Communication

Examining the Effects of Induced Plant Defenses on *Spodoptera frugiperda* Performance

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Abstract: Knowing the duration insect pests are in the environment is vital for growers to determine management schemes and apply treatments. Unfortunately, experiments to determine long-term insect performance across plant cultivars are infrequently conducted. With that in mind, we report here the performance of *Spodoptera frugiperda*, the fall armyworm, on jasmonic acid (JA) induced/non-induced soybean cultivars. JA induction increases plant defensive compounds and can be considered an equivalent to a plant's response to herbivory. *S. frugiperda* is a global pest, with infestations in soybeans becoming an emerging problem, making information on this pest's performance on soybeans warranted. Thus, we reared larvae on two different soybean cultivars with contrasting defensive strategies when induced with JA and measured 7-day survival, development time to pupation, and pupal mass. Plant cultivar and JA induction were both important causes of mortality. Although plant cultivars varied in their amounts of constitutive/inducible defenses, this did not cause an interactive effect between plant cultivar and induction. Insect development to pupation was also extended when fed on induced plants regardless of cultivar, while pupal mass was not affected. Overall, induced plant defenses lowered larval survival and extended development time which would alleviate pest pressure and extend the period growers have for detecting infestations.

Keywords: *Glycine max*; Bayesian modeling; jasmonic acid; fall armyworm; slow-growth high-mortality hypothesis; plant-herbivore interactions

1. Introduction

Knowing the duration during which herbivore pests are present in the environment feeding on a plant commodity is vital for developing and implementing a sound management scheme. These data, in turn, can be used to create life tables to document the maturation of an organism. When combined with phenological observations and data, the resulting information can also be used to time crop planting dates, predict pest emergence, and determine likely pesticide treatment dates/intervals [1]. For general phytophagous insects, though, these predictions can be problematic or prone to error if data has not been collected from pests feeding on numerous different host plants and/or cultivars for calibration [2].

Further still, upon herbivore attack, plants induce defenses to protect themselves from herbivore damage, which is mediated by the jasmonic (JA) and salicylic acid (SA) phytohormone pathways [3,4]. These plant defenses are toxic and antinutritive to herbivore pests. This increases herbivore mortality and slows their development [5–7]. Within a plant species, because of differences in plant secondary metabolite concentration and inducibility upon herbivore damage, different cultivars can greatly affect insect life history and performance [5–9].

Collecting these data is vital for applied research and making informed management decisions [1]. From an empirical perspective, knowing the maturation schedule of an insect pest across plant cultivars varying in resistance to herbivory is useful for parameterizing

models, whether for determining pest population dynamics, entomopathogen spread, or other lines of inquiry [10–12]. This information is also useful for implementing control efforts, such as how biopesticides will perform when applied in the environment [13,14]. Understandably, one cannot test every cultivar and species combination a generalist phytophagous insect consumes, especially if the breadth of their host plant diet extends to hundreds of species, so research should focus on cultivars within a crop commodity with known variations in plant resistance traits to insect herbivores. This relates to how current plant domestication syndrome research is conducted [6]; information that would allow researchers and growers to make sound predictions while also balancing labor and resource costs [2,14].

With that framework in mind, we report here the performance (i.e., survival, development time, and pupal mass) of the fall armyworm on jasmonic acid (JA) induced and non-induced *Glycine max* (soybean) cultivars. We also document female fall armyworm fecundity over a mass gradient when reared on an artificial diet to gauge how differences in pupal mass affect fecundity. We predict that larvae-fed induced host plants would have higher mortality and lower performance than those on uninduced plants. We also predict that plant cultivars should interact with inducible defenses to influence insect performance due to varying secondary metabolite profiles and inducibility between cultivars. Lastly, we predict that lighter female moths would lay fewer eggs (i.e., be less fecund) than heavier female moths.

