Introduction

Plants employ two modes of resistance to defend themselves against herbivore attack: constitutive resistance, which is expressed in a plant irrespective of prior history of herbivore attack, and inducible resistance, which is triggered by herbivore feeding (Stout, 2019). In general, the same physical and chemical traits have been implicated in constitutive and inducible resistance. Tradeoffs between constitutive and induced resistance have long been hypothesized (Brody & Karban, 1992; Herms & Mattson, 1992; Agrawal, Conner & Rasmann, 2010; Kempel, Sch

Ma a s a d d s

Simpson 1992). The adjusted mean larval weight gains were compared using Tukey-Kramer mean separations.

Similarly, the impact of soybean genotype and JA treatment on foliar consumption and food conversion efficiency (mg/cm^2

and least on Cook, followed by Braxton. Braxton did not differ significantly from Cook. Weight gains on all other genotypes except Braxton were intermediate between Davis and Cook. JA treatment significantly reduced larval growth (Table 1). The overall weight gains of larvae on the JA treatment were reduced by 29% compared to weight gains before induction across all genotypes. The negative impact of JA treatment on larval growth did not differ significantly among genotypes (as indicated by a lack of genotype by JA treatment interaction; Table 1).

Foliar consumption by larvae differed among genotypes but was not significantly affected by JA treatment or the interaction between genotype and JA treatment (Table 1). Consumption was lowest on Cook and consumption on this genotype differed significantly from consumption on Bragg, Davis, Centennial and Stonewall. Consumption on the remaining genotypes was intermediate. Initial larval weight significantly affected foliar consumption (F = 11.5, df = 1, 183, P = 0.0009).

Foliar conversion efficiency in larvae was affected by genotype and application of JA, but no interaction between these two factors was found (Table 1). Initial larval weight significantly affected conversion efficiency (F = 8.83, df = 1, 190, P = 0.003).

The relationship between constitutive and inducible resistance based on larval weight gains was marginally significant (F = 3.5; df = 1, 9, P = 0.09). The slope of the relationship was −0.51 ± 0.27 (R^2 = 0.20) (Fig. 1). The relationship between constitutive and inducible resistance based on foliar consumption could not be determined because the consumption estimates in four out of 11 genotypes were higher in induced than uninduced leaf disks (Table 1).

G [illegible] **1** The same genotypes used in the GC experiment were used in GHI. Larval weight gain of S. frugiperda was significantly impacted by genotype (Table 2). The lowest larval weight gain, on Bragg, differed significantly from weight gains on genotypes Davis, Williams 82 and Asgrow 5533. In the remaining genotypes, weight gains were intermediate. Application of JA resulted in significantly lower weight gains in larvae, with an overall 77% decrease in growth compared to no JA application. However, the effect of JA on weight gains was consistent across genotypes since the interaction between genotype and JA was not significant (Table 2). The effect of initial weight (covariate) on weight gain was significant, indicating that initial weight of larvae impacted weight gain on soybeans (F = 8.988, df = 1, 166, P = 0.003).

Foliar consumption by larvae was also significantly impacted by genotype (Table 2), although post-hoc comparisons of foliar consumption by Tukey-Kramer did not reveal differences among genotypes. JA application resulted in a 65% reduction in consumption compared with consumption prior to the application of JA. Furthermore, a significant interaction between genotype and JA treatment was found and was evidenced by differences in the rankings of consumption among genotypes in the induced and uninduced states (Table 2). Initial weight of larva as a covariate was significant for foliar consumption (F = 12.77, df = 1, 178, P = 0.0005).

Foliar conversion efficiency was significantly influenced by soybean genotype, and application of JA (Table 2). Conversion efficiency in Asgrow 5533 was greatest and differed significantly from conversion efficiencies on Bragg and Cook. In the remaining genotypes, intermediate levels of conversion efficiency were found. Conversion efficiencies on induced soybeans was 40% less than those on soybeans

