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Jasmonic acid-induced resistance to fall armyworm in soybeans: Variation among genotypes and tradeoffs with constitutive resistance

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Abstract

A negative correlation between constitutive and inducible resistance across plant populations is expected for a variety of reasons; however, empirical evidence for such trade-offs remain ambiguous, particularly for crop plants. The current study investigated the relationship between constitutive and inducible resistance in vegetative-stage soybeans (V5-V6) against larvae of the generalist defoliator, *Spodoptera frugiperda*. Eighteen soybean genotypes differing in their constitutive resistance to coleopteran or lepidopteran defoliators were used over four experiments. Exogenous jasmonic acid (JA, 2 mM) was used to induce plants. Constitutive resistance of each genotype was estimated by measuring weight gains, foliar consumption, and foliar conversion efficiency in short-term feeding assays on excised leaf disks of terminal trifoliate leaves of plants not treated with JA. JA was applied to plants immediately after removing leaf material for assays of constitutive resistance, and induced resistance was estimated 48 h after application of JA using leaf disks from the remaining leaf tissue of the same trifoliate used for measuring constitutive resistance. Larval weight gains before JA treatments revealed genotypic variability in constitutive resistance. . Overall, reductions in weight gain (28.7% to 76.7%), foliar consumption (3.7% - 65%) and conversion efficiency (10.9% - 42.2%) were found in JA treatments. Significant ($P < 0.05$) or marginally significant ($P < 0.10$) negative correlations between constitutive resistance (larval weight gains on non-induced plants) and induced resistance (differences in weight gains before and after induction) were found in all four experiments, suggesting tradeoff between the two modes of resistance does exist in soybean for this herbivore. Additional evidence for tradeoffs between constitutive and inducible resitance was also found in the analysis of consumption data. Comparisons of consumption and conversion efficiencies suggest that similar antibiotic and antixenotic factors are involved in constitutive and inducible resistance to fall armyworm in soybean.

Keywords: Host plant resistance; Constitutive resistance; Fall armyworm; Foliar consumption; Foliar conversion efficiency; Induced resistance; Ja; Resistance; Soybean; Tradeoffs

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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, Schädler, Chrobock, Fischer & Kleunen, 2011). Several mechanisms might be responsible for such tradeoffs. Expression of chemical and physical resistance-related traits is costly for plants, and constitutive and induced defenses are assumed to be in competition for the same (limited) pool of resources in plants (Koricheva, Nykanen & Gianoli, 2004). In addition, a species already well defended by high constitutive resistance is thought to benefit only negligibly by further induced resistance (Karban & Baldwin, 1997; Mattson et al. 1988). Finally, crosstalk among hormonal pathways underlying constitutive and inducible resistance might also lead to tradeoffs (Guo, Major & Howe, 2018) Regardless of the mechanisms potentially underlying tradeoffs, empirical evidence for trade-offs between constitutive and inducible resistance remains ambiguous.

Much of the evidence for trade-offs between constitutive and inducible resistance that does exist comes from studies of non-domesticated plants (Koricheva et al., 2004). Fewer studies have examined both modes of resistance in cultivated crops despite the potential for both modes of resistance to reduce damage from pests. Studies in cotton (Brody & Karban, 1992), grape (Loeb-English, Karban & Walker, 1998) and soybean (Underwood, Morris, Gross & Lockwood, 2000) revealed no relationships between constitutive and induced resistance, but the evidence is not yet sufficient to form a consensus. It has been argued that artificial selection for crop improvement that aims to incorporate certain desirable agronomic traits in crop varieties, such as high yield or quality, could disrupt or alter other important traits, such as resistance against herbivores (Brody & Karban 1991; Rodriguez-Saona et al., 2011). Narrow genetic diversity of plant resistance traits in domesticated crop plants could be one reason for the absence of the expected tradeoff between both modes of resistance (Brody & Karban, 1992; Rodriguez-Saona et al., 2011). Therefore, genetic variation in resistance-related traits is needed to study the relationship between the two modes of resistance in crop plants.

Soybean germplasm contains sufficient genetic variation in constitutive resistance to defoliating insects to allow an investigation of the relationship between inducible and constitutive resistance. Breeding efforts in both the U.S. and Japan have resulted in the development of a number of constitutively resistant soybean lines possessing quantitative trait loci (QTLs) for both antibiosis and antixenosis resistance against defoliators (Beach & Todd, 1987; Beach, Todd & Baker, 1985; Komatsu, Takahashi & Nakazawa, 2010; Lambert & Kilen 1984, a, b; Rector, All, Parrott & Boerma, 1998, 1999 & 2000; Rowan, Boerma, All & Todd, 1991; Van Duyn, Turnipseed & Maxwell, 1971; Warrington, Zhu, Parrott, All & Boerma, 2008). However, only two studies have evaluated both modes of resistance in multiple soybean genotypes. A study by Underwood et al. (2000) revealed no relationship between constitutive and induced resistance against defoliating adults of Mexican bean beetle, *Epilachna varivestris*, Shikano, Shumake, Peiffer, Felton and Hoover (2017) found variation among soybean genotypes in both constitutive and inducible resistance to *Spodoptera frugiperda* (J. E. Smith) larvae, but the relationship between the two modes of resistance was not explicitly determined.