Background and Study System

The fall armyworm, *Spodoptera frugiperda*, (Lepidoptera: Noctuidae), is a global insect pest of economic importance. It is native to the western hemisphere but was introduced into Africa in 2016 and has now spread to Asia and Australia [15–18]. This insect pest is fond of cereal crops such as corn, sorghum, rice, and cotton, but is a generalist herbivore utilizing numerous plant species [15,19]. Specifically, in poorly managed *Zea mays* (corn) fields under crop rotation with legumes, these insects have also been known to infest soybeans, causing economic damage. In Brazil, because of crop rotation, *S. frugiperda* is reported to have switched onto soybeans as a preferred host, much like the corn rootworm did in North America [20,21]. *S. frugiperda* larvae are also ravenous herbivores and highly cannibalistic, which at high densities during an outbreak appear to "march" across the landscape, consuming entire fields [15,16,22,23].

2. Materials and Methods

2.1. Plant Cultivars and Propagation

Two *G. max* cultivars were used in this experiment: Gasoy (USDA accession number P.I. 553046) and Braxton (USDA accession number P.I. 548659). We purposefully chose soybean cultivars that have previously been investigated and are known to vary in secondary metabolite concentration and inducibility; Gasoy induces higher peroxidase activity (POD) while Braxton has higher constitutive phenolics [24,25]. Seeds were first germinated by placing them between two moist paper towels before being covered and placed in the dark at room temperature (~23 °C). Seeds that successfully germinated after 72 h were then planted in 10×20, 18-cell insert trays containing a 2:1:1:2 mixture of Sunshine Mix #3 (Sun Gro Horticulture, Agawam, MA, USA), Vermiculite, Perlite, and Osmocote 14-14-14 slow-release fertilizer (The Scotts Miracle-Gro Company, Marysville, OH, USA). The seedlings were then moved to a grow room and placed on a 16L:8D cycle at 28 °C and 80% humidity. At 3 weeks post-germination, the seedlings were transplanted from the cell insert into 15.24 cm^2 pots using the same soil mixture. Plants used in the experiment ranged in age from 5 to 8 weeks old and were approximately the same size regarding the number of fully developed tri-foliate leaves.

2.2. Experimental Procedure

S. frugiperda eggs were obtained from a commercially available colony (Benzon Research Inc., Carlisle, PA, USA) which originated from Mississippi, USA. These insects have been bred on a priority artificial diet and reared in a colony for multiple generations, and are used annually in field trials. For the subsequent experiments, newly hatched fall armyworm neonates (Benzon Research Inc., Carlisle, PA, USA) were fed on 1 of 5 diet treatments: a proprietary artificial diet (Southland Products Inc., Lake Village, AR, USA); uninduced *G. max* c.v. Braxton; uninduced *G. max* c.v. Gasoy; JA-induced *G. max* c.v. Braxton; or JA-induced *G. max* c.v. Gasoy. We initially set up ~2000 insects and roughly divided them evenly across the treatments. Soybeans in the JA induction treatment were initially induced 24 h before being fed to larvae by spraying them until runoff with a 1 mM solution of JA (Tokyo Chemical Industry, Tokyo, Japan) dissolved in 0.5% ethanol. Non-induced plants were sprayed with a 0.5% ethanol solution as a control. Plants in the different induction treatments were also isolated in separate bioclimatic chambers (Conviron, Winnipeg, MB, Canada) on a 16L:8D cycle at 28 °C and 80% humidity to prevent volatile induction of the uninduced plants. Insects in the different diet treatments were also separated so that insects feeding on artificial diet, non-induced plants, and induced plants were in separate bioclimatic chambers (Conviron, Winnipeg, MB, Canada) each on a 16L:8D cycle at 28 °C and 80% humidity. Additionally, larvae were not directly placed on plants to ensure that feeding did not further induce the JA-sprayed plants or induce control plants. Larvae were instead fed leaf cuttings of plants ad libitum in 1 oz souffle cups with 30 mm Whatman filter paper discs applied with 50 μL of DI water to keep the leaves from drying out. Generally, across plant species, leaves not fully expanded are more well-defended and contain higher toxic secondary metabolites, so only fully expanded leaves were fed to the larvae, with leaves being removed mechanically at the pulvinus where the petiole meets the stem to prevent induction caused by wounding/injuring, although cutting soybean leaves does not induce plant defenses [21,26]. To maintain plant induction, the JA-induction treated plants were sprayed every other day for the duration of the experiment.

