FACTORS INFLUENCING DAMAGE FROM *DELIA ANTIQUA* IN ONION AND ACTIVITY OF SPINOSAD SEED TREATMENTS USED IN THEIR CONTROL

A Thesis
Presented to the Faculty of the Graduate School
of Cornell University
In Partial Fulfillment of the Requirements for the Degree of
Master of Science

by
Erica Moretti
May 2020

ABSTRACT

Onion maggot, *Delia antiqua* Meigen (Diptera: Anthomyiidae), is the most important early-season insect pest of commercial onion in the northeastern United States and Canada. Larvae of the pest feed on belowground tissue of onions and can cause substantial damage to seedlings. *Delia antiqua* is managed with seed treatments, and damage from the pest is highly variable across onion growing regions. The goals of the research presented here was to investigate factors associated with *D. antiqua* damage to determine what may be influencing the disparities in damage observed across the region and to evaluate the mechanism of control of the principal seed treatment, spinosad (Regard SC), used in its management. Relationships between plant damage and surrounding landscape, planting date, soil temperature, and soil organic matter were identified. Spinosad uptake in plant tissue, susceptibility of larvae through contact and ingestion, and behavior of larvae exposed to spinosad-treated plants revealed insights into the seed treatment's mechanism of control and highlighted areas in need of further research. Collectively, the results from these studies fill key gaps in our understanding of *D. antiqua* activity and control and will be used to inform areas of future research and improve management of this economically important pest.

BIOGRAPHICAL SKETCH

Erica grew up in the rolling hills of Indiana, Pennsylvania with her parents and two older sisters. She studied Environmental Science, minoring in Chemistry and Philosophy, at Allegheny College in Meadville, Pennsylvania where she earned her Bachelor of Science degree in May 2017. During her time as an undergraduate student, Erica developed her interests in agriculture and entomology working in the college's student garden and conducting research on native bees under the guidance of Dr. Beth Choate. Erica continued to gain experience in entomology by participating in the Cornell Summer Scholar Program in Geneva, New York where she studied European corn borer behavior with Dr. Rebecca Schmidt-Jeffris and Dr. Brian Nault. It was at this time that she gained further interest in integrated pest management. In the summer of 2017, Erica began her graduate studies at Cornell University in the Department of Entomology under the supervision of Brian Nault where she initially studied onion thrips resistance along with Dr. Jeff Scott. Following a rainy summer bereft of onion thrips, Erica transitioned her research to onion maggot on which she completed her thesis research.

For my parents

for their unending support

ACKNOWLEDGMENTS

First and foremost, I would like to express immense gratitude to my major advisor Dr. Brian Nault for his support, advice, encouragement, and unshakable positive attitude; thank you for encouraging me to pursue my research questions. In addition, I would like to thank my committee members, Drs. Kyle Wickings and Alan Taylor for their collaboration and advice. I would like to express my appreciation of Nault lab members, past and present, for providing such a welcoming community and excellent workplace for the past three years. A special thanks to Riley Harding whose tireless work managing the lab has ensured successful field seasons every year. Among the many technicians that assisted throughout my research, I would like to especially thank Kellie Damann and Mason Clark who drove countless miles with me across New York to evaluate maggot damage in onion fields. Thank you to Ashley Leach, for encouraging me to pursue onion maggot research questions and setting an amazing example of research integrity and diligence. Thank you to the best office mate in existence, Lindsy Iglesias, who kept me grounded and smiling throughout the last two years. Thank you to Abby Wentworth and members of the Wickings Lab for providing advice on soil sampling and analysis. Many thanks to the faculty, staff, technicians, and students of Cornell AgriTech for maintaining such a supportive and enjoyable workplace. Lastly, special thanks to the onion growers whose collaboration made this research possible. The research presented here was funded in part by a Northeast Sustainable Agriculture Research & Education (SARE) graduate student grant.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION

Onion Production Globally and in New York

Dry bulb onion, *Allium cepa* L., is a vegetable crop of global importance. It is produced in over 170 countries, led by China, India, and the United States (FAO, 2018). In the US, over 125,000 acres of onions are planted annually, with production valued at over $1 billion USD (NASS, 2017). Within the US, this economically important crop is produced commercially in 20 states, with top producing states including California, Oregon, Washington, Idaho, Georgia, Texas, and New York.

New York state is the number one producer of onions in the northeastern US, planting approximately 7,000 acres of onion annually and ranking it seventh in national onion production. Within the state, onion production is concentrated in Orange, Oswego, Orleans, Genesee, Madison, Yates, and Steuben counties, where onions are grown primarily on muck soils (Stivers, 1999), high organic matter histosols derived from drained lakebeds or wetlands with organic matter ranging from 20-80 percent (Lucas, 1982). The majority of onions produced are dry-bulb, long-day varieties sold as fresh-market produce. Approximately 70 percent of acreage is direct seeded while the remaining 30 percent is transplanted from bare root or plug seedlings. Most onions are planted between April and mid-May and harvested in August and September.

In New York, onion production is valued at $40-60 million USD, making it one of the most important specialty crops grown in the state (NASS, 2017).

Production is highly specialized, and the crop is intensively managed from seeding to harvest (Brewster 2008). Some of the most important limitations to production are pests, pathogens, and weeds. Principal insect pests of onion included foliar feeders, specifically onion thrips, *Thrips tabaci* Lindeman, cutworms, primarily black cutworm *Agrotis ipsilon* Hufnagel, and root feeders, which include seedcorn maggot, *Delia platura* Meigen, and onion maggot, *D. antiqua* Meigen (Hoffmann et al., 1996). Although seedcorn maggot and onion maggot co-occur in onion plantings, onion maggot remains the dominant maggot species infesting the crop in New York, and it is the most important early season pest of the crop (Nault et al. 2006a).

***Biology and Pest Status of* D. antiqua**

Onion maggot (Diptera: Anthomyiidae) is one of the most important insect pests of *Allium* crops, including onion and shallot, *A. cepa* (L.), leek, *A. ameloparsum* (L.), garlic, *A. sativum* (L.), and chives, *A. schoenoprasum* (L.) in northern temperate regions worldwide (Hoffmann et al., 1996). It is currently found throughout Europe, Asia, and North America, and its range is expected to broaden within these locations (Ning et al., 2017; Walters and Eckenrode, 1996). In North America, onion maggot is the most important early-season pest of onion in the northeast, northcentral and portions of the western United States and in Canada.

Closely related to other root feeding maggot species, including bean seed fly, *D. florilega*, cabbage maggot, *D. radicum*, and seedcorn maggot, onion maggot feeds on subterranean tissues of onions and related crops. Females use both visual (Harris and Miller, 1988, 1984, 1983) and olfactory cues (Gouinguené et al., 2005; Ikeshoji et al., 1981; Ishikawa et al., 1983, 1981; Judd and Borden, 1989) for host searching and selection and can oviposit hundreds of eggs over their 2-4 week lifespan (Loosjes, 1976). Flies deposit eggs, which are elongated in shape, ~1.25 mm, and white in color, on or at the base of onion plants (Havukkala et al., 1992). Once emerged, larvae move into the soil and feed on the belowground portion of the plants (roots and bulb), entering through the basal plate. The tapered, off-white larvae reach a maximum length of ~8 mm and develop through three instars before pupating in the soil at depths of 5-10 cm (Smith and Nault, 2014). In northern temperature regions, onion maggot undergoes three generations annually in the growing season and overwinters as pupae in the soil, emerging in spring, typically in early- to mid-May (Eckenrode et al., 1975; Vernon et al., 1987; Whitfield et al., 1985). Of the three generations, the first tends to be the most damaging because feeding on seedling onions results in high plant mortality.

Because onion maggot is a belowground pest, evidence of feeding is often not apparent until the plant has been damaged irrevocably. Small onion plants damaged by maggots appear flaccid and have droopy leaves (Figure 1.1). Damage by first-generation larvae on seedling onions tends to be aggregated in the field, as a result of clustered oviposition (Judd and Borden, 1992) and larval movement to adjacent undamaged plants (Whitfield et al., 1985; Workman, 1958). Seedling onions are at greatest risk for damage by first-generation larvae. Workman (1958) estimated that a single *D. antiqua* larva can consume an average of 28 seedling onions (1 mm diam) over its development. Larger onions can sustain more feeding; for example, one larva can complete its development on a single plant with diameter exceeding 4.5 mm (Workman, 1958). Feeding on developing bulbs, which usually occurs during the second generation of the pest, results in bulb distortion and creates entryways for fungal and bacterial pathogens that can cause bulb rot (Smith and Nault, 2014). Mature onions are less likely to be damaged by larvae, which often fail to penetrate the large, intact bulbs (Finch et al., 1986a). However, mature bulbs, especially if they have been damaged by harvest equipment, are still susceptible to feeding, which can render them unmarketable. In NY State, damage can exceed 80% in onions that are not treated with insecticides (Nault et al. 2006a, Moretti and Nault 2020).

Figure 1.1 Onion maggot damage early in the season. Plants infested with onion maggot become flaccid and limp (A) from the larvae feeding within the belowground portion of the plant (B). Photos courtesy of E. Moretti

Environment

Climate (specifically temperature), moisture dynamics, soil type, and surrounding habitat influence the survival and abundance of *D. antiqua*.

Temperature and Moisture. It has long been suggested that cooler temperatures and increased soil moisture are associated with increased onion maggot damage. This relationship has anecdotally been reported since the 1920s; since then, laboratory studies and observations have confirmed this association (Loosjes, 1976). The developmental optimum for *D. antiqua* has been estimated at approximately 22^{o}C (Miles, 1958; Robinson and Zurlini, 1979). Adult activity tends to decline in hotter temperatures (Finch et al., 1986b), and oviposition ceases at temperatures exceeding 30^{o}C (Keller and Miller, 1990). Laboratory tests have demonstrated improved egg viability and larval success under conditions of low temperature and high moisture (Ellington 1963). Workman (1958) similarly observed that at low moisture (<10% w/v) in muck soils, egg hatch was delayed, and larval survival and movement was hindered below 23% w/v soil moisture. In a field trial, Workman (1958) also observed that rows of onion receiving additional water had more damage than those that were not watered. Similar effects of temperature and moisture are shared among *Delia spp*., including *D. florilega* (Kim and Eckenrode, 1987; Throne and Eckenrode, 1986), *D. radicum* (Lepage et al., 2012), and *D. platura* (Hesler et al., 2018; Throne and Eckenrode, 1986).

Soil Type. For belowground pests, the soil environment has a profound effect on survival and movement (Villani and Wright, 1990). Dustan (1932) observed that onion maggot larvae perform better in “lighter” soils, i.e. soils with more organic matter compared to clay-rich soils. Potential mechanisms suggested to explain this relationship included an increase in mobility of larvae through the soil with greater organic matter, and increased habitat suitability due to elevated soil moisture content with increasing soil organic matter (Loosjes, 1976). However, to date, no studies have specifically evaluated the effects of soil characteristics on *D. antiqua* larval movement and survival.

Landscape. *Delia antiqua* flies display an edge-effect adjacent to onion field edges bordered by wooded areas, in contrast to those bordered by other vegetable crops. Finch et al. (1986b) observed elevated activity of flies adjacent to field perimeters next to wooded habitats, and Werling et al. (2006) confirmed that this effect is present in first-generation flies. Forested edges adjacent to fields may provide flies with protection from desiccation during the hottest time of day and may harbor protein-rich food sources for flies. Female flies require a protein-rich meal prior to oviposition, and flies have been observed feeding on floral resources, which may include pollen (Finch et al., 1986b; Loosjes, 1976).

Non-Chemical Management

Many different non-chemical approaches to *D. antiqua* management are known. These include crop rotation, crop sanitation, delayed planting, installation of protective barriers, biological control and sterile insect technique. Many of these tactics only marginally impact pest pressure (e.g. crop sanitation, delayed planting, biocontrol) and do not reduce maggot damage below economically damaging levels. While some of these tactics are extremely effective (e.g., crop rotation and protective barriers), they are not economically practical and cannot be deployed at the scale of commercial onion production.

Crop Rotation. Crop rotation can considerably reduce damage by *D. antiqua* (Finch et al. 1986a). Because onion production is highly specialized, onions are grown nearly exclusively on a very limited acreage of muck soil, growers often do not rotate out of onion. Moreover, there are many cases in which crop rotation will not reduce damage, even if carried out. Martinson et al. (1988) demonstrated that while crop rotation can be effective, its efficacy is dependent on distance from overwintering sites (i.e. other onion fields, cull piles). When rotated fields are near (<500m) overwintering sites, crop rotation does not reduce maggot damage to below economically damaging levels (stand reduction < 20%) relative to non-rotated controls. In fields rotated out of onion located at least 1500 m away from potential overwintering sites, crop rotation is highly effective, substantially reducing subsequent damage. Given these findings, onions grown in large, contiguous pockets of muck adjacent to other onion fields or cull piles (e.g. Elba muck) are unlikely to benefit from crop rotation.

Crop Sanitation. Crop sanitation, including the removal of cull and volunteer onions, proper disposal of culls and volunteers, and avoiding damaging bulbs in the field is an important facet of *D. antiqua* management. Onion is a biennial, so bulbs remaining in the field post-harvest will re-sprout the following year. These large "volunteer" onions are attractive to ovipositing females (Mowry, 1993) in the spring, and because these onions are not chemically protected, they can host many larvae early in the season.

Later in the growing season, cull onions and damaged bulbs serve as an important food source for second and third generation *D. antiqua* (Finch and Eckenrode, 1985). Although large bulbs tend to escape damage from larvae, as larvae often fail to penetrate developed bulbs, damaged or rotten bulbs can support large populations of overwintering pupae (Eckenrode and Nyrop, 1986; Finch et al., 1986a;

Finch and Eckenrode, 1985). Damaged bulbs and seedlings also release volatiles attractive to ovipositing females (Dindonis and Miller, 1980). Utilizing damaged bulbs as traps crops has been considered, but never implemented effectively or adopted widely (Cowles and Miller, 1992; Miller and Cowles, 1990).

Delayed Planting. *Delia antiqua* flies preferentially oviposit on larger onions (Harris et al., 1987; Nault et al., 2011). In laboratory choice and no-choice tests, females preferentially oviposited on eight-week-old onion over four-week old onions when given a choice, and without a choice, deposited fewer eggs on smaller onions (Nault et al., 2011). This preference can be exploited through delayed planting. Nault et al. (2011) demonstrated in field trials with staggered plantings that there was greater damage by *D. antiqua* in earlier planted plots than in later planted plots. Delayed planting creates asynchrony between the crop and the first generation of the pest, thus allowing the crop to escape the pest in time.

