 d)	0.42	0.28	125.43	1.49	0.140	-0.14	0.98
Age (4 d)	0.49	0.43	122.07	1.14	0.259	-0.36	1.34
Scotophase hour 3	1.54	0.50	124.52	3.06	0.003	0.54	2.53
Scotophase hour 4	0.78	0.43	124.15	1.81	0.072	-0.07	1.64
Scotophase hour 5	0.76	0.40	124.47	1.93	0.056	-0.02	1.55
Scotophase hour 6	0.67	0.25	127.58	2.67	0.009	0.18	1.17
Age (2 d): Scotophase hour 3	-1.78	0.56	124.50	-3.18	0.002	-2.90	-0.67
Age (3 d): Scotophase hour 3	-1.42	0.47	123.30	-3.02	0.003	-2.36	-0.49
Age (4 d): Scotophase hour 3	-1.68	0.59	121.19	-2.86	0.005	-2.85	-0.52
Age (2 d): Scotophase hour 4	-0.60	0.50	124.74	-1.20	0.233	-1.58	0.39
Age (3 d): Scotophase hour 4	-0.43	0.39	122.81	-1.11	0.268	-1.19	0.33
Age (4 d): Scotophase hour 4	-0.14	0.52	120.14	-0.27	0.791	-1.17	0.89
Age (2 d): Scotophase hour 5	-0.53	0.46	124.95	-1.15	0.253	-1.43	0.38
Age (3 d): Scotophase hour 5	-0.29	0.34	122.27	-0.87	0.388	-0.96	0.37
Age (4 d): Scotophase hour 5	-0.17	0.51	122.43	-0.33	0.739	-1.18	0.84
Age (2 d): Scotophase hour 6	-0.68	0.35	128.22	-1.93	0.056	-1.38	0.02

Note: Marginal R^2: 0.21; conditional R^2: 0.37

Pheromone blend composition

Component amounts (Z7-12:OAc, Z9-14:OAc, Z11-16:OAc) were converted to percentages of their sum for each vial. Composition was summarized descriptively (percentages and ternary plots) and reported as Mean±SD at the selected reference window; no clr-based inferential mixed modeling of composition was performed.

Software and reporting

Analyses were conducted in R (v4.5.1; R Core Team 2025) using lme4 (v1.1-37), lmerTest (v3.1-3), emmeans (v2.0.0), ggplot2 (v4.0.0), ggtern (v4.0.0), dplyr (v1.1.4), and tidyr (v1.3.1).

RESULTS AND DISCUSSION

Pheromone yield varies with female age and diel phase

Across nine Indonesian populations, total pheromone amount (Total_ng; ng per gland) showed clear dependence on female age and time after scotophase onset (Figure 2). The faceted heatmaps indicate a broad period of elevated yield during the early-to-mid scotophase, with higher values concentrated in the 3-6 hours window after lights-off, whereas lower yields were more common at 2 hours and in later/less-supported combinations. Although peak magnitudes varied among populations, the temporal pattern was broadly consistent across sites (Bogor, South Lampung, Blitar, Sumenep, Bandung, Jember, Banyuwangi, Kediri, and Cirebon). Cell-wise summaries of the full Age×Hour grid (sample sizes, population coverage, mean, SD, and coefficient of variation (CV)) are provided in Table 1, and population-level summaries are provided in Table 4.

Optimal extraction windows (ranking for robustness)

To identify operationally robust extraction windows for Indonesia, global Age×Hour combinations were ranked by mean total pheromone amount (ng per gland) on the original scale while prioritizing robustness (minimum replication per cell, n≥3 vials/injections) and generality (broad population coverage) (Table 5). Under these criteria, the selected global reference window was Age 3 days; 5 hours after scotophase onset. Although some cells showed higher mean totals (e.g., 4 days; 5 hours), these were supported by fewer vials and fewer populations; therefore, 3 days; 5 hours was selected as the national reference because it provides stronger replication and broader population coverage while remaining within the high-yield period. Mean totals also differed among populations, which was accommodated in the mixed-model framework by including Population as a random intercept (see Mixed-model inference, below); nevertheless, the early-night high-yield period was broadly conserved across sites (Figure 2, Table 1 and Table 4). For local applications, the "best window" for each population is reported descriptively as the sampled Age×Hour cell with the highest mean total pheromone amount (Table 6). These population-specific maxima are provided to illustrate local variation and are not intended to replace the national reference window; we recommend using Age 3 days; 5 hours for standardized comparisons, while population-specific windows may be adopted in local optimization when maximizing extraction yield is the primary goal and adequate within-population replication is available.