Larvae were then assayed for mortality 7 days post-emergence from eggs. After this point, dead insects were removed, and the remaining live insects were arbitrarily culled by half, given the limited plant material for rearing insects to later instars. This left us with ~800 caterpillars to rear and use for further experiments. The remaining individuals reared from the different diets were then fed until pupation, after which pupation was recorded, with pupae also being sexed and massed (Mettler Toledo, Greifensee, Switzerland). We used mortality (at seven days after insects hatched and were placed on diet treatments), development time (in days to pupation), and pupal mass (mg) as proxies for larval performance within a generation.

Adult fecundity, taken as the total number of eggs laid per female, was also assessed for individuals on the artificial diet treatment in a separate experiment. Individuals used in this experiment were reared as larvae using the same setup/procedure as above. Upon pupation and then ecolsion, sex, pupal mass (mg), and adult mass (mg) were recorded for all individuals. Female moths that eclosed were then placed individually in large 3.7 L containers (Rubbermaid, Atlanta, GA, USA) with 2 male moths that also eclosed within 24 h of each other and provided a 20% sucrose-electrolyte solution (m/v; The Gatorade Company, Chicago, IL, USA). Cages were checked daily, with the number of eggs laid counted until the females died. A total of ~1800 neonates were set up at the onset of this experiment which resulted in 18 breeding pairs (n = 18). Given this methodology and the low number of final breeding pairs, it was not feasible to conduct this experiment on the larvae reared from JA-induced/non-induced *G. max*. However, the relationship between pupal mass and fecundity in this experiment can be used to infer how differences in pupal weights between various feeding treatments impact adult fecundity.

2.3. Statistical Analysis

All statistical analyses were conducted using the open-source R statistical software 4.0.2 [27]. Generalized linear models (GLMs) were fit for all immature performance parameters with the fixed effects of plant cultivar crossed with plant induction and insect sex (when known) using Bayesian methods employed in the R2jags package [28]. For adult fecundity (taken as the total number of eggs laid), females reared on an artificial diet were fit against their pupal mass using a linear model. For insect mortality, we fit the GLM with a Bernoulli distribution. Development time, final pupal mass, and fecundity (all after being log-transformed to meet assumptions of normality) were fit using a Gaussian error distribution (development time and total eggs laid were modeled better by a Gaussian than Poisson distribution). All Bayesian models were run using 3 separate chains for at least 10,000 iterations with a burn-in of 1000 and a thinning rate of 1, and then the chains were checked for convergence (please see the Supplementary Material for further documentation). To compare across different effects/models (Supplementary Material Tables S1–S4), we used a Bayesian information theoretic approach and calculated the Deviance Information Criterion (DIC) and the Watanabe-Akaike Information Criterion (WAIC) to determine the best fit model. For the diet treatments, we fit three models—a null model with no effects, a main effects model, and a model that accounted for the interactions between the treatments. For the fecundity experiment, we compared the null model to a standard linear model. WAIC calculations for models were performed in the loo package [29]. Data were visualized using the package vioplot when not using the native R plotting functionality [30].

