

Induced defences in plants reduce herbivory by increasing cannibalism

John Orrock*, Brian Connolly and Anthony Kitchen

Plants are attacked by myriad herbivores, and many plants exhibit anti-herbivore defences. We tested the hypothesis that induced defences benefit tomato plants by encouraging insects to eat other members of their species. We found that defences that promote cannibalism benefit tomatoes in two ways: cannibalism directly reduces herbivore abundance, and cannibals eat significantly less plant material. This previously unknown means of defence may alter plant-herbivore dynamics, plant evolution and pathogen transmission.

Plants are not passive bystanders in their interactions with herbivores: plants alter their chemistry, morphology and other components of their phenotype to reduce herbivory¹, often using cues from their environment to initiate these defences before any actual attack occurs^{2–4}. Because induced defences in plants are so ubiquitous¹ and may have important effects on herbivores^{1,5} and other trophic levels⁶, fundamental goals in plant–herbivore ecology are to understand the benefits of induced defences to plants in terms of reduced herbivory⁷, to describe how induced defences operate (for example whether they reduce herbivore feeding, survival or reproduction), and to characterize how plants' induced defences may affect other organisms^{6,8}. We advance these goals by demonstrating a means by which induced defences in plants reduce herbivory: altering cannibalism among herbivores.

We found that induced defences reduce damage to tomato (*Solanum lycopersicum*) plants by both directly reducing herbivore feeding and increasing rates of cannibalism among individual herbivores. We induced defences in undamaged tomato plants^{9,10} according to one of four treatments (Fig. 1a). Plants that were strongly induced before exposure to generalist insect herbivores (*Spodoptera exigua*) caused herbivores to begin consuming each other earlier (Fig. 1a), leading to increased average rates of cannibalism (Fig. 1a inset) and reduced herbivory on strongly induced plants (Fig. 1b). Over five times as much plant biomass remained at the end of the experiment when plants received the high-induction treatment than remained in the control treatment (Fig. 1b); the amount of plant biomass was also greater in the medium-induction treatment than the control treatment (Fig. 1b). Control plants were often completely defoliated (Supplementary Fig. 1).

This dynamic unfolded because, like many omnivorous herbivores^{11,12}, cannibalism in *S. exigua* occurs more readily when herbivores are nutritionally stressed¹³. Our work confirms that the low quality of induced plant tissue was responsible for this change in herbivore behaviour: cannibalism happened sooner (Fig. 1a) and more conspecifics were consumed (Fig. 1a, inset; Fig. 1c) when herbivores were offered tissue from induced plants. Our findings also show that *S. exigua* use cannibalism to compensate for the low quality of defended plant tissue: growth rates were significantly lower for *S. exigua* feeding on induced plants compared with

control plants, but the growth rate of cannibals was not as compromised (Supplementary Fig. 2). Consistent with the hypothesis that induced defences in plants can moderate the initiation of cannibalism in herbivores, *S. exigua* that were fed control leaves exhibited lower rates of cannibalism (Fig. 1c) and *S. exigua* on whole plants with little or no induced defence only began to consume each other later (Fig. 1a), when the quantity of remaining aboveground plant material was minimal and as the plant had sufficient time to mount chemical defences¹⁴.

Given that promoting cannibalism has considerable benefits for induced plants (Fig. 1b,d), and that facultative cannibalism is relatively common among herbivores^{11,12,15,16}, even in field and laboratory settings where herbivores can disperse^{11,12}, our work suggests that promoting cannibalism may be an important, but unappreciated, component of the evolution of induced defences in plants. Induced defences that promote cannibalism provide several benefits for the plant. First, induced defences directly reduce the consumption of plant tissue by individual herbivores¹ (Fig. 1d). Second, we have found that induced defences reduce herbivory by triggering earlier cannibalistic behaviour (Fig. 1a,c) that reduces the number of herbivores (Fig. 1a). Third, our results demonstrate that induced defences reduce herbivory because cannibals consume less plant material (Fig. 1d). Encouraging cannibalism as a defensive strategy has similarities with plant defences that attract natural enemies of herbivores⁶, but also differs in an important way. Like predation and parasitism, cannibalism reduces herbivory by increasing herbivore mortality. However, unlike predation and parasitism, cannibalism also benefits plants because herbivores that exhibit cannibalism also stop consuming as much plant biomass (Fig. 1d).