Table 4. Per-population Age × Hour grid for total pheromone amount (Total_ng; ng per gland) in *Spodoptera frugiperda*: sample size (N: vials/injections) and summary statistics per cell

Population	Age (d)	Hour after scotophaseonset (h)	N (vials/ injections)	N (total females	Mean total (ng/gland)	SD (ng)	SE (ng)	CV
Banyuwangi	2	5	1	2	61.68	NA	NA	NA
Banyuwangi	3	4	2	6	63.79	40.67278205	28.76	0.637604359
Banyuwangi	3	5	2	6	136.325	13.92293252	9.845	0.102130442
Banyuwangi	3	6	2	6	113.37	49.21463197	34.8	0.434106307
Blitar	1	5	1	3	23.19	NA	NA	NA
Blitar	2	2	2	5	59.535	20.64044694	14.595	0.34669433
Blitar	2	4	2	4	63.525	33.75020667	23.865	0.531290148
Blitar	2	5	4	9	223.9225	55.8531016	27.9265508	0.249430502
Blitar	2	6	1	3	41.67	NA	NA	NA
Blitar	3	3	1	3	58.89	NA	NA	NA
Blitar	3	4	4	9	75.6725	27.04614252	13.52307126	0.357410453
Blitar	3	5	10	21	176.579	367.4933043	116.2115866	2.081183517
Blitar	3	6	4	9	283.1675	345.0668639	172.5334319	1.218596286
Blitar	4	5	2	4	477.515	604.3995212	427.375	1.265718399
Bogor	1	3	1	2	652.67	NA	NA	NA
Bogor	1	4	1	2	192.01	NA	NA	NA
Bogor	1	5	1	1	319.7	NA	NA	NA
Bogor	2	3	2	4	36.94	45.79223515	32.38	1.239638201
Bogor	2	4	2	3	442.045	489.5795221	346.185	1.10753322
Bogor	2	5	2	4	173.525	51.96527735	36.745	0.299468534
Bogor	3	3	2	4	47.69	24.63560026	17.42	0.516577904
Bogor	3	5	4	7	272.915	160.5594107	80.27970535	0.588312884
Bogor	4	3	3	6	59.99	52.54775067	30.33845799	0.875941835
Bogor	4	4	2	3	267.62	119.3454825	84.39	0.445951284
Cirebon	2	3	1	1	125.56	NA	NA	NA
Cirebon	2	4	1	2	134.46	NA	NA	NA
Cirebon	2	5	1	2	132.9	NA	NA	NA
Cirebon	2	6	2	4	142.27	28.77924599	20.35	0.202286118
Jember	1	4	1	2	22.56	NA	NA	NA
Jember	1	6	1	3	33.3	NA	NA	NA
Jember	2	2	1	3	46.18	NA	NA	NA
Jember	2	3	1	3	8.05	NA	NA	NA
Jember	2	5	2	6	98.195	92.01580544	65.065	0.937072208
Jember	2	6	1	1	20.33	NA	NA	NA
Jember	3	4	2	5	33.165	2.609224023	1.845	0.078674025
Jember	3	5	3	6	33.36666667	13.2253746	7.635673586	0.396364873
Jember	3	6	1	2	43.58	NA	NA	NA
Kediri	1	5	2	4	109.56	0.650538239	0.46	0.005937735
Kediri	1	6	1	2	77.45	NA	NA	NA
Kediri	2	5	1	3	271.57	NA	NA	NA
Kediri	2	6	2	5	265.8	49.27120051	34.84	0.185369453
Kediri	3	5	4	8	181.24	147.0267202	73.51336012	0.811226662
Kediri	4	4	2	4	270.575	100.3879497	70.985	0.371017092
Kediri	4	5	1	2	101.15	NA	NA	NA
Kediri	4	6	1	1	273.39	NA	NA	NA
South Lampung	2	3	2	4	94.105	46.49227086	32.875	0.494046765
South Lampung	2	4	1	3	140.36	NA	NA	NA
South Lampung	2	5	1	3	50.12	NA	NA	NA
South Lampung	3	4	2	4	341.295	43.25372181	30.585	0.126734121
South Lampung	3	5	1	1	216.99	NA	NA	NA
Sumenep	2	3	1	2	305.47	NA	NA	NA
Sumenep	2	4	2	4	204.225	156.9706344	110.995	0.768616155
Sumenep	2	5	6	17	135.5466667	88.58613338	36.16513751	0.653547118
Sumenep	2	6	4	10	61.6025	19.58542039	9.792710193	0.317932233
Sumenep	3	2	3	6	37.36	13.56547456	7.832030388	0.363101567
Sumenep	3	3	4	7	131.065	190.3782292	95.18911462	1.452548195
Sumenep	3	4	6	12	86.91666667	80.45117517	32.84405473	0.925612754
Bandung	2	4	1	3	102.64	NA	NA	NA
Bandung	2	6	1	3	44.43	NA	NA	NA
Bandung	3	5	4	10	151.21	53.87511052	26.93755526	0.356293304
Bandung	3	6	1	2	288.14	NA	NA	NA

Pheromone composition is Z9-major with modest geographic variation

Across populations and sampling cells, gland extracts were dominated by Z9-14:OAc, with Z11-16:OAc as an intermediate component and Z7-12:OAc remaining low (Figure 3). Within the optimized extraction framework, the relative composition was broadly consistent in component ordering (Z9-14:OAc>Z11-16:OAc>Z7-12:OAc), although the exact percentages varied modestly among populations and sampling cells. Thus, Indonesian FAW females share a Z9-major acetate chemotype while retaining population-level differences in the minor/intermediate components. For national formulation guidance anchored to a standardized sampling point, composition at the selected global window (Age 3 days; 5 hours) is summarized in Table 7, and composition by population at this window is provided in Table 8.