3. Results

The model that included interactive effects for 7-day post-hatching survival fit the data reasonably well (Table S1A,B). However, the best fit and most parsimonious model included only the main effects of cultivar and JA treatment (Figure 1; Tables 1 and S1B). In general, neonates feeding on Gasoy increased their probability of survival by 15.4% compared to neonates feeding upon Braxton (Figure 1). Treating plants with JA to induce plant defenses reduced the probability of neonate survival regardless of cultivar by 9.6% (Figure 1; Table 1). For comparison, larvae reared on the artificial diet had a survival probability of 0.878 ($\pm$0.019 S.E.).
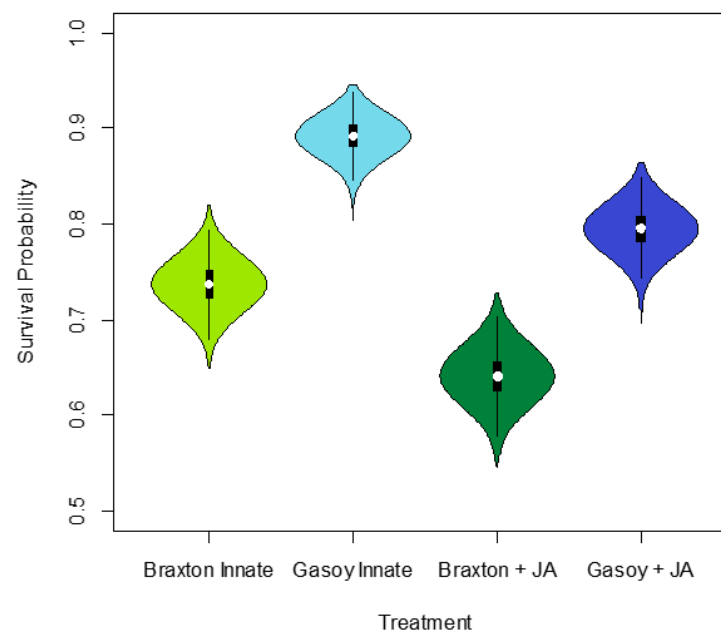

Figure 1. Probability of *S. frugiperda* 7-day survival (*y*-axis) on different plant cultivars crossed with induction treatments (*x*-axis). Cultivar affected insect survival with JA induction increasing larval mortality. Estimates in the figure are displayed as violin plots, represented as a traditional boxplot overlayed on a kernel density plot of the distribution of the Bayesian posterior estimates.

Table 1. Bayesian GLM with group means parameterization of *S. frugiperda* mortality at 7 days across different *G. max* cultivars crossed for innate and induced jasmonic acid plant defenses. Differences between treatment group means inferred by non-overlapping 95% Credible Intervals (C.I.).

Treatment Group	Mean	S.D.	2.5% C.I.	25% C.I.	50% C.I.	75% C.I.	97.5% C.I.	$\hat{R}$	N. eff
Braxton Innate	1.034	0.107	0.827	0.962	1.032	1.105	1.249	1.001	27,000
Gasoy Innate	2.117	0.175	1.783	1.997	2.114	2.233	2.471	1.001	27,000
Braxton + JA	0.581	0.102	0.383	0.512	0.581	0.650	0.782	1.001	13,000
Gasoy	1.358	0.119	1.127	1.276	1.356	1.437	1.598	1.002	3200

For development time to pupation, the main effects model that included plant cultivar, pupal sex, and JA induction best fit the data (Figure 2; Tables 2 and S2C). Development time to pupa was influenced by plant cultivar and JA induction but not gender (Table 2). Larvae feeding on JA-induced plants took about 3 days longer to develop (a ~16% increase) than on control plants, while larvae on Gasoy took about half a day longer to develop than larvae on Braxton, both regardless of gender (Figure 2; Table 2). For comparison, female larvae reared on the artificial diet pupated in 13.795 (±0.094 S.E.) days, while male larvae reared on the artificial diet pupated in 13.858 (±0.148 S.E.).
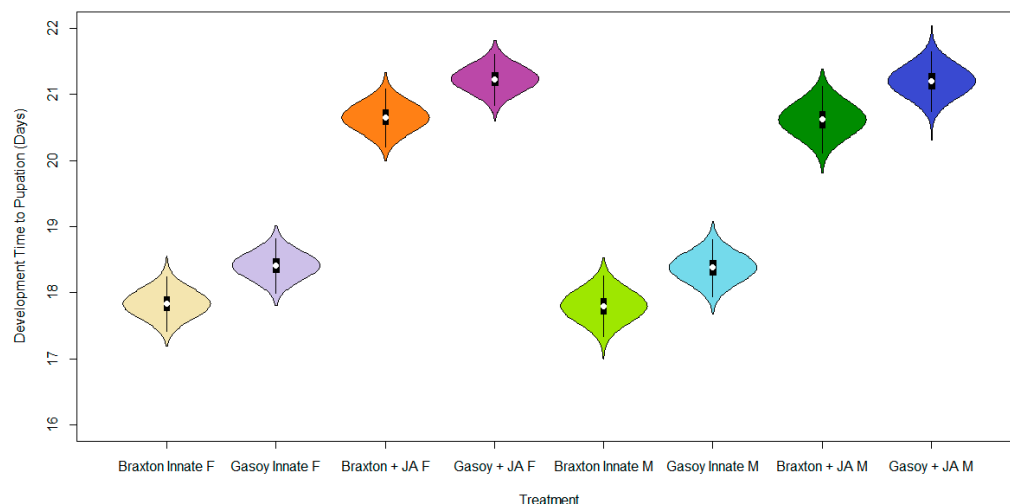