Despite this being an apparently effective approach for maggot management, delayed planting is not frequently implemented by growers to manage the pest. Delayed planting is most effective when the crop is planted as late as the last week in May (Nault et al., 2011). However, growers are unlikely to direct-seed past the third week in May. Onions seeded too late in the spring fail to reach their maximum potential bulb size or to mature in the field properly, risking lower yields. Growers are constrained early in the season by field conditions (fields that are too wet in the spring and cannot be planted) and later in the spring by bulb development. These constraints are more important determinants of when to plant the crop relative to potentially reducing the severity of maggot damage.

Host Plant Resistance. While *Allium spp.* differ in susceptibility to *D. antiqua*, there is little variation in susceptibility among onion (McFerson et al., 1996). Numerous onion germplasm accessions have been screened for resistance to larval feeding by *D. antiqua*. While some differences have been observed, the majority of accessions are equally susceptible to feeding (Harris et al., 1987; Mcdonald et al., 2002; McFerson et al., 1996). Therefore, in the absence of onion breeding lines with traits that confer resistant qualities to onion maggot, there are no commercially available resistant cultivars.

Barriers. Because *D. antiqua* oviposits on or at the base of onion plants, the use of physical barriers to exclude flies has been considered; row covers effectively reduce infestations of both *D. platura* and *D. radicum* (Hough-Goldstein, 1987; Matthews-Gehringer and Hough-Goldstein, 1988). Non-woven fibers applied to the soil surface forming a web-like barrier are effective at reducing oviposition by *D. antiqua* (Hirai, 2019; Hoffmann et al., 2001); however, the installation of a physical barrier is not practical for large-scale onion production and should only be considered in small-scale management applications.

Biological Control. *Delia spp.* pests are susceptible to a number of natural enemies and biocontrol agents. Predators of *Delia spp.* include many (60-100) species of staphylinid and carabid ground beetles, generalists that feed on eggs and early instars (Finch, 1989). Some staphylinid beetles, including *Aleochara bilineata* Gyllenhal and *A. bipustulata* Linnaeus, parasitize *Delia* pupae in addition to feeding on eggs (Finch, 1989; Whistlecraft et al., 1985). The braconid fly *Aphaereta pallipes* Say, which has a broad host range, also parasitizes *D. antiqua* successfully

(Whistlecraft et al., 1984). In addition to predators and parasitoids, other biocontrol agents of *Delia* include entomopathogenic fungi (EPFs) and nematodes (EPNs).

Screenings of EPFs suggest that *Entomophthora muscae*, *Metarhizium anispliae,* and *Beauveria bassiana* are all capable of infecting and killing *Delia sp*. pests (Raymond I. Carruthers et al., 1985; Davidson and Chandler, 2005; Majchrowicz et al., 1990; Poprawski et al., 1985; Zhang et al., 2016). *Entomophthora muscae* is a broad muscoid pathogen naturally occurring in many *D. antiqua* populations (Raymond I. Carruthers et al., 1985; Smith and Nault, 2014); however, the conditions favorable for the survival and transmission of the fungi are often not favorable to the pest nor do they reflect field conditions, which are inhospitable to the pathogen (Carruthers and Haynes, 1986, 1985). Moreover, fungicides used to manage plant pathogens can negatively affect EPFs (Carruthers et al., 1985), limiting the commercial use of products employing these pathogens as pest control.

Similarly, EPNs, including commercially available species such as *Steinernema feltiae* and *Heterorhabditis bacteriophora*, infect *D. antiqua* (Finch, 1989; Morris, 1985; Yildrim and Hoy, 2003); however, field conditions are not often favorable to their coexistence. Recent screenings of several New York onion fields revealed that among the fields evaluated, there were no resident populations of EPNs, suggesting that they are not currently contributing to pest control in the region (D. Willett and C. Filgueiras, personal communication).

Despite the variety of biocontrol agents, there is little evidence that any will reduce *D. antiqua* populations below economically damaging levels, at least given the existing cropping and pest management practices. Thus, the role of biocontrol for *D. antiqua* management is currently limited.

Sterile Insect Technique. Sterile insect technique (SIT) is a pest management tactic in which large numbers of a pest are reared and sterilized, then released into the wild population. Sterile males compete with fertile males to mate with fertile females, reducing the number of viable offspring (Klassen, 2005). In combination with traditional pest management tactics, SIT can substantially reduce resident populations of a pest over wide areas over time. This approach is most well-known for its role in the successful eradication of screwworm, *Cochliomyia hominivorax* Coquerel, in the US that began in the 1950s (Klassen and Curtis, 2005).

SIT was first applied to the management of *D. antiqua* in the Netherlands in the 1970s (Loosjes, 1976). High numbers of the insect are reared in the laboratory, and one-day prior to emergence, pupae are exposed to either x-ray or gamma radiation, sterilizing male sperm cells and arresting development of female ovaries (Ticheler et al., 1980). Flies are then marked with dye to monitor the ratio of sterile/fertile males as the season progresses and are released into high pressure areas. This process has become commercialized in the Netherlands and is carried out by De Groene Vlieg BioControl & Diagnostics. Despite its efficacy, adoption of this practice has not expanded past 16% of onion acreage in the Netherlands, as many growers opt out of adoption and continue employing chemical control instead (Klassen, 2005). In addition to the Netherlands, a company in Quebec, Canada (PhytoData, Inc) commercialized this process in 2011 (Cranmer, 2019). In 2017, SIT was implemented in nearly 680 hectares of onion in Quebec; however, efficacy and adoption data from the province is not widely available.

Currently, there are no companies in the US commercially producing sterilized *D. antiqua* and there are no readily available estimates for how costly this approach will be. As a result, although SIT has the potential to substantially reduce *D. antiqua* damage, it has not been adopted in the US.

Chemical management

Given the practical and economic limitations of non-chemical management tools, growers heavily rely upon chemical management tactics. Currently, *D. antiqua* is managed principally with insecticides applied as seed treatments and in-furrow applications of chlorpyrifos at planting (Reiners et al., 2019). Because of the movement and dispersal of flies during the day, sprays targeting flies are not likely to make contact with the pest and are not recommended for fly management, despite some growers continuing this practice (Finch et al., 1986b).

Prior to the introduction of seed treatments in onion pest management, insecticides used to manage *D. antiqua* were exclusively incorporated into the soil in granular or drench form. In the 1940s, growers relied on broad-spectrum products belonging to organochlorine, organophosphate, and carbamate classes, to which *D. antiqua* developed resistance rapidly (Finlayson et al., 1959; Howitt, 1958; Ritcey and Mcewen, 1984; Taylor et al., 2001). Since being labeled in the early 1980s, chlorpyrifos (Lorsban®, Corteva, Indianapolis, IN,USA), has been the principal insecticide applied in-furrow to manage maggot pests of onion (Taylor et al., 2001).

However, it also has become ineffective due to resistance in many areas (Hessney and Eckenrode 2000, Nault et al. 2006b). Moreover, it is slowly being phased out of use due to its negative non-target effects and high-risk to human health.

Given the limitations with chlorpyrifos (both regulatory and resistance-related), growers rely almost exclusively on insecticide seed treatments for maggot pest management. Because the first generation of maggots are the most damaging, and rescue treatments are not available once a field is infested, seed-treatments are employed prophylactically. Currently, there are several seed treatments available to growers (Table. 1.1). At this time, the two most effective insecticides applied as seed treatments for *D. antiqua* management are spinosad, a spinosyn that acts as a nicotinic acetocholine allosteric inhibitor (Bacci et al., 2016; Dripps et al., 2011; B. A. Nault et al., 2006; Wilson et al., 2015), and cyromazine, a growth disrupter that works by stiffening the larval cuticle (Hayden and Grafius, 1990; Kotze and Reynolds, 1991; Taylor et al., 2001; Yildirim and Hoy, 2003). Spinosad is available alone as Regard SC or as part of a seed treatment package including thiamethoxam (FarMore FI500, Syngenta); however, thiamethoxam alone is not effective against *D. antiqua* (Nault et al. 2006a, Wilson et al. 2015). There are also two neonicotinoid insecticides labeled for use on onion, clothianidin and imidacloprid; however, despite performing well in some field trials (B. A. Nault et al., 2006; Wilson et al., 2015), the product has not performed as well as either spinosad or cyromazine in field trials in New York (Hoepting and Nault, 2012). Both treatments perform better as seed treatments than when applied directly to the soil (Yildirim and Hoy 2003, Nault unpublished). Current recommendations advise that growers annually rotate between these two active ingredients in order to reduce selection pressure on *D. antiqua* to adapt to either one (Hoepting and Nault, 2012; Moretti et al., 2019).

Table 1.1. Seed treatments labeled for *Delia antiqua* management in New York. Adapted from Reiners et al. 2019.

Insecticides	IRAC Group	Trade-Name	Company
clothianidin + imidacloprid	4A	Sepresto 75WS	Bayer, Triangle Park, NC
cyromazine	17	Trigard	ADAMA, Raleigh, NC
spinosad + thiamethoxam	5 + 4A	FarMore FI500*	Syngenta, Greensboro, NC
spinosad	5	Regard SC	Syngenta, Greensboro, NC

*FarMore FI500 package also includes three fungicide: azoxystrobin, fludioxonil, and mefenoxam.

Research Goals

Delia antiqua is a devastating pest of onion and its management is crucial for the economic sustainability of onion production, particularly in the Great Lakes region of North America. Despite employing similar onion production and pest management practices across this region, onion growers experience highly variable damage from *D. antiqua*. Some growers seldom report problems with the pest, while others consistently report substantial losses (>30%). Therefore, identifying factors that explain why differences in onion maggot damage occur among fields would be invaluable for predicting risk for maggot attack as well as helping inform deployment of specific pest management practices.

Moreover, spinosad has been the primary insecticide used to manage onion maggot in commercial onion fields. Since 2011, it has been delivered in the seed treatment package, FarMore FI500, and has provided excellent control. Yet, very little is understood regarding the mechanism for how spinosad protects onion seedlings from becoming damaged by onion maggot. While other studies have shown that spinosad can move systemically within plants (Van Leeuwen et al., 2006; van Leeuwen et al., 2005; Weintraub and Mujica, 2006) it is not known if this occurs in onion. Furthermore, it remains unclear whether larval control is achieved through contact in the soil, or if spinosad is taken up by the plant, and larva are controlled by mortality via ingestion. Understanding the mechanism for how spinosad protects onion seedlings from onion maggot may provide insight into future delivery tactics as well as future compatibility with other management strategies and resistance management strategies.

To address these gaps in our knowledge about *D. antiqua* population ecology and management, I had two main objectives:

Objective 1: To assess environmental and management factors associated with *D. antiqua* damage across onion fields experiencing variable pressure from the pest to determine which factors are associated with increased plant damage.

Objective 2: To improve our understanding of spinosad seed treatments used in the management of *D. antiqua* by evaluating uptake and dissipation of spinosad in onion plants during the first-generation of *D. antiqua*, quantifying susceptibility of larvae to spinosad through different modes of contact (ingestion and contact), and assessing behavior of larvae exposed to onion seedlings grown with spinosad-treated seeds.

REFERENCES

Bacci, L., Lupi, D., Savoldelli, S., Rossaro, B., 2016. A review of Spinosyns, a derivative of biological acting substances as a class of insecticides with a broad range of action against many insect pests. Journal of Entomological and Acarological Research 48, 40. https://doi.org/10.4081/jear.2016.5653

Carruthers, R.I., Haynes, D.L., 1986. Temperature, moisture, and habitat effects on *Entomophthora muscae* (Entomophthorales: Entomophthoraceae) conidial germination and survival in the onion agroecosystem. Environ Entomol 15, 1154–1160. https://doi.org/10.1093/ee/15.6.1154

Carruthers, R.I., Haynes, D.L., 1985. Laboratory transmission and in vivo incubation of *Entomophthora muscae* (Entomophthorales: Entomophthoracae) in the onion fly, *Delia antiqua* (Diptera: Anthomyiidae). Journal of Invertebrate Pathology 45, 282–287. https://doi.org/10.1016/0022-2011(85)90105-3

Carruthers, Raymond I., Haynes, D.L., MacLeod, D.M., 1985. *Entomophthora muscae* (Entomophthorales: Entomophthoracae) mycosis in the onion fly, *Delia antiqua* (Diptera: Anthomyiidae). Journal of invertebrate pathology 45, 81–93.

Carruthers, R. I., Whitfield, G.H., Haynes, D.L., 1985. Pesticide-induced mortality of natural enemies of the onion maggot, *Delia antiqua* (Dip.: Anthomyiidae). Entomophaga 30, 151–161. https://doi.org/10.1007/BF02372248

Cowles, R.S., Miller, J.R., 1992. Diverting *Delia antiqua* (Diptera: Anthomyiidae) Oviposition with cull onions: field studies on planting depth and a greenhouse test of the stimulo-deterrent concept. Environmental Entomology 21, 453–460. https://doi.org/10.1093/ee/21.3.453

Cranmer, T., 2019. Can Onion Maggot be managed without insecticides? [WWW Document]. ONvegetables. URL https://onvegetables.com/2019/03/01/can-onion-maggot-be-managed-without-insecticides/ (accessed 3.17.20).

Davidson, G., Chandler, D., 2005. Laboratory evaluation of entomopathogenic fungi against larvae and adults of onion maggot (Diptera : Anthomyiidae). J. Econ. Entomol. 98, 1848–1855.

Dindonis, L.L., Miller, J.R., 1980. Host-finding responses of onion and seedcorn flies to healthy and decomposing onions and several synthetic constituents of onion. Environ Entomol 9, 467–472. https://doi.org/10.1093/ee/9.4.467

Dripps, J.E., Boucher, R.E., Chloridis, A., Cleveland, C.B., DeAmicis, C.V., Gomez, L.E., Paroonagian, D.L., Pavan, L.A., Sparks, T.C., Watson, G.B., 2011. CHAPTER 5. The

Spinosyn Insecticides, in: López, Ó., Fernández-Bolaños, J.G. (Eds.), RSC Green Chemistry. Royal Society of Chemistry, Cambridge, pp. 163–212. https://doi.org/10.1039/9781849732901-00163

Dustan, A.G., 1932. The Effect of some Physical Factors on Onion Maggot Infestations in Light and Heavy Soils. Annual Report of the Quebec Society for the Protection of Plants 32, 20-27..

Eckenrode, C., Vea, E., Stone, K., 1975. Population trends of onion maggots correlated with air thermal units accumulations. Environ. Entomol. 4, 785–789.

Eckenrode, C.J., Nyrop, J.P., 1986. Impact of physical injury and commercial lifting on damage to onion bulbs by larvae of onion maggot (Diptera: Anthomyiidae). Journal of Economic Entomology 79, 1606–1608. https://doi.org/10.1093/jee/79.6.1606

Ellington, J.J., 1963. Field and laboratory observations on the life history of the onion maggot ylemyia antiqua (Meigen). Cornell University.