Mixed-model inference for total pheromone amount

Total pheromone amount (Total_ng; ng per gland) was analyzed as log10(Total_ng) using a linear mixed model with Age (1-4 days), Hour (2-6 hours after scotophase onset), and their interaction as fixed effects and Population as a random intercept (N: 130 vials/injections). The Age×Hour interaction was significant (LRT χ^2: 19.176, df: 10, p: 0.0381), indicating that diel patterns in pheromone yield differed among age classes. Estimated marginal means for sampled Age×Hour cells are provided in Table 2, and fixed-effect estimates and model fit (marginal and conditional R^2) are provided in Table 3. Descriptive summaries (Figures 2-3, Tables 5-7) are shown on the original ng per gland and percentage scales for interpretability.

Synthesis and implications for standardization

Overall, total pheromone yield supports a reproducible national reference extraction window of Age 3 days; 5 hours after scotophase onset for standardized chemical profiling in Indonesian *S. frugiperda*. Across populations, gland extracts show a Z9-major chemotype with broadly consistent component ordering (Z9-14:OAc>Z11-16:OAc>Z7-12:OAc), while exact percentages vary modestly among sites. Composition at the reference window provides a locally derived baseline (≈80:16:4), and we recommend 80:15:5 as an operational starting blend with minor adjustments around this ratio for subsequent behavioral and multi-site field validation.

Table 5. Top-ranked global extraction windows (Age×Hour) for total pheromone amount (Total_ng; ng per gland) across Indonesian *Spodoptera frugiperda* populations, ranked on the original scale while considering pheromone yield, replication robustness (minimum replication per cell, n≥3 vials/injections) and population coverage. SD: standard deviation, CV: coefficient of variation

Rank	Age (d)	Hour after scotophase onset (h)	N (vials/injections)	Population coverage (n)	Mean total (ng/gland)	SD (ng/gland)	CV
1	4	5	3	2	352.00	479.00	1.36
2	4	4	4	2	269.00	90.10	0.34
3	3	6	8	4	211.00	249.00	1.18
4	2	4	9	6	200.00	234.00	1.17
5*	3	5	28	7	171.00	233.00	1.37

Note: *Selected global reference window used for national standardization (Age 3 days; 5 hours after scotophase onset)

Table 6. Highest observed mean extraction window (Age×Hour) for each Indonesian population of *Spodoptera frugiperda* based on the highest observed mean Total_ng (ng per gland) among sampled combinations within that population. These maxima are descriptive (maximum mean within sampled cells) and do not by themselves imply field-optimized performance. SD: standard deviation, CV: coefficient of variation

Population	Age (d)	Hour of scotophase (h)	N (vials/ injections)	N (total females)	Mean total (ng/gland)	Median total (ng/gland)	SD total (ng/gland)	CV total
Banyuwangi	3	5	2	6	136.32	136.32	13.92	0.10
Blitar	4	5	2	4	477.52	477.52	604.40	1.27
Bogor	2	4	2	3	442.04	442.04	489.58	1.11
Cirebon	2	6	2	4	142.27	142.27	28.78	0.20
Jember	2	5	2	6	98.19	98.19	92.02	0.94
Kediri	4	4	2	4	270.58	270.58	100.39	0.37
South Lampung	3	4	2	4	341.29	341.29	43.25	0.13
Sumenep	2	4	2	4	204.23	204.23	156.97	0.77
Bandung	3	5	4	10	151.21	139.30	53.88	0.36