The objective of the current study was to evaluate the relationship between constitutive and inducible resistance in soybean genotypes with putative differences in their levels of constitutive resistance using a generalist defoliator, fall armyworm, *S. frugiperda*. Because soybean defenses are highly responsive to exogenous jasmonic acid (JA), a phytohormone involved in regulating responses to insect feeding (Creelman & Mullet 1997; Creelman, Tierney & Mullet, 1992; Gordy, Leonard, Blouin, Davis & Stout, 2015; Howe, 2004; Iverson, Hammond & Iverson, 2001; Shikano et al., 2017), applications of JA were used to induce soybean plants. The use of JA not only enabled the same plants to be evaluated for both constitutive and induced resistance, but also eliminated the need to use herbivores to induce plants, a procedure which can be problematic due to difficulty in controlling the amount of leaf tissue consumed (Baldwin, 1996; Cipollini, Purrington & Bergelson, 2003). Although other defoliators such as Chrysodeixis includens (Walker), the soybean looper, and *Anticarsia gemmatalis* (Hübner), the velvetbean caterpillar, are more important pests of soybean in the southern U.S., *S. frugiperda*, a sporadic pest on soybeans, was employed in this experiment because this insect is known to be responsive to JA-induced defenses in soybean (Gordy et al., 2015). As measures of induced resistance, these experiments employed the differences in *S. frugiperda* weight gains and consumption when fed plants in the constitutive and induced states following Kempel et al. (2011) . To provide further insight into changes in plant resistance induced by JA application, the increase in larval weight per unit area of foliage consumed was also calculated.

Materials and methods

Soybean genotypes and plant growth. Four independent experiments were conducted to evaluate the relationship between constitutive and inducible resistance in vegetative-stage soybeans by using feeding assays with *S. frugiperda* larvae. One experiment (GC) used soybeans grown in a walk-in growth room (Life Sciences Annex, Louisiana State University (LSU), Baton Rouge, LA) during February and March 2014. The three other experiments (GHI, GHII, and GHIII) were conducted using soybeans grown in a greenhouse on the LSU campus from March to October 2014 (Baton Rouge, LA).

In all, 18 soybean genotypes were used in these experiments (Table S1). These soybeans belong to different maturity groups (groups 3 to 8) (Table S1). Of these 18 genotypes, 10 had been previously shown to possess varying levels of constitutive and induced resistance to *E. varivestis* (Underwood et al., 2000). Eight of these genotypes were also found to possess varying levels of constitutive resistance to *S. frugiperda* (Shikano et al., 2017). Seven of the genotypes had been reported to possess varying levels of resistance to other lepidopteran larvae such as cutworms (Rowan et al., 1991;Warrington et al., 2008; Van Duyn et al., 1971; 1972). The ten genotypes from Underwood et al. (2000), namely Bragg, Braxton, Centennial, Clark, Cook, Davis, Gasoy 17, Johnston, Stonewall, and Williams 82, were evaluated for resistance twice, once using plants grown in a growth chamber (GC) and once using plants grown in a greenhouse (GHI). The seven putatively lepidopteran-resistant genotypes were PI 227,687 ('Miyako white'), PI 229,358 ('Soden-daizu'), Crockett, Lamar, Lyon, Shore, and Roy. Constitutive and inducible resistance were evaluated in these genotypes in experiment GHII. The final greenhouse experiment (GHIII) utilized a subset of eight genotypes short-listed from genotypes used in the first and second greenhouse experiments: Bragg, Crockett, Davis, Gasoy, Lamar, Lyon, Soden-daizu, and Stonewall. In all experiments a commercially grown soybean genotype, Asgrow 5533 was also employed for comparison.

Seeds of all genotypes except Asgrow 5533 were obtained from USDA-Genetic Resources and Information Network. Seeds of Agrow 5533 were obtained from a commercial supplier (Asgrow Seed Co., LLC, Creve Coeur, MO). No chemical treatments were applied to seeds. The potting soil for growing soybeans was a commercial mix of Sphagnum moss, perlite, and vermiculite (Sunshine Mix #8, Sungro Horticulture Agawam, MA 01,001). Additional vermiculite was added to the potting soil at a ratio of 1:3 and the soil mix was slightly moistened. Because varietal differences in root nodulation were not the focus of these experiments, a complex fertilizer (N:P:K 14−14−14; Osmocote^{TM}) was added to the wet soil and thoroughly mixed (40 g fertilizer /16 L soil mix). The soil mix was used to fill circular plastic pots (12.5 cm diameter and depth) with a capacity of 0.8 L containing drainage holes at the bottom. One or two soybean seeds were placed in each pot at a depth of 2.5 cm. For all experiments, 11−14 pots were prepared for each soybean genotype.

The growth chamber experiment, GC, was conducted in a growth room measuring 12.0m X 3.5m. Pots were placed in twelve plastic trays (75.0× 75.0 cm) with each tray containing one pot of each genotype (11 pots/tray). Trays were placed on steel racks (2.4 × 0.9 × 0.5 m) at a height of approximately 1.5 m above the floor. As a light source, a light assemblage (1.8 × 0.2 m) with four florescent tube lights (Philips^{TM} 80watt tube bulbs) was suspended such that the lights were maintained about 25 cm above the tops of plants. The light assemblage was repositioned twice per week to ensure the light source was ca. 25 cm above plants. Plants were watered as needed with tap water. To minimize positional effects on soybeans in the growth room, the trays were shifted from one rack to another randomly once a week. Similarly, pot positions in each tray were changed weekly until resistance was evaluated. A timer connected to each light assemblage unit was adjusted to provide light and dark periods (14:10 L:D). A range of relative humidity (85 ± 5%) and temperature (27 ± 0.5 °C) was maintained in the growth room. To maintain uniform RH, air flow in the room was aided by a fan.

For the greenhouse experiments, GHI-GHIII, pots were placed on greenhouse benches (2.4 × 1.1 m) and watered as needed. Soybean genotypes that tended to grow prostate (especially indeterminate varieties such as Lyon, Stonewall and Centennial) were staked to wooden pegs to secure them upright. Pots were randomly placed on benches and their positions were changed within and between the benches at weekly intervals to minimize positional effects. No additional lighting was provided (ambient lighting) and temperature was maintained at 28 ± 5 °C.

