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SCHREYER HONORS COLLEGE

DEPARTMENT OF BIOLOGY

HERBIVORE IMPACT ON TRANS-SEASONAL INDUCTION OF TRICHOME DEFENSES
IN *SOLANUM CAROLINENSE*

REBECCA KOLSTROM
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A thesis
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Reviewed and approved* by the following:

Andrew Stephenson, Ph.D
Distinguished Professor of Biology
Associate Dean for Research and Graduate Education
Thesis Supervisor

Jim Marden, Ph.D
Professor of Biology
Honors Advisor

* Signatures are on file in the Schreyer Honors College.

ABSTRACT

Previous studies of the common horsenettle have shown that inbreeding adversely affects resistance to herbivores and compromises the ability of horsenettle to upregulate both chemical and physical defenses in response to herbivory. In this project, inbred and outbred plants from several maternal families were either exposed to herbivory by *M. sexta* caterpillars (+H) or not exposed to herbivory (-H). Rhizome cuttings from these plants were used to regenerate the plants, which were used to test whether herbivory induces physical defenses that persist trans-seasonally. Photographs were taken of close-view leaf cross sections of the regenerated +H and -H plants. Trichomes were counted in each of these photographs. Our results show significant differences between damaged and undamaged progeny with +H progeny exhibiting significantly more trichomes. We also found significant effects of inbreeding on trichome production. These data suggest that damage during one growing season induces defenses that persist into the next growing season. We are currently exploring the effects of parental herbivory on other induced defenses in both inbred and outbred plants.

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Chapter 1

INTRODUCTION

Flowering plants are subject to exploitation from a variety of predators, particularly insect herbivores, which can cause significant damage to the plant material. Herbivores may use a variety of methods to find desired plants and often, non-contact cues, such as volatile organic compounds (VOC's), are used by insect larvae to locate plant hosts and accurately assess host quality (Bruce et al., 2005; Kariyat et al., 2014).

Additionally, flowering plants can experience inbreeding, which is a widespread, population-level condition that can lead to a reduction in fitness via a greater expression of deleterious, recessive alleles and the absence of heterozygote advantage (Barrett & Eckert, 1990; Kariyat et al., 2011; Kariyat et al., 2014). Inbreeding is extremely common among flowering plants, and estimates indicate that over 50% of plant species self-pollinate more than 20% of the time (Barrett & Eckert, 1990). Studies have shown that herbivores perform better on inbred plants, which is most likely related to the induction of defense-related genes (Delphia et al., 2009; Kariyat et al., 2012). The negative effects of inbreeding have also been shown to be more severe under stress conditions. Studies performed using herbivorous spittlebug nymphs have shown that the severity of inbreeding depression was increased by a factor of three under introduced herbivore pressure (Carr & Eubanks, 2002; Hayes et al., 2004).

Solanum carolinense, commonly known as horsenettle, is an herbaceous perennial weed found throughout North America (Kariyat et al., 2012). Horsenettle is a member of the nightshade family, and is a close relative to solanaceous plants such as potatoes, tomatoes, and eggplant (“Horsenettle – Weed Management”, 2015). Therefore, research performed on horsenettle can easily be related to its close, and agriculturally important relatives. Horsenettle reproduces sexually through pollination by bees, and asexually by spreading horizontal rhizomes, or root-like structures, underground (up to 1 meter from the original parent individual) (Hardin et al., 1972; Ilnicki et al., 1962). The flowers have both male and female parts, and therefore, horsenettle has the potential to either self-pollinate or be fertilized by pollinators (“Horsenettle – Weed Management”, 2015). Branching in the aboveground portion of horsenettle plants may be either simple, or complex with multiple branches. Plants can grow up to 4 feet tall. Horsenettle flowers from May to September, and produces small, yellow, bitter fruits, which set about 30 days after flowering (“Horsenettle – Weed Management”, 2015). A study performed by Mena-Ali et al. (2008) has shown that horsenettle does experience inbreeding in both the field and in the greenhouse.