Figure 2. Estimate of *S. frugiperda* development time to pupation (*y*-axis) on different plant cultivars with induction treatments by sex (*x*-axis). Larvae reared on Gasoy and JA-induced plants had extended development times. Estimates in the figure are displayed as violin plots, represented as a traditional boxplot overlayed on a kernel density plot of the distribution of the Bayesian posterior estimates.

Table 2. Bayesian GLM with main effects parameterization of *S. frugiperda* development time to pupation across different *G. max* cultivars, innate/induced jasmonic acid plant defenses, and individuals' sex. Note that the 95% Credible Intervals (C.I.) for sex overlap zero.

Treatment Group	Mean	S.D.	2.5% C.I.	25% C.I.	50% C.I.	75% C.I.	97.5% C.I.	$\hat{R}$	N. eff
Intercept	17.827	0.157	17.519	17.722	17.826	17.932	18.136	1.001	45,000
Cultivar	0.580	0.164	0.261	0.467	0.579	0.691	0.901	1.001	45,000
+JA	2.824	0.164	2.503	2.714	2.823	2.935	3.144	1.001	45,000
Sex	−0.030	0.166	−0.355	−0.143	−0.030	0.082	0.294	1.001	45,000

In terms of pupal mass, the main effects model, which included cultivar, pupal gender, and JA induction best fit the data (Figure 3; Tables 3 and S3B). Given the credible intervals, pupal mass was only influenced by plant cultivar and not gender or induction, with individuals on Gasoy being on average 1 mg heavier than individuals on Braxton (Figure 3). However, there did seem to be a trend for gender and interaction between

cultivar and gender (Table S3A). Interestingly, while female mass was similar regardless of cultivar induction treatment, male pupae on Gasoy tended to weigh more than individuals on Braxton regardless of induction. However, to reiterate, the best fit model for the data remained the main effects model (Tables 3 and S3B). For comparison, female pupae reared on the artificial diet weighed 123.652 (±3.038 S.E.) mgs while male pupae were 118.475 (±2.765 S.E.) mgs.
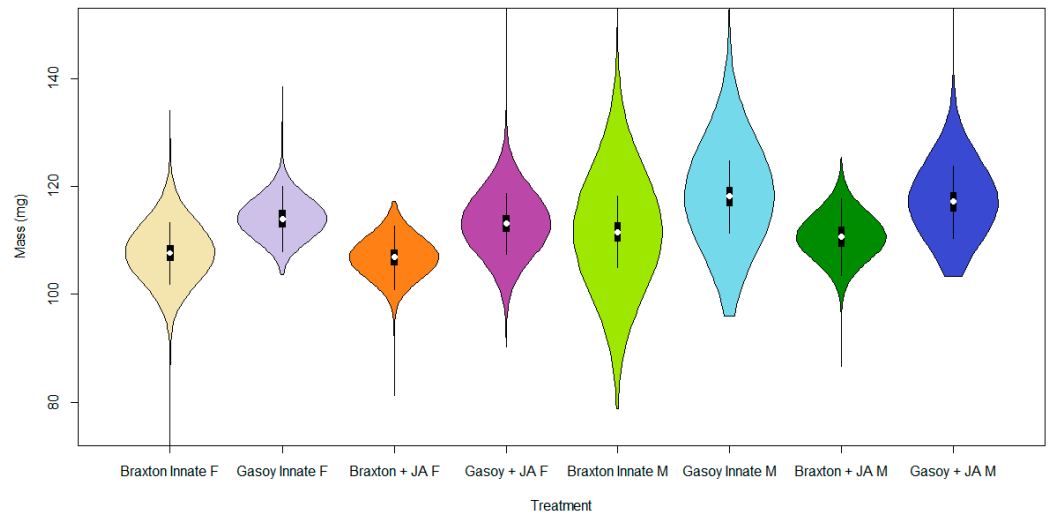