Inducing treatments and plant sampling: In all four experiments, each individual plant of each genotype was used to assess both constitutive and induced resistance. The protocol involved the sequential use of two leaflets from the same trifoliate of each plant to assess first constitutive and then induced resistance. Nine to 14 plants were evaluated per variety per experiment. The use of the same plant rather than separate plants for evaluation of constitutive and inducible resistance distinguishes these experiments from many previous tests for tradeoffs in which inducible and constitutive resistance were evaluated in separate groups of plants of the same genotype (e.g., Kempel et al., 2011). The use of the same trifoliate to assess both modes of resistance within an individual plant was intended to minimize the impact of within-plant spatial variation in plant resistance. Exogenous JA was used to trigger induced resistance in these experiments.

Constitutive and induced resistance were assessed using the youngest fully expanded trifoliate (5th or 6th node from the base) of plants possessing five or six fully expanded trifoliate leaves (V5-V6 stage). To assess constitutive

resistance, three leaf disks, each measuring 2.0 cm in diameter, were punched from the trifoliate leaf using a metallic cork borer (Hummert Scientific; size 13). Previous studies have demonstrated that the mechanical damage involved in removing leaf disks does not induce soybeans (Lin, Kogan & Fischer, 1990). Midribs of leaflets were avoided because young fall armyworm larvae do not feed on leaf veins. These leaf disks were used immediately for a feeding assay to evaluate constitutive resistance as described below. After removing leaf disks, a known amount of racemic mixture of JA (TCI, Portland, OR) was dissolved in 1 ml of 95% ethyl alcohol, and the resultant solution was diluted in water to obtain a 2 mM JA solution. The spray solution was applied to entire plants using a gas propellant-powered hand sprayer (Preval, Coal City, IL, USA) connected to a glass bottle with threaded opening (300 ml). For effective delivery of atomized spray particles, the spray assembly was held obliquely at a distance of 15 cm from the plants. A spray volume of 300 ml covered approximately 10 soybean plants. To avoid unintentional exposure of soybeans to JA spray by drift, plants were sprayed in batches by removing pots from the greenhouse bench and placing them in front of an exhaust fan for treatment.

In both greenhouse and growth chamber experiments, plants were placed on benches for 48 h after JA treatment to allow induction to occur After this period, the leaflet adjacent to the leaflet used for assessment of constitutive resistance was removed and used to obtain three leaf disks for evaluation of induced resistance.

Insect growth and feeding assays: Fourth-instar *S. frugiperda* were used for bioassays. Insects were obtained as eggs from a commercial supplier (Benzon Research, Philadelphia, PA). The colony of *S. frugiperda* maintained by the commercial supplier was a mixed strain but genetically closer to the corn strain than the grass strain (personal communication). This colony was inherited from USDA's lab at Stoneville, MS approximately 20 y ago. No feral or other lab insects had been added to the colony for the past 15 y. In each experiment, larvae derived from a single batch of eggs were used to assess both modes of resistance by staggering egg hatching. To do this, paper towels laden with *S. frugiperda* eggs were cut into small pieces and separated into two halves. One half of the eggs was placed in 8-cell trays and incubated in an incubator (Percival Scientific, Perry, IA, USA) at 29 °C; (85% RH;14L:10D) to accelerate hatching and the other half was stored in the refrigerator at 5 °C for 48 h and then placed in eight-cell trays. After hatching, neonates were transferred to a standard artificial diet (Southland Products Inc., Lake Village, AR, USA) in 40 ml plastic cups using a camel hair paint brush (3−4 neonates/cup). Twelve to 20 trays with neonates on artificial diet were incubated (29 °C; 14L:10D) for each bioassay (each tray containing 30 cups).

Fourth instars were stage-synchronized by selecting them at head capsule slippage during the end of the third instar and placing them individually in empty plastic cups. Larvae were weighed to the nearest 0.1 mg within 12 h of ecdysis. The beginning mean weight of insects used in assays was 8.1 ± 0.1 mg. Each Petri dish (12.5 cm diameter, 1.5 cm deep) containing three leaf disks obtained from a trifoliate of a single plant was an experimental unit and one larva was released per Petri dish. Dishes were lined with moistened cotton batting to maintain leaf turgor. A range of 10 − 14 Petri dishes were used per genotype for all assays. Petri dishes were placed in an incubator (29 °C; 85% RH; 14L:10D) following the release of larvae. Larvae were allowed to feed for 36 h except for GHII, in which a feeding period of 30 h was used. In no case did larvae consume all leaf material available to them.

Measures of resistance: Three variables were used to characterize larval performance on induced and non-induced soybean leaf disks. *Larval weight gain* was calculated by subtracting larval weight at the beginning of a feeding period from the weight of the same larva at the end of the feeding assay to the nearest 0.1 mg. Larvae were starved for four hours to empty the gut contents before weights were measured at beginning and end of feeding assays.

T*otal foliar consumption* was used as a second metric of plant resistance. To measure foliar area removed due to larval feeding, public-domain image analysis software was used (Image J, NIH) (https://imagej.nih.gov/ij). Leaf disks from each Petri dish, cleaned of frass, were attached to paper with transparent tape and scanned to capture images using a flat-bed desk top scanner set at 200 dpi resolution. The scale of measurement was set in mm by using two points of known distance on a ruler in gray scale. To obtain the area of the undamaged portion of the leaf disk in mm^2, images were converted to gray scale and were processed in binary mode. To obtain the area of the damaged portion (i.e., the foliar area consumed), the undamaged portion of leaf area in each Petri dish was subtracted from the total area of three leaf disks as estimated from the average of three independent measurements.