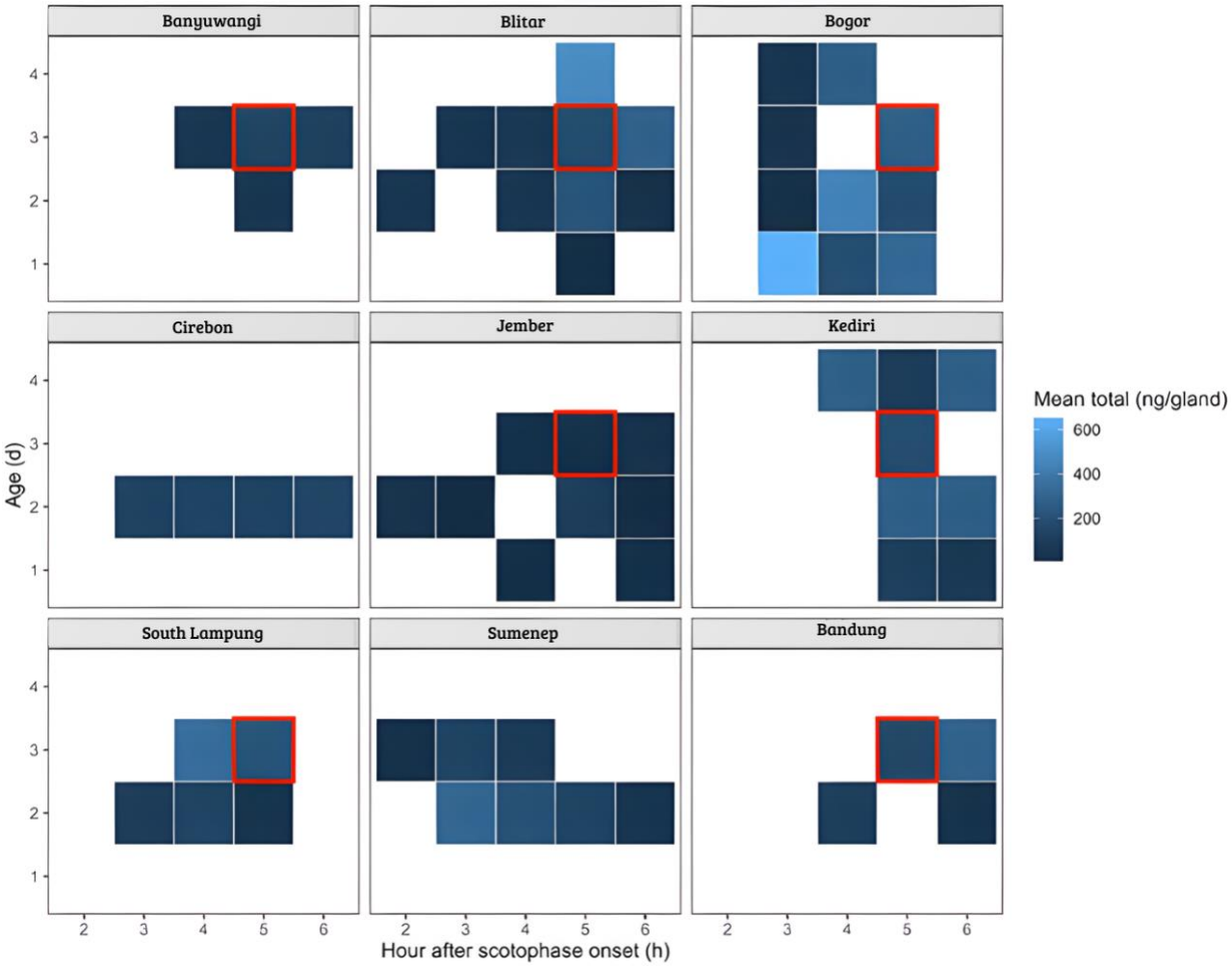

Figure 2. Heatmap of mean total pheromone amount (Total_ng; ng per gland) in virgin females of *Spodoptera frugiperda* across the Age (days post-emergence; 1-4 days) × Hour after scotophase onset (2-6 hours) grid; panels represent populations. Values are means per cell based on vial/injection as the experimental unit; each vial contained glands from 1-3 females (pooled). White cells indicate unsampled combinations. The selected global reference window (Age 3 days; 5 hours) is outlined where sampled. CV: coefficient of variation; scotophase: dark phase

Table 7. National pheromone blend composition at the selected global reference window (Age 3 days; 5 hours after scotophase onset) in *Spodoptera frugiperda* female gland extracts. Values are Mean±SD (% of total) across vials (n: 28 vials; 59 females pooled). SD: standard deviation

Component	Mean±SD (%)
Z9-14:OAc	80.18±13.61
Z11-16:OAc	16.15±13.44
Z7-12:OAc	3.67±5.31

Discussion

Consistent with reports from both the native and invaded ranges (Cruz-Díaz et al. 2022), Indonesian populations of *S. frugiperda* exhibited a clear Z9-major acetate motif. The main contribution of this study is methodological: by fixing a narrow and biologically justified age-scotophase sampling window, we minimized avoidable temporal variance and made geographic differences interpretable as biological signals rather than procedural artifacts. On that common footing, Indonesian populations were Z9-weighted with moderate Z11-16:OAc and consistently low Z7-12:OAc, supporting the concept of regional "pheromonal dialects" in FAW (Sisay et al. 2024).

According to published ratios, Z9-14:OAc is usually dominant across regions, but its proportion can vary significantly (about 88-99.6%), accompanied by changes in minor components like Z11-16:OAc and Z7-12:OAc (Andrade et al. 2000; Haenniger et al. 2020; Wakamura et al. 2021; Wang et al. 2022; Akter et al. 2025). Indonesia's profile falls comfortably within Z9 dominance but has a distinct weighting of intermediate/minor components, supporting the practicality of deriving local reference compositions before formulation and field deployment.