Horsenettle possesses a number of defense-related traits, including physical defenses such as spines and trichomes (Kariyat et al., 2012). Spines are located in the highest densities on the internodes (Kariyat et al., 2013). Although larger than trichomes, spines are thought to be less effective in deterring insect herbivores (Nykänen & Koricheva, 2004). Trichomes are hair-like structures located on leaves, flowers, and other tissues (Agren & Schemske, 1993). Horsenettle possesses only non-glandular, stellate, trichomes, which do not produce toxins to deter herbivores, but do provide mechanical barriers to these insect pests (Medeiros & Moreira,

2002). Research in other plant systems has shown that plants with a greater number of trichomes have a greater ability to impede herbivore movement, and experience less damage than plants with fewer trichomes (Cooper & Ginnett, 1998; Medeiros & Moreira, 2002). (See Figure 1)

Studies previously performed on *Solanum carolinense* have revealed that tobacco hornworm (*Manduca sexta*), a specialist herbivore, has a significant preference for inbred horsenettle as compared to outcrossed horsenettle (Kariyat et al., 2014). There has also been a proven preference for undamaged horsenettle compared to damaged horsenettle, even in the absence of visual indicators of defenses (Kariyat et al., 2014). Additional experiments have shown that physical defenses in horsenettle, namely spines and trichomes, are affected by inbreeding (Kariyat et al., 2013). Inbred plants possess fewer structural defenses than outbred plants (Kariyat et al., 2013). Inbreeding can also lead to a general decrease in plant vigor, which can affect herbivore resistance and volatile production. Fewer resources are available to be allotted for defense pathways, leaving plants more vulnerable to herbivores. There is also strong evidence supporting the suggestion that plant growth is slowed during the most vulnerable life stages, due to the effects of inbreeding (Kariyat et al., 2012). (See Figure 2)

Additionally research indicates that physical defenses may be induced or upregulated when a plant experiences herbivory by a chewing insect. The induction, or up-regulation, of these defenses is the product of jasmonic acid, a secondary metabolite known to be important in the activation of defense responses to insect herbivores (Howe & Jander, 2008). Herbivore damage by tobacco hornworm larvae can induce the production of additional trichomes on new growth, as well as increase the number of internode spines within an individual plant. The

induction of structural defenses has significant energetic costs that require more resources, and therefore inbred plants have a lower ability to produce additional defense structures (Kariyat et al., 2013).

Our research aims to examine whether herbivory in the parent generation of horsenettle affects trans-seasonal induction of physical defenses in next-season plants produced via the rhizome. Essentially, the project will determine if herbivory in one season of horsenettle affects the defense phenotype in the next season via a memory stored in the rhizome. The results of this experiment will contribute to a larger study, which will examine a broader view of the impact of herbivory on trans-seasonal induction of defenses in plants. It is predicted that herbivore damage on a parental population will induce physical defenses that can be transmitted through rhizome, and will persist into the next season.

Chapter 2

METHODS

Parental Plant Population:

Solanum carolinense plants were grown from the rhizomes of three maternal families: A5, A7, and B9. Original horsenettle cuttings were acquired from a large wild population in State College, Pennsylvania. An experimental, parental population of horsenettle was grown from the rhizomes of these original three families. Plants were grown in 6-inch pots under constant conditions. The parental generation was comprised of three inbred and three outcrossed pairings from each family. Half of these plants were assigned to the damage treatment, and the other half was assigned to the undamaged treatment. Thus, in this setup, each genotype in the damage treatment had an exact clone in the undamaged treatment. Plants were grown in all-purpose potting soil (Pro-Mix, Premier Horticulture Inc., Quakertown, PA). ½ tsp of Osmocote fertilizer and ¼ tsp micronutrient fertilizer was applied to each plant upon planting. All plants were grown in a growth chamber at 23°C, with a 16:8 hour light/dark cycle. Two heavy screens separated damage treatment and undamaged treatment plants, so that chemical cues could not be transmitted between the two experimental groups.

Larval Rearing:

Manduca sexta, commonly known as the tobacco hornworm, is a specialist herbivore of solanaceous plants that was used in this study. It grows through five instars to maturity. The caterpillar then begins to excrete bodily fluids and reduce its movement as it enters into the

pupation stage of its life cycle. After a period of approximately 21 days, the pupae eclose into adult moths (Reinecke et al., 1980).

Manduca Sexta larvae were reared in the lab, and fed a wheat-based, artificial diet (Frontier Scientific Services Inc., Newark DE) Eggs were allowed to hatch in breathable plastic cups containing a layer of artificial diet. As larvae molted into larger instars, they were moved to plastic boxes (approx. 35cm long x 10cm high x 15cm wide) containing chunks of artificial diet. Late-third to early-fourth instar caterpillars were used for this experiment.