For the third variable, *foliar food conversion efficiency*, a measure analogous to the efficiency of conversion of ingested food developed by Waldbauer (1968) and termed "leaf utilization" by Shikano et al. (2017), was used. The food conversion efficiency was calculated as the ratio of weight gain by the insect to area of foliage consumed expressed as mg of weight gained per cm^2 of leaf tissue consumed.

Statistical analysis. The effects of soybean genotype and application of JA on larval weight gain were determined in a modified split-plot design by using Proc Mixed in SAS 9.4 version (SAS Institute Inc, Cary, NC, USA). Because feeding assays were conducted on the same experimental unit (plant) before and after the spray of JA, the plant within genotype was used as a random error term. Larval weight gain for all experiments was adjusted for differences in initial weights of larvae by using initial weight as a covariate in the analysis (Horton & Redak 1993; Raubenheimer &

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) was analyzed using a modified split plot design as described above for larval weight gains. Initial weight of larva was used as a covariate. Foliar consumption data were log -transformed to meet the assumptions of normality and homoscedasticity, based on the output from Proc Univariate, before being analyzed in Proc Mixed.

Because larval weight gain can be viewed as a more herbivore-centric metric of plant resistance and foliar consumption can be considered as a more phytocentric measure (Stenberg & Muola, 2017), both weight gain and consumption estimates were used to evaluate the relationship between plant constitutive and inducible resistance. The procedure for evaluating the relationships between constitutive and inducible resistance in each of the four experiments followed Kempel et al. (2011) for both measures of resistance. The strength of induced resistance for each genotype with respect to larval weight gain was calculated by subtracting the mean mass gain of larvae feeding on leaf disks of plants before induction with JA (non-induced) from the mean mass gain of larvae feeding on JA-induced leaf disks (induced). Because large weight gains indicate low resistance in plants, both the mass gains on non-induced leaf disks (constitutive resistance) and the differences in mass gains (induced resistance) were multiplied by −1 for easier visualization (i.e., higher values correspond to higher resistance) (Kempel et al., 2011).

The strength of induced resistance based on foliar consumption was measured by using a procedure similar to that described for weight gains. It was calculated by subtracting the mean foliar area consumed on leaf disks of plants before induction with JA (non-induced) from the mean foliar area consumed on JA-induced leaf disks (induced). Because large foliar consumption indicates low resistance in plants, both the consumption on non-induced leaf disks (constitutive resistance) and the differences in consumption (induced resistance) were multiplied by −1 for easier visualization (i.e., higher values correspond to higher resistance).

Relationships among constitutive and inducible resistance based on both weight gains and consumption data were analyzed by regression analysis in SAS using Proc Reg in SAS v 9.4 (SAS Institute Inc, Cary, NC, USA). The number of pair-wise estimates of constitutive and induced resistance in each experiment was equal to the number of genotypes (11 genotypes for the growth chamber and first greenhouse experiment; 9 and 8 for the second and third greenhouse experiments, respectively). To identify possible outliers in each experiment, regression diagnostics in SAS were used, and an R- studentized value of > 2.37 was used as the criterion for eliminating the data point.

Results

The growth chamber (GC) experiment employed genotypes previously evaluated for constitutive and inducible resistance to *E. varivestris* by Underwood et al. (2000) and some of the genotypes evaluated for constitutive and inducible resistance by Shikano et al. (2017). Weight gains of fall armyworm larvae were significantly impacted by genotype (Table 1). The influence of initial weights of larvae (covariate) on weight gain was significant ($F = 24.9$; df = 1, 180, $P < 0.00010$). Of all genotypes, growth was greatest on Davis

Table 1. 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 GC experiment involving 11 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). Results of post-hoc mean comparisons are only shown when the interaction between variety and JA treatment was significant.

Genotype	Larval weight gain (mg)		Consumption (cm^2)		Conversion efficiency (mg/cm^2)	
	Constitutive	Induced	Constitutive	Induced	Constitutive	Induced
Cook	17.57 ± 1.99	12.44 ± 1.99	4.35 ± 0.49	3.97 ± 0.49	4.21 ± 0.31	3.14 ± 0.31
Braxton	19.26 ± 1.92	13.11 ± 2.10	4.95 ± 0.49	4.54 ± 0.52	4.04 ± 0.31	2.63 ± 0.33
Asgrow 5533	21.85 ± 1.99	18.63 ± 1.99	4.69 ± 0.49	5.49 ± 0.49	4.73 ± 0.31	3.44 ± 0.31
Clark	23.17 ± 1.98	13.65 ± 1.99	5.13 ± 0.49	4.74 ± 0.49	4.62 ± 0.31	2.96 ± 0.31
Stonewall	23.40 ± 1.99	20.10 ± 1.99	5.47 ± 0.49	6.33 ± 0.49	4.28 ± 0.31	3.32 ± 0.31
Williams	23.43 ± 1.99	16.18 ± 1.99	5.64 ± 0.49	4.86 ± 0.49	4.14 ± 0.31	3.23 ± 0.31
Gasoy	23.56 ± 1.99	16.64 ± 1.99	5.74 ± 0.49	4.80 ± 0.49	4.10 ± 0.31	3.63 ± 0.31
Bragg	23.79 ± 1.99	16.64 ± 1.98	6.44 ± 0.49	5.82 ± 0.49	3.68 ± 0.31	2.92 ± 0.31
Centennial	25.58 ± 1.99	18.07 ± 2.10	5.76 ± 0.49	6.11 ± 0.52	4.47± 0.31	2.93 ± 0.33
Davis	26.66 ± 1.99	22.90 ± 1.99	5.77 ± 0.49	6.16 ± 0.49	4.69 ± 0.31	3.77 ± 0.31
Johnston	29.62 ± 1.98	15.41 ± 1.98	5.91 ± 0.49	4.84 ± 0.49	5.08 ± 0.31	3.54 ± 0.31
Genotype	$F_{10, 98.9} = 3.30$; $P = 0.010$		$F_{10, 98.6} = 2.61$; $P = 0.007$		$F_{10, 99.0} = 2.04$; $P = 0.040$	
JA	$F_{1, 103.0} = 72.0$; $P < 0.0001$		$F_{1, 103.0} = 0.98$; $P = 0.32$		$F_{1, 103.0} = 73.80$; $P < 0.0001$	
Genotype*JA	$F_{10, 98.2} = 1.57$; $P = 0.13$		$F_{10, 98.0} = 1.15$; $P = 0.30$		$F_{10, 98.7} = 0.80$; $P = 0.63$	

