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The effects of Nematode Infection and MI-Mediated Resistance in Tomato (Solanum Lycopersicum) on Plant Fitness

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THE EFFECTS OF NEMATODE INFECTION AND MI-MEDIATED RESISTANCE IN TOMATO (*SOLANUM LYCOPERSICUM*) ON PLANT FITNESS

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Abstract

The Mi gene in tomato (Solanum lycopersicum) is a single, dominant resistance (R) gene that confers resistance against several species of insects and root-knot nematodes. This study examined the impact of root-knot nematode infestation and the plant growth and reproduction of near-isogenic tomato cultivars with and without Mi. The objectives of this experiment were to examine the potential fitness costs and benefits of the R gene-mediated herbivore resistance, and to explore the role of nematodes as a selection pressure favoring plants that carry Mi. Mi-mediated resistance dramatically reduced nematode reproduction on tomato. In the presence of nematodes, plants that carried Mi produced larger fruits and greater foliar biomass than susceptible plants. Both resistant and susceptible plants, however, were able to compensate for heavy nematode infestation, and neither genotype showed a significant reduction in yield or estimated lifetime seed production in response to infestation. Therefore, Mi-mediated resistance did not provide a fitness benefit to the plants under the infestation level tested. Seeds from plants that carried Mi also had lower germination rates than seeds from susceptible plants, suggesting that there may be a metabolic fitness cost associated with Mi-mediated nematode resistance.

Introduction

Plants display an array of sophisticated biochemical and morphological traits that limit attack from a variety of pests, such as pathogens, insects, and other herbivores. "Acquired" or "induced" resistance is dependent upon a conglomeration of traits that are upregulated by pest damage, and that can reduce the severity of subsequent assaults from a broad range of potential attackers (Agrawal, 2005; Cipollini et al., 2003). This phenotypic plasticity is presumed to be controlled by many interacting genes in the plant. In contrast, R gene-mediated pest resistance rapidly blocks initial attacks by one or a small number of pest species, and is controlled by simple but highly specific gene-for-gene interactions between the plant and the pest (Dangl and Jones, 2001; Kaloshian, 2004). According to this model, the presence of a single resistance (R) gene in the plant allows the rapid detection of a corresponding avirulence (Avr) gene in the pest, resulting in incompatibility (Flor, 1971).

Regardless of whether it is acquired or R-gene mediated, any plant trait that blocks pest establishment or limits their proliferation can be considered a source of resistance. However, Karban and Baldwin (1997) propose that the term "plant defense" should be reserved for traits that have also been shown to enhance plant fitness in the presence of pests. Fitness represents the plant's lifetime reproductive success and is the critical trait on which natural selection acts. The term "plant defense" implies that the trait in question is an adaptation to pest pressure.

Plant-herbivore interactions have long been used as model systems to study co-evolution (Agrawal, 1998; Baldwin, 1998; De Meaux and Mitchell-Olds, 2003). The theory of co-evolution proposes that reciprocal genetic changes have occurred in plants and their associated herbivores, driven by the costs and benefits of these changes to Darwinian fitness. According to this hypothesis, plants have developed a variety of resistance traits (e.g., thorns, trichomes, toxic chemicals, and antinutritive proteins) to combat herbivory and limit its fitness costs (Agrawal and Tuzun and Bent, 1999; Sagers and Phyllis, 1995). Through selection, insects have responded with adaptations to cope with the new plant traits, such as detoxifying enzymes or behavioral avoidance mechanisms (Gardner and Agrawal, 2002; Strauss and Agrawal, 1999). Many of the plant traits that deter herbivores, however, could potentially have developed in response to other selective pressures. For example, leaf trichomes have been identified in biological functions such as toxin removal, UV protection, and water retention (Smith and Hare, 2004). These abiotic fators may aid in the selection of trichome production or trichome density (Gianoli and Gonzallez-Teuber, 2005; Karkkainen et al., 2004). Therefore, before making any inferences about the adaptive significance or evolutionary history of a particular form of resistance, empirical tests are needed to assess the costs and benefits of this trait to plant fitness in the presence and absence of pests.