Figure 3. Estimate of *S. frugiperda* pupal mass (*y*-axis, back-transformed to linear) across different treatment groups (*x*-axis). Final pupal mass was only influenced by the cultivar. Estimates in the figure are displayed as violin plots, represented as a traditional boxplot overlayed on a kernel density plot of the distribution of the Bayesian posterior estimates.

Table 3. Bayesian GLM with main effects model of *S. frugiperda* pupal mass across different *G. max* cultivars, innate/induced jasmonic acid plant defenses, and individuals' gender. Note that the 95% Credible Intervals (C.I.) for innate/induced jasmonic acid plant defenses and sex overlap zero.

Treatment Group	Mean	S.D.	2.5% C.I.	25% C.I.	50% C.I.	75% C.I.	97.5% C.I.	$\hat{R}$	N. eff
Intercept	2.032	0.009	2.015	2.026	2.032	2.038	2.050	1.001	110,000
Cultivar	0.025	0.009	0.007	0.019	0.025	0.013	0.043	1.001	140,000
+JA	−0.004	0.009	−0.022	−0.010	−0.004	0.003	0.014	1.001	43,000
Sex	0.015	0.009	−0.003	0.009	0.015	0.022	0.034	1.001	100,000

The total number of eggs laid was influenced by female mass (Figure 4; Table 4). Heavier females laid more eggs over their adult lifespan compared to lighter females. However, while the best fit model for the data was the main effects model, there was also support for the intercept-only null model (Table S4A,B).

Table 4. Bayesian LM of total number of eggs laid by *S. frugiperda* female pupal mass (mg).

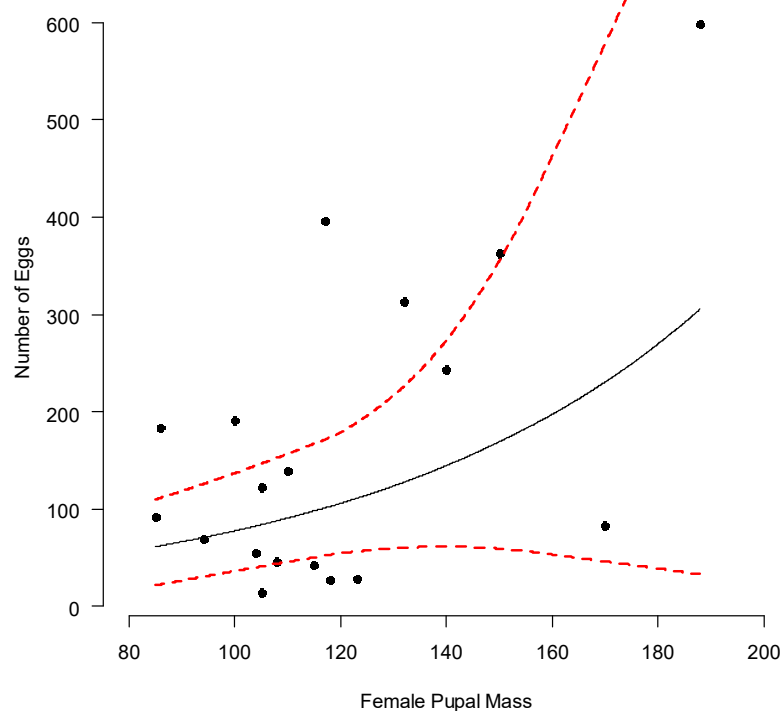| Parameter	Mean	S.D.	2.5% C.I.	25% C.I.	50% C.I.	75% C.I.	97.5% C.I.	$\hat{R}$	N. eff
Intercept	2.793	1.175	0.452	2.036	2.794	3.539	5.126	1.001	13,000
Slope	0.016	0.010	−0.004	0.009	0.016	0.022	0.035	1.001	12,000

Figure 4. Regression of total number of eggs laid by *S. frugiperda* females (*y*-axis, back-transformed to linear) using female pupal mass (mg) as the predictor (*x*-axis). Heavier females laid more eggs than lighter females. Filled circles represent the raw data, with the solid black line representing the regression and the dashed red lines represent the 95% credible intervals.