FAOSTAT [WWW Document], 2018. URL http://www.fao.org/faostat/en/#home (accessed 3.30.20).

Finch, S., 1989. Ecological considerations in the management of delia pest species in vegetable crops. Annual Review of Entomology 34, 117–137. https://doi.org/10.1146/annurev.en.34.010189.001001

Finch, S., Cadoux, M.E., Eckenrode, C.J., Spittler, T.D., 1986a. Appraisal of current strategies for controlling onion maggot (Diptera: Anthomyiidae) in New York State. Journal of Economic Entomology 79, 736–740. https://doi.org/10.1093/jee/79.3.736

Finch, S., Eckenrode, C.J., 1985. Influence of unharvested, cull-pile, and volunteer onions on populations of onion maggot (Diptera: Anthomyiidae). Journal of Economic Entomology 78, 542–546. https://doi.org/10.1093/jee/78.3.542

Finch, S., Eckenrode, C.J., Cadoux, M.E., 1986b. Behavior of onion maggot (Diptera: Anthomyiidae) in commercial onion fields treated regularly with parathion sprays. Journal of economic entomology 79, 107–113.

Finlayson, D.G., Crowell, H.H., Howitt, A.J., Scott, D.R., Walz, A.J., 1959. Chemical control of the onion maggot in onions grown from seed in various types of soil in northwestern north america in 1955 and 1956. J Econ Entomol 52, 851–856. https://doi.org/10.1093/jee/52.5.851

Gouinguené, S.P., Buser, H.-R., Städler, E., 2005. Host-plant leaf surface compounds influencing oviposition in *Delia antiqua*. Chemoecology 15, 243–249. https://doi.org/10.1007/s00049-005-0319-3

Harris, M.O., Miller, J.R., 1988. Host-acceptance behaviour in an herbivorous fly, *Delia antiqua*. Journal of Insect Physiology, Host Finding and Feeding in Adult Phystophagous Insects 34, 179–190. https://doi.org/10.1016/0022-1910(88)90048-0

Harris, M.O., Miller, J.R., 1984. Foliar form influences ovipositional behaviour of the onion fly. Physiological Entomology 9, 145–155. https://doi.org/10.1111/j.1365-3032.1984.tb00693.x

Harris, M.O., Miller, J.R., 1983. Color stimuli and oviposition behavior of the onion fly, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae)1. Annals of the Entomological Society of America 76, 766–771. https://doi.org/10.1093/aesa/76.4.766

Harris, M.O., Miller, J.R., Ponti, O.M.B., 1987. Mechanisms of resistance to onion fly egg-laying. Entomologia Experimentalis et Applicata 43, 279–286. https://doi.org/10.1111/j.1570-7458.1987.tb02223.x

Havukkala, I., Harris, M., Miller, J., 1992. Onion fly egg distribution in soil - a new sampling method and the effect of two granular insecticides. Entomol. Exp. Appl. 63, 283–289.

Hayden, J., Grafius, E., 1990. Activity of cyromazine on onion maggot larvae (Diptera: Anthomyiidae) in the soil. Journal of Economic Entomology 83, 2398–2400. https://doi.org/10.1093/jee/83.6.2398

Hesler, L.S., Allen, K.C., Luttrell, R.G., Sappington, T.W., Papiernik, S.K., 2018. Early-season pests of soybean in the United States and factors that affect their risk of infestation. J Integr Pest Manag 9. https://doi.org/10.1093/jipm/pmx028

Hessney, M.L., Eckenrode, C.J., 2000. Onion maggot resistance to Lorsban, 1999. Arthropod Manag Tests 25. https://doi.org/10.1093/amt/25.1.L9

Hirai, G., 2019. The effect of non-woven fabric floating row covers on the emergence, growth, and bulb yield of direct-seeded onions (*Allium cepa* L.) in a Subarctic Area. The Horticulture Journal 88, 67–75. https://doi.org/10.2503/hortj.OKD-172

Hoepting, C.A., Nault, B.A., 2012. New developments for managing onion maggot. Cornell Cooperative Extension. VegEdge 8, 10–13.

Hoffmann, M.P., Kuhar, T.P., Baird, J.M., Gardner, J., Schwartz, P., Shelton, A.M., 2001. Nonwoven fiber barriers for control of cabbage maggot and onion maggot (Diptera: Anthomyiidae). J Econ Entomol 94, 1485–1491. https://doi.org/10.1603/0022-0493-94.6.1485

Hoffmann, M.P., Petzoldt, C.H., Frodsham, A.C., 1996. Integrated Pest Management for Onions. Cornell University, Ithaca, NY.

Hough-Goldstein, J.A., 1987. Tests of a spun polyester row cover as a barrier against seedcorn maggot (Diptera: Anthomyiidae) and cabbage pest infestations. J Econ Entomol 80, 768–772. https://doi.org/10.1093/jee/80.4.768

Howitt, A.J., 1958. Chemical control of *Hylemya antiqua* (Meig.) in the Pacific Northwest. J Econ Entomol 51, 883–887. https://doi.org/10.1093/jee/51.6.883

Ikeshoji, T., Ishikawa, Y., Matsumoto, Y., 1981. Behavioral and EAG synergism of varous compounds to dipropyl disulfide in the ovipositional attraction of the onion fly : *Hylemya antiqua* MEIGEN : Diptera : Anthomyiidae. Applied Entomology and Zoology 16, 432–442. https://doi.org/10.1303/aez.16.432

Ishikawa, Y., Ikeshoji, T., Matsumoto, Y., Tsutsumi, M., Mitsui, Y., 1983. 2-Phenylethanol : an attractant for the onion and seed-corn flies, *Hylemya antiqua* and *H. platura* (Diptera : Anthomyiidae). Applied Entomology and Zoology 18, 270–277. https://doi.org/10.1303/aez.18.270

Ishikawa, Y., Ikeshoji, T., Matsumoto, Y., Tsutsumi, M., Mitsui, Y., 1981. Field trapping of the onion and seed-corn flies with baits of fresh and aged onion pulp. Applied Entomology and Zoology 16, 490–493. https://doi.org/10.1303/aez.16.490

Judd, G.J.R., Borden, J.H., 1992. Aggregated oviposition in *Delia antiqua* (Meigen): A case for mediation by semiochemicals. J Chem Ecol 18, 621–635. https://doi.org/10.1007/BF00987824

Judd, G.J.R., Borden, J.H., 1989. Distant olfactory response of the onion fly, *Delia antiqua*, to host-plant odour in the field. Physiological Entomology 14, 429–441. https://doi.org/10.1111/j.1365-3032.1989.tb01112.x

Keller, J.E., Miller, J.R., 1990. Onion fly oviposition as influenced by soil temperature. Entomologia Experimentalis et Applicata 54, 37–42. https://doi.org/10.1111/j.1570-7458.1990.tb01309.x

Kim, T.H., Eckenrode, C.J., 1987. Bionomics of the bean seed maggot, *Delia florilega* (Diptera: Anthomyiidae), Under Controlled Conditions. Environ Entomol 16, 881–886. https://doi.org/10.1093/ee/16.4.881

Klassen, W., 2005. Area-Wide Integrated Pest Management and the Sterile Insect Technique, in: Dyck, V.A., Hendrichs, J., Robinson, A.S. (Eds.), Sterile Insect Technique: Principles and Practice in Area-Wide Integrated Pest Management. Springer Netherlands, Dordrecht, pp. 39–68. https://doi.org/10.1007/1-4020-4051-2_2

Klassen, W., Curtis, C.F., 2005. History of the Sterile Insect Technique, in: Dyck, V.A., Hendrichs, J., Robinson, A.S. (Eds.), Sterile Insect Technique: Principles and Practice in Area-Wide Integrated Pest Management. Springer Netherlands, Dordrecht, pp. 3–36. https://doi.org/10.1007/1-4020-4051-2_1

Kotze, A.C., Reynolds, S.E., 1991. An examination of cuticle chitin and protein in cyromazine-affected *Manduca sexta* larvae. Pesticide Biochemistry and Physiology 41, 14–20. https://doi.org/10.1016/0048-3575(91)90055-Q

Lepage, M.P., Bourgeois, G., Brodeur, J., Boivin, G., 2012. Effect of soil temperature and moisture on survival of eggs and first-instar larvae of *Delia radicum*. Environ. Entomol. 41, 159–165. https://doi.org/10.1603/EN10313

Loosjes, M., 1976. Ecology and genetic control of the onion fly, *Delia antiqua* (Meigen). PUDOC, Wageningen.

Lucas, R., E., 1982. Organic Soils (Histosols): Formation, Distribution, Physical and Chemical Properties and Management for Crop Production. Michigan State University, Agricultural Experiment Station.

Majchrowicz, I., Poprawski, T.J., Robert, P.-H., Maniania, N.K., 1990. Effects of entomopathogenic and opportunistic fungi on *Delia antiqua* (Diptera: Anthomyiidae) at low relative humidity. Environmental Entomology 19, 1163–1167. https://doi.org/10.1093/ee/19.4.1163

Martinson, T.E., Nyrop, J.P., Eckenrode, C.J., 1988. Dispersal of the onion fly (Diptera: Anthomyiidae) and larval damage in rotated onion fields. Journal of economic entomology 81, 508–514.

Matthews-Gehringer, D., Hough-Goldstein, J., 1988. Physical barriers and cultural practices in cabbage maggot (Diptera: Anthomyiidae) Management on broccoli and chinese cabbage. J Econ Entomol 81, 354–360. https://doi.org/10.1093/jee/81.1.354

Mcdonald, M.R., Kooi, K.V., Kornatowska, B., Janse, S., 2002. Screening onion breeding lines for resistance to onion maggot (*Delia antiqua* Meigen) damage. J Ent. Soc. Ont. 133, 10.

McFerson, J.R., Walters, T.W., Eckenrode, C.J., 1996. Variation in Allium spp. damage by onion maggot. HortScience 31, 4.

Miles, M., 1958. Studies of British Anthomyiid Flies. IX.—Biology of the onion fly, *Delia antiqua* (Mg.). Bulletin of Entomological Research 49, 405–414. https://doi.org/10.1017/S0007485300053700

Miller, J.R., Cowles, R.S., 1990. Stimulo-deterrent diversion: A concept and its possible application to onion maggot control. J Chem Ecol 16, 3197–3212. https://doi.org/10.1007/BF00979619

Moretti, E., Nault, B., Hoepting, C., 2019. Seed treatment recommendations for onion maggot control in 2020. VegEdge 15, 4–5.

Moretti, E., Nault, B.A., 2020. Onion Maggot Control in Onion, 2019. Arthropod Manag Tests 45. https://doi.org/10.1093/amt/tsaa007

Morris, O.N., 1985. Susceptibility of 31 species of agricultural insect pests to the entomogenous nematodes *Steinernema feltiae* and *Heterorhabditis bacteriophora*. The Canadian Entomologist 117, 401–407. https://doi.org/10.4039/Ent117401-4

Mowry, T., 1993. Ovipositional patterns and larval movement of *Delia antiqua* (Diptera, Anthomyiidae) on sprouted bulb and seedling onions. J. Econ. Entomol. 86, 1440–1445.

NASS, 2017. 2016-2017 Agricultural statistics annual bulletin: New York.

Nault, B. A., Straub, R.W., Taylor, A.G., 2006. Performance of novel insecticide seed treatments for managing onion maggot (Diptera : Anthomyiidae) in onion fields. Crop Prot. 25, 58–65. https://doi.org/10.1016/j.cropro.2005.03.020

Nault, B.A., Werling, B.P., Straub, R.W., Nyrop, J.P., 2011. Delaying onion planting to control onion maggot (Diptera: Anthomyiidae): Efficacy and underlying mechanisms. Journal of Economic Entomology 104, 1622–1632. https://doi.org/10.1603/EC11175

Nault, Brian A., Zhao, J.-Z., Straub, R.W., Nyrop, J.P., Hessney, M.L., 2006. Onion maggot (Diptera : Anthomyiidae) resistance to chlorpyrifos in New York onion fields. J. Econ. Entomol. 99, 1375–1380.

Ning, S., Wei, J., Feng, J., 2017. Predicting the current potential and future world wide distribution of the onion maggot, *Delia antiqua* using maximum entropy ecological niche modeling. PLOS ONE 12, e0171190. https://doi.org/10.1371/journal.pone.0171190

Poprawski, T.J., Robert, P.-H., Majchrowicz, I., Boivin, G., 1985. Susceptibility of *Delia antiqua* (Diptera: Anthomyiidae) to eleven isolates of entomopathogenic hyphomycetes. Environmental Entomology 14, 557–561. https://doi.org/10.1093/ee/14.5.557

Reiners, S., Curtis, P.D., Helms, M., McGrath, M.T., Nault, B.A., Seaman, A., 2019. Cornell integrated crop and pest management guidelines for commercial vegetable production, in: N.Y. State Integ. Pest Manag. Progr. Cornell University, Geneva, NY.

Ritcey, G., Mcewen, F.L., 1984. Control of the onion maggot, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae), with furrow treatments. J Econ Entomol 77, 1580–1584. https://doi.org/10.1093/jee/77.6.1580

Robinson, A.S., Zurlini, G., 1979. The response of two strains of *Hylemya antiqua* (diptera: anthomyiidae) to a constant and an alternating temperature regime. The Canadian Entomologist 111, 1207–1217. https://doi.org/10.4039/Ent1111207-11

Smith, E.A., Nault, B.A., 2014. Onion Maggot Factsheet. Cornell University Department of Entomology.

Stivers, L., 1999. Crop Profile: Onions in New York.

Taylor, A.G., Eckenrode, C.J., Straub, R.W., 2001. Seed coating technologies and treatments for onion: challenges and progress. HortScience 36, 199–205.

Throne, J.E., Eckenrode, C.J., 1986. Development rates for the seed maggots *Delia platur*a and *D. florilega* (Diptera: Anthomyiidae). Environ Entomol 15, 1022–1027. https://doi.org/10.1093/ee/15.5.1022

Ticheler, J., Loosjes, M., Noorlander, J., 1980. Sterile-insect technique for control of the onion maggot, *Delia antiqua*, in: Integrated Control of Insect Pests in the Netherlands. Wageningen, WageningenCetnre for Agricultural Publishing and Documentation, pp. 93–97.

van Leeuwen, T., Dermauw, W., Van De Veire, M., Tirry, L., 2005. Systemic use of spinosad to control the two-spotted spider mite (Acari: Tetranychidae) on tomatoes grown in rockwool. Experimental and Applied Acarology 37, 93–105. https://doi.org/10.1007/s10493-005-0139-8

Van Leeuwen, T., Van de Veire, M., Dermauw, W., Tirry, L., 2006. Systemic toxicity of spinosad to the greenhouse whitefly *Trialeurodes vaporariorum* and to the cotton leaf worm *Spodoptera littoralis*. Phytoparasitica 34, 102–108. https://doi.org/10.1007/BF02981345

Vernon, R.S., Judd, G.J.R., Borden, J.H., 1987. Commercial monitoring programme for the onion fly, *Delia antiqua* (Meigen)(Diptera: Anthomyiidae) in south-western British Columbia. Crop Protection 6, 304–312.