The majority of studies that have examined the costs and benefits of resistance have focused on traits that contribute to induced insect resistance, such as trichome density in wild radish (*Raphanus* spp.) and nicotine synthesis in a wild tobacco (*Nicotiana attenuata*) (Agrawal, 1999; Karban et al., 1997). Fewer research groups have assessed the effects of R genes on plant reproductive success, although dramatic progress has recently been made in studying R gene mediated bacterial resistance in *Arabidopsis thaliana* (Korves and Bergelson, 2004; Tian et al., 2003). Data from this system suggests that wild Arabidopsis populations experience

intermittent periods of extreme pathogen attack, during which plants that carry *RPM1* and other R genes for disease resistance have a strong selective advantage. During periods of low pathogen incidence, however, susceptible plants boast higher fitness than resistant genotypes. Bergelson and coworkers propose that as a result of these trade-offs, both resistant and susceptible alleles of R gene loci are maintained in Arabidopsis populations through balancing selection (Korves and Bergelson, 2004; Tian et al., 2003).

The goal of the present study was to use tomato as a model system to measure the fitness costs and benefits of R gene mediated herbivore resistance. The *Mi* gene is present in many tomato cultivars and confers resistance to three common root-knot nematode species (*Meloidogyne incognita, M. javanica, M. arenaria*), as well as three insect species (potato aphid, *Macrosiphum euphorbiae*; sweetpotato whitefly, *Bemisia tabaci*; tomato psyllid, *Bactericerca cockerelli*) (Casteel et al., 2006). This gene was introduced into cultivated tomato, *Solanum lycopersicum*, by crossing it with a wild relative, *S. peruvianum* (Smith, 1944). Our study focused on the effects of *Mi* on root-knot nematode, which are the most damaging of these herbivores on tomato. Root-knot nematodes disrupt the vascular system of their host plant causing symptoms that include stunted plant growth, chlorosis or premature death, and that increase susceptibility to drought and other pathogens (Jenkins and Taylor, 1967; Olsen, 2000). These endoparasites cause severe yield reductions in agricultural crops including cultivated tomato, and *Mi* is the only known source of root-knot nematode resistance in cultivated tomato (Williamson, 1998). In plants that carry *Mi*, a hypersensitive reaction (HR), which involves rapid localized cell death, stops the nematode from establishing a feeding site (Williamson, 1998). *Mi*-mediated resistance dramatically reduces root-knot nematode numbers and has been shown to increase tomato yield in both greenhouse and field experiments (Sorribas et al., 2005; Lopez-Perez et al., 2006). However, the impact of *Mi* on seed production has not been examined. To this end we conducted a full factorial experiment to assess the effects of nematode infection and *Mi*-mediated resistance on plant growth and reproduction. The goals of this study were to examine the potential fitness costs and benefits of *Mi*, and to explore the potential role of nematodes as a selection pressure favoring *Mi*-mediated resistance.

Methods and Materials

Plant Materials. Two near-isogenic tomato cultivars Castlerock II (*Mi*-, susceptible) and Sun 6082 (*Mi*+, resistant) were used for this assay. All plants were grown in 11-liter plastic pots of autoclaved sand (Play Sand, Quikrete, Atlanta, GA) under stable greenhouse conditions (~24°C-27°C; 16:8 L:D photoperiod). Tomatoes were watered three times daily with a nutrient solution containing 1000 mg/L CaNO (Hydro Agri North America, Tampa, FL), 500 mg/L MgSO (Giles Chemical Corp, Waynesville, NC), and 500 mg/L Hydroponic 4-18-38 Growmore fertilizer (Growmore, Gardena, CA).