Damage Treatment:

Plants in the damage treatment were exposed to *M. sexta* caterpillar herbivory. Healthy *M. sexta* were chosen and starved for 4 hours prior to the beginning of each damage session. At the beginning of each damage session, one caterpillar was placed on a lower leaf of each plant assigned to the damage treatment. Caterpillars were allowed to feed on the horsenettle plants and roam freely throughout the entire plant for 4 hours. Since plants were not enclosed, caterpillars were checked each hour to ensure that they were still located on their original plant. A total of 18 damage sessions were completed over the damage period of 2.5 months.

Second Season Plant Population:

After the 2.5 month damage period was complete, the parental generation of plants was harvested and rhizomes were collected from each plant. Six 1-inch rhizome cuttings were taken from each damaged and undamaged replicate genotype, and immediately replanted, creating the

second season of plants. Once again, these plants were grown in a growth chamber at 23°C with a 16L:8D hour light cycle. They were grown in ProMix soil and given ½ tsp of Osmocote fertilizer and ¼ tsp of micronutrient fertilizer. Plants grew for 6-8 weeks, and were once again separated by two heavy screens.

Trichome Images and Scoring:

Once all plants had fully matured, pictures of the leaf surfaces were taken using a DinoLite® microscopic camera. Pictures were taken between the second and third lateral veins of the second or third topmost, fully developed leaf. These pictures were scored using the program Preview for Macintosh. A blind observer counted all visible trichomes, and these counts were used to quantify trichome density. A trichome was counted if more than 50% of the trichome was visible in the image. For instance, the full center of the trichome would have to be visible to the observer in order for the trichome to be included in the density count. (See Figure 7)

Statistical Analysis:

Data were analyzed using Minitab 17.1. Data were log transformed to fit the normality assumption. The data were then run using a General Linear Model ANOVA. The model included three main factors: Family (random), Breeding (fixed – either inbred or outbred), and Damage (fixed – either damaged or undamaged) and one interaction term: Breeding x Damage. A Tukey Mean Comparison was performed to determine differences between the treatment means for Breeding, Damage, and Breeding x Damage.

Chapter 3

RESULTS

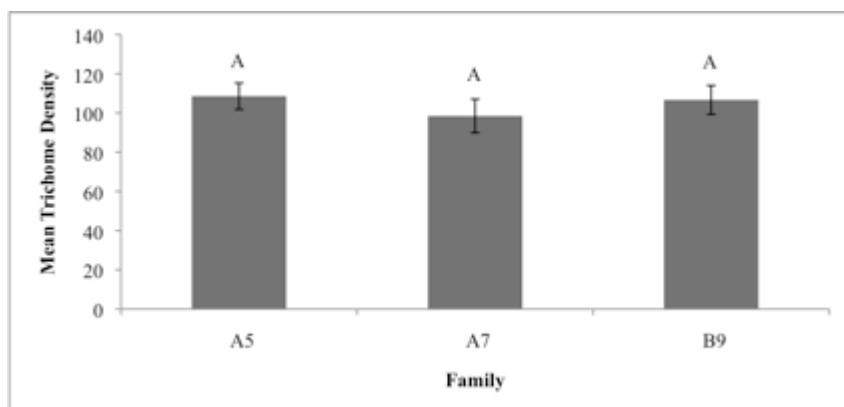


Figure 1. Mean trichome density of second season plants from three families.

There is no statistically significant difference in the mean density of trichomes between families ($p=0.373$).