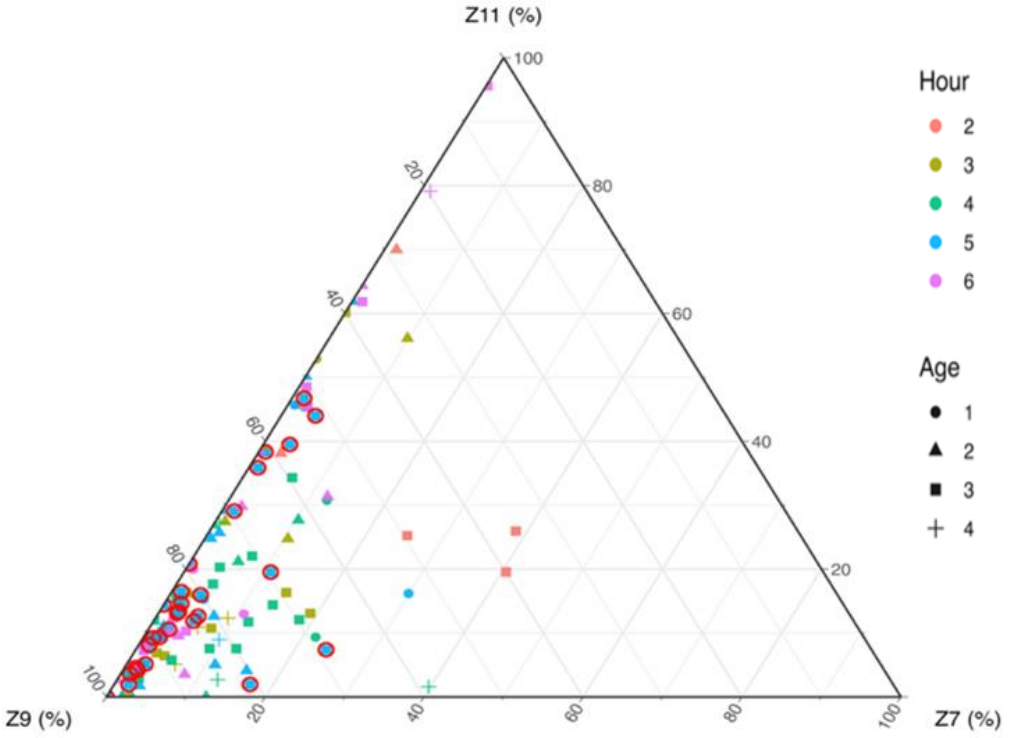

Figure 3. Ternary plot of pheromone blend composition (% of total) of Z9-14:OAc, Z11-16:OAc, and Z7-12:OAc in *Spodoptera frugiperda* female gland extracts (GC-FID). Point shape indicates female age (days) and point color indicates hour after scotophase onset (hours). Red-outlined points indicate the selected global reference window (Age 3 days; 5 hours). OAc: acetate

Table 8. Pheromone blend composition (% of total; Z9-14:OAc, Z11-16:OAc, Z7-12:OAc) by population at the selected global reference window (Age 3 d; 5 h) in *Spodoptera frugiperda*

Population	N (vials/ injections)	N (total females)	Z9-14:OAc mean (%)	Z9-14:OAc SD	Z11-16:OAc mean (%)	Z11-16:OAc SD	Z7-12:OAc mean (%)	Z7-12:OAc SD (%)
Banyuwangi	2	6	66.93238963	21.48369481	29.68725287	24.11636365	3.380357494	2.632668841
Blitar	10	21	84.66358328	14.23339703	12.63955658	12.50565214	2.696860138	3.14798416
Bogor	4	7	72.98436461	10.18722072	20.28819779	13.2251817	6.727437605	11.51924831
Jember	3	6	68.89346901	11.50304345	28.18880977	11.78662908	2.917721225	1.212520293
Kediri	4	8	86.87704284	5.902650329	10.62401003	5.325867091	2.498947129	1.80800336
South Lampung	1	1	80.93460528	NA	1.963224112	NA	17.10217061	NA
Bandung	4	10	84.34997966	14.63071017	14.08926297	14.91781187	1.560757368	0.423300438

Geographic variability in FAW pheromone composition has been linked to host-associated strains (corn and rice strains), which can differ in component ratios (Unbehend et al. 2013; Nagoshi and Meagher 2022; Sisay et al. 2024). Because this paper does not present new strain-genotyping results, we do not infer strain identity from pheromone chemistry alone. Instead, we interpret the country-wide consistency of the Z9-major architecture as evidence of a broadly shared chemotype across Indonesian maize-associated populations, while still allowing modest regional variation in the exact percentages of Z11 and Z7. This pattern is compatible with the broader view that FAW pheromone composition reflects evolutionary background and invasion history and that strain background may contribute to ratio sensitivity in male responses (Unbehend et al. 2013; Cruz-Esteban et al. 2018).

The recommended extraction window is congruent with circadian control of pheromone biosynthesis and female calling in noctuid moths (Cardé and Haynes 2004; Tabata et al. 2023). Calling behavior and pheromone production are under light-dark regulation, and mid-scotophase peaks are common across Noctuidae (Levi-Zada and Byers 2021). Female age further shapes output, with 2-3 days post-emergence often representing an early reproductive phase with high pheromone production (Zhang et al. 2015; Levi-Zada and Byers 2021). PBAN (pheromone biosynthesis activating neuropeptide), which is released rhythmically and initiates enzymatic activity in the pheromone gland, is the mechanism by which pheromone biosynthesis is activated

(Jurenka and Rafaeli 2011). Consequently, sampling during the initial high-yield interval of the night focuses on a physiologically relevant period while mitigating variability associated with the end of the night.