Nematode cultures and inoculation. Root-knot nematodes, *Meloidogyne javanica* (VW4 isolate), were obtained from Dr. V. M. Williamson (University of California, Davis). Nematodes were maintained on susceptible tomato plants (cv. Moneymaker), under the same greenhouse conditions and fertilization regime described above. Nematode eggs were collected from colony plants inoculated at least seven weeks. Eggs were extracted from infected root systems using a 1% sodium hypochlorite solution, and were resuspended in water and quantified by examining serial dilutions with a light microscope (Hussey and Barker, 1973). Experimental plants were inoculated with 20,000 nematode eggs via pipette on each side of the root crown, while control plants were mock-inoculated with water.

Fitness Factors. Four tomato plant treatment conditions were used: susceptible inoculated, susceptible control, resistant inoculated, and resistant control. For each condition, 8 plants/treatment) were grown and allowed to fruit. The fruit was collected and weighed as it became ripe. Fruit was collected twice a week for ten weeks, and at ten weeks all remaining green fruit was collected. Three tomatoes of average size were chosen from each plant for seed extraction. Seeds were counted and weighted (AG285, Mettler Toledo, Columbus, OH) for analysis. Total foliar biomass (stems and leaves) was collected after four months of growth, and dried for five days at 26°C before being weighed. Whole root systems were collected and sent to a nematology diagnostics facility (Dr. Kirkpatrick, University of Arkansas, Hope) for nematode egg quantification. Whole root systems were dried and weighed after nematode extraction.

Germination. Germination rates were measured from a sub-sample of the seeds collected (10 seeds/plant; eight plants/ treatment group). Seeds were sown in 1 cup plastic square pots of vermiculite (Vermiculite, Schultz, Atlanta, GA) and grown in greenhouse conditions same as above, and watered daily with tap water. Germination rate was recorded every two days for ten days after planting.

Statistics. Tomato yield, seed count and weight, root and foliar dry weight, and nematode reproduction were compared on our four treatment groups using full factorial 2-way analysis of variance (ANOVA) and student's t-test (JMP version 5.01, SAS Institute, Cary, NC).

Results

Nematode Infection. Nematode data was transformed for analysis using the formula 'log +1'. *Mi*-mediated resistance significantly reduced nematode reproduction, as measured by the number of egg masses per gram of root mass (Figure 1) ($F=0.835$; $df=1, 28$; $P=0.0004$).

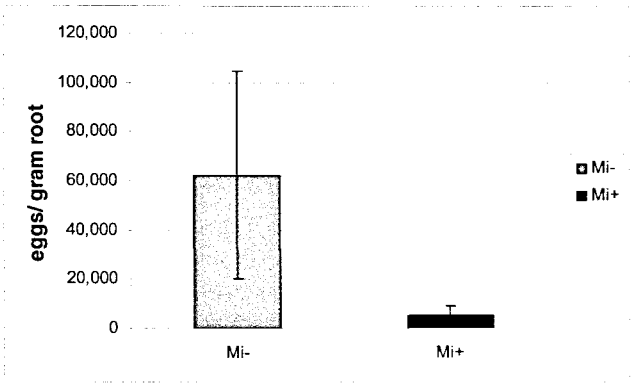

Figure 1. Effects of *Mi*-mediated resistance on nematode reproduction.

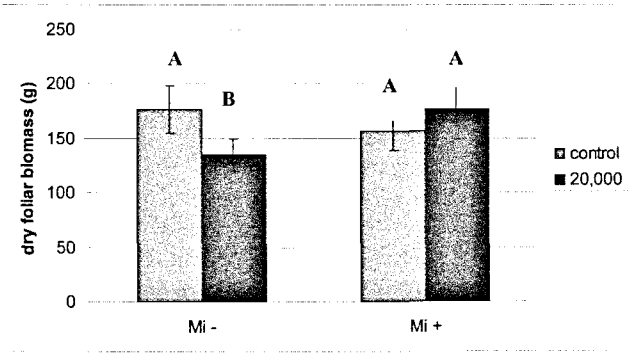

Figure 2. Effects of *Mi*-mediated resistance and nematode inoculation on dry foliar weight of tomato plants.