Villani, M.G., Wright, R.J., 1990. Environmental influences on soil macroarthropod behavior in agricultural systems. Annual review of entomology 35, 249–269.

Walters, T.W., Eckenrode, C.J., 1996. Integrated management of the onion maggot (Diptera: Anthomyiidae). J Econ Entomol 89, 1582–1586. https://doi.org/10.1093/jee/89.6.1582

Weintraub, P.G., Mujica, N., 2006. Note: Systemic effects of a spinosad insecticide on *Liriomyza huidobrensis* larvae. Phytoparasitica 34, 21–24. https://doi.org/10.1007/BF02981335

Werling, B.P., Nyrop, J., Nault, B., 2006. Spatial and temporal patterns of onion maggot adult activity and oviposition within onion fields that vary in bordering habitat. Entomol. Exp. Appl. 118, 49–59. https://doi.org/10.1111/j.1570-7458.2006.00363.x

Whistlecraft, J.W., Harris, C.R., Tolman, J.H., Tomlin, A.D., 1985. Mass-rearing technique for *Aleochara bilineata* (Coleoptera: Staphylinidae). J Econ Entomol 78, 995–997. https://doi.org/10.1093/jee/78.4.995

Whistlecraft, J.W., Harris, C.R., Tomlin, A.D., Tolman, J.H., 1984. Mass rearing technique for a braconid parasite, *Aphaereta pallipes* (Say) (Hymenoptera: Braconidae). J Econ Entomol 77, 814–816. https://doi.org/10.1093/jee/77.3.814

Whitfield, G.H., Carruthers, R.I., Lampert, E.P., Haynes, D.L., 1985. Spatial and temporal distribution of plant damage caused by the onion maggot (Diptera: Anthomyiidae). Environ Entomol 14, 262–266. https://doi.org/10.1093/ee/14.3.262

Wilson, R.G., Orloff, S.B., Taylor, A.G., 2015. Evaluation of insecticides and application methods to protect onions from onion maggot, *Delia antiqua*, and seedcorn maggot, *Delia platura*, damage. Crop Prot. 67, 102–108. https://doi.org/10.1016/j.cropro.2014.10.002

Workman, R.B., 1958. The biology of the onion maggot, *Hylemyia antiqua* (Meigen), under field and greenhouse conditions. Oregon State College.

Yildirim, E., Hoy, C.W., 2003. Cyromazine seed treatments to control onion maggot, *Delia antiqua*, on green onions. J. Econ. Entomol. 96, 6.

Yildrim, E., Hoy, C.W., 2003. Interaction between cyromazine and the entomopathogenic nematode *Heterorhabditis bacteriophora* Poinar "GPS11" for control of onion maggot, *Delia antiqua* (Meigen). Crop Protection 22, 923–927. https://doi.org/10.1016/S0261-2194(03)00091-7

Zhang, H., Wu, S., Xing, Z., Wang, X., Lei, Z., 2016. Bioassay and scanning electron microscopic observations reveal high virulence of entomopathogenic fungus, *Beauveria bassiana*, on the Onion Maggot (Diptera: Anthomyiidae) adults. J. Econ. Entomol. 109, 2309–2316. https://doi.org/10.1093/jee/tow235

CHAPTER 2

ENVIRONMENTAL FACTORS AND PRODUCTION PRACTICES THAT AFFECT *DELIA ANTIQUA* DAMAGE IN ONION FIELDS

Abstract

Many factors can directly and indirectly influence pest dynamics in cultivated crops. Identifying the suite of factors associated with a pest's population dynamics is an important component of pest management. Onion maggot, *Delia antiqua* Meigen (Diptera: Anthomyiidae), is a significant pest of onion in temperature regions worldwide. In the Great Lakes region of North America, *D. antiqua* is the most important early-season pest of onion and causes considerable damage to seedling onions. Despite growers employing the same production tactics, using the same insecticide seed treatments, and cultivating the crop on similar soil types, damage across field sites is highly variable. The commonality of production and management suggests that other factors may be important in explaining the disparities in damage across the region, and previous studies have indicated that temperature and precipitation, soil organic matter content, surrounding landscape composition, planting date, and plant size at peak fly activity are all important factors affecting *D. antiqua*. However, no study has evaluated the relationship between all of these factors and *D. antiqua* damage in onion fields. In a two-year study (2018-19), the aforementioned factors were monitored in commercial onion fields (2018: n=15; 2019: n=13) in central and western New York, USA. Fly activity was positively associated with onion

plant damage in both years of the study. Onion fields surrounded primarily by forest compared with vegetable fields and those planted late compared with early in the season had higher levels of damage by *D. antiqua*. Plant damage also was negatively associated with soil temperature and positively associated with soil organic matter content, but these effects were context dependent and were only observed in the first year of the study. Based on these factors, predictive models for damage by *D. antiqua* were developed to inform management decisions such as selective deployment of insecticides and crop rotation.

Introduction

Insect pest populations in cultivated crops are influenced by environmental factors as well as crop production practices, including pest management. The most important environmental factors are typically temperature and precipitation (Porter et al., 1991), but also include temporal and spatial dynamics such as host availability and landscape complexity (Van Vuren and Smallwood, 1996). Influential crop production and pest management practices include cultivar, fertilization, planting date, crop rotation, chemical control, biological control, harvest date, and crop sanitation, among others. For belowground pests that are in direct contact with the soil environment, soil moisture, organic matter, pH, and texture are often significant factors (Brown and Gange, 1990; Villani and Wright, 1990). Identifying the suite of factors that exert the largest effect on pest populations is key for understanding the distribution of a pest across a region and can ultimately help make advancements in pest management.

Onion maggot (*Delia antiqua*) is a significant pest of *Allium* crops, specifically onion (*Allium cepa* L.), and occurs throughout temperate regions worldwide (Eckenrode et al., 1975). In North America, *D. antiqua* is the most important early-season pest of onion in the Great Lakes region. *Delia antiqua* damages onion crops by directly feeding on seedlings and bulbs and indirectly by facilitating entry of pathogens (Ellis and Eckenrode, 1979; Loosjes, 1976; McDonald et al., 2004). In New York, where nearly 3,000 ha of onion are planted annually, crop losses of unprotected plants can exceed 50% (Nault et al., 2006; Taylor et al., 2001). The pest overwinters as a pupa in the soil, and flies emerge in early spring, typically in mid-May. Females oviposit on or at the base of onion plants, and larvae move into the root zone, enter the basal plate, and feed within the belowground portion of the plant (roots and bulb) (Loosjes, 1976). While *D. antiqua* undergoes three generations annually in the Great Lakes region (Eckenrode et al., 1975; Vernon et al., 1987; Whitfield et al., 1985), the first, which occurs from mid-May to mid-July, is the most damaging because feeding kills onions (Workman, 1958). For this reason, early-season protection and prediction of at-risk fields is crucial for maintaining the profitability of this crop.

Growers manage *D. antiqua* principally through the prophylactic use of insecticides at planting, specifically seed treatments (Nault et al., 2006). However, options for effective seed treatments are limited by available chemistries (Reiners et al., 2019) and resistance of the pest to chlorpyrifos (Hessney and Eckenrode, 2000; Nault et al., 2006). Spinosad, found in the seed treatment package FarMore FI500 (Syngenta), and cyromazine (Trigard, ADAMA) are the two most effective and commonly used active ingredients applied as seed treatments for the management of

D. antiqua (Nault et al., 2006; Wilson et al., 2015; Yildirim and Hoy, 2003). In an onion field in New York with a history of severe *D. antiqua* infestations, spinosad and cryomazine performed equally well in protecting the crop from *D. antiqua* damage (Moretti and Nault, 2020). Despite the widespread adoption of these effective seed treatments as well as additional similar cultivation practices, including cultivars, seeding densities, crop rotational strategies, and planting in the same soil types (high organic matter muck soils), onion growers experience highly variable *D. antiqua* damage. In New York, some growers experience virtually no damage, while others report substantial losses (>30%) annually. The commonality of these pest management strategies and crop production practices suggests that other factors are likely influencing pest pressure and damage.

Since the 1920s, precipitation and temperature have been anecdotally linked to *D. antiqua* damage and continue to be cited as an important factor limiting *D. antiqua* survival across life stages (Dill and Kirby, 2016; Loosjes, 1976; UMassAmherst, 2015). In laboratory studies, Ellington (1963) demonstrated that *D. antiqua* adult activity, larval survival, and egg viability is hindered in hot, dry conditions, while Keller & Miller (1987) observed a precipitous decrease in oviposition at temperatures approaching 30^{o}C. In field experiments, Workman (1958) observed that onions receiving an augmented water regimen had more damage from *D. antiqua* than rows that remained dry. Similar temperature and moisture responses have been observed in closely related species including *Delia florilega* (Kim and Eckenrode, 1987; Throne and Eckenrode, 1986), *D. radicum* (Lepage et al., 2012), and *D. platura* (Hesler et al., 2018; Throne and Eckenrode, 1986). Together, these studies along with anecdotal reports suggest that onions grown in cooler, wetter conditions may have greater activity and damage of *D. antiqua* than those produced in hotter and drier conditions.

For belowground pests, soil properties profoundly impact insect survival and resulting damage. Soil moisture has been identified as a key factor influencing both the mobility and survival of soil dwelling insects (Brown and Gange, 1990; Villani and Wright, 1990). Dustan (1932) observed that onion maggot larvae perform better in "lighter" soils, i.e. soils with more organic matter compared to clay-rich soils. Potential mechanisms suggested to explain this relationship include an increase in mobility of larvae through the soil with greater organic matter, and increased habitat suitability due to elevated soil moisture content with increasing soil organic matter (Loosjes, 1976). In the Great Lakes region, commercial onion production is concentrated on muck soils, high organic matter histosols, derived from drained lakebeds or wetlands with organic matter ranging from 20-80% (Lucas, 1982). Organic matter content, and thus water holding capacity (Hudson, 1994; Sullivan, 2002), of fields across the region can vary dramatically and may play a role in the severity of *D. antiqua* larval damage. Previous research suggests that *D. antiqua* adult activity and damage will be elevated in fields with higher organic matter.

In addition to within-field conditions, the landscape surrounding a cultivated crop strongly influences pest dynamics (Karp et al., 2018). In many systems, additional non-crop or natural habitat surrounding the cultivated crops serves as habitat for predators and parasitoids, which can enhance biocontrol of pest populations (Chaplin-Kramer et al., 2011; Veres et al., 2013). However, in other systems, surrounding natural habitat can instead serve as a source of pests (Tscharntke et al., 2016). The response of pests to landscape composition adjacent to the host crop tends to be study specific (Karp et al., 2018). In onion agroecosystems, Werling et al. (2006) identified elevated first-generation *D. antiqua* adult activity along onion field edges adjacent to wooded areas, such as forests and hedgerows, in contrast to field edges bordered by other vegetable crops. This indicates that forested habitats surrounding onion fields may provide a refuge and resources for *D. antiqua* adults early in the growing season. Consequently, onion fields surrounded by a greater proportion of forest or wooded habitat may be at higher risk for *D. antiqua* infestation.

Finally, synchrony between the pest and its host can impact pest survival and crop damage (Kennedy and Storer, 2000). Host availability and plant size may influence *D. antiqua* colonization and establishment within fields. In laboratory choice tests, Nault et al. (2011) confirmed that females preferentially oviposited on eight-week old onions over four-week old onions and when presented with an onion in no-choice tests, deposited fewer eggs on younger plants. Field trials with staggered onion plantings confirmed that delayed plantings, which create asynchrony between the host crop and ovipositing females, can significantly reduce the number of plants killed by larvae (Nault et al., 2011). Therefore, onion fields planted later in the spring should have lower *D. antiqua* damage than those planted earlier because onion plants should be smaller during peak fly activity.

Collectively, these separate studies have indicated that climate (temperature and precipitation), soil conditions, landscape, and planting date are key factors influencing *D. antiqua* survival, colonization, and subsequent larval damage. However, no study has assessed these factors across onion fields with varied pressure from the pest or identified which of these factors or combinations thereof can best explain differences in damage across fields. The goal of this research was to identify the suite of factors and their interactions that likely have the greatest impact on *D. antiqua* fly activity and plant damage in commercial onion fields in an attempt to understand this variability. While our study did not explore all factors known to impact insect pest populations, we focused on factors suspected to have the greatest impact on *D. antiqua* based on previous studies and anecdotal reports. The objectives of this study were to 1) determine the effects of temperature and precipitation, soil properties, landscape, planting date, and plant size at peak fly activity on *D. antiqua* adult activity and larval damage early in the season, and 2) identify which combination of these factors best explain *D. antiqua* adult activity and larval damage. Implications for predicting risk of onion fields for *D. antiqua* attack and future management are discussed.

Materials & Methods

Site selection and description

Environmental factors, fly activity, and damage were monitored in commercial onion fields in six counties in central and western New York in 2018 (n=15) and 2019 (n=13). Fields that had a history of onion production were monitored in Orleans (n=4, 2018-19), Genesee (n=1, 2018-19), Yates (n=2, 2018-19), Steuben (n=2, 2018), Oswego (n=4, 2018; n=4, 2019), and Wayne (n=2, 2018-2019). Except for field sites in Steuben county, two sites in Oswego county, and two sites in Orleans county, all field sites were sampled in both 2018 and 2019. Field sites were selected to be a minimum of 1.5 km apart and were located within continuous pockets of Palms or Carlisle muck (NRCS, n.d.).While some of these fields had been rotated out of onion in recent years, no field had been rotated out of onion in the absence of onions within 1.5 km, rendering rotation largely ineffective for *D. antiqua* management (Martinson et al., 1988). All fields were direct-seeded with long-day varieties of dry bulb onions in April and May. Because no *D. antiqua* resistant cultivars exist (Ellis & Eckenrode 1979; McFerson et al. 1996), cultivar was disregarded in this study. In 2018, all seeds were treated with FarMore® FI500 (Syngenta, Greensboro, NC, USA), and 80 percent of growers (12/15) co-applied chlorpyrifos (Lorsban®, Corteva, Indianapolis, IN, USA) at the recommended rate of 0.43 kg ai/acre. In 2019, 62% of participating growers (8/13) treated seeds with FarMore® FI500, while the remainder used Trigard® (ADAMA, Raleigh, NC, USA). The majority of growers (9/13) co-applied chlorpyrifos at planting at the recommended rates in 2019 as well. Trigard® and FarMore® FI500 perform equivalently well for *D. antiqua* control (Moretti and Nault, 2020), whereas the addition of chlorpyrifos typically does not improve control (Moretti et al., 2019).