Although headspace collections more directly represent the airborne signal perceived by males, this study quantified gland titer to capture biosynthetic capacity and stored reserves as a stable baseline for standardizing extraction across sites. Importantly, gland titers and headspace emission do not necessarily scale linearly because emission depends on calling posture/behavior and can rapidly draw down gland stores; thus, high titers may occur without high headspace release (and vice versa) at a given moment (Levi-Zada and Byers 2021). Consequently, the optimized age-scotophase window is intended primarily to standardize chemical profiling and provide a reproducible reference point for downstream formulation work, rather than to fully substitute for emission-based characterization.

Regional shifts in minor/intermediate components matter operationally because male attraction can be ratio-sensitive and differ by geography and strain background; field evidence indicates population- and strain-dependent preferences for lure blends (Unbehend et al. 2013). Therefore, deploying blends optimized for distant populations may lead to suboptimal performance when transferred across regions with different pheromone dialects. Based on the national composition summarized at the standardized reference window, we propose an Indonesia-specific reference blend of approximately 80:16:4 (Z9:Z11:Z7) as a chemically informed starting point for optimization, bracketed operationally by 75-85:10-20:0-5 to accommodate observed variation and practical formulation constraints. We emphasize that this proposed ratio is not a field-validated formulation; final lure optimization will require systematic behavioral assays and multi-site field trials.

Acetate-rich FAW differs chemically from aldehyde-dominated *Helicoverpa armigera*, and *Spodoptera litura* has distinct isomer patterns (Fite et al. 2020; He et al. 2026). A potential complication in maize agroecosystems is overlap with other noctuids (e.g., *Mythimna* spp.), where partial component overlap could contribute to incidental captures in some settings (Chang et al. 2025). Because the Indonesian profile supports moderate-to-high Z11-16:OAc within the proposed bracket, selectivity should be verified empirically during field validation, and trap design/ placement may need adjustment to reduce non-target captures (Fleischer et al. 2005; Spears et al. 2016). Recording and reporting non-target captures is now widely regarded as best practice in pheromone-based trapping studies and should be incorporated into Indonesian field validations.

Key limitations should be considered when interpreting the present study. First, chemical analyses used GC-FID without parallel GC-MS. While retention-time matching with authentic standards and external-standard quantification support robust identification and quantification of the three target acetates, GC-FID alone cannot resolve unknown trace components, structural isomers, or novel compounds that may contribute to attraction at low abundance; therefore, our conclusions are restricted to the three quantified acetate components. Second, the study quantified laboratory gland titers rather than field emissions. Because emission depend on calling behavior and environmental context, gland-derived ratios may not perfectly match airborne emission ratios under field conditions, even within the same diel window. Third, blend composition was summarized descriptively rather than modeled formally; thus, subtle Age×Hour effects on minor components cannot be excluded under the present unbalanced design and per-cell replication. Future research should integrate targeted GC-MS profiling (paired with GC-FID) within the optimized window to confirm major components and screen for additional trace compounds that are behaviorally relevant (Unbehend et al. 2013; Guo et al. 2022; Akter et al. 2025).

In conclusion, we recommend a standardized reference window of 3 days old virgin females at 5 hours into scotophase (3 days; 5 hours) as a robust point for cross-population comparisons in Indonesia. When strict comparability is not required, sampling can be extended within the early-night high-yield interval (≈3-6 hours after lights-off) to improve recovery. Within the reference window, the Indonesian gland profile is consistently Z9-dominant (Z9>Z11>Z7), supporting an Indonesia-specific reference blend of ~80:16:4 (Z9:Z11:Z7), bracketed operationally by 75-85:10-20:0-5. This ratio is a chemically informed starting point rather than a field-validated formulation and should be confirmed and refined through behavioral assays and multi-site field trials to support locally adapted FAW pheromone lures in Indonesian maize agroecosystems.

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REFERENCES

Akter S, Hossain MS, Ali R, Regmi R, Park SJ, Mainali B. 2025. Variations in sex pheromone of the Australian population of fall armyworm: Influence of age and mating status. J Chem Ecol 51 (3): 55. https://doi.org/10.1007/s10886-025-01607-0.

Andrade R, Rodriguez C, Oehlschlager AC. 2000. Optimization of a pheromone lure for *Spodoptera frugiperda* (Smith) in Central America. J Braz Chem Soc 11: 609-613. https://doi.org/10.1590/S0103-50532000000600009.

Asfiya W, Subagyo VNO, Dharmayanthi AB, Fatimah F, Rachmatiyah R. 2020. Intensitas serangan *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) pada pertanaman jagung di Kabupaten Garut dan Tasikmalaya. Jurnal Entomologi Indonesia 17 (3): 163-167. https://doi.org/10.5994/jei.17.3.163. [Indonesian]

Bird L, Miles M, Quade A, Spafford H. 2022. Insecticide resistance in Australian *Spodoptera frugiperda* (J.E. Smith) and development of testing procedures for resistance surveillance. PLoS One 17 (2): e0263677. https://doi.org/10.1371/journal.pone.0263677.

Cardé RT, Haynes KF. 2004. Structure of the pheromone communication channel in moths. In: Cardé RT, Millar JG (eds). Advances in Insect Chemical Ecology. Cambridge University Press, Cambridge.