Plant Growth. When foliar dry masses were analyzed, there was a significant interaction between plant genotype and nematode inoculation (Figure 2) (F=16.7227; df= 1, 28; P= 0.0003). Nematode inoculation significantly reduced foliar dry weight of the susceptible (Mi-) genotype (t=3.976; df=28; P=0.0004), but did not reduce the dry weight of the resistant (Mi+) cultivar (t= -1.807; df=28; P=0.0814). Nematode inoculation did not significantly affect whole root weight (Figure 3) (F=0.0274; df=1,28; P=0.8697), nor was there a significant interaction between inoculation and plant genotype (F=0.202; df=1,28; P=0.6566). Root weight was significantly higher for the resistant genotype than for susceptible genotype (F=5.936; df=1,28; P=0.0214).

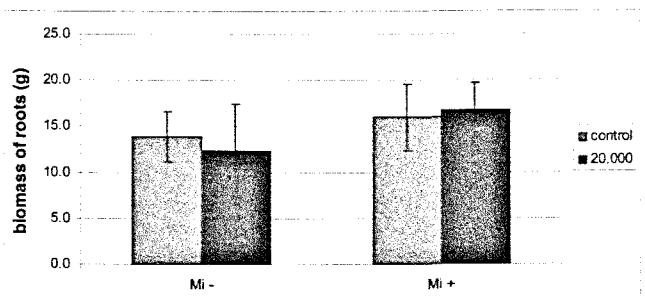

Figure 3. Effects of Mi-mediated resistance and nematode inoculation on root weight of tomato plants.

Fruit Production. Neither nematode inoculation nor plant genotype had a significant effect on the number or total weight of mature fruits collected (Table 1). When the average weight per mature fruit was analyzed, there was a significant interaction between genotype and nematode inoculation. In the presence of nematodes, resistant plants produced significantly larger fruits than susceptible plants (t=2.48; df=28; F=0.019). There was no significant difference among treatments in the number, total weight, or average weight of green fruits collected from the plants at the termination of the experiment, when fruit production was waning (Table 2).

Genotype	*Inoculation*	*Mature Fruit/ Plant (mean ± S.D.)*	*Avg Mature Fruit Wt. (g) (mean ± S.D.)*	*Yield of Total Mature Fruit (g) (mean ± S.D.)*
Mi-	control	14.9 ± 7.1	37.8 ± 4.3ab	560.6 ± 272.0
	inoculated	14.5 ± 6.7	33.3 ± 7.7b	489.6 ± 287.1
Mi+	control	11 ± 5.7	35.6 ± 11.5ab	415.8 ± 280.2
	inoculated	13.9 ± 7.5	43.9 ± 8.9a	582.4 ± 309.0
ANOVA results	Genotype effect	$F_{1,28}$=0.8847 P=0.3550	$F_{1,28}$=1.9572 P=0.1728	$F_{1,28}$=0.0655 P=0.7999
	Inoculation effect	$F_{1,28}$=0.2731 P=0.6054	$F_{1,28}$=0.4107 P=0.5268	$F_{1,28}$=0.2211 P=0.6418
	Interaction	$F_{1,28}$=0.4615 P=0.5025	$F_{1,28}$=4.4575 P=0.0438	$F_{1,28}$=1.3678 P=0.2520

Table 1. Mature fruit production.

Genotype	*Inoculation*	*Avg. Green Fruit/ Plant (mean ± S.D.)*	*Avg. Green Fruit Wt. (g) (mean ± SEM)*	*Yield of Total Green Fruit (g) (mean ± S.D.)*
Mi-	control	1 ± 0.9	20.5 ± 8	286.3 ± 46.2
	inoculated	2.3 ± 2.4	16.5 ± 5.2	433.9 ± 55.3
Mi+	control	1.5 ± 2.4	15.1 ± 5.8	345.3 ± 66.1
	inoculated	1.5 ± 1.0	23.3 ± 5.2	363.3 ± 38.7
ANOVA results	Genotype effect	$F_{1,28}$=0.0366 P=0.8496	$F_{1,28}$=0.0117 P=0.9147	$F_{1,28}$=0.0015 P=0.9692
	Inoculation effect	$F_{1,28}$=0.9162 P=0.3467	$F_{1,28}$=0.1062 P=0.7470	$F_{1,28}$=0.3097 P=0.5823
	Interaction	$F_{1,28}$=0.9162 P=0.3467	$F_{1,28}$=0.8739 P=0.3579	$F_{1,28}$=0.1897 P=0.6665

Table 2. Green fruit production.