Plants may initiate changes in defence in response to airborne chemical cues, such as methyl jasmonate (MeJA) and jasmonic acid^{2–4}. Such a strategy is expected to evolve when cues of risk are indicative of increasing likelihood of herbivory^{3,4,17} and when such pre-emptive induced defences yield benefits that outweigh their costs⁴. Because application of high levels of MeJA can cause changes in plant defence^{9,10}, our results also clearly demonstrate the value that plants can receive by inducing defences before an actual attack. Although plants in control- and low-MeJA treatments would have induced defence once attack was under way¹⁴, this defence comes too late: many of these plants were entirely consumed (Fig. 1b; Supplementary Fig. 1). For plants that had higher levels of induced defence at the start of herbivore exposure, increased levels of early cannibalism (Fig. 1a,c) reduced the potential for extreme levels of biomass loss (Fig. 1b,d).

An important question is the degree to which the plant-mediated cannibalism revealed in our laboratory-based study provides insight into dynamics in natural systems. Given that induced defences are

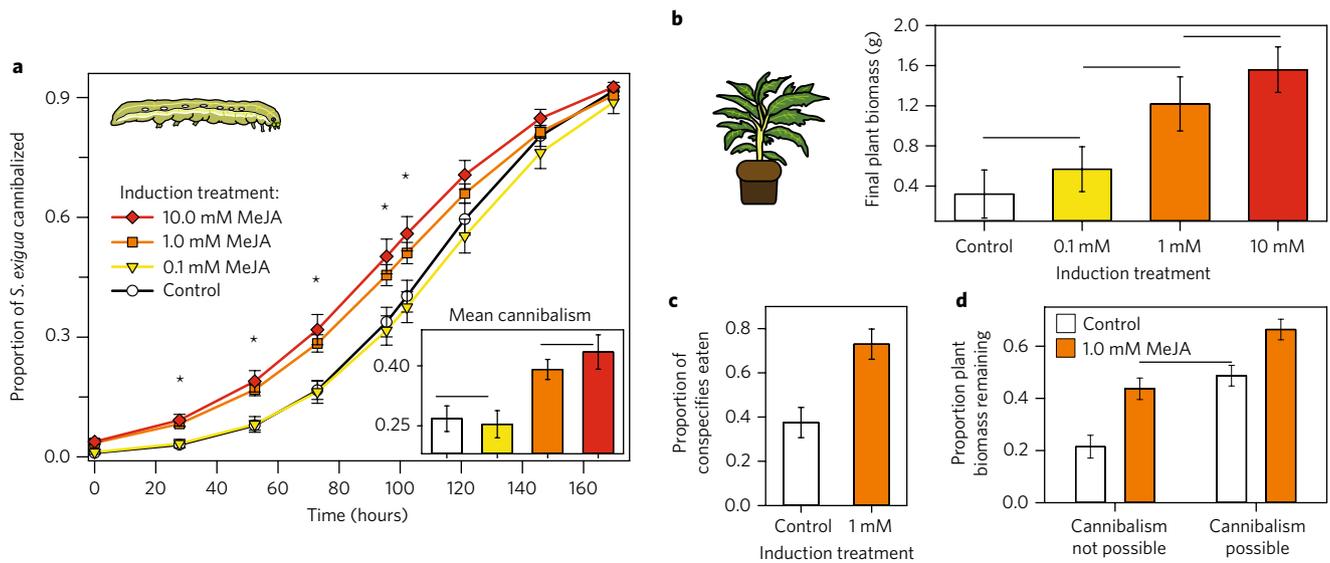


Figure 1 | Induced defences in plants lead to increased rates of cannibalism among herbivores, which result in significant decreases in losses of plant biomass. **a**, Induced defences in plants cause earlier herbivore cannibalism. The plots show estimates (\pm s.e.m.) of *S. exigua* mortality due to cannibalism as a function of induced defence in the plants. Plant induction treatment levels spanned a range of concentrations (plants were sprayed with 0.1 mM, 1.0 mM and 10.0 mM MeJA) and also included a control solution. There was a significant effect of the induction treatment (binomial generalized linear mixed model (generalized LMM), $F_{3,36} = 4.95$, $P = 0.006$) on the proportion of *S. exigua* consumed by other *S. exigua*, a significant effect of the time that had elapsed during the experiment (generalized LMM, $F_{1,316} = 552.97$, $P < 0.001$), and no interaction between treatment and time elapsed (generalized LMM, $F_{3,316} = 1.66$, $P = 0.18$). Asterisks: significant differences (linear contrasts within omnibus binomial generalized LMM, $P < 0.05$) when high- and medium-induction treatments are compared with low-induction and control treatments. Inset: mean (\pm s.e.m.) cannibalism across the entire trial; bars that do not share a horizontal line are significantly different (linear contrasts, $P < 0.02$). **b**, Plants with defences induced before attack lose less biomass. Defences that promoted early cannibalism led to significant increases in the amount of plant tissue remaining at the end of the experiment (general linear model (GLM), $F_{3,34} = 7.04$, $P < 0.001$); bars that do not share a horizontal line are significantly different (linear contrasts within omnibus GLM, $P < 0.02$). **c**, Plant defences cause herbivores to eat more herbivores. In a second experiment in which we manipulated the presence or absence of dead conspecifics, individual *S. exigua* demonstrated greater levels of cannibalism when housed with leaves of induced plants (1.0 mM MeJA) versus