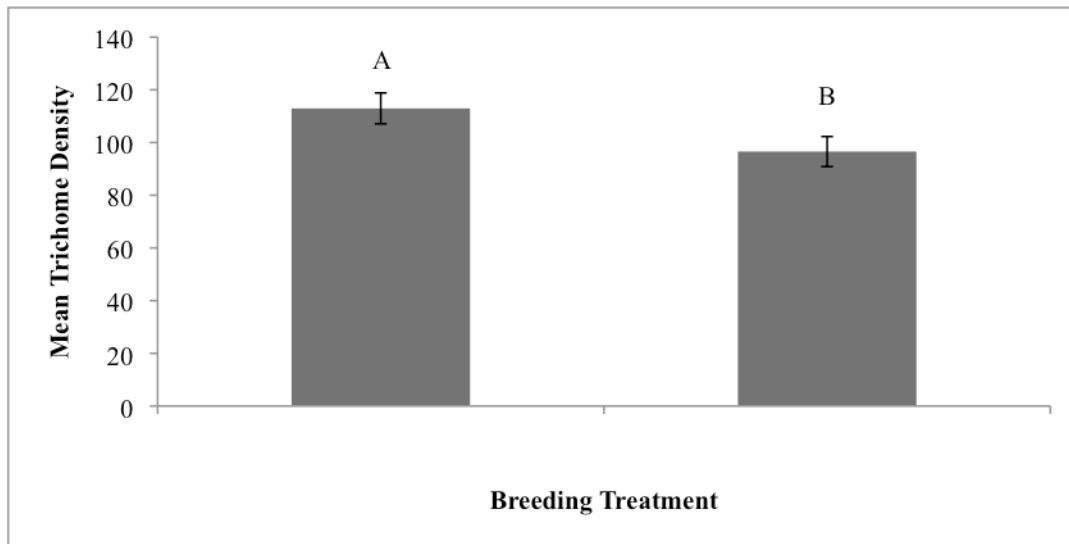


Figure 2. Mean trichome density of second season plants from outcrossed and inbred parents.

There was a visibly and significantly higher mean density of trichomes in outbred horsette leaves than in inbred horsette leaves.

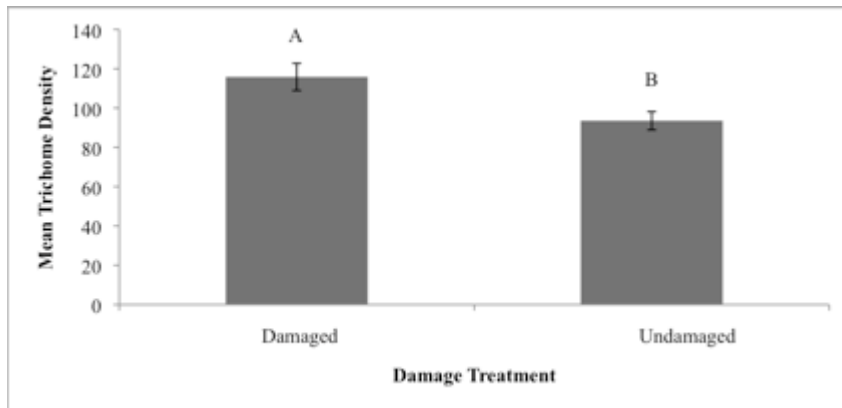


Figure 3. Mean trichome density of second season plants from damaged and undamaged parents.

There was a visible and statistically significant difference in the mean density of trichomes with damaged plants exhibiting higher densities than undamaged plants ($p=0.019$).

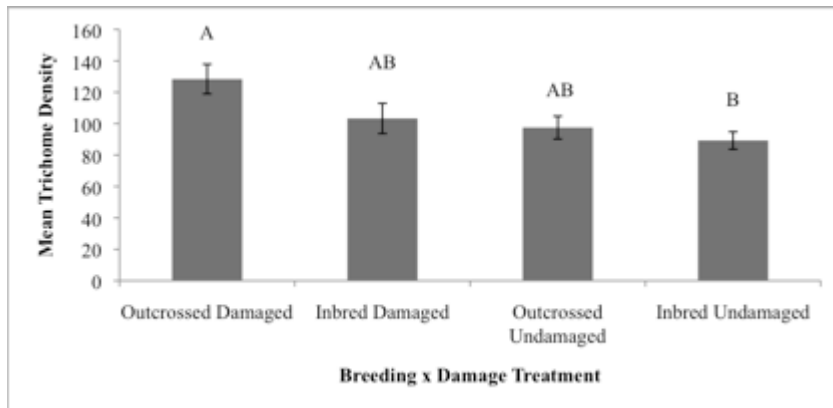


Figure 4. Breeding x Damage interaction effect on the mean trichome density of second season plants.

There were overall non-significant differences in mean trichome density based on an interaction between breeding and damage, but a Tukey multiple comparison test revealed a significant difference in trichome density between outcrossed damaged plants and inbred undamaged plants ($p=0.287$).