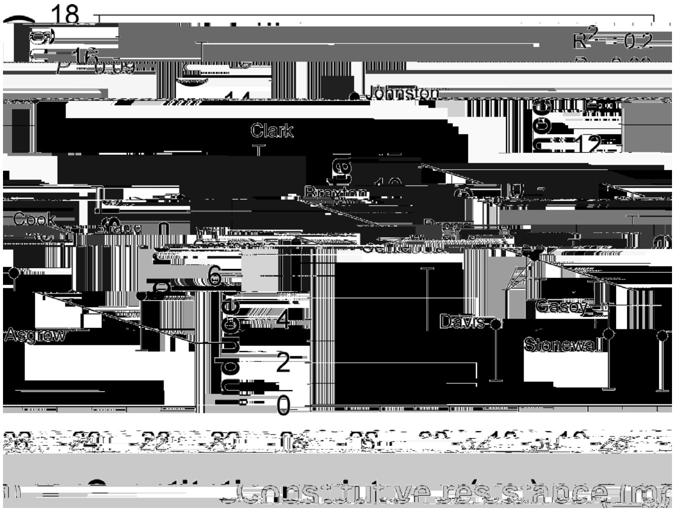


Fig. 1. Relationship between mean constitutive (−1 × weight gain of larvae on non-induced plants) and induced resistance [−1 × (weight gain of larvae on induced plants - weight gain on non-induced plants)] for 11 genotypes of soybeans in the GC experiment. Each point represents data from larvae from 10 plants per genotype before and after induction with jasmonic acid. This graph shows a marginally significant ($P < 0.10$) relationship between constitutive resistance and induced resistance.

before induction. The interaction between JA treatment and soybean genotype was not significant for conversion efficiency (Table 2). Finally, initial weight differences did not influence foliar conversion efficiency (F = 2.25, df = 1, 177, P = 0.13).

Inducible and constitutive resistance as measured by larval weight gain were negatively correlated with one another in this experiment (F = 10.54, df = 1, 9, P = 0.01; R^2= 0.49); that is, induced resistance decreased as constitutive resistance increased (slope = −0.47 ± 0.15) (Fig. 2A) Similarly, the relationship between the two modes of resistance as measured by foliar consumption was negative (F = 5.54, df = 1, 9, P = 0.04; R^2 = 0.31) because induced resistance decreased with increases in constitutive resistance (slope = −0.88 ± 0.37) (Fig 3A)

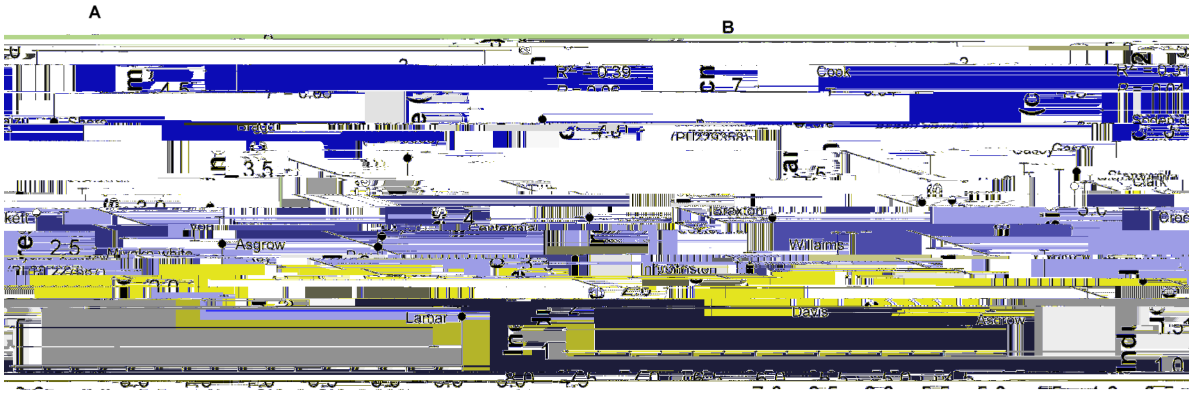
G [illegible] II (GHII) This experiment used genotypes that had been developed for resistance to lepidopteran pests. Larval weight gain of S. frugiperda was impacted by genotype (Table 3). The lowest larval weight gain on Lamar differed significantly from weight gains on Miyako White and

Fig. 2. Relationship between mean constitutive (−1 × weight gain of larvae on non-induced plants) and induced resistance [−1 × (weight gain of larvae on induced plants - weight gain on non-induced plants)] on soybeans in GHI (A), GHII (B) and GHIII (C) experiments with 11,eight and eight genotypes in GHI, II and III, respectively. Each point represents data from larvae before and after induction with jasmonic acid from eight to ten plants per genotype in GHI and II, and 11−14 plants per genotype in GHIII experiments. The graphs show a significant (P < 0.05) relationship in GHI (A) and GHIII (C) and a marginally significant (P < 0.10) relationship in GH II (B) between constitutive resistance and induced resistance.