control plants (Welch's *t*-test, $t_{19,28} = 3.67$, $P = 0.002$). **d**, Induced defences and increased cannibalism both reduce herbivory. The experiment described in **c** also demonstrated that induced defences (GLM, $F_{1,37} = 23.41$, $P < 0.001$) and cannibalism (GLM, $F_{1,37} = 36.94$, $P < 0.001$) both led to reduced herbivory by individual *S. exigua*, and these effects were additive (GLM, induction \times cannibalism interaction term: $F_{1,37} = 0.31$, $P = 0.58$); bars that do not share a horizontal line are significantly different (linear contrasts within omnibus GLM, $P < 0.004$). Data used to create panels **b**, **c** and **d** are also illustrated with boxplots in Supplementary Figs 3, 4 and 5, respectively.

common in many plant species¹, and that cannibalism occurs in many primarily herbivorous species^{11,12,15,16}, even in field and laboratory settings where herbivores can disperse^{11,12}, changes in cannibalism caused by plant defences could be an unevaluated mechanism contributing to the dynamics of plant and herbivore populations, as well as the dynamics of predators and pathogens^{5,6,18,19}. For example, plant defences that promote cannibalism might alter pathogen dynamics within herbivore populations by changing the frequency and/or density of herbivores¹⁶; this might arise if cannibals consume conspecifics, if cannibals have different dispersal capacity, if cannibals alter the dispersal of conspecifics, or some combination of all of these. Such behaviourally mediated shifts in herbivore density might be a particularly important way that increased cannibalism alters dynamics in field settings where movement is less constrained. Increased cannibalism might also alter the nature of pathogen transmission if infected individuals are more or less likely to be cannibalized^{18,20}. As such, induced defences in plants may also accelerate the spread of viruses by increasing cannibalistic behaviour. Such a dynamic would be beneficial for the plant as well as serving to increase the efficacy of strategies to control herbivorous pests in agricultural settings via induction of plant defence with jasmonic acid¹⁹, via the introduction of herbivore viruses²⁰, or both.

Methods

Experiment 1: Examining how induced defences alter cannibalism and herbivory when herbivores access entire plants. The effects of plant induction on rates of

intraspecific predation were evaluated with tomato (*S. lycopersicum* L., var. 'MoneyMaker') plants. Plants were grown for 21 days under a 12 hour light, 12 hour dark photoperiod ($\sim 220 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) at 23°C, at which point every plant had three or four true leaves. Plants received one of four treatments applied on two consecutive days: control (0.125% Triton-X), low (0.1-mM MeJA + 0.125% Triton-X), medium (1.0-mM MeJA + 0.125% Triton-X), and high (10-mM MeJA + 0.125% Triton-X); see Supplementary Information. We used 10 plants for each treatment level, for a total of 40 plants. Concentrations of tomato plant proteins associated with herbivore deterrence significantly increase following exposure to MeJA^{9,10} or jasmonic acid (a derivative of MeJA); see Supplementary Information.

