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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

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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 informati[p 0889a0 0 08893 0 0 time1 0 0 1 0 0 cm / Ida5 D, QQ0 gest ions42.]ence, and determine likely p(pe c22Lo36.283ne)-252rvations an -757.64 cmBedict agthe 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

2.2. Experimental Procedure

S. frugiperda

2.3. Statistical Analysis

Table 1. Bayesian GLM with group means parameterization of *S. frugiperda* mortality at 7 days across different *G. max* cu28.9664 Tfbvarsx

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.

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].

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/app12083907/s1, Figure S1: Posterior predictive fit for *S. frugiperda* mortality at 7 days across different *G. max* cultivars crossed for innate and induced jasmonic acid plant defenses, Figure S2: Posterior predictive fit estimates for *S. frugiperda* survival at 7 days across different *G. max* cultivars crossed for innate / induced jasmonic acid plant defenses, Figure S3: Posterior predictive

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