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).

Greenhouse 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

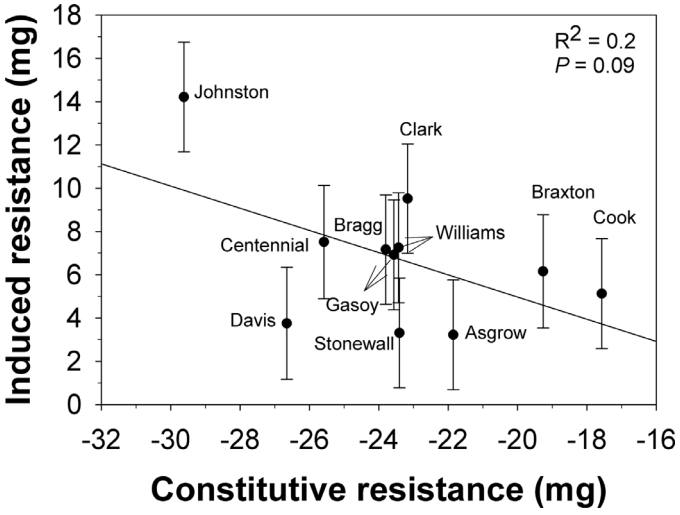

Fig 1. Relationship between mean constitutive (−1 × weight gain of larvae on non-induced plants) and induced resistance [−1 × (weight gain of larvae on induced plants - weight gain on non-induced plants)] for 11 genotypes of soybeans in the GC experiment. Each point represents data from larvae from 10 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.

Table 2. 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 GHI experiment involving 11 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). Results of post-hoc mean comparisons are only shown when the interaction between variety and JA treatment was significant. Means for a given variable accompanied by the same letter did not differ significantly (Tukey's Honestly Significant Difference, α= 0.05).

Genotype	Larval weight gain (mg)		Consumption (cm^2)		Conversion efficiency (mg/cm^2)	
	Constitutive	Induced	Constitutive	Induced	Constitutive	Induced
Bragg	15.80 ± 1.91	1.34 ± 1.91	6.13 ± 0.51 abc	1.06 ± 0.51 f	2.52 ± 0.68	1.21 ± 0.68
Stonewall	17.51 ± 1.92	3.92 ± 1.91	5.76 ± 0.51 abcd	1.74 ± 0.51 f	3.20 ± 0.68	2.89 ± 0.68
Gasoy	18.06 ± 1.91	4.30 ± 1.91	6.51± 0.51 a	2.14 ± 0.51 f	2.78 ± 0.68	1.87 ± 0.68
Braxton	20.96 ± 1.91	4.02 ± 2.01	6.27 ± 0.51 abc	1.86 ± 0.54 f	3.37 ± 0.68	1.94 ± 0.72
Clark	20.75 ± 1.91	4.33 ± 1.91	6.55 ± 0.51 a	1.97 ± 0.51 f	3.09 ± 0.68	2.20 ± 0.68
Cook	21.95 ± 1.91	1.44 ± 1.92	7.43 ± 0.51 a	1.17 ± 0.51 f	2.99 ± 0.68	1.41 ± 0.68
Johnston	22.76 ± 2.14	7.09 ± 2.28	7.22 ± 0.57 a	3.19 ± 0.61 def	3.15 ± 0.76	2.21 ± 0.81
Centennial	23.76 ± 1.91	6.16 ± 2.01	7.30 ± 0.51 a	2.56 ± 0.54 ef	3.38 ± 0.68	2.14 ± 0.72
Davis	25.54± 2.14	9.06 ± 2.14	6.40 ± 0.57 ac	3.47± 0.57 bdef	3.73 ± 0.76	2.76 ± 0.76
Williams	26.24 ± 2.29	7.95 ± 2.29	6.50 ± 0.61 ab	3.40 ± 0.61 cdef	4.15 ± 0.81	2.04 ± 0.81
Asgrow 5533	26.56 ± 1.91	6.16 ± 1.91	4.85 ± 0.51 abcde	2.26 ± 0.51 f	7.01 ± 0.68	2.21 ± 0.68
Genotype	$F_{10, 91.9} = 3.14$; $P = 0.002$		$F_{10, 91.8} = 2.13$; $P = 0.03$		$F_{10, 92.3 =} 2.02$; $P = 0.04$	
JA	$F_{1, 93.1} = 520.0$; $P < 0.0001$		$F_{1, 93.8} = 363.0$; $P < 0.0001$		$F_{1, 94.2 =} 27.21$; $P < 0.0001$	
Genotype*JA	$F_{10, 90.7} = 1.06$; $P = 0.40$		$F_{10, 91.3 =} 2.18$; $P = 0.02$		$F_{10, 91.8 =} 1.78$; $P = 0.08$	

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)

Greenhouse 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 Asgrow 5533. With the exception of Crockett, weight gains on the remaining genotypes were significantly lower than on Miyako White and Asgrow. Application of JA resulted in smaller weight gains in larvae compared to weight gains before JA applications (Table 3). An overall inhibition of 50% in growth was found with JA treatment. The effect of JA application on larval growth was consistent across soybean genotypes (no genotype by JA interaction; Table 3). The effect of initial weight (covariate) on weight gain was not significant, indicating that differences in initial weight of larvae did not impact weight gain on soybeans ($F = 2.30$, df = 1, 130, $P = 0.13$).