G[illegible] **III**: For GHIII, a selection of genotypes from the previous three experiments was used. Larval growth of S. frugiperda was significantly influenced by both genotype and application of JA (Table 4). Also, the interaction between genotype and JA was significant (Table 4). Of all the genotypes, larvae gained the most weight on Asgrow followed by Gasoy, and weight gain was significantly higher on Asgrow than on the rest of the genotypes except Gasoy. The intermediate weight gains in five of the nine genotypes used in this experiment (Bragg >Crockett>Lyon>Soden-daizu>Stonewall) did not differ significantly from the lowest weight gain on Lamar. Weight gain on Lamar was significantly different from weight gains on Davis, Asgrow and Gasoy. Treatment with JA resulted in ~30% reduction in weight gain compared to weight gains before treatment with JA. The significant interaction between genotype and JA treatment was manifested as differences in the effect of JA on weight gains among genotypes (Table 4). The influence of initial weight on larval growth was significant (F = 10.04, df = 1, 219, P = 0.002).

Foliar consumption was also significantly influenced by genotype, JA application and the interaction of genotype and JA (Table 4). Low consumption on Soden-daizu along with Gasoy and Lamar differed significantly from higher consumption on Davis, Crockett, Bragg and Stonewall. Consumption was intermediate in Lamar and Asgrow and these genotypes were significantly less consumed than Davis or Crockett. Consumption after JA was >35% lower after JA application than before JA application. Genotypes differed in the effect of JA application on foliar consumption (Table 4).

Conversion efficiency was impacted by genotype, JA application and the interaction of these factors (Table 4). The highest conversion efficiency, on Gasoy, differed significantly from conversion efficiencies on all genotypes except Asgrow and Lyon. Conversion efficiency was lowest on



F 3. Relationship between mean constitutive (−1 × foliar consumption on non-induced plants) and induced resistance [−1 × (foliar consumption on induced plants − foliar consumption on non-induced plants)] on soybeans in GHI (A), GHII (B) and GHIII (C) experiments with 11,eight and eight genotypes in GHI, II and III, respectively. Each point represents data from larvae before and after induction with jasmonic acid from eight to ten plants per genotype in GHI and II, and 11−14 plants per genotype in GHIII experiments. The graphs show a significant ($P < 0.05$), marginally significant($P < 0.10$) and highly non-significant ($P = 0.3$) relationship between constitutive resistance and induced resistance in GHI (A), GHII (B) and GHIII experiments, respectively.

Tab 3. Larval growth (mg ± s.e.), foliar consumption (cm^2 ± s.e.) and food conversion efficiency (mg/ cm

Table 4. Larval growth (mg ± s.e.), foliar consumption (cm^2 ± s.e.) and food conversion efficiency (mg/ cm^2 ± s.e.) for S. frugiperda larvae fed on soybean leaf disks in the GHIII experiment involving nine soybean genotypes. Weight gains, consumption and conversion efficiencies were estimated in bioassays conducted before application of JA (constitutive) and after the application of JA (induced). Means in both the columns for each variable followed by the same letter show no difference across varieties before and after application of JA (Tukey's Honestly Significant Difference, α= 0.05).

	Larval weight gain (mg)		Consumption (cm^2)		Conversion efficiency (mg/cm^2)	
	Constitutive state	Induced state	Constitutive	Induced	Constitutive	Induced
Lamar	21.65 ± 1.24 abcd	13.00 ± 1.24 e	3.48 ± 0.23 cde	2.24 ± 0.23 fgh	6.36 ± 0.98 de	6.14 ± 0.98 de
PI 229,358	21.67 ± 1.19 abcd	16.47 ± 1.19 cde	2.73 ± 0.22 ef	2.28 ± 0.22 fgh	8.02 ± 0.95 cde	8.40 ± 0.95 cde
Stonewall	22.07 ± 1.19 abc	15.10 ± 1.19 e	4.07 ± 0.22 abcd	2.57 ± 0.22 efg	5.53 ± 0.95 de	6.40 ± 0.95 de
Lyon	23.24 ± 1.19 ab	15.01 ± 1.19 e	2.62 ± 0.22 ef	1.48 ± 0.22 gh	9.20 ± 0.95 bcd	11.92 ± 0.95 bc
Crockett	23.80 ± 1.19 ab	17.03 ± 1.19 cde	4.38 ± 0.22 abc	3.22 ± 0.22 def	5.49 ± 0.95 de	6.10 ± 0.95 de
Bragg	25.81 ± 1.29 a	16.41 ± 1.29 cde	4.81 ± 0.24 ab	2.56 ± 0.24 efgh	5.48 ± 1.02 de	7.82 ± 1.02 cde
Asgrow 5533	26.58 ± 1.24 a	26.59 ± 1.19 a	3.41 ± 0.23 cde	2.25 ± 0.22 fgh	7.85 ± 0.98 cde	13.37 ± 0.95 ab
Davis	27.23 ± 1.19 a	15.98 ± 1.19 de	4.87 ± 0.22 a	3.89 ± 0.22 bcd	5.65 ± 0.95 de	4.18 ± 0.95 e
Gasoy	28.00 ± 1.34 a	18.98 ± 1.34 bcde	3.56 ± 0.25 cde	1.35 ± 0.25 h	8.11 ± 1.07 cde	17.90 ± 1.07 a
Genotype	$F_{8, 112} = 9.98$; $P < 0.0001$		$F_{8, 109} = 17.11$; $P < 0.0001$		$F_{8, 112} = 14.07$; $P < 0.0001$	
JA	$F_{1, 112} = 170.73$; $P < 0.0001$		$F_{1, 108} = 234.60$; $P < 0.0001$		$F_{1, 112} = 27.63$; $P < 0.0001$	
Genotype*JA	$F_{8, 112} = 3.84$; $P = 0.0005$		$F_{8, 108} = 4.56$; $P < 0.0001$		$F_{8, 111} = 6.49$; $P < 0.0001$	