One hour after the second MeJA treatment, eight randomly selected third-instar *Spodopetera exigua* larvae (25.97 ± 2.13 mg, mean starting mass \pm standard error (s.e.m.) of one randomly selected larva per group of eight) were sealed into each plastic container, yielding eight larvae for each of 40 replicate plants. The number of *S. exigua* was monitored at least once daily for eight consecutive days (see Supplementary Information). At the end of the experiment, plants were clipped at ground level and immediately weighed to determine above-ground biomass.

Experiment 2: Using leaf-feeding trials to examine the unique contribution of induced defences and cannibalism to plant defence. In this experiment, the same variety of tomato used in experiment 1 was grown for 21 days in a growth chamber at 25°C with a 12:12 photoperiod. Plants were grown in standard potting mix in square (6 \times 6 cm) plastic pots that were 9 cm tall. Plants were sprayed with either a control solution of 0.125% Triton-X or a medium-induction solution of 1.0-mM MeJA + 0.125% Triton-X (identical to the respective solutions used in experiment 1). Two identical sprays were given to each plant, one on day 22 (19 February 2017) and another on day 24 (21 February 2017); see Supplementary Information. On 22 February, a leaflet from each plant was clipped and placed in a 2 fl oz plastic cup. A single third-instar larva of *S. exigua* was weighed and placed in each cup. A cannibalism treatment with two levels (conspecifics added to cup, or no conspecifics added to cup) was randomly assigned to each cup (stratified by

induction treatment). For cups assigned to receive conspecifics, we added a total of four third-instar and fourth-instar larvae of *S. exigua* that had been killed by briefly flash-freezing them in a freezer at -80°C . This resulted in 9 replicates of the 'control + no conspecific' treatment, 10 replicates of the 'induced + no conspecific' treatment, 11 replicates of the 'control + conspecific' treatment, and 11 replicates of the 'induced + conspecific' treatment.

Two dead larvae were added at the start of the trial on 22 February; another two dead larvae were added 24 hours later on 23 February. The trial was concluded after 48 hours, when the amount of dead larvae consumed was visually estimated and the living larvae and remaining plant material were weighed.

Data availability. The data from this study supporting our findings are freely available from the Environmental Data Initiative: <http://doi.org/10.6073/pasta/bfbd6eca5e1534cd236526a4656e75b0>.

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Author contributions

J.O. conceived the study; J.O. and B.C. designed the study; A.K., B.C. and J.O. conducted the experiments; J.O. performed all analyses and led manuscript preparation; B.C. and A.K. contributed to manuscript revision.

Competing interests

The authors declare no competing financial interests.

Additional information

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Supplementary Materials

Plant induced defenses reduce herbivory by increasing cannibalism

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Supplementary Methods

Additional information for Experiment 1:

Tomatoes were grown in individual clear plastic containers (9 x 12 cm circular cups with dome lids) filled with ~382 cm³ of RediEarth Sunshine Professional Growing Mix; four holes were punctured in the bottom of each cup and containers were placed in individual plastic trays to 1) eliminate interplant signaling via a shared water source and 2) provide a refillable water supply that limited physical disturbance to plant tissue during watering.

We used spray application of methyl jasmonate (MeJA) to induce changes in plant chemistry, as MeJA application is known to cause changes in plant defensive chemistry in the absence of any actual herbivory¹⁻⁵. To apply MeJA treatments, each plant and its corresponding plastic dish were covered with a hollow, rigid green plastic cylinder (37 cm tall; diameter 14 cm). The open end of the cylinder was covered by a thin film of plastic to ensure MeJA spray did not volatilize and cross contaminate neighboring plants. For each treatment application, the plastic film was removed from the top of the cylinder, the nozzle of a spray bottle was inserted into the opening (~22 cm from the plant) and two sprays (~6.00 mL) were applied to each plant. Immediately after spray treatments, plastic covering was replaced over the top of the cylinder. Plants were left covered for a minimum of 1 hour before being moved. We measured plant height and the number of true leaves on each plant prior to the initiation of the herbivory trial.

One hour after the second MeJA treatment, eight randomly selected third-instar *Spodopetera exigua* larvae were sealed into each plastic container, yielding 8 larvae for each of 40 replicate plants. We selected 8 larvae per plant based on previous studies that manipulate *S. exigua* density to examine plant induced defense⁶ as well as on field studies that suggest the potential for high densities of *S. exigua* in some settings^{7,8}, including densities used in our study (see Figure 1 in Kolodny-Hirsch et al. 1993⁸).