Foliar consumption by larvae was impacted by genotype (Table 3). Consumption was highest on Miyako White, Crockett and Asgrow, and consumption on these genotypes differed significantly from consumption on NC Roy, Lyon, and Lamar. Consumption was lowest on Lamar and consumption on this genotype differed significantly from consumption on all other genotypes except Roy and Lyon. JA application significantly reduced foliar consumption, and the decrease in consumption after JA was greater than 50% compared to consumption before JA application. Furthermore, the interaction between genotype and JA treatment for consumption was significant, as evidenced by differences in the ranking of consumption among varieties in induced and uninduced states (Table 3). Initial weight of larva as a covariate was not significant for consumption ($F = 2.53$, df = 1, 129, $P = 0.11$).

Foliar conversion efficiency was influenced both by soybean genotype and JA treatment (Table 3). Conversion efficiencies were low in Lamar, Soden-daizu, and Crockett and conversion efficiencies on these genotypes differed significantly from conversion efficiency on Asgrow, on which larvae showed the highest conversion efficiency. The remaining genotypes supported intermediate levels of conversion efficiency. No interaction between genotype and JA treatment was found for conversion efficiency (Table 3).

The relationship between constitutive and inducible resistance in GHII was marginally significant based on both larval weight ($F = 4.3$, df = 1, 6, $P = 0.08$) (slope: −0.30 ± 0.15; $R^2 = 0.32$) (Fig. 2B) and foliar consumption ($F = 5.4$, fd = 1, 6, $P = 0.06$) (slope: −0.45 ± 0.19; $R^2 = 0.39$) (Fig. 3B)

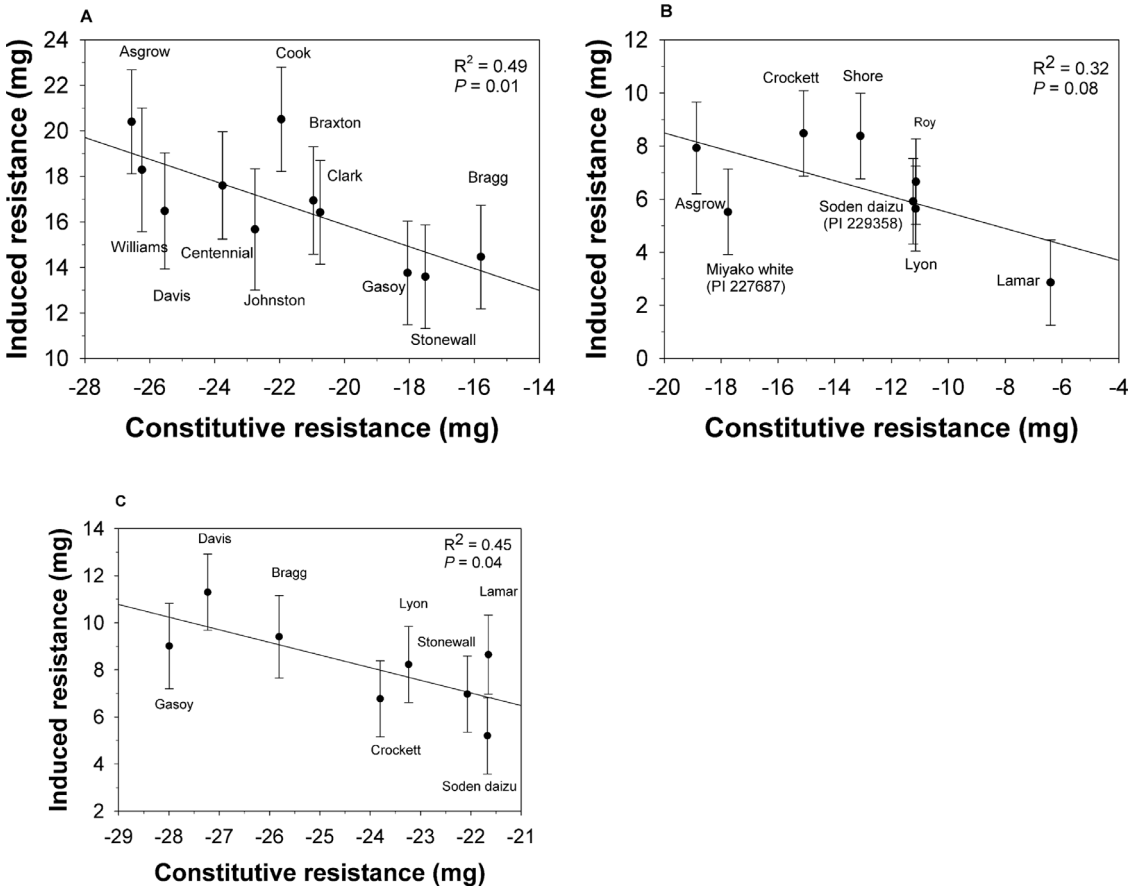

Fig 2. Relationship between mean constitutive (−1 × weight gain of larvae on non-induced plants) and induced resistance [−1 × (weight gain of larvae on induced plants - weight gain on non-induced plants)] on soybeans in GHI (A), GHII (B) and GHIII (C) experiments with 11,eight and eight genotypes in 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.