4. Discussion

Our results indicate that plant cultivar and JA induction were both important initial causes of mortality at 7 days for insects. However, contrary to our expectations, although plant cultivars varied in their amounts of constitutive/inducible phenolic compounds and POD, plant induction and cultivar did not cause an interactive effect (Figure 1; Table 1). POD produces deleterious reactive oxygen species harming insects but also uses phenolic compounds as a substrate, producing toxins like quinone and quinone methides, which can bind to plant-derived amino acids reducing their digestibility [24,31]. Given the results, it would seem *S. frugiperda* is not capable of mounting an effective strategy against POD at these early life stages. Interestingly, the Braxton cultivar exhibited a 9.6% decrease in insect survival when JA was applied, even though this cultivar does not express higher amounts of phenolic compounds or POD when induced with JA [24]. Thus, our results also indicate that other plant secondary metabolites or structural defenses, such as protease inhibitors (PIs) or trichomes [32–35], are important contributors to plant defense against general insects concerning soybeans. Specifically, for the soybean cultivars we investigated, PIs have also been implicated in lowering insect pest performance [26,36].

Insect development to pupation was also extended when fed on induced plants and by cultivar, although the latter only marginally (Figure 2; Table 2). Again, cultivar and JA induction did not interact even though cultivars varied in their amounts of constitutive and inducible phenolics/POD, which can be seen by the main effects model being considerably better than the main interactive effects model (Tables 2 and S2A,B). Although there did seem to be a trend for interaction between cultivar and sex on pupal mass (Table S3A), the better fit main effects models to these data suggest pupal mass was only marginally influenced by plant cultivar (Figure 3; Table S3B). This difference is likely not biologically relevant, though, comprising less than a one percent difference in average mass. Induction also did not impact pupal mass regardless of the model. This outcome is perhaps not surprising since the impetus to pupate rather than molt into a new instar is hormonally coordinated

and contingent on a genetically set fixed size/mass rather than development time [37]. Insects, especially lepidopterans like the fall armyworm, can have supernumerous instars to meet their target pupal mass due to poor quality food or varying temperatures. Lastly, the total number of eggs laid by females was influenced by female pupal mass (Figure 4; Table 4). This is also not unsurprising since heavier females are bigger and thus have more space/resources to develop eggs over their adult lifespan compared to lighter/smaller females. Although, our data also suggest females lay ~100 eggs regardless of their mass, with heavier females perhaps laying the same number of eggs but allocating more resources to each one. Work by Huang et al. (2021) [38] would suggest the former hypothesis, with female mass influencing fecundity and the variability in our data being perhaps attributed to the fewer number of male copulatory partners.

From a management perspective, plant cultivar and inducible JA defenses had the strongest effects on early larval mortality, which would be the most susceptible and naïve life stages to plant defenses. Different induced plant defenses were equally effective at decreasing 7-day larval survival, but the higher constitutive phenolic defenses varying between cultivars were more effective at lowering larval survival before JA induction. Later life performance metrics such as development time to pupation and pupal mass were less influenced or unaffected (respectively) by plant cultivar and induced defenses. Further, individuals that survive to pupation would have similar fecundity due to the similar body sizes of individuals in the different treatment groups; extending the development rate of larvae would allow growers more time to apply treatment methods and could increase the insect pest's susceptibility to natural enemies as predicted by the slow-growth high mortality hypothesis [39]. However, induced plant defenses that act as a feeding retardant, such as in this case, would lower the efficacy of any *per os* entomopathogens used as a microbial biological control, such as *Spodoptera frugiperda* multiple nucleopolyhedrovirus [11,12]. *S. frugiperda* exhibits size susceptibility to nucleopolyhedroviruses (NPVs), meaning smaller insects are more susceptible than larger insects. Still, insect herbivores that have slower development and feeding because of plant defenses are less susceptible to NPV control measures because they consume viral particles on foliage slower, resulting in a lower treatment dose being administered per time [10,12]. Furthermore, induced plant defenses can inactivate NPVs, interfere with their transmission inside the larva's gut, and lower pathogen efficacy/production [10,11,24,40].