Data collection

Field sites were sampled from mid-May (15 May) to mid-July (17 July) in 2018 and 2019, corresponding to the first flight of adults from overwintered pupae until subsequent pupation of first-generation *D. antiqua* in the field.

Fly abundance

Fly activity was monitored near onion field edges, which were bordered by either forests or weedy areas, nearest to where *D. antiqua* damage was later evaluated. To monitor activity, three 15 x 15 cm yellow sticky cards (Olson Products, Medina, OH, USA) were spaced 30 m apart along the field edge (as described in Werling et al. 2005). Cards were fastened to wooden stakes at a height of ~25 cm (approximating onion height) using spring loaded clamps (Woodworkers' Supply, Casper, WY, USA). Sticky cards were collected and replaced on a weekly basis, and flies were identified to species using Huckett (1987) and Savage et al. (2016).

Plant damage

Plant damage by *D. antiqua* was evaluated weekly in each field by walking transects totaling 100 m. In 2018, two 50 m transects and in 2019, four 25 m transects were evaluated. In both years, transects were placed a minimum of 25 m apart and extended from the onion field edge toward the center of the field. The number of damaged plants in a total of four rows of onions adjacent to each transect was counted (two rows on either side of the transect). *Delia antiqua* damage was identified by plants with flaccid leaves; plants were removed and assessed for active feeding by larvae or in the absence of larvae, larval entry or exit wounds.

Because *D. antiqua* and seedcorn maggot (*Delia platura*) can co-occur in onion fields, in 2019, we confirmed the species identification of larvae in heavily infested fields. Larvae from infested plants were collected in tubs and returned to the lab. Larvae were reared in 19 x 13.5 x 14.5 cm rearing boxes fitted with a screened lid lined with 3 cm of moistened unwashed mason sand. Larvae were fed portions of yellow bulb onions and were maintained at 21ºC, 40% RH, and photoperiod of 16:8 (L:D) until emergence. Flies were frozen, pinned, and identified to species. Flies were successfully reared from larvae collected in fields from four sites in Oswego county, one site in Wayne county, and three sites in Orleans county. At each field site, the majority of flies (> 85%) were identified as *D. antiqua*, confirming that it is the dominant maggot pest species in these fields.

Precipitation, soil temperature, and plant size

Precipitation and average weekly soil temperatures were monitored each week. Soil temperature, rather than ambient air temperature, was measured to more accurately assess the conditions that egg and larval stages of *D. antiqua* experience. Muck soil, which tends to be dark in color, is usually warmer than air temperature, and measures of air temperature likely underestimate the conditions eggs and larvae experience. Precipitation was assessed using a simple rain gauge consisting of an inverted 2 L bottle with the bottom removed and fitted with a 10 cm diameter funnel to direct rainfall into the bottle. Rain gauges were affixed ~1.5 m above the ground to a steel pole, placed along the edge of each field, unobstructed by trees or other structures. Soil temperature was monitored using continuous data loggers (i-button®, Thermochron, DS1921G, OnSolution Pty Ltd, Baulkham Hills, NSW, AUS) which recorded temperature every 20 min. Data loggers were placed in 50 mL Falcon Tubes (Corning™ , Corning, NY, USA) filled with rinsed and dried calclined clay (Turface® MVP, Profile Products LLC, Buffalo Grove, IL, USA). Tubes were sealed with

Parafilm to exclude moisture and were buried at a depth of 5 cm, the depth where most *D. antiqua* larvae occur (Loosjes, 1976)

Plant growth was assessed each week by selecting 10 plants from transects within each field. Plant size was estimated using neck diameter, measured at the widest point of the neck with digital calipers (General® Tools & Instruments LLC, New York, NY, USA) (Lancaster, 1996).

Soil collection and analysis

Soil was sampled at field sites the week of 9 July in 2018 and 17 July in 2019. Soil was only sampled once for each field site over the two-year sampling period; those sampled in 2019 were field sites that had been moved or added. A total of nine samples (n=9) were taken in each field within a 100 m x 100 m area. At each sampling location, five soil cores (5 cm diameter, 6-10 cm depth) were taken within a 1 m radius, and cores were taken between onion rows to avoid roots. Cores were bulked for each sample, and soil was air-dried and stored in plastic bags until processing. For analysis, roots were removed from samples and soil was passed through a 2 mm sieve. Water holding capacity (WHC) was quantified following standard procedures (Barrett et al., 2009), and organic matter was determined using loss on ignition at 500 ^{o}C for 2 hr (Storer, 1984).

Landscape Analysis

Land cover around all sites was quantified using ArcGIS (ArcGIS version10.7.1, ESRI, 2018) with data from the United States Department of

Agriculture Cropland Data Layer (CDL; USDA National Agriculture Statistics Service, 2018). Land cover was designated as agriculture (all crop systems excluding onion production), forest, and developed, and each land cover was quantified in a 1.5 km radius around each field site. This distance is the best estimate of how far adult *D. antiqua* can travel (Martinson et al., 1988). Because onion fields surveyed were all surrounded by landscapes composed primarily of either forest or agriculture, percent surrounding forest was selected as the dependent variable.

Statistical Analysis

Analyses were performed in R (R Core Team, 2017). To test the relationships between first-generation *D. antiqua* (fly abundance or damaged plants) and soil temperature, precipitation, soil organic matter, landscape, and planting date and plant size at peak fly activity, generalized linear mixed effects models were used in the analyses (lme4 package and function glmer()) (Bates et al., 2015). Because plant damage differed substantially between years, data were analyzed separately. For each model, the dependent variable was cumulative number of plants damaged in each field over the observation period and was modeled with a Poisson distribution. Average fly abundance across the observation period; climate factors, including soil temperature averaged across the nine-week sampling period (“soil temperature”) and cumulative rainfall (“precipitation”); temporal factors, including planting date (“planting date”) and neck diameter (“neck diameter”) during the week of peak flight; proportion of forest at 1500 m (“forest”); and soil organic matter (“organic matter”) served as fixed effects for each model. Both percentage of forest in the landscape and soil organic matter were arcsine square root transformed and fly abundance (average flies per card per week) was log transformed prior to analysis. Dependent variables were mean centered and scaled, and in all models, field site was included as an observation level random effect to adjust for overdispersion. The relationships between soil organic matter and water holding capacity (WHC) were analyzed using linear regressions with Pearson correlation coefficients.

To assess which factors or combinations of factors were most important in determining damage in fields in each year, we used best subsets regressions. Prior to analysis, collinearity between continuous variables was assessed with variance inflation factors (VIF). Using the dredge() function ('MuMIn'; Barton, 2019) all possible mixed effects models were constructed with fixed effects "soil temperature", "precipitation", "planting date", "neck diameter", "forest", and "organic matter". All models included a minimum of one fixed effect, were limited to one, two-way interaction, and only included factors or interactions that were statistically significant ($\alpha < 0.05$). Model selection was based on the lowest delta Akaike's information criterion value corrected for small sample sizes (AICc), and uncertainty of model selection was measured with Akaike's weight. Marginal R-squared values for each model were determined using the 'MuMIn' package.

Results

Fly abundance and plant damage

In 2018 and 2019 average fly capture across weeks of adult activity ranged from 0.3-17.9 and 0-16.2 flies per card per week, respectively. Cumulative number of damaged plants observed in fields ranged from 0-853 in 2018 and 1-384 in 2019. In the majority of field sites in 2018 (13 of 15), peak fly activity occurred during the first two weeks of June, but in 2019, peak fly activity in the majority of field sites occurred about a week later. In both years, the greatest number of damaged plants was observed during the last two weeks of June. In 2018, fly abundance and plant damage were positively associated ($F_{1, 12} = 86.19$, $p < 0.001$, $R^2_m = 0.89$; Figure 2.1A). In 2019, fly abundance and plant damage were still positively associated, but the relationship was weaker ($F_{1,9} = 4.48$, $p = 0.034$, $R^2_m = 0.29$; Figure 2.1B); only field sites with plant damage were used in this analysis. Because the abundance of flies and plant damage were positively associated, the remainder of the analyses focused on how the various factors impacted plant damage.

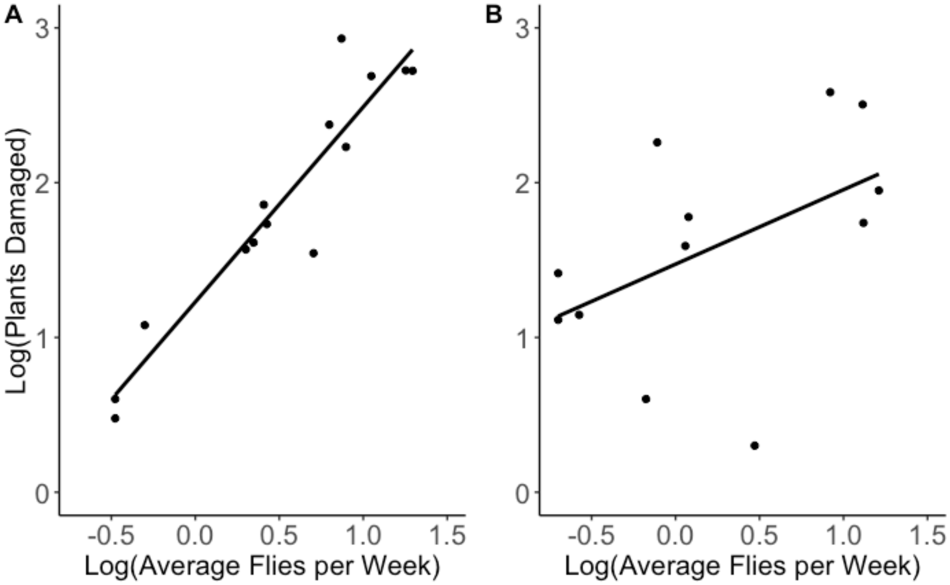

Figure 2.1. Relationship between fly capture (average number of flies per card per week, log transformed) and the cumulative number of plants damaged (log transformed) observed across the nine-week sampling period in 2018 (A) and 2019 (B).

Soil temperature and precipitation

In 2018, neither cumulative precipitation ($F_{1,10} = 0.07$, p = 0.58) nor the interaction between precipitation and average soil temperature ($F_{1,10} = 0.64$, p = 0.42) had a significant relationship with larval damage, but there was a significant effect of average soil temperature ($F_{1,10} = 14.14$, $p < 0.001$). Fields with higher average soil temperatures over the nine-week observation period had lower damage ($R^2_m = 49$; Figure 2.2A). However, this relationship was not upheld the following year (Figure 2.2B). In 2019, there was no significant relationship between larval damage and average soil temperature ($F_{1,8} = 0.00$, p = 0.96), cumulative precipitation ($F_{1,8} = 2.98$, p = 0.13), or their interaction ($F_{1,8} = 3.24$, p = 0.072).

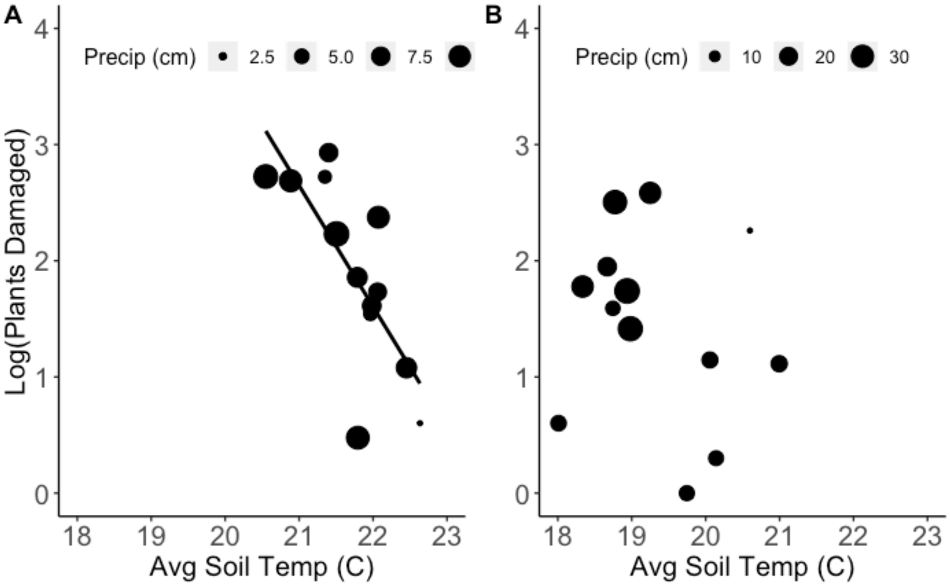

Figure 2.2. Relationship between weekly soil temperature, averaged over the nine-week sampling period and cumulative number of plants damaged from first generation onion maggot in 2018 (A) and 2019 (B). Point size reflects cumulative precipitation (cm).

Soil characteristics

Soil organic matter content ranged from 40-85%, and all soils were acidic, with pH ranging from 4.8-6.3. As expected, organic matter and WHC were positively correlated across the fields (Pearson correlation: $r = 0.83$, $p < 0.001$). In 2018, organic matter had a significant positive relationship with larval damage ($F_{1,12} = 8.70$, $p = 0.003$, $R^2_m = 0.39$), but in 2019, there was no effect ($F_{1,10} = 0.3$, $p = 0.58$; Figure 2.3).

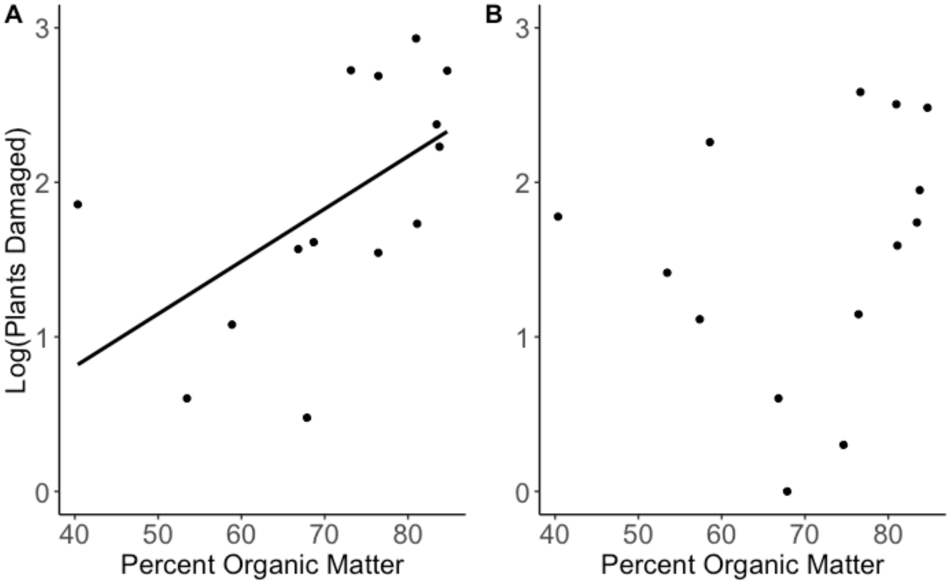

Figure 2.3. Relationship between soil organic matter and cumulative number of plants damaged in 2018 (A) and 2019 (B).