Seed production. Nematode infection significantly reduced the average number of seeds per fruit and per gram of fruit weight, as well as the amount of seed produced relative to the total plant biomass (Table 3). Plant genotype (Mi- and Mi+) did not significantly influence any of these parameters. The season-wide seed production per plant was estimated by multiplying the total number of grams of ripe

fruit produced by the average number of seeds per gram for the tomatoes sampled. This estimated seed production did not differ significantly among treatments. Seed weights and germination rates were also evaluated as a measure of seed quality and viability. The average size of individual seeds did not differ among treatments (genotype: F=1.234; df=1,28; P=0.276, treatment: F=0.3381; df=1,28; P=0.5656, interaction: F=2.5532; df=1,28; P=0.1213). Germination rates on days 5, 7, and 10 after planting were all significantly lower for the resistant cultivar than for the susceptible plants ($P \leq 0.01$ for all time points), whereas nematode infection did not influence germination rates or interact significantly with genotype ($P > 0.05$ for all time points) (Figure 4).

Genotype	*Inoculation*	Average seeds/ fruit *(mean* ± SEM)#*	Average seeds/ (g) fruit *(mean* ±S.D.)*	Average seeds/ (g) dry foliar and root weight *(mean* ±S.D.)*	Estimated lifetime seed production *(mean* ±S.D.)*
Mi-	control	39.6 ± 9a	0.25 ± 0.19	0.62 ± 0.4	363.5 ± 227.9
	inoculated	21.6 ± 6.8b	0.14 ± 0.1	0.43 ± 0.41	256.9 ± 260.7
Mi+	control	56.1 ± 7.9a	1.03 ± 1.57	0.99 ± 0.41	333.3 ± 214.5
	inoculated	26.5 ± 6.4b	0.16 ± 0.1	0.41 ± 0.26	315.6 ± 422.4
ANOVA results	Genotype effect	$F_{1,28}$=1.9659 P=0.1719	$F_{1,28}$=2.0929 P=0.591	$F_{1,28}$=0.5971 P=0.4462	$F_{1,28}$=0.0188 P=0.8919
	Inoculation effect	$F_{1,28}$=9.7250 P=0.0042	$F_{1,28}$=3.0511 P=0.0916	$F_{1,28}$=0.8049 P=0.3773	$F_{1,28}$=0.3591 P=0.5538
	Interaction	$F_{1,28}$=0.5815 P=0.4521	$F_{1,28}$=1.8620 P=0.1833	$F_{1,28}$=0.3755 P=0.5450	$F_{1,28}$=0.1833 P=0.6719

Table 3. Seed production.
Values followed by the same letter are not significantly different from each other, P>0.05

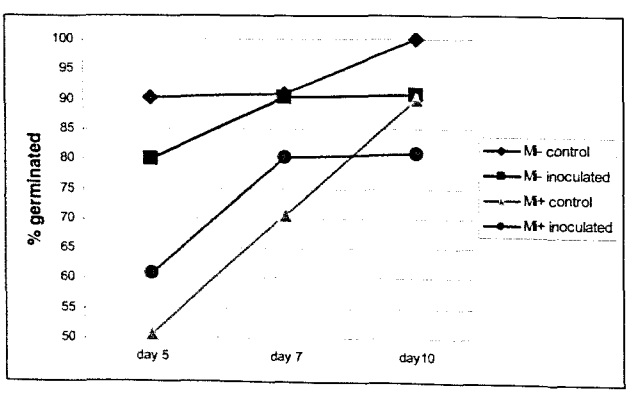

Figure 4. Effects of *Mi*-mediated resistance and nematode infestation on germination rate.