To assess cannibalism, the number of *S. exigua* was counted daily. When counting *S. exigua* during these monitoring events, the top of the soil was also searched to ensure that no individuals were in the soil. During both sessions, we assumed that any *S. exigua* that disappeared were consumed. This assumption was supported by direct observations of cannibalism and no indication that any *S. exigua* ever escaped from their holding container. At the end of the experiment, the entire soil column in each pot was also checked for any living larvae; none were found. At the end of the experiment, we also noted whether plants were completely defoliated (visually assessed as having less than 10% of leaf biomass remaining).

The experiment was conducted in two sessions (8-15 April 2016 and 15-22 May 2016) with 6 replicates of each treatment (24 plants; 192 *S. exigua*) during the first session, and 4 replicates of each treatment (16 plants; 128 *S. exigua*) during the second session.

Additional information for Experiment 2:

Application of treatments to plants: On day 21, each potted plant was placed within a larger 16-ounce plastic cup. A smaller translucent 9 ounce plastic cup was affixed to the top of the bottom cup with two pieces of masking tape, effectively enclosing each plant and preventing the potential for cross-contamination. Spray application of treatments were performed in a fume hood to avoid potential contamination between treatments during application. Between sprays, plants were returned to the growth chamber.

One hour after the second MeJA treatment, eight randomly selected third-instar *Spodopetera exigua* larvae were sealed into each plastic container, yielding 8 larvae for each of 40 replicate plants. We selected 8 larvae per plant based on previous studies that manipulate *S. exigua* density to examine plant induced defense⁶ as well as on field studies that suggest the potential for high densities of *S. exigua* in some settings⁷.

To estimate rates of mass loss in tomato leaves due to water loss over the two-day feeding trial, we weighed a single, fresh tomato leaf and placed it in a plastic cup with a lid (identical to those used in feeding trials). This was replicated for leaves from ten individual tomato plants. The cups were placed on the same area where herbivory trials were conducted and weighed after two days. After two days, the mean proportion of leaf mass lost due to water loss was 0.265 ± 0.016 . As expected, this value was smaller than the proportion of leaf mass lost for leaves in the feeding trial (Fig. 1d). However, it was similar to the mean leaf mass observed when herbivores were fed leaves with induced defenses and herbivores had conspecifics available to consume (on average, the proportion of biomass lost by leaves in this treatment combination was 0.336 ± 0.039), suggesting that herbivores in this situation consumed very little plant material.

Statistical analyses:

The rate and severity of intraspecific predation in *S. exigua* was assessed with a generalized linear mixed effects model (generalized LMM) with a binomial response distribution⁹. The experimental induction treatment was evaluated as a fixed effect with four levels: control, low induction, medium induction, and high induction. The time interval at which censuses were conducted was treated as a continuous covariate and we also evaluated the interaction between treatment and census period. Session (first or second) and shelf where the trial was conducted (top or bottom) was included as random model effect. Repeated measures were modelled using a first-order autoregressive covariance structure; other covariance structures were evaluated (e.g., compound symmetry), but none yielded an improved fit based on AIC values. To evaluate plant height and leaf number prior to the start of herbivory trials, general linear mixed models were used that also included session and shelf as random effects. All analyses conducted for experiment 2 utilized general linear models.

Supporting Results

Experiment 1

Prior to the initiation of experimental treatments, there were no significant differences among treatments for plant height (general linear mixed model (GLMM), $F_{3,34} = 0.41$, $P = 0.75$), plant width (GLMM, $F_{3,34} = 2.03$, $P = 0.13$), or the number of leaves (GLMM, $F_{3,34} = 1.27$, $P = 0.30$).