Landscape

Forest and agriculture (excluding onion-cropping systems) constituted the majority of the landscape surrounding onion fields. The amount of forest surrounding each field site in a 1500 m radius ranged from 6-62%, while agriculture ranged from 2-64%. Proportion of agriculture and forest were negatively correlated (Pearson correlation: r = -0.60, p = 0.02); that is, fields surrounded by more forest had less agriculture, and conversely, fields surrounded by more agriculture had less forest. The amount of forest in the landscape in a 1500 m radius surrounding each onion field site had a significant association with larval damage (Figure 2.4). Field sites surrounded by a greater proportion of forest had more larval damage in both 2018 ($F_{1,12} = 15.87$, $p<0.001$, $R^2_m = 0.54$) and 2019 ($F_{1,10} = 7.42$, $p = 0.007$, $R^2_m = 0.39$).

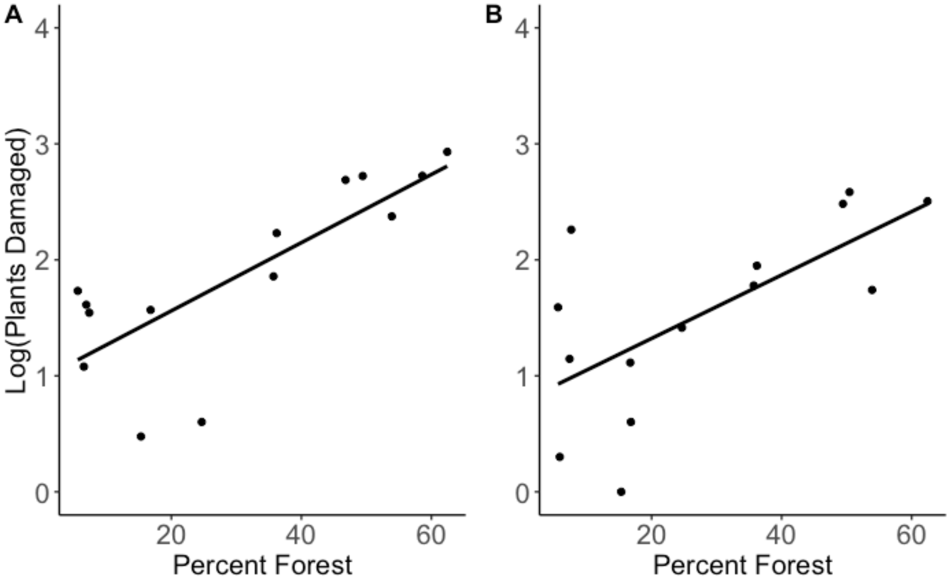

Figure 2.4. Relationship between the percentage of forested land within a 1.5 km radius around field sites and cumulative plants damaged by onion maggot in 2018 (A) and 2019 (B).

Planting Date and plant size

In both 2018 and 2019, planting date had a significant relationship with larval damage. Fields that were planted later had higher damage than those planted earlier in the spring (2018: $F_{1,10} = 4.05$, $p = 0.046$; 2019: $F_{1,8} = 6.63$, $p = 0.039$; Figure 2.5), although this relationship was weaker in 2018 ($R^2_m = 0.21$) than in 2019 ($R^2_m = 0.34$).

However, there was no relationship between plant size (neck diameter) at peak fly activity and larval damage in either year (2018: $F_{1,10} = 0.02$, p = 0.90; 2019: $F_{1,8} = 0.01$, p = 0.91). Moreover, there was no interaction between planting date and plant size in either year (2018: $F_{1,10} = 3.57$, p = 0.06; 2019: $F_{1,8} = 0.41$, p = 0.52). Despite the majority of fields having peak fly activity in the same weeks in 2018 and 2019, plant size at peak fly activity differed substantially from field to field and did not have a relationship with planting date. Fields planted later did not consistently have smaller onions and contrarily, fields planted earlier did not have larger onions at peak fly activity.

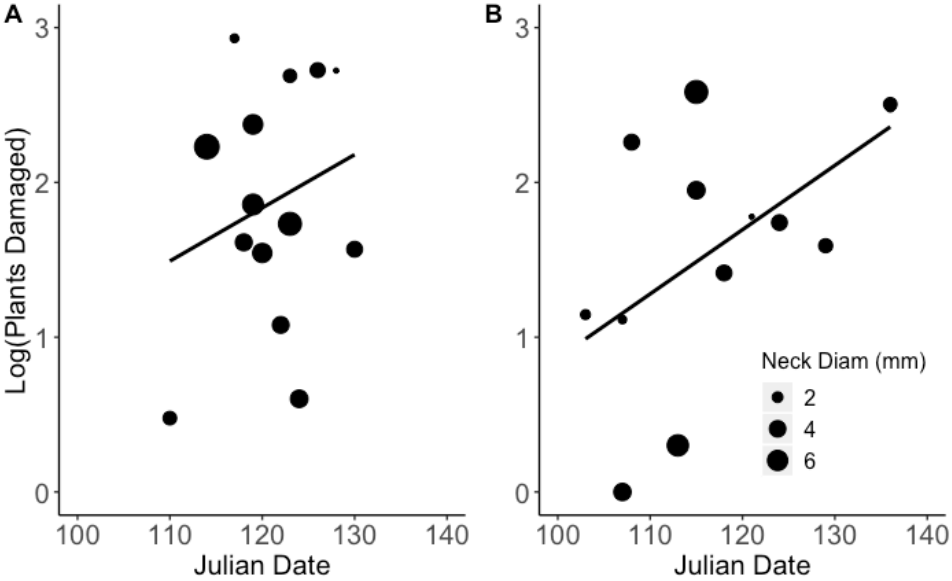

Figure 2.5. Relationship between planting date (Julian Date) and cumulative plants damaged across the nine-week sampling period in 2018 (A) and 2019 (B). Julian date 110 – 140 corresponds to 20 April – 20 May in both years. Point size reflects plant size at peak flight, measured as average plant neck width (mm) of onions sampled during the week where fly activity was at its maximum.

Best predictors of plant damage

In 2018, plant damage was best predicted using the model that included the interaction of forest and planting date plus average soil temperature (“forest x planting date + soil temperature”) (Table 2.1). Together, these variables explained a substantial amount of variation in larval damage observed across field sites ($R^2_m = 0.90$). For the other two top models in 2018, “forest x planting date + soil temperature + organic matter” and “planting date x soil temperature” appeared to be important factors affecting larval damage (Table 2.1). In 2019, forest was the best model and planting date the second best model for estimating larval damage (Table 2.1). However, neither factor explained more than 40 percent of the variation in damage or were substantially better than the null model (~1) based on AIC weight.

Table 2.1. Best candidate models explaining *D. antiqua* larval damage in commercial onion fields in New York, USA, in 2018 and 2019

Rank	Factors in model	df	ΔAICc	Weight	R^2_m
2018					
Null	~1	2	13.9	<0.001	0.00
1	**Forest * Planting Date + Soil Temperature**	6	0.00	0.420	0.90
2	**Forest * Planting Date + Soil Temperature + Organic Matter**	7	1.53	0.196	0.94
3	**Planting Date * Soil Temperature**	5	2.42	0.125	0.84
4	Forest + Organic Matter	4	4.29	0.049	0.71
5	Forest + Organic Matter + Planting Date	5	4.31	0.049	0.79
6	Organic Matter + Planting Date * Soil Temperature	6	4.36	0.048	0.88
7	Forest + Planting Date * Soil Temperature	6	4.71	0.040	0.86
8	Organic Matter + Planting Date + Soil Temperature	5	4.88	0.037	0.77
9	Planting Date + Soil Temperature	4	4.88	0.037	0.68
2019					
Null	~1	2	2.45	0.153	0.00
1	**Forest**	3	0.00	0.616	0.39
2	**PlantDate**	3	0.95	0.384	0.34

Only showing ΔAICc < 5

Discussion

Delia antiqua is a devastating pest of onion in the Great Lakes region. In commercial onion fields across central and western New York, damage from this pest is highly variable. Because the majority of onion production practices and onion pest management tactics are identical, we hypothesized that other factors may be influencing the variability of this pest across the region. Based on anecdotal reports and published manipulative studies, we identified several factors that should influence *D. antiqua* damage and evaluated their association with fly activity and larval damage across onion field sites. This was the first study to assess the interactive effects of environmental factors and production practices on *D. antiqua*. While we consider our study comprehensive, it did not include all factors that might influence pest dynamics. Rather, it highlighted specific environmental factors and a production practice that are considered most likely to influence *D. antiqua*. Across both years of the study, surrounding landscape and planting date had consistent, significant associations with larval damage. Larval damage was higher in onion fields surrounded by forest and planted later than those surrounded by agricultural crops and planted early. Both soil temperature and soil organic matter also significantly impacted larval damage, but only during the first year of the study.

Soil temperature, precipitation, and soil organic matter

Consistent with previous studies, in one of two years there was a negative relationship between levels of *D. antiqua* damage and soil temperatures. While increased seasonal temperatures have been associated with increased herbivory, longevity, and fecundity in some species, increased temperatures can be detrimental to others (Karuppaiah and Sujayanad, 2012). In *D. antiqua* and other closely related species, increased temperatures, particularly temperatures approaching 30° C, have been associated with reduced oviposition, lower hatch rates, and elevated larval and adult mortality in laboratory studies (Ellington, 1963; Keller and Miller, 1990; Lepage et al., 2012).

Average weekly soil temperatures across field sites were warmer in 2018 (21-23°C) than in 2019 (18-21°C). In 2019, there was no effect of soil temperature on larval damage, suggesting that *D. antiqua* was not affected across this temperature range. In contrast, average weekly temperatures across the nine-week observation period in 2018 were warmer, but only ranged from 21-23°C, which is near the developmental optimum identified for *D. antiqua* (Miles, 1958; Robinson and Zurlini, 1979). This suggests that in 2018, but not 2019, across the temperatures observed, a critical temperature threshold detrimental to *D. antiqua* was met that lead to greater mortality. Seasonal averages, such as those measured in this study, can underestimate the detrimental effects of short-duration temperature extremes (Ma et al., 2015a). Increases in average seasonal temperatures are often associated with increases in high temperature events (Easterling et al., 2016, 1997; Ma et al., 2015b), and exposure to short-term heat events can elicit species-specific responses, which vary depending on both the frequency and magnitude of the event (Ma et al., 2004ab, 2015). To date, responses of *D. antiqua* to temperature in the laboratory are limited to constant temperature exposure (Ellington, 1963; Keller and Miller, 1990). More information regarding exposure of *D. antiqua* to short-term heat events are necessary to simulate field-accurate temperatures.

Similar to the temperature response, an association between organic matter and *D. antiqua* damage was only observed in the first year of the study. Across the fields sampled in this study, the percentage of organic matter was positively correlated with water holding capacity ($r = 0.834^*$). Soil moisture strongly influences the survival and mobility of belowground insects and enhanced soil moisture generally increases survival (Brown and Gange, 1990; Erb and Lu, 2013; Villani and Wright, 1990). Ellington et al. (1963) observed suppressed egg hatch rates and egg development of *D. antiqua* at high vapor pressure deficit. Similarly, in a series of trials, Workman (1958) found reduced and delayed egg hatch of *D. antiqua* within low moisture muck soils (<10% w/v). Larvae had limited survival below 23% moisture, and neonates failed to penetrate the soil surface, suggesting limited mobility as well as enhanced mortality under low moisture conditions (Workman, 1958).

The absence of an association between soil organic matter content and larval damage in the second year of the study may have been influenced by rainfall. Cumulative precipitation was not a significant predictor of *D. antiqua* damage in either year, and it was not identified in any of the cumulative models for predicting *D. antiqua* activity in either year of the study (Table 2.1). However, compared with 2018, field sites in 2019 experienced much higher levels of rainfall. In 2018, cumulative rainfall ranged from 2.4-13.5 cm, but in 2019 it ranged from 7.6-36.6 cm. In a year when water was not limiting (2019) and fields were likely at or near saturation, as evidenced by frequent periods of standing water (E. Moretti, personal observation), differences in organic matter were not associated with larval damage. In contrast, when water was more limiting in 2018, the percentage of organic matter was associated with increased damage.

Although temperature and moisture dynamics within fields were associated with *D. antiqua* damage in commercial onion, these factors appeared to be context dependent. For example, soil moisture may be an important factor influencing damage in drier conditions, but not under wetter conditions. Growers may expect more field-field variation in plant damage based on organic matter content in a water-limited year compared to a wet year. Moisture management within fields, through either tiling to remove excess water or irrigation to add water to the crop allows growers to manipulate soil moisture throughout the growing season, and may be a tactic worth pursuing for *D. antiqua* management.

Landscape

Across both years, more larval damage was observed in fields surrounded by high proportions of forest (Figure 2.4), and this landscape parameter was identified in the majority of candidate models combining all factors measured in the study (Table 2.1). Werling et al. (2006) observed enhanced activity (measured as fly capture) of first-generation *D. antiqua* flies adjacent to onion field edges in contrast to onion field centers. The edge effect was particularly pronounced adjacent to edges bordered by wooded habitat in contrast to those bordered by other vegetable crops. Their findings confirmed observations of an “edge effect” of *D. antiqua* activity by others (Finch et al., 1986; Vernon et al., 1989, 1987). Although none of the previous studies measured subsequent larval damage, our results indicated that elevated adult activity in fields surrounded by a greater proportion of forest translated to increased damage from first-generation larvae.

In contrast to open habitat, habitats adjacent to forested edges have lower temperatures, increased shading and relative humidity, and experience less drastic changes in temperature throughout the day (Cadenasso et al., 1997). Finch et al. (1986) suggested that flies move into forested edges to seek shelter from direct sunlight and heat, particularly midday when temperatures reach their maximum. Access to forested habitat providing shade and a cooler, more humid environment may be particularly important early in the season, when the onion canopy is under-developed and shelter from sunlight and desiccation in the field is limited (Werling et al. 2006). In addition to offering a sheltered environment, adjacent wooded habitat may also provide valuable early-season food resources. Female flies require a protein-rich meal to oviposit (Loosjes 1976), and adult flies have been observed feeding on flowers (Baker, 1928; Finch et al. 1986), suggesting that pollen serves as an important resource which can be found in abundance in or around wooded habitats.