There was no significant difference in the mean trichome density among families (A5 = 108.6 ± 6.7 ; A7 = 98.5 ± 8.6 ; B9 = 106.7 ± 7.4 ; Mean \pm SE; Appendix A: Table 1, Table 2; $p = 0.373$; Figure 1)

Second season outcrossed plants exhibited a significantly higher mean trichome density than second season inbred plants (Outcrossed = 112.9 ± 5.9 ; Inbred = 96.6 ± 5.7 ; Mean \pm SE; Appendix A: Table 1, Table 2; $p = 0.035$; Figure 2).

Second season plants whose parents were exposed to damage treatment exhibited a significantly higher mean trichome density than second season plants whose parents were undamaged (Damaged = 115.8 ± 6.9 ; Undamaged = 93.6 ± 4.6 ; Mean \pm SE; Appendix A: Table 1, Table 2; $p = 0.019$; Figure 3).

There was one main interaction term, Breeding \times Damage, which gave non-significant differences in mean trichome density (Outcrossed Damaged = 128.4 ± 9.4 ; Inbred Damaged = 103.3 ± 9.6 ; Outcrossed Undamaged = 97.5 ± 7.3 ; Inbred Undamaged = 89.3 ± 5.6 ; Mean \pm SE; Appendix A: Table 1, Table 2; $p = 0.287$; Figure 4). However, there is an interesting visual trend in these data, with mean trichome densities decreasing in the order of Outcrossed Damaged, Inbred Damaged, Outcrossed Undamaged, Inbred Undamaged.

Chapter 4

DISCUSSION

Previous studies have examined the effects of inbreeding and herbivory on constitutive and induced defense pathways. However, no studies have examined the effects on the inheritance of defenses across seasons. Previous research in the system has determined that herbivores preferentially choose inbred plants due to a reduced number of physical defenses, and that herbivore damage can induce physical defenses within an individual (Kariyat et al., 2012). Our results from this study indicate that these inducible defenses may persist beyond the reaches of a single season.

Our results indicate that there are significant differences in trichome density between inbred and outcrossed lines of horsenettle in the second season, implying that breeding has an effect on trichome density. The results of the breeding x damage interaction show an interesting visual trend, with outcrossed damaged plants having the highest mean trichome density, and inbred damaged plants having the lowest mean trichome density. With increases in sample size, data from the non-significant interaction treatment may become significant and show the importance of the Breeding x Damage interaction. However, without additional data, we conclude that the effects of inbreeding and damage are independent. The damage treatment was also significant, showing a significantly higher mean trichome density in second season plants that were previously damaged by *Manduca sexta* caterpillars compared to plants that were left undamaged in the first season. This indicates that plants that experienced herbivory in the first season had induced defenses that persisted across seasons. This suggests a significant trans-seasonal persistence of defenses.

The ability to transmit/store a memory of herbivory from one season to the next allows plants to have greater resistance to insects in areas with high herbivore pressure, and this ability to protect itself in future seasons could be extremely important to plant populations that exist in heavily predated areas. There is a high chance that herbivores will be present in similar distributions from season to season, provided there are no considerable changes to the landscape itself. If this prediction holds true, plants have the ability to adapt to their environment both within a season and across multiple seasons.

We hypothesize that the plant storing a memory, possibly via small RNA signals within the rhizome, causes these induced changes (Holeski et al., 2012). The ability to retain induced defenses into subsequent seasons allows plants reproducing asexually by runners to pre-defend themselves from future herbivory, and in a way that may increase their future fitness.

The data concerning the induction of trichome defenses are the beginning of a larger study examining a broad view of trans-seasonal defense induction. Additional implications of inbreeding and herbivory will be examined, in order to better understand how these processes affect plant defense pathways, and the ability of individuals and populations to protect themselves against herbivores, specifically insect herbivores.

The first of these continued studies examines the trans-seasonal effects of inbreeding and previous damage on caterpillar larval growth. Trichomes and spines may affect an herbivore's ability to digest plant material and their use of nutrients for metabolic and cellular processes.