Greenhouse 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

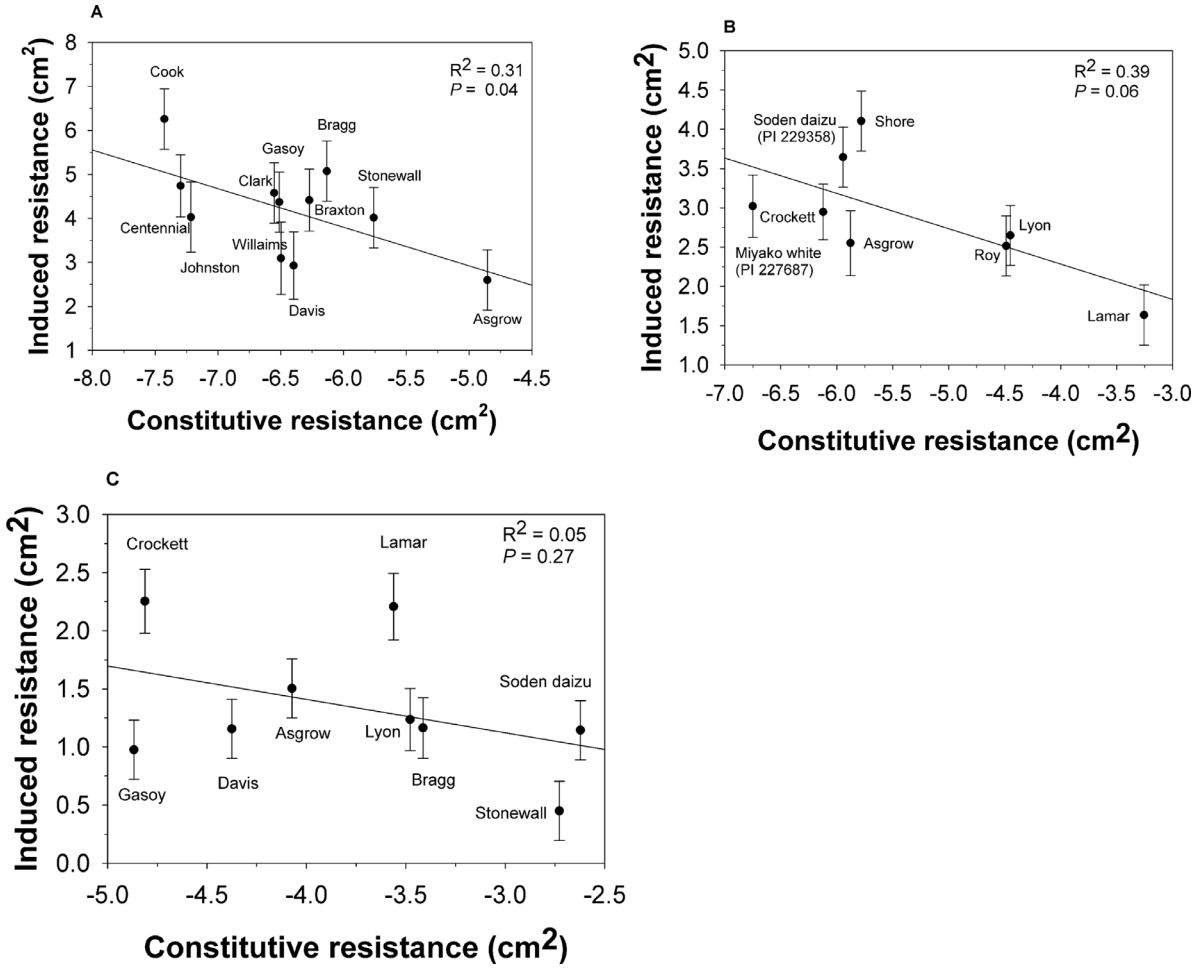

Fig 3. Relationship between mean constitutive (−1 × foliar consumption on non-induced plants) and induced resistance [−1 × (foliar consumption on induced plants − foliar consumption on non-induced plants)] on soybeans in GHI (A), GHII (B) and GHIII (C) experiments with 11,eight and eight genotypes in 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.

Table 3. 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 GHII experiment involving eight 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). Results of post-hoc mean comparisons are only shown when the interaction between variety and JA treatment was significant. Means for a given variable accompanied by the same letter did not differ significantly (Tukey's Honestly Significant Difference, α= 0.05).