Chang X, Zhang S, Wang Z, Yang X, Lv L, Wang M. 2025. Functional characteristics of pheromone binding proteins from *Mythimna separata*. Insect Sci 32 (6): 1997-2008. https://doi.org/10.1111/1744-7917.70029.

Cruz-Díaz M, Robledo N, Reyes-Prado H, Tapia-Marur D, Castrejón-Gómez VR. 2022. *Spodoptera frugiperda* (Lepidoptera: Noctuidae) females can detect the sex pheromone emitted by conspecific females. Fla Entomol 105 (2): 126-132. https://doi.org/10.1653/024.105.0204.

Cruz-Esteban S, Rojas JC, Sánchez-Guillén D, Cruz-López L, Malo EA. 2018. Geographic variation in pheromone component ratio and antennal responses, but not in attraction, to sex pheromones among fall armyworm populations infesting corn in Mexico. J Pest Sci 91 (3): 973-983. https://doi.org/10.1007/s10340-018-0967-z.

Deshmukh SS, Prasanna BM, Kalleshwaraswamy CM, Jaba J, Choudhary B. 2021. Fall armyworm (*Spodoptera frugiperda*). In: Omkar (eds). Polyphagous Pests of Crops. Springer, Singapore.

Fite T, Damte T, Tefera T, Negeri M. 2020. Evaluation of commercial trap types and lures on the population dynamics of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) and its effects on non-target insects. Cogent Food Agric 6 (1): 1771116. https://doi.org/10.1080/23311932.2020.1771116.

Fiteni E, Durand K, Gimenez S, Meagher RLJ, Legeai F, Kergoat GJ. 2022. Host-plant adaptation as a driver of incipient speciation in the fall armyworm (*Spodoptera frugiperda*). BMC Ecol Evol 22 (1): 133. https://doi.org/10.1186/s12862-022-02090-x.

Fleischer SJ, Harding CL, Blom PE, White J, Grehan J. 2005. *Spodoptera frugiperda* pheromone lures to avoid nontarget captures of *Leucania phragmatidicola*. J Econ Entomol 98: 66-71. https://doi.org/10.1093/jee/98.1.66.

Goergen G, Kumar PL, Sankung SB, Togola A, Tamò M. 2016. 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 11 (10): e0165632. https://doi.org/10.1371/journal.pone.0165632.

Guo H, Gong XL, Li GC, Mo BT, Jiang NJ, Huang LQ, Wang CZ. 2022. Functional analysis of pheromone receptor repertoire in the fall armyworm, *Spodoptera frugiperda*. Pest Manag Sci 78 (5): 2052-2064. https://doi.org/10.1002/ps.6831.

Haenniger S, Goergen G, Akinbuluma MD, Kunert M, Heckel DG, Unbehend M. 2020. Sexual communication of *Spodoptera frugiperda* from West Africa: Adaptation and implications. Sci Rep 10: 2892. https://doi.org/10.1038/s41598-020-59708-7.

He Y, Ye JJ, Liu SR, Chen MY, Bai TF, Li JW, Yan SW, Huang JR, Deng JY, Keesey IW, Zhang J, Yan Q, Dong SL. 2026. Optimizing sex pheromone lures for male trapping specificity between *Spodoptera frugiperda* and *Mythimna loreyi*. Pest Manag Sci 82 (1): 319-327. https://doi.org/10.1002/ps.70197.

Jiang YY, Zhang YY, Zhou XY, Hong XY, Chen L. 2022. Population genetics reveal multiple independent invasions of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in China. Bull Entomol Res 112 (6): 796-806. https://doi.org/10.1017/S0007485322000190.

Jing DP, Guo JF, Jiang YY, Zhao JZ, Sethi A, He KL, Wang ZY. 2020. Initial detections and spread of invasive *Spodoptera frugiperda* in China and comparisons with other noctuid larvae in cornfields using molecular techniques. Insect Sci 27 (4): 780-790. https://doi.org/10.1111/1744-7917.12700.

Jurenka R, Rafaeli A. 2011. Regulatory role of PBAN in sex pheromone biosynthesis of heliothine moths. Front Endocrinol 2: 46. https://doi.org/10.3389/fendo.2011.00046.

Keerthi MC, Suroshe SS, Doddachowdappa S, Shivakumara KT, Mahesha HS, Rana VS. 2023. Bio-intensive tactics for the management of invasive fall armyworm for organic maize production. Plants 12 (3): 685. https://doi.org/10.3390/plants12030685.

Levi-Zada A, Byers JA. 2021. Circadian rhythms of insect pheromone titer, calling, emission, and response: A review. Sci Nat 108 (5): 35. https://doi.org/10.1007/s00114-021-01746-w.

Maharani Y, Dewi VK, Puspasari LT, Rizkie L, Hidayat Y, Dono D. 2019. Cases of fall army worm *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) attack on maize in Bandung, Garut and Sumedang District, West Java. Cropsaver 2 (1): 38-46. https://doi.org/10.24198/cropsaver.v2i1.23013.