Current research in the lab has shown that trichomes can penetrate the gut lining of the *M. sexta*

caterpillar, which may in turn affect caterpillar growth, development, and reproduction. These effects may contribute to how resources are allocated within the caterpillar, and may help to quantify the effectiveness of plant defenses. Another continued study examines how *M. sexta* damage in one season affects leaf area consumption by caterpillars in the second season. We hypothesize that caterpillars will consume a larger amount of leaf material from plants that were undamaged in the first season, as opposed to those that were damaged by *M. sexta* caterpillars. This may be the result of increased physical defenses in plants previously damaged in the first season. All of these experiments, together, will examine the extent of trans-seasonal defense induction, and how plants can confer resistance to their progeny by inducing defensive pathways. Trichome data will be the driving force behind both of these additional studies, as these structures provide mechanical barriers to insect herbivores and may affect herbivore digestion.

As these studies are completed and more is understood about the trans-seasonal induction of defenses in plant species, the concept of over-wintering will be introduced. The belowground portions of horsetail undergo a period of over-wintering and re-sprout in the spring (Kariyat et al., 2011). This vernalization period can be used as a signal for the plant to begin reproductive growth, and end its period of vegetative growth (Henderson et al., 2003; Doyle & Amasino, 2009). Therefore, we would like to examine whether or not these induced defenses can be retained through a vernalization period. To do this, rhizomes will be placed in a cold treatment for a period of 1 month, allowed to re-sprout, and examined to determine whether trans-seasonal defenses persist after experiencing cold temperatures for an extended period of time.

This research is the first to examine the effects of inbreeding and herbivory on the trans-seasonal induction of defenses. Eventually, this project will provide a broad and extensive view of defense induction beyond a single season, and how it relates to plant-herbivore interactions. Results of these studies may be applied in a larger context to agriculturally important relatives of horsetettle, such as tomato, potato, and tobacco.

Appendix A
HORSENETTLE IMAGES



Figure 5. This image shows a second instar tobacco hornworm caterpillar feeding on a horsetail leaf. The large structures oriented vertically are spines. The hair-like projections on the leaf tissue are trichomes.

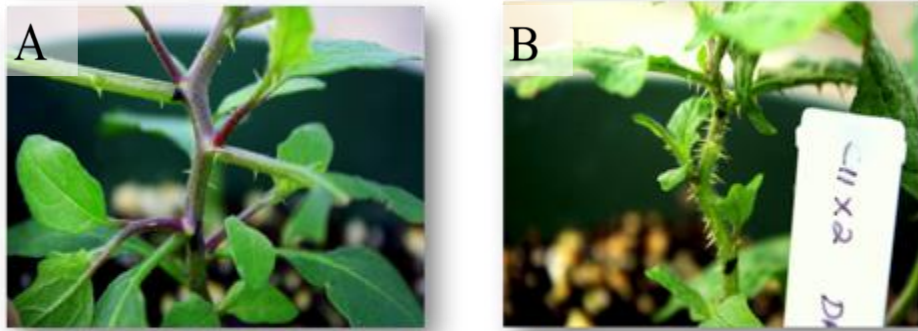


Figure 6. Inbred and outbred plants with spines.

Image A represents an inbred plant. The number of internode spines can be contrasted with Image B, which represents an outcrossed plant.

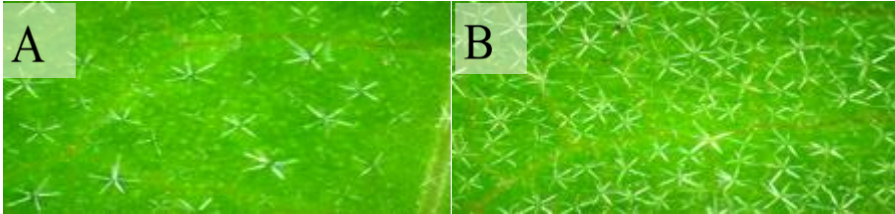


Figure 7. Images taken using the DinoLite camera.

Each trichome is visible as a single, asterisk-shaped structure. Figure 7A is an image taken from an undamaged, second season plant. Figure 7B is an image taken of a damaged, second season plant. Images were taken on the second or third bottom-most leaf between the second and third lateral veins.