Experiment 2

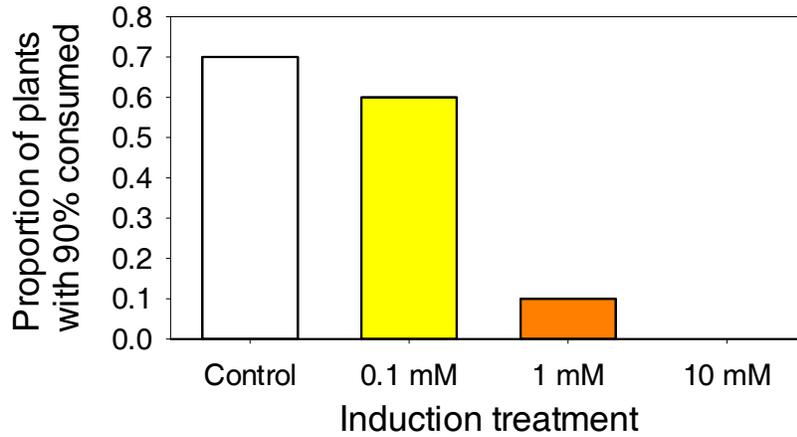
Plant induction and no-choice feeding assays: These trials indicate that there was a strong interaction between plant induced defense and opportunities for cannibalism in affecting *S. exigua* growth rate (Supplementary Fig. S2; general linear model (GLM), $F_{1,37} = 46.00$, $P < 0.001$), as well as significant main effects of induced defenses (GLM, $F_{1,37} = 96.27$, $P < 0.001$) and cannibalism (GLM, $F_{1,37} = 125.72$, $P < 0.001$). This interaction arose because there was a significant reduction in *S. exigua* growth rate when individuals were reared for 48 hours on induced leaves, but only when those individuals did not have the opportunity to cannibalize dead conspecifics (Supplementary Fig. S2). Although the amount of leaf material consumed varied greatly, leaf material was only totally consumed in 1 of the 41 trials (i.e., 2%).

After weighing, plant samples were placed in a drying oven at 50°C for 48 hours to ascertain the relationship between wet and dry leaf biomass; this relationship was highly significant (GLM, $r^2 = 0.96$, $F_{1,40} = 1088$, $P < 0.001$).

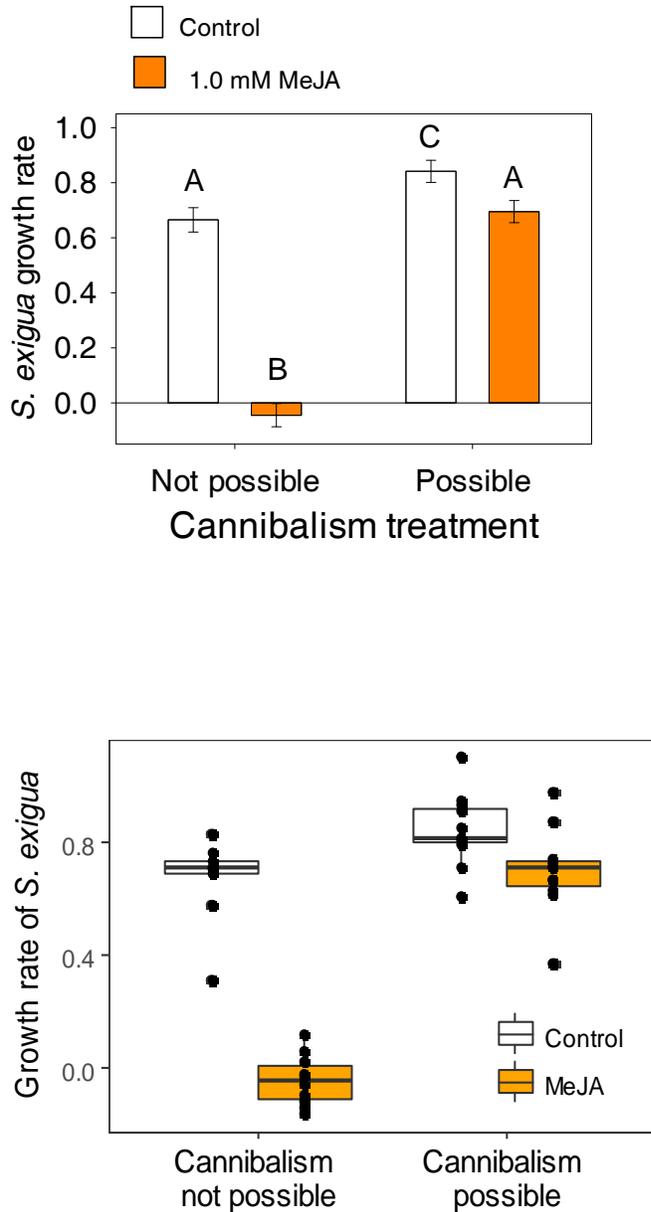
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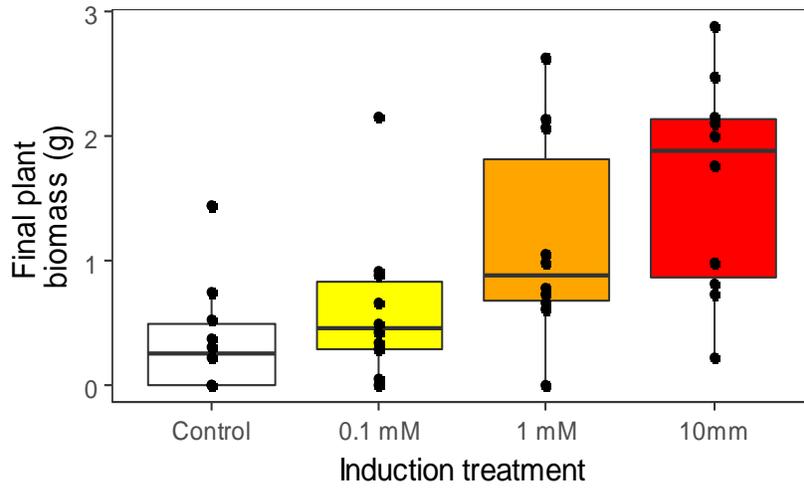
Supplementary Figure S1. Plant induced defenses affected the likelihood that plants would have at least 10% of their biomass remaining after the conclusion of the herbivory trial. Data presented are pooled across sessions of the experiment and across shelves where trials were conducted. Differences in the frequency of plants experiencing 90% loss of biomass are significantly different among treatments ($X^2 = 16.26$, 3 d.f., $P = 0.001$).