Muthukumar M, Kennedy JS. 2021. A review of the scientific literature on the use of reproductive pheromones in the management of *Spodoptera frugiperda* (Lepidoptera: Noctuidae). J Entomol Sci 56: 475-486. https://doi.org/10.18474/JES20-89.

Nagoshi RN, Meagher RL. 2022. The *Spodoptera frugiperda* host strains: What they are and why they matter for understanding and controlling this global agricultural pest. J Econ Entomol 115 (6): 1729-1743. https://doi.org/10.1093/jee/toac050.

Ramya N, Padala VK, Sagar D, Rupali JS, Kumar H, Reshma R. 2024. Decoding the copulation and courtship patterns of an invasive pest, *Spodoptera frugiperda* (J.E. Smith, 1797) from India. Curr Sci 126 (9): 1152-1158. https://doi.org/10.18520/cs/v126/i9/1152-1158.

Rizvi SAH, George J, Reddy GVP, Zeng X, Guerrero A. 2021. Latest developments in insect sex pheromone research and its application in agricultural pest management. Insects 12 (6): 484. https://doi.org/10.3390/insects12060484.

Schöfl G, Heckel DG, Groot AT. 2009. Time-shifted reproductive behaviours among fall armyworm (Noctuidae: *Spodoptera frugiperda*) host strains: Evidence for differing modes of inheritance. J Evol Biol 22 (7): 1447-1459. https://doi.org/10.1111/j.1420-9101.2009.01759.x.

Sianturi YPPA, Dadang, Sartiami D. 2022. Bioactivity of extracts from *Syzygium aromaticum, Annona muricata,* and *Piper retrofractum* against *Spodoptera frugiperda*. IOP Conf Ser Earth Environ Sci 1083: 012075. https://doi.org/10.1088/1755-1315/1083/1/012075.

Sisay B, Subramanian S, Weldon CW, Krüger K, Khamis F, Tefera T. 2024. Evaluation of pheromone lures, trap designs and placement heights for monitoring the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in maize fields of Kenya. Crop Prot 176: 106523. https://doi.org/10.1016/j.cropro.2023.106523.

Spears LR, Looney C, Ikerd H, Koch JB, Griswold T, Strange JP, Ramirez RA. 2016. Pheromone lure and trap color affects bycatch in agricultural landscapes of Utah. Environ Entomol 45 (4): 1009-1016. https://doi.org/10.1093/ee/nvw085.

Tabata J, Nakano R, Yasui H, Nakamura K, Takehara K, Matsuda H. 2023. Sex pheromone of the fall armyworm, *Spodoptera frugiperda*: Identification of a trace component that enhances attractiveness and specificity. Entomol Exp Appl 171 (7): 535-541. https://doi.org/10.1111/eea.13287.

Tawakkal MI, Buchori D, Maryana N, Pudjianto. 2021. New association between *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) and native natural enemies: Bioprospection of native natural enemies as biological control agents. IOP Conf Ser Earth Environ Sci 771: 012030. https://doi.org/10.1088/1755-1315/771/1/012030.

Tay WT, Rane RV, Padovan A, Walsh TK, Elfekih S, Downes S. 2022. Global population genomic signature of *Spodoptera frugiperda* (fall armyworm) supports complex introduction events across the Old World. Commun Biol 5 (1): 297. https://doi.org/10.1038/s42003-022-03230-1.

Trisyono YA, Suputa S, Aryuwandari VEF, Hartaman M, Jumari J. 2019. Occurrence of heavy infestation by the fall armyworm *Spodoptera frugiperda*, a new alien invasive pest, in corn in Lampung Indonesia. Jurnal Perlindungan Tanaman Indonesia 23: 156-160. https://doi.org/10.22146/jpti.46455.

Unbehend M, Hänniger S, Meagher RL, Heckel DG, Groot AT. 2013. Pheromonal divergence between two strains of *Spodoptera frugiperda*. J Chem Ecol 39 (3): 364-376. https://doi.org/10.1007/s10886-013-0263-6.

Wakamura S, Arakaki N, Yoshimatsu SI. 2021. Sex pheromone of the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) of a "Far East" population from Okinawa, Japan. Appl Entomol Zool 56 (1): 19-25. https://doi.org/10.1007/s13355-020-00703-9.

Wang C, Zhang S, Guo MB, Hou XQ, Yang B, Wang GR. 2022. Optimization of a pheromone lure by analyzing the peripheral coding of sex pheromones of *Spodoptera frugiperda* in China. Pest Manag Sci 78 (7): 2995-3004. https://doi.org/10.1002/ps.6924.

Yu SJ, Nguyen SN, Abo-Elghar GE. 2003. Biochemical characteristics of insecticide resistance in the fall armyworm, *Spodoptera frugiperda* (J.E. Smith). Pestic Biochem Physiol 77: 1-11. https://doi.org/10.1016/S0048-3575(03)00079-8.

Zhang YN, Zhu XY, Fang LP, He P, Wang ZQ, Chen G. 2015. Identification and expression profiles of sex pheromone biosynthesis and transport related genes in *Spodoptera litura*. PLoS One 10 (10): e0140019. https://doi.org/10.1371/journal.pone.0140019.