Discussion

In this experiment, we observed only a modest effect of nematodes on plant performance. Nematode infection reduced the foliar dry weight of susceptible plants, and the number of seeds per fruit collected from resistant as well as from susceptible plants. However, nematodes did not significantly influence the fruit yield or the estimated total seed production of either genotype. These results indicate that the tomato plants in this study were able to compensate for high levels of nematode infestation without a negative effect on fitness. This is consistent with data presented in two recent studies of nematode infestation on tomato. Lopez-Perez et al. (2006) inoculated greenhouse-grown plants with 0, 10^2, 10^3, 10^4, and 10^5 root-knot nematode eggs, and found that only the highest inoculum level significantly reduced the total fruit mass produced by a susceptible (*Mi*-) tomato cultivar. In a field study, Sorribas et al. (2005) grew a susceptible cultivar in naturally infested soil for three consecutive years and observed abundant galls and nematode eggs on the roots (~40,000 – 50,000 eggs/ gram root mass). Although this study concluded that total yield over three years was lower in infested versus fumigated soil, a year-by-year analysis of the data shows that nematodes significantly reduced yield in only one out of three field seasons.

The susceptible plants grown in this study appear to have used some form of tolerance to maintain normal reproductive levels when challenged with nematodes. In contrast to resistance, defined as any trait that reduces infestations, tolerance reduces the impact of infestations on plant fitness (Restif and Koella, 2004). The physiological and molecular mechanisms underlying tolerance are not thoroughly understood, but are thought to involve relocation of resources such as photoassimilates to less vulnerable parts of the plant (Agrawal, Strauss and Stout, 1999). Plants display varying degrees of tolerance against biotic and abiotic stresses, and selection for tolerance in crop plants has been a goal of agricultural breeding for decades (Wiley, New York, 1951). More recently, experiments to determine how plants use tolerance are increasing. A recent study by Schwachtje et al. showed *Nicotiana attenuata* relocates sugars to roots, immediately following simulated herbivore attack, for storage and future regrowth (Schwachtje et al., 2006).

While the plants in our study were able to compensate for nematode infection, this is not always the case; root-knot nematodes are a major agricultural pest that can cause dramatic yield losses on tomato (Olsen, 2000; Sorribas, 2005). The growing conditions used for this study may have helped limit the impact of nematode infection on plant fitness. Nematodes reduce root translocation and predispose their host plants to drought stress and disease (Olsen, 2000). The plants in this experiment were grown in greenhouse conditions with daily irrigation and fertilization, whereas plants grown in field conditions may have a more limited amount of water and nutrients to allocate for growth and reproduction. Furthermore, plants in this study were grown in autoclaved sand, absent of root pathogens and other pests that might otherwise attack plants stressed by nematode infestation. Therefore, plants grown in the "optimum" conditions of our greenhouse only had to defend themselves against one pest, allowing plentiful resources to be used for growth and reproduction.

Because nematode infection in this study did not significantly reduce the estimated total seed production by susceptible plants, we were not able to measure any

potential benefit of *Mi*-mediated resistance to plant fitness. *Mi* dramatically reduced nematode populations on tomato plants and conferred a modest benefit for fruit size and foliar biomass in the presence of nematodes; however, it had no major impact on yield or seed production. Notably, seeds from resistant plants also had lower germination rates than seeds from susceptible plants. Resistance could be associated with a metabolic cost to the plant, as reported by Korves and Bergelson (2004) for R-gene mediated pathogen resistance. However, the two cultivars used in our study are not perfectly isogenic, and the observed difference in germination could be due to genetic differences unrelated to *Mi*. To test this, we would need to test the germination rates of cultivars that carry *Mi* in other genetic backgrounds.