Given the consistent, positive association between surrounding forest habitat and *D. antiqua* damage, the surrounding landscape should be used to predict onion fields that may be at either greater risk (surrounded by forest) or lower risk (surrounded by other vegetable fields) to *D. antiqua* attack. Moreover, in crop fields where a pest infestation exhibits a strong edge-effect (e.g., *D. antiqua*), pest management tactics could target field edges rather than the entire field. Historically, targeting *D. antiqua* flies with foliar insecticide sprays in onion fields has proven ineffective. Flies are active and mobile, making them difficult to target with insecticide sprays (Finch et al. 1986). However, flies could be targeted with insecticide-baited traps along field edges in onion fields with surrounding forests to complement insecticide seed treatments that are currently used to manage *D. antiqua* (Zhou et al., 2016, Willet et al. 2020ab).

Planting Date and plant size

Prior work assessing the influence of planting date on *D. antiqua* plant damage showed a negative relationship between time of onion planting and subsequent larval damage. Nault et al. (2011) demonstrated that delayed planting significantly reduced larval damage by first generation *D. antiqua*, and using laboratory choice and no-choice tests, confirmed that plant size mediated this outcome. Females preferentially oviposit on larger onion plants (8-wk old) compared with smaller seedlings (4-wk old), and lay fewer eggs on smaller onions (Harris et al., 1987; Nault et al., 2011).

In contrast to Nault et al.'s (2011) conclusions, across fields in western and central New York, less *D. antiqua* damage was observed in the earliest planted fields compared to those planted later (Figure 2.5). This relationship was stronger in 2019, and weaker in 2018. Although peak fly activity occurred in roughly the same weeks across the field sites surveyed, there was no association between planting date and plant size. Onions seeded earlier in the spring were not necessarily larger than those planted later. In Nault et al.'s (2011) study, small plots of different aged onion plants were grown adjacent to each other in the same field, affording flies a host choice. In contrast, flies in our study were not presented with host choices per se, as fields consisted of a single-aged stand of onion. Females will oviposit on non-preferential hosts, albeit less than ideal hosts (Cowles and Miller, 1992; Miller and Cowles, 1990; Nault et al., 2011). Onion fields consist of a single aged stand, there are no choices, and as a consequence, delayed-planting is unlikely to reduce damage when an established population of *D. antiqua* is already present.

What mediated an increase in *D. antiqua* damage in later-planted onion fields remains unclear. Onion fields that are the driest and most well-drained tend to be prepared for planting first. Because *D. antiqua* damage tends to be lower in drier conditions (Workman, 1958; Ellington, 1963), well-drained fields may be drier and more likely to be planted earlier, and consequently, less likely to experience damage from the pest. Nevertheless, a short window exists for planting direct-seeded onions in the Great Lakes region. Planting date is constrained early in the growing season by weather and field conditions and later in the season by plant development. Onions that are seeded too late will fail to reach their maximum potential bulb size and maturity. For this reason, growers will not direct-seed onions later than approximately the third week in May. In an effort to delay planting to escape the first generation of *D. antiqua*, growers risk smaller bulbs or a crop that will not mature normally. Although planting date was important for models predicting larval damage in fields, manipulation of planting date for management of this pest is inherently risky and likely will not be adopted by growers.

Predicting plant damage

Understanding the roles of key environmental factors and management practices in pest dynamics can help inform predictive models of damage, risk assessments, and strategic deployment of management practices (Rijal et al., 2014; Van Vuren and Smallwood, 1996). The predictive relationships assessed herein identified landscape (forest in the surrounding landscape) and planting date as the most important factors for explaining the variation in *D. antiqua* damage across field sites (Table 2.1). Among the factors assessed, these attributes had a consistent relationship with *D. antiqua* damage across both years of the study (Figure 2.4, 2.5). The effects of temperature and soil organic matter were inconsistent across the two years of the study; however, our results suggest that specific thresholds for temperature or determinants of soil moisture (e.g., precipitation, soil organic matter content, and drainage) exist. Identifying these thresholds will be important so that these factors can be used predict fields at-risk for *D. antiqua* damage.

Because onion production is highly specialized, rotation out of onion is often not economical despite it being extremely effective (Martinson et al., 1988). Building better predictive models should be pursued in order to help growers identify fields at the greatest risk for invasion. Given the economic constraints and limited chemical tactics in onion production, accurate risk predictions are invaluable for management decision-making.

Conclusion

Factors in the environment as well as management practices influence pest abundance and damage in cultivated crops. In systems where management is largely similar among growers, identifying key factors associated with damage is important for understanding variability in pest pressure and identifying conditions where the pest may be particularly problematic. In the Great Lakes region, *D. antiqua* activity is highly variable across onion growing regions, despite grower's employing the same production and pest management strategies in the same soil types. In this study, we explored the association of several factors identified to be key to *D. antiqua* survival and colonization to try to explain the disparities in damage observed across central and western New York. Onion fields surrounded primarily by forest compared with vegetable fields and those planted later in the season compared with early in the season were at greatest risk for higher levels of damage by *D. antiqua*. Factors such as lower soil temperature and high organic matter also were associated with higher levels of *D. antiqua* damage, but these effects were variable and context dependent. More information is needed for these two factors to be reliable predictors of *D. antiqua* damage, particularly if short-duration temperature extremes and the interactions between precipitation and soil moisture are important. This study is the first to evaluate these factors' association with *D. antiqua* damage in onion fields. Identifying high-risk fields will help growers make decisions regarding strategic deployments of management tactics, such as using insecticide-baited traps for *D. antiqua* flies, or more costly management practices, such as crop rotation or transplanting onions that are more resilient to *D. antiqua* attack.

REFERENCES

Barrett, J., Ball, B., Simmons, B., 2009. Standard procedures for soil research in the McMurdo Dry Valleys LTER. http://mcm.lternet.edu/sites/default/files/Standard_soil_methods_MCM_2010.pdf (accessed 10.14.19)

Barton, K., 2019. Package "MuMIn." https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf (accessed 1.10.20)

Bates, D., Maechler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Brown, V.K., Gange, A.C., 1990. Insect herbivory below ground, in: Begon, M., Fitter, A.H., Macfadyen, A. (Eds.), Advances in Ecological Research. Academic Press, pp. 1–58. https://doi.org/10.1016/S0065-2504(08)60052-5

Cadenasso, M.L., Traynor, M.M., Pickett, S.T., 1997. Functional location of forest edges: gradients of multiple physical factors. Can. J. For. Res. 27, 9.

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol. Lett. 14, 922–932. https://doi.org/10.1111/j.1461-0248.2011.01642.x

Cowles, R.S., Miller, J.R., 1992. Diverting Delia antiqua (Diptera: Anthomyiidae) Oviposition with cull onions: Field studies on planting depth and a greenhouse gest of the stimulo-deterrent concept. Environ.Entomol. 21, 453–460. https://doi.org/10.1093/ee/21.3.453

Dill, J., Kirby, C.A., 2016. Onion Maggot - Cooperative Extension: Insect Pests, Ticks and Plant Diseases - University of Maine Cooperative Extension. Cooperative Extension. https://extension.umaine.edu/ipm/ipddl/publications/5031e/ (accessed 2.19.20).

Dustan, A.G., 1932. The effect of some physical factors on onion maggot infestations in light and heavy soils. Annual Report of the Quebec Society for the Protection of Plants. 32, 20-27.

Easterling, D.R., Horton, B., Jones, P.D., Peterson, T.C., Karl, T.R., Parker, D.E., Salinger, M.J., Razuvayev, V., Plummer, N., Jamason, P., Folland, C.K., 1997. Maximum and minimum temperature trends for the globe. Science 277, 364–367. https://doi.org/10.1126/science.277.5324.364

Easterling, D.R., Kunkel, K.E., Wehner, M.F., Sun, L., 2016. Detection and attribution of climate extremes in the observed record. Weather. Clim. 11, 17–27. https://doi.org/10.1016/j.wace.2016.01.001

Eckenrode, C., Vea, E., Stone, K., 1975. Population trends of onion maggots correlated with air thermal units accumulations. Environ. Entomol. 4, 785–789.

Ellington, J.J., 1963. Field and laboratory observations on the life history of the onion maggot *Hylemyia antiqua* (Meigen). Cornell University.

Ellis, P.R., Eckenrode, C.J., 1979. Factors influencing resistance in *Allium sp*. to onion maggot. Bull. Entomol. Soc. Am. 25, 151–154. https://doi.org/10.1093/besa/25.2.151

Erb, M., Lu, J., 2013. Soil abiotic factors influence interactions between belowground herbivores and plant roots. J. Exp. Bot. 64, 1295–1303. https://doi.org/10.1093/jxb/ert007

Finch, S., Eckenrode, C.J., Cadoux, M.E., 1986. Behavior of onion maggot (Diptera: Anthomyiidae) in commercial onion fields treated regularly with parathion sprays. J. Econ. Entomol. 79, 107–113.

Harris, M.O., Miller, J.R., Ponti, O.M.B., 1987. Mechanisms of resistance to onion fly egg-laying. Entomol. Exp. Appl. 43, 279–286. https://doi.org/10.1111/j.1570-7458.1987.tb02223.x

Hesler, L.S., Allen, K.C., Luttrell, R.G., Sappington, T.W., Papiernik, S.K., 2018. Early-season pests of soybean in the United States and factors that affect their risk of infestation. J. Integr. Pest. Manag. 9. https://doi.org/10.1093/jipm/pmx028

Hessney, M.L., Eckenrode, C.J., 2000. Onion maggot resistant to lorsban, 1999. Arthropod Manag. Tests 25. https://doi.org/10.1093/amt/25.1.L9

Huckett, H.C., 1987. Anthomyiidae, in: Manual of Nearctic Diptera. Canada Communication Group, Ottawa, Canada, pp. 1099–1114.

Hudson, B.D., 1994. Soil organic matter and available water capacity. J. Soil Water Conserv. 49, 189–194.

Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A.E., Martínez-Salinas, A., O'Rourke, M.E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J.A., Schellhorn, N.A., Tscharntke, T., Wratten, S.D., Zhang, W., Iverson, A.L., Adler, L.S., Albrecht, M., Alignier, A., Angelella, G.M., Zubair Anjum, M., Avelino, J., Batáry, P., Baveco, J.M., Bianchi, F.J.J.A., Birkhofer, K., Bohnenblust, E.W., Bommarco, R., Brewer, M.J., Caballero-López, B., Carrière, Y., Carvalheiro, L.G., Cayuela, L., Centrella, M., Ćetković, A., Henri, D.C., Chabert, A., Costamagna, A.C., De la Mora, A., de Kraker, J., Desneux, N., Diehl, E., Diekötter, T., Dormann, C.F., Eckberg, J.O., Entling, M.H., Fiedler, D., Franck, P., Frank van Veen, F.J., Frank, T., Gagic, V., Garratt, M.P.D., Getachew, A., Gonthier, D.J., Goodell, P.B., Graziosi, I., Groves, R.L., Gurr, G.M., Hajian-Forooshani, Z., Heimpel, G.E., Herrmann, J.D., Huseth, A.S., Inclán, D.J., Ingrao, A.J., Iv, P., Jacot, K., Johnson, G.A., Jones, L., Kaiser, M., Kaser, J.M., Keasar, T., Kim, T.N., Kishinevsky, M., Landis, D.A., Lavandero, B., Lavigne, C., Le Ralec, A., Lemessa, D., Letourneau, D.K., Liere, H., Lu, Y., Lubin, Y., Luttermoser, T., Maas, B., Mace, K., Madeira, F., Mader, V., Cortesero, A.M., Marini, L., Martinez, E., Martinson, H.M., Menozzi, P., Mitchell, M.G.E., Miyashita, T., Molina, G.A.R., Molina-Montenegro, M.A., O'Neal, M.E., Opatovsky, I., Ortiz-Martinez, S., Nash, M., Östman, Ö., Ouin, A., Pak, D., Paredes, D., Parsa, S., Parry, H., Perez-Alvarez, R., Perović, D.J., Peterson, J.A., Petit, S., Philpott, S.M., Plantegenest, M., Plećaš, M., Pluess, T., Pons, X., Potts, S.G., Pywell, R.F., Ragsdale, D.W., Rand, T.A., Raymond, L., Ricci, B., Sargent, C., Sarthou, J.-P., Saulais, J., Schäckermann, J., Schmidt, N.P., Schneider, G., Schüepp, C., Sivakoff, F.S., Smith, H.G., Stack Whitney, K., Stutz, S., Szendrei, Z., Takada, M.B., Taki, H., Tamburini, G., Thomson, L.J., Tricault, Y., Tsafack, N., Tschumi, M., Valantin-Morison, M., Van Trinh, M., van der Werf, W., Vierling, K.T., Werling, B.P., Wickens, J.B., Wickens, V.J., Woodcock, B.A., Wyckhuys, K., Xiao, H., Yasuda, M., Yoshioka, A., Zou, Y., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. Proc Natl Acad Sci USA 115, E7863–E7870. https://doi.org/10.1073/pnas.1800042115

Karuppaiah, V., Sujayanad, G.K., 2012. Impact of Climate Change on Population Dynamics of Insect Pests. World J. Agric. Res. 8, 240-246.

Keller, J.E., Miller, J.R., 1990. Onion fly oviposition as influenced by soil temperature. Entomol. Exper. Appl. 54, 37–42. https://doi.org/10.1111/j.1570-7458.1990.tb01309.x

Kennedy, G.G., Storer, N.P., 2000. Life systems of polyphagous arthropod pests in temporally unstable cropping systems. Annu. Rev. Entomol. 45, 467–493. https://doi.org/10.1146/annurev.ento.45.1.467

Kim, T.H., Eckenrode, C.J., 1987. Bionomics of the bean seed maggot, *Delia florilega* (Diptera: Anthomyiidae), under controlled conditions. Environ. Entomol. 16, 881–886. https://doi.org/10.1093/ee/16.4.881

Lancaster, J., 1996. Bulbing in onions: Photoperiod and temperature requirements and prediction of bulb size and maturity. Ann. Bot. 78, 423–430. https://doi.org/10.1006/anbo.1996.0138

Lepage, M.P., Bourgeois, G., Brodeur, J., Boivin, G., 2012. Effect of soil temperature and moisture on survival of eggs and rirst-instar larvae of *Delia radicum*. Environ. Entomol. 41, 159–165. https://doi.org/10.1603/EN10313

Loosjes, M., 1976. Ecology and genetic control of the onion fly, *Delia antiqua* (Meigen). PUDOC, Wageningen.

Lucas, R., E., 1982. Organic Soils (Histosols): Formation, distribution, physical and chemical properties and management for crop production. Michigan State University, Agricultural Experiment Station.