Davis. Application of JA increased conversion efficiency in larvae by 32% across genotypes.

The regression diagnostics on this data set showed that the data point for Asgrow 5533 was an outlier (R studentized value = 6.2) (suppl table 2). Inducible and constitutive resistance based on larval weights were negatively correlated in the remaining genotypes (F = 6.8, df = 1, 6, P = 0.0400) (Fig. 2C). The slope of this relationship was −0.54 ± 0.21 and the value of R^2 was 0.45 (Fig 2C). The relationship between constitutive and inducible resistance as measured by consumption was not statistically significant (F = 1.42, df = 1, 7, P = 0.27) (Fig. 3C).

Discussion

The current study provides support for the existence of a tradeoff between constitutive and inducible modes of resistance in soybean genotypes bred for varying levels of resistance to Lepidopteran defoliators (Boethel, 1999). Following Kempel et al. (2011), induced resistance was measured as the difference in larval weight gains on soybean leaflets before and after induction (treatment with JA), whereas constitutive resistance was measured as larval weight gain on leaflets not treated with JA. A significant ($P < 0.05$) or marginally significant ($P < 0.10$) negative correlation between the two modes of resistance was found in all four experiments (GC, GHI, GHII, and GHIII), with each experiment comprising 8−11 genotypes and at least 10 plants per genotype per treatment in each experiment. The negative relationships between constitutive and inducible modes of resistance found in experiments GHI and GC contrast with the results of Underwood et al. (2000), who used the same soybean genotypes that were used in GHI but found no correlation between induced and constitutive resistance to Mexican bean beetle (E. varivestris) adults. Resistance in Underwood et al. (2000), however, was measured differently, using dual-choice preference tests with leaf disks from injured and non-injured plants. Brody and Karban (1992) and English-Loeb, Karban and Walker (1998) also failed to find trade-offs between constitutive and inducible resistance to pest mite species in two other crop species (cotton and grapes, respectively). In addition, the results of this study contrast with Kempel et al. (2011), who failed to find a tradeoff between constitutive and inducible resistance to Spodoptera littoralis in 40 cultivated plant species.

Evidence for a tradeoff between constitutive and inducible resistance was also investigated using the foliar consumption data. Using foliar consumption as a metric for resistance, a significant, marginally significant, and non-significant relationship between induced and constitutive resistance was found in GHI, GHII, and GHIII, respectively. These data from the greenhouse experiments are largely supportive of the relationships found using weight gains as a metric of plant resistance. The relationship between constitutive and inducible resistance was not investigated for the GC experiment, because higher consumption after JA treatment was found for four genotypes in this experiment; this anomalous result may have be explained by the more artificial conditions for plant growth in this experiment.

Aside from differences potentially stemming from the use of different crops and arthropod species, one potential reason for disagreement between this study and previous studies investigating tradeoffs in crop plants is that prior studies used natural feeding by arthropods to induce plants. The current study, in contrast, used exogenous JA to induce resistance in plants. The percent reductions in mean larval growth resulting from treatment with JA were substantial (from 29% to 76%) and were observed consistently in all genotypes except in Asgrow 5533 in GH III. The induction of resistance by JA in soybeans is consistent with prior reports on induction by this elicitor against S. frugiperda in soybeans (Gordy et al., 2015; Shikano et al., 2017). Plant biochemical and morphological responses to JA are thought to largely (but not perfectly) mimic those following chewing herbivory (Zhang, Shu, Dicke & Liu, 2010), and the use of JA rather than natural herbivory to induce plants minimized potential variation in induced resistance arising from differences in the intensity of the initial inducing event when genotypes with different levels of constitutive resistance are used. Furthermore, the use of JA enabled assessment of constitutive and inducible resistance in leaflets from the same

Declaration of Competing Interests

None.

Acknowledgments

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