Appendix B
TRICHOME DATA

Treatment	Source of Variation	Mean	Standard Error
a) Breeding Treatment	Outcrossed	112.9	5.9
	Inbred	96.6	5.7
b) Damage Treatment	Damaged	115.8	6.9
	Undamaged	93.6	4.6
c) Family Treatment	A5	108.6	6.7
	A7	98.5	8.6
	B9	106.7	7.4
d) Breeding x Damage Treatment	Outcrossed Damaged	128.4	9.4
	Inbred Damaged	103.3	9.6
	Outcrossed Undamaged	97.5	7.3
	Inbred Undamaged	89.3	5.6

Table 1. Results of Mean and Standard Error calculations for the effects of breeding, damage, family, and breeding x damage treatments on trichome density.

Treatment	DF	SS	F	P
Breeding	1	0.10451	3.37	0.035
Family	2	0.06175	1.00	0.373
Damage	1	0.17667	5.70	0.019
Breeding x Damage	1	0.03551	1.15	0.287

Table 2. Results of ANOVA tests for the effect of breeding (fixed), family (random), damage (fixed), and breeding x damage treatments.

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ACADEMIC VITA

REBECCA KOLSTROM

rlk5210@psu.edu

EDUCATION

- **Bachelor of Science in Biology (Ecology)**
Minor in Wildlife and Fisheries Science:
Pennsylvania State University, University Park, PA, anticipated May 2015
Schreyer Honors College

EXPERIENCE AND SKILLS

The Pennsylvania State University

01/13 – 05/15

Research Assistant, Plant Ecology Lab, Dr. Andrew Stephenson

*In the Stephenson lab, I performed experimental procedures in various studies. These tested inbreeding depression, transmission of diseases, disease resistance, and volatile signaling. Under supervision of a graduate student, I performed Honors Thesis Research, which examined maternal gene expression in *Solanum carolinense*. I was exposed to research in a variety of environments, which included a laboratory, various greenhouses, and field settings in Penn State's agricultural station. The research done in the Stephenson lab will contribute to scientific papers examining trans-seasonal effects of defense induction.*

- **Laboratory Skills**
 - PCR
 - DNA Analysis
 - Gel Electrophoresis
 - NMR
 - Autoclaving
 - Infrared Spectrometry
 - Gas Chromatography
- **Greenhouse Skills**
 - Plant Maintenance
 - Rhizome Collection
 - Pest Management
 - Pest Removal
 - Disease Identification
 - Disease Monitoring and Control
- **Relevant Coursework**
 - Populations and Communities
 - Ornithology
 - Animal Behavior
 - Conservation Biology
 - Physiological Ecology
 - Mammalogy
 - Invertebrate Zoology
 - Ecological and Environmental Problem Solving
- **Relevant Academic Presentations**
 - Eastern Branch Meeting of the Entomological Society of America
*Research done in the Stephenson lab was presented in the Student Poster Competition in Rehoboth Beach, Delaware. The poster was registered under the Plant-Ecosystems and Host-Plant Resistance categories and displayed research performed to examine how inbreeding affects herbivore resistance and defense induction in *Solanum carolinense*, and how these defenses are transmitted trans-seasonally.*

- **Additional Skills**
 - Proficiency in German Language
 - Competence in Adobe Photoshop
 - Mastery of Microsoft Office
 - Proficiency in analytical computer programs, including Microsoft Excel, Minitab, and SAS

ACADEMIC HONORS AND AWARDS

- **Schreyer Honors College** *08/11 – Present*
Academic Excellence Scholarship
- **Pennsylvania State University Dean’s List** *(5 semesters)*

ACTIVITIES

- **Science LionPride** *01/13 – Present*
Science LionPride is an undergraduate organization associated with the Pennsylvania State University and the Eberly College of Science. Involvement included leading tours of Penn State’s Science Campus for prospective students and distinguished alumni. The organization also helped to coordinate special events hosted by the College of Science.
- **Penn State Dance Marathon** *10/11 – Present*
As a Rules and Regulations Captain for THON 2015, I culminated four years of involvement in the organization with a leadership role. My position included leading a committee of 40 students and planning/carrying out security operations throughout the fundraising season and during the weekend of the Dance Marathon.

ADDITIONAL WORK EXPERIENCE

- **Hershey Entertainment and Resorts** **- Retail Employee** *05/09 – 09/09*
- **Hershey Trolley Works – Performer and Tour Guide (Seasonal)** *09/09– Present*
- **Pennsylvania State University – Dining Hall Staff** *02/14-06/14*