Ma, C.S., Hau, B., Poehling, H.M., 2004a. The effect of heat stress on the survival of the rose grain aphid, Metopolophium dirhodum (Hemiptera : Aphididae). Eur. J. Entomol. 101, 327–331. https://doi.org/10.14411/eje.2004.042

Ma, C.S., Hau, B., Poehling, H.M., 2004b. Effects of pattern and timing of high temperature exposure on reproduction of the rose grain aphid, *Metopolophium dirhodum*. Entomol. Exp. Appl. 110, 65–71. https://doi.org/10.1111/j.0013-8703.2004.00123.x

Ma, G., Hoffmann, A.A., Ma, C.-S., 2015a. Daily temperature extremes play an important role in predicting thermal effects. J. Exp. Biol. 218, 2289–2296. https://doi.org/10.1242/jeb.122127

Ma, G., Rudolf, V.H.W., Ma, C., 2015b. Extreme temperature events alter demographic rates, relative fitness, and community structure. Glob. Change. Biol. 21, 1794–1808. https://doi.org/10.1111/gcb.12654

Martinson, T.E., Nyrop, J.P., Eckenrode, C.J., 1988. Dispersal of the onion fly (Diptera: Anthomyiidae) and larval damage in rotated onion fields. J. Econ. Entomol. 81, 508–514.

McDonald, M.R., de los Angeles Jaime, M., Hovius, M.H.Y., 2004. Management of diseases of onions and garlic, in: Naqvi, S.A.M.H. (Ed.), Diseases of Fruits and Vegetables: Volume II: Diagnosis and Management. Springer Netherlands, Dordrecht, pp. 149–200. https://doi.org/10.1007/1-4020-2607-2_6

Miles, M., 1958. Studies of British Anthomyiid Flies. IX.—Biology of the Onion Fly, *Delia antiqua* (Mg.). B. Entomol. Res. 49, 405–414. https://doi.org/10.1017/S0007485300053700

Miller, J.R., Cowles, R.S., 1990. Stimulo-deterrent diversion: A concept and its possible application to onion maggot control. J. Chem. Ecol. 16, 3197–3212. https://doi.org/10.1007/BF00979619

Moretti, E., Nault, B., Hoepting, C., 2019. Seed treatment recommendations for onion maggot control in 2020. VegEdge 15, 4–5.

Moretti, E., Nault, B.A., 2020. Onion maggot control in onion, 2019. Arthropod Manag Tests 45. https://doi.org/10.1093/amt/tsaa007

Nault, B.A., Straub, R.W., Taylor, A.G., 2006. Performance of novel insecticide seed treatments for managing onion maggot (Diptera : Anthomyiidae) in onion fields. Crop Prot. 25, 58–65. https://doi.org/10.1016/j.cropro.2005.03.020

Nault, B.A., Werling, B.P., Straub, R.W., Nyrop, J.P., 2011. Delaying onion planting to control onion maggot (Diptera: Anthomyiidae): Efficacy and underlying mechanisms. J. Econ. Entomol. 104, 1622–1632. https://doi.org/10.1603/EC11175

NRCS, n.d. SSURGO Database. Web Soil Survey. URL http://weboilsurvey.nrcs.usda.gov/ (accessed 1.20.18).

Porter, J.H., Parry, M.L., Carter, T.R., 1991. The potential effects of climatic change on agricultural insect pests. Agr. Forest Meteorol. 57, 221–240. https://doi.org/10.1016/0168-1923(91)90088-8

Reiners, S., Curtis, P.D., Helms, M., McGrath, M.T., Nault, B.A., Seaman, A., 2019. Cornell integrated crop and pest management guidelines for commercial vegetable production, in: N.Y. State Integ. Pest Manag. Progr. Cornell University, Geneva, NY.

Rijal, J.P., Brewster, C.C., Bergh, J.C., 2014. Effects of biotic and abiotic factors on grape root borer (Lepidoptera: Sesiidae) infestations in commercial vineyards in Virginia. Environ. Entomol. 43, 1198–1208. https://doi.org/10.1603/EN14094

Robinson, A.S., Zurlini, G., 1979. The response of two stains of *Hylemya antiqua* (Diptera: Anthomyiidae) to a constant and an alternative temperature regime. Can. Entomol. 111, 1207–1217. https://doi.org/10.4039/Ent1111207-11

Savage, J., Fortier, A.-M., Fournier, F., Bellavance, V., 2016. Identification of *Delia* pest species (Diptera: Anthomyiidae) in cultivated crucifers and other vegetable crops in Canada. Can. J. Arthropod Identif. 29, 1–40. https://doi.org/doi:10.3752/cjai.2016.29

Storer, D.A., 1984. A simple high sample volume ashing procedure for determination of soil organic matter. Commun. Soil Sci. Plan. 15, 759–772. https://doi.org/10.1080/00103628409367515

Sullivan, P., 2002. Drought Resistant Soil. http://www.attra.ncat.org/attra-pub/PDF/drought.pdf (accessed 2.6.20)

Taylor, A.G., Eckenrode, C.J., Straub, R.W., 2001. Seed coating technologies and treatments for onion: challenges and progress. HortScience 36, 199–205.

Throne, J.E., Eckenrode, C.J., 1986. Development rates for the seed maggots *Delia platura* and *D. florilega* (Diptera: Anthomyiidae). Environ. Entomol. 15, 1022–1027. https://doi.org/10.1093/ee/15.5.1022

Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E.A., Martínez-Salinas, A., Meehan, T.D., O'Rourke, M., Poveda, K., Rosenheim, J.A., Rusch, A., Schellhorn, N., Wanger, T.C., Wratten, S., Zhang, W., 2016. When natural habitat fails to enhance biological pest control – Five hypotheses. Biol. Conserv. 204, 449–458. https://doi.org/10.1016/j.biocon.2016.10.001

UMassAmherst, 2015. Onion Maggot. Center for Agriculture, Food and the Environment. URL https://ag.umass.edu/vegetable/fact-sheets/onion-maggot (accessed 2.19.20).

Van Vuren, D., Smallwood, K.S., 1996. Ecological management of vertebrate pests in agricultural systems. Biol. Agric. Hortic. 13, 39–62. https://doi.org/10.1080/01448765.1996.9754765

Veres, A., Petit, S., Conord, C., Lavigne, C., 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. Agric. Ecosyst. Environ.166, 110–117. https://doi.org/10.1016/j.agee.2011.05.027

Vernon, R.S., Hall, J.W., Judd, G.J.R., Bartel, D.L., 1989. Improved monitoring program for *Delia antiqua* (Diptera: Anthomyiidae). J. Econ. Entomol. 82, 251–258. https://doi.org/10.1093/jee/82.1.251

Vernon, R.S., Judd, G.J.R., Borden, J.H., 1987. Commercial monitoring programme for the onion fly, *Delia antiqua* (Meigen)(Diptera: Anthomyiidae) in south-western British Columbia. Crop Prot. 6, 304–312.

Villani, M.G., Wright, R.J., 1990. Environmental influences on soil macroarthropod behavior in agricultural systems. Annu. Rev. Entomol. 35, 249–269.

Werling, B.P., Nyrop, J., Nault, B., 2006. Spatial and temporal patterns of onion maggot adult activity and oviposition within onion fields that vary in bordering habitat. Entomol. Exp. Appl. 118, 49–59. https://doi.org/10.1111/j.1570-7458.2006.00363.x

Whitfield, G.H., Carruthers, R.I., Haynes, D.L., 1985. Phenology and control of the onion maggot (Diptera: Anthomyiidae) in Michigan onion production. Agric. Ecosyst. Environ. 12, 189–200. https://doi.org/10.1016/0167-8809(85)90110-0

Willett, D., Filgueiras, C., Nyrop, J., Nault, B., 2020a. Field monitoring of onion maggot (Delia antiqua) fly through improved trapping. J. Appl. Entomol. In Press

Willett, D.S., Filgueiras, C.C., Nyrop, J.P., Nault, B.A., 2020b. Attract and kill: spinosad containing spheres to control onion maggot (*Delia antiqua*). Pest Manag. Sci. In press.

Wilson, R.G., Orloff, S.B., Taylor, A.G., 2015. Evaluation of insecticides and application methods to protect onions from onion maggot, *Delia antiqua*, and seedcorn maggot, *Delia platura*, damage. Crop Prot. 67, 102–108. https://doi.org/10.1016/j.cropro.2014.10.002

Workman, R.B., 1958. The biology of the onion maggot, *Hylemyia antiqua* (Meigen), under field and greenhouse conditions. Oregon State College.

Yildirim, E., Hoy, C.W., 2003. Cyromazine seed treatments to control onion maggot, *Delia antiqua,* on green onions. J. Econ. Entomol. 96, 6.

Zhou, F., Zhu, G., Zhao, H., Wang, Z., Xue, M., Li, X., Xu, H., Ma, X., Liu, Y., 2016. Sterilization effects of adult-targeted baits containing insect growth regulators on *Delia antiqua*. Sci. Rep. 6, 1–9. https://doi.org/10.1038/srep32855

CHAPTER 3

TRANSLOCATION OF SPINOSAD SEED TREATMENTS IN ONION AND ACTIVITY AGAINST *DELIA ANTIQUA* (DIPTERTA: ANTHOMYIIDAE)

Abstract

Onion maggot, *Delia antiqua* (Meigen), is a serious pest of onion in northern temperate regions. Over the last decade, *D. antiqua* has been managed principally using a pesticide seed treatment package containing spinosad, a reduced-risk, biologically derived insecticide. Onion is the only crop in which spinosad is registered as a seed treatment. As a consequence, very little is known regarding its activity, specifically translocation within onion and how it protects onion seedlings against *D. antiqua* larvae, when applied as a seed treatment. Translocation of spinosad within onion plants and numbers of plants killed by *D. antiqua* larvae were assessed in a field trial. Mortality of *D. antiqua* larvae was assessed when exposed to spinosad via ingestion and contact, and feeding behavior of larvae was examined in choice and no choice tests with spinosad-treated onion plants. Spinosad was detected in both aboveground and belowground plant tissue, indicating that spinosad is translocated into the foliage, and spinosad was also detected in the soil. Spinosad content within plants declined over time, which corresponded with an increase in plant mortality from *D. antiqua* feeding. Larval age and mode of exposure influenced the susceptibility of *D. antiqua* larvae to spinosad. In choice assays, larvae preferred feeding on untreated plants (75%) compared with spinosad-treated ones; however, without a choice, larvae did not discriminate between untreated and treated plants. Overall, results indicated that spinsoad has minor systemic activity in onion and was more than twice as lethal to young larvae than old larvae; spinosad was equally toxic to small and large larvae when exposed dermally to spinosad. Results from this study provide valuable insight into potential mechanisms of control and their importance for how spinosad protects onion seedlings from *D. antiqua*.

Introduction

Onion maggot, *Delia antiqua* (Meigen), is a severe pest of onion in northern temperate regions worldwide (Eckenrode et al., 1975). Similar to other root feeding maggots, larvae feed on the belowground portions of plants, including the roots and developing bulb. In the Great Lakes region of the United States and Canada, *D. antiqua* has three generations annually; however, the first generation, which spans mid-May to mid-June is the most devastating, as small seedlings are highly vulnerable to feeding (Eckenrode et al., 1975; Whitfield et al., 1985). Flies oviposit on or at the base of onion plants, and larvae move to the root zone and begin feeding on the subterranean tissues of onion, entering through the basal plate. A single larva can consume over 20 seedlings throughout its development (Workman, 1958), and stand losses of unprotected seedings can exceed 50%, making management of the pest essential early in the season (Nault et al. 2006a, Moretti and Nault 2020).

To manage *D. antiqua*, growers rely almost exclusively on seed treatments. There are no rescue treatments for *D. antiqua* once it is established in the field (Reiners et al., 2019), and due to their diurnal movement between onion fields and adjacent habitats, targeting flies has not been effective (Finch et al., 1986). As a consequence, growers target larvae prophylactically with insecticides applied in-furrow as a drench at planting or as seed treatments. The only insecticide currently labeled for application as an in-furrow drench is chlorpyrifos (e.g., Lorsban Advanced, Corteva, Indianapolis, IN, USA), which is being phased out of production and is likely to have its registration revoked. Moreover, *D. antiqua* populations have developed resistance to chlorpyrifos, and it is no longer effective on many farms (Hessney and Eckenrode 2000, Nault et al. 2006b, Moretti et al. 2019), leaving only seed treatments as a defense against infestations. Among the insecticides labeled for use as seed treatments for *D. antiqua* management, spinosad (Regard SC, Syngenta, Greensboro, NC, USA) has been one of the most effective and widely adopted (Hoepting and Nault, 2012; Wilson et al., 2015).

Since its registration in 1997, spinosad has been labeled for use on pests of many agricultural and horticultural crops. Spinosad is a mixture of two structurally similar compounds, spinosyn A and spinosyn D, and belongs to a novel class of insecticides, the spinosyns, which are bacterial fermentation products of the soil actinomycete *Saccharopolyspora spinosa* (Thompson et al., 2000, 1997). Spinosyns have a novel mode of action, acting as allosteric modulators of the nicotinic acetylcholine receptor (nAChR) in insect nervous systems (Dripps et al., 2011; Jeschke and Nauen, 2019; Orr et al., 2009; Sparks et al., 2001; Watson et al., 2010). Spinosad is considered a “reduced-risk” insecticide (US EPA, 1999), owing to its relatively low toxicity to non-target organisms (Biondi et al., 2012; Schoonover and Larson, 1995), rapid dissipation (Cleveland et al., 2002; Kollman, 2002), and low leaching potential (Hedia and El-Aswad, 2016; Kollman, 2002). Unlike many other biologically-derived insecticides, spinosad is active through both contact and ingestion and is highly effective against several insect orders, principally Lepidoptera, Thysanoptera, and Diptera (Bret et al., 1997; Thompson et al., 1997).

Spinosad was labeled in 2011 for use as a seed treatment in onion for management of maggot pests and is available alone as Regard SC (Syngenta, Greensboro, NC) or as part of the seed treatment package FarMore FI500 (Syngenta, Greensboro, NC). Since its registration, spinosad has been the primary insecticide used to manage *D. antiqua* in commercial onion fields. Despite evidence that spinosad seed treatment can be effective against other *Delia* spp. on other crops, like cabbage maggot, *D. radicum*, on cabbage (Ester et al., 2003), onion is the only crop in which spinosad is registered as a seed treatment. As a consequence, very little is known regarding spinosad's activity and mechanism of maggot control in onion when applied as a seed treatment. Specifically, it remains unclear whether larval mortality from the seed treatment occurs when larvae contact spinosad in the soil or if spinosad moves systemically in onion plants and mortality occurs via ingestion, or both. Although the physical properties of spinosad, including its large molecular weight and low water solubility, suggest that systemic activity of the insecticide is unlikely (Jeschke and Nauen, 2019), studies in tomatoes and beans have demonstrated some systemic activity (Van Leeuwen et al., 2006; van Leeuwen et al., 2005; Weintraub and Mujica, 2006).

Given the gap in our understanding about spinosad activity when applied as a seed