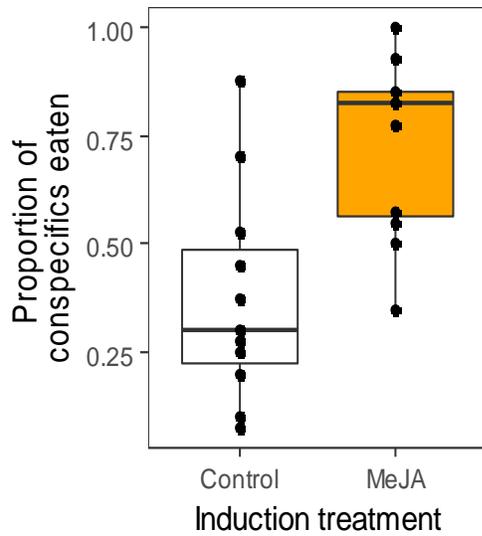
Supplementary Figure S2. Growth rate of *S. exigua* in the presence or absence of four dead conspecifics when offered a single leaf in a no-choice feeding trial for 48 hours; each leaf was obtained from a different tomato plant that was sprayed twice with one of two defense-induction treatments (Control or 1.0 mM MeJA). Top panel presents data as least-squared means with error bars that represent 1 SE. Bars that have a different letter are significantly different (linear contrasts following omnibus GLM, all $P < 0.02$). Lower panel presents same data as a box-and-whisker plot with individual data points plotted.



Supplementary Figure S3. A box-and-whisker plot of the data from Figure 1b. Plant induced defenses that promoted early cannibalism led to significant increases in the amount of plant tissue remaining at the end of the experiment (general linear model (GLM), $F_{3,34} = 7.04$, $P < 0.001$).



Supplementary Figure S4. A box-and-whisker plot of the data from Figure 1c. Individual *S. exigua* demonstrated greater levels of cannibalism when housed with leaves of induced plants (1.0 mM MeJA) vs. control plants (Welch's t-test, $t_{19,28} = 3.67$, $P = 0.002$).



Supplementary Figure S5. A box-and-whisker plot of the data from Figure 1d. Both induced defenses (GLM, $F_{1,37} = 23.41$, $P < 0.001$) and cannibalism (GLM, $F_{1,37} = 36.94$, $P < 0.001$) led to reduced herbivory by individual *S. exigua*, and these effects were additive (GLM, induction \times cannibalism interaction term: $F_{1,37} = 0.31$, $P = 0.58$).