In the future, it would be useful to test the effects of *Mi* on plant fitness in the presence of higher nematode densities that might have a greater impact on plant reproduction. It would also be worthwhile to test the effects of *Mi* on the fitness of plants challenged by multiple pests. As mentioned previously, nematodes can impact plants by predisposing them to attack by other pests. Furthermore, *Mi* also affects aphids, whiteflies, and psyllids, all of which could have an additive effect on plant fitness, and could be important selection pressures on tomato. Future studies could also examine the effects of *Mi* on reproduction rates in *S. peruvianum*, the wild tomato species from which this gene was introduced into cultivated tomato. It is interesting to note that nematodes in this study had a larger effect on seed production than on fruiting; they reduced the number of seeds per fruit (Table 3), but did not affect the number or total weight of fruit produced (Table 1). This could be due to the fact that we worked with cultivated varieties that were artificially selected for fruit production. In addition, it may be useful for future experiments to consider ecological factors such as competition among plants, weather and water availability, light, flowering time, pollinators, and migration patterns of other herbivores (Hiel, 2002). The diversity of a plants' environment plays a role in fitness through an unlimited number of factors that are difficult to simulate in a greenhouse experiment, due to methodological limitations (Agrawal, 2005; Hiel, 2002). Further work is necessary to investigate the costs and benefits of *Mi*-mediated resistance.

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Mentor Comments

Dr. Fiona Goggan describes the rigor of Mr. Corbett's research and the recognition of its quality at a regional meeting of the primary professional organization in their field.

The research project described in this manuscript was the basis for Brandon Corbett's undergraduate Honors thesis in Biology, which he successfully defended in April 2007. To initiate his thesis project in my laboratory, Brandon conducted a literature survey on the evolution of plant defenses against insects and pathogens. The evolution of plant resistance (R) gene families that confer disease resistance is a very active and exciting research area. Few if any studies, however, have examined the maintenance and diversification of genes for herbivore resistance in an evolutionary context. Furthermore, most of the relevant studies of disease resistance infer the evolutionary history of R genes from DNA and amino acid sequence comparisons among homologous genes. In other words, the focus of these studies is at the molecular level, and few of these studies examine the biotic interactions and environmental factors that presumably drive the process of natural selection. In response to this gap in the literature, Brandon and I developed a project to quantify the costs and benefits of an herbivore resistance gene in the presence and absence of herbivory. The herbivore chosen for this study was the root-knot nematode, which has a world-wide distribution, can infect over 1,000 plant species, and is associated with severe yield losses on a wide variety of crops. Much to our surprise, Brandon's results indicated that susceptible as well as resistant tomato genotypes could sustain heavy nematode infestations without a significant loss in reproductive success. The findings of the greenhouse study reported in this manuscript were also corroborated by a field trial in which Brandon participated. These results may help explain why the Mi nematode resistance gene is not present in all populations of the Solanum species from which it was derived. This study also underlines the fact that any single resistance gene is only one part of a larger suite of different mechanisms by which plants adapt to herbivory. In particular, it highlights the importance of tolerance, which typically receives less study than resistance. Brandon continues to work on this project, and is currently examining the effects of different nematode inoculum levels on the costs and benefits of resistance. He has also begun to explore possible mechanisms of tolerance in tomato.

The academic rigor of Brandon's project and program of study are evidenced by his graduating with honors. Throughout this project, I have been very impressed by Brandon's hard work, perseverance, and dedication to research. Although the field of plant-herbivore interactions lies outside of Brandon's long-term interest in medicine, he enthusiastically approached his Honors project as an opportunity to gain hands-on experience in research, and to learn concepts of experimental design and analysis that can be applied to any area of biology. As a result, his project was a resounding success. Based on his research proposal, Brandon won a scholarship from the University of Arkansas Honors College to support the project. He also presented his results at the southeastern branch meeting of the Entomological Society of America, the primary professional organization in my discipline. Although undergraduates do not typically participate in this

type of conference, Brandon succeeded in winning first place in the Masters-level poster competition. As part of this competition, the judges talk with the competitors and assess their ability to explain their work and answer questions. I believe that Brandon's poise and knowledge of his topic as well as the quality of his poster contributed to his winning this award. I am also very proud that Brandon is the recipient of the Inquiry student paper award. In short, it has been a pleasure to work with Brandon, and I'm sure that this project will be only one of many successes in his career.