Given all this, it would be advisable for growers to monitor their commodities biweekly. At the same time, *S. frugiperda* can quickly detect infestations for rapid deployment of control measures while insects are still young. Induced plant defenses could lower larval survival up to 9.6% and extend development time by ~3 days which would alleviate pest pressure and extend the period growers have to detect *S. frugiperda*. Likewise, planting a resistant cultivar higher in phenolic compounds will greatly lower young larvae survival, with only marginal changes in *S. frugiperda* development time that would not impact the detection window. If microbial biocontrol with NPVs is to be applied, it would be most effective on younger instars before they cause significant amounts of foliar damage that triggers an induced plant defensive response [41]. Cultivars with high constitutive plant defenses and plantings that experience high levels of damage from numerous generations of *S. frugiperda* infestations might present a particular problem for microbial biocontrol with NPVs. Thus, an integrated pest management approach should be used to enhance the effectiveness of NPVs. Augmentative biological control specifically could be an effective additive treatment to NPV applications in the field since natural enemies either avoid sick prey or have neutral effects on pathogen spread, given the increased development time of pests allowing predators more time to forage and hunt them [42,43].

fit for *S. frugiperda* development time in days to pupation across different *G. max* cultivars with innate/induced jasmonic acid plant defenses and sex of individual for the main effects parameterization model, Figure S4: Posterior predictive fit estimates for *S. frugiperda* development time in days to pupation across different *G. max* cultivars with innate/induced jasmonic acid plant defenses and sex of individual for the main effects parameterization model, Figure S5: Posterior predictive fit for *S. frugiperda* pupal mass across different *G. max* cultivars with innate/induced jasmonic acid plant defenses and sex of individual for the main effects parameterization model, Figure S6: Posterior predictive fit estimates for *S. frugiperda* pupal mass across different *G. max* cultivars with innate/induced jasmonic acid plant defenses and sex of individual for the main effects parameterization model, Figure S7: Posterior predictive fit for the total number of eggs laid by *S. frugiperda* female pupal mass, Figure S8: Posterior predictive fit estimates for the total number of eggs laid by *S. frugiperda* female pupal mass, Table S1: (A) Bayesian GLM with main interactive effects parameterization of *S. frugiperda* mortality at 7 days across different *G. max* cultivars crossed for innate and induced jasmonic acid plant defenses. (B) DIC and WAIC scores for different models fit to *S. frugiperda* mortality at 7 days across different *G. max* cultivars and innate/induced jasmonic acid plant defenses, Table S2: (A) Bayesian GLM with main interactive effects parameterization of *S. frugiperda* development time to pupation across different *G. max* cultivars crossed for innate/induced jasmonic acid plant defenses and individuals' sex. (B) DIC and WAIC scores for different models fit to *S. frugiperda* development time to pupation across different *G. max* cultivars and innate/induced jasmonic acid plant defenses, Table S3: (A) Bayesian GLM with main interactive effects parameterization of *S. frugiperda* pupal mass across different *G. max* cultivars crossed for innate/induced jasmonic acid plant defenses and individuals' sex. (B) DIC and WAIC scores for different models fit to *S. frugiperda* pupal mass across different *G. max* cultivars and innate/induced jasmonic acid plant defenses. Table S4: (A) Bayesian LM of the total number of eggs laid for the intercept-only model (null model). (B) DIC and WAIC scores for different models fit to the total number of eggs laid by *S. frugiperda* pupal mass (mg).

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