Genotype	Larval weight gain (mg)		Consumption (cm^2)		Conversion efficiency (mg/cm^2)	
	Constitutive state	Induced state	Constitutive	Induced	Constitutive	Induced
Lamar	6.40 ± 1.31	3.54 ± 1.31	3.26 ± 0.32 cde	1.62 ± 0.32 f	1.87 ± 0.29	2.13 ± 0.29
Roy	11.14 ± 1.31	4.48 ± 1.31	4.49 ± 0.32 bc	1.97 ± 0.32 ef	2.49 ± 0.29	2.17 ± 0.29
Lyon	11.15 ± 1.30	5.51 ± 1.30	4.45± 0.32 bc	1.80± 0.32 ef	2.37± 0.29	3.56 ± 0.29
PI229358	11.24 ± 1.31	5.32 ± 1.31	5.94 ± 0.32 ab	2.30 ± 0.32 def	1.83 ± 0.29	2.12 ± 0.29
Shore	13.10 ± 1.31	4.72 ± 1.31	5.78 ± 0.32 ab	1.63 ± 0.32 f	2.24 ± 0.29	2.96 ± 0.29
Crockett	15.10 ± 1.31	6.62 ± 1.31	6.12 ± 0.32 a	3.17 ± 0.32 cdef	2.42 ± 0.29	2.02 ± 0.29
PI227687	17.76 ± 1.31	12.24 ± 1.38	6.75 ± 0.32 a	3.73 ± 0.32 cd	2.63 ± 0.29	3.16 ± 0.29
Asgrow 5533	18.87 ± 1.46	10.94 ± 1.30	5.88 ± 0.32 ab	3.33 ± 0.31 cde	3.18 ± 0.29	3.30 ± 0.29
Genotype	$F_{7, 71.2} = 11.24$; $P < 0.0001$		$F_{7, 70.5} = 13.64$; $P < 0.0001$		$F_{7, 71.5} = 13.64$; $P = 0.002$	
JA	$F_{1, 75.1} = 115.50$; $P < 0.0001$		$F_{1, 74.30} = 411.96$; $P < 0.0001$		$F_{1, 76.30} = 4.09$; $P = 0.04$	
Genotype*JA	$F_{7, 70.1} = 2.30$; $P = 0.23$		$F_{7, 69.3} = 4.00$; $P = 0.0010$		$F_{7, 71.2} = 1.79$; $P = 0.10$	

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 plants separated in age by only two days. Thus, the use of JA rather than natural herbivory to induce plants probably allowed a more precise determination of the influence of genotype on induced resistance by reducing variation in larval growth on induced plants arising from other sources.

Another distinctive feature of the current study was the use of genotypes with a wide range of constitutive resistance against *S. frugiperda*. Larval weight gains on putatively susceptible genotypes such as Asgrow 5533 and Davis were, as expected, generally higher than on other varieties, and were generally consistent with patterns in constitutive resistance found by Shikano et al. (2017). Also, as expected, the genotypes used in GHII and GHIII that had been bred for resistance to lepidopteran defoliators showed higher levels of resistance than other varieties. The only exception to this pattern was found with Miyako White (PI 227,687). The low constitutive resistance in Miyako White was inconsistent with several studies showing high levels of resistance to different defoliators in this genotype and may have been due to the use of the terminal trifoliate leaf for assays. A previous study investigating effects of leaf position on larvae of soybean looper on Miyako White and the susceptible genotype Davis reported high larval growth rates on apex leaves compared to growth rates on leaves from the third and lower leaves on both genotypes (Reynolds & Smith, 1985). The intermediate levels of resistance in most of the genotypes used in GHI and GC was somewhat surprising given the high degree of susceptibility previously found in these genotypes against several defoliators of economic importance to soybeans, including lepidopterans (Hartwig, Lambert & Kilen, 1990; Lambert & Kilen, 1984 a, b; Rowan et al., 1991) and *E. varivestris* (Underwood et al., 2000). Such differences could be attributable to the different herbivore species used and to the different methods employed in measuring resistance, because most of the previous studies used feeding preference to measure resistance

Wider variation in constitutive resistance among the genotypes used in the four experiments in this study could partly explain differences in the results of this study and the results of Underwood et al. (2000). These authors found no significant correlation between constitutive and inducible resistance to *E. varivestris* using many of the same genotypes used in GC, GHI, and GHIII. However, Underwood et al. (2000) used only six genotypes to investigate the relationship between inducible and constitutive resistance, and variation in constitutive resistance among these genotypes was not large, potentially hindering the ability to detect a negative relationship.

The presence of antibiosis resistance in a plant is difficult to determine from data on foliar consumption alone because reductions in foliar consumption can result from both antixenosis (non-preference) as well as antibiosis. For this reason, a 'conversion efficiency' index (weight gain per unit area of foliage consumed), modified from Waldbauer (1968), was used in this study to help differentiate antixenotic effects from antibiotic effects. A comparison of foliar conversion efficiencies among genotypes before and after induction by JA revealed a lack of interaction between JA treatment and genotype in three of four experiments; that is, JA-induced reductions in conversion efficiencies (antibiosis) tended to be similar among genotypes. Shikano et al. (2017) also showed no genotypic differences in JA-induced effects on larval growth and leaf utilization in *S. frugiperda* larvae fed on eight different soybean genotypes. These results are consistent with the idea that the biochemical and morphological traits induced by JA application were similar among varieties, and that similar factors (secondary metabolites, morphological traits, or resistance-related proteins) may have contributed to resistance in the induced and non-induced states in the various genotypes. However, quantification of multiple resistance-related traits in multiple genotypes before and after induction will be needed to further support the hypothesis that the biochemical and morphological traits responsible for resistance are similar in induced and non-induced plants.

Negative correlations between constitutive and inducible resistance have been more commonly found in wild plant species than in cultivated plant species (Kempel et al., 2011). The current study provides evidence that negative correlations between the two modes of resistance exist in some crop-pest interactions. Methodological issues may have prevented detection of these tradeoffs in previous studies. Furthermore, differences in the results of the GC and GHI experiments, which utilized the same genotypes, indicate that both constitutive and inducible resistance in soybean are influenced by the conditions under which plants are grown and other environmental factors. Understanding potential tradeoffs between constitutive and inducible resistance in crop plants and the environmental conditions that affect both is critical to understanding the contribution of induced resistance to overall crop resistance and to manipulating phenotypic plasticity for management of crop pests. Further studies of potential tradeoffs using other crop species are needed.

Declaration of Competing Interest

None.

Acknowledgments

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2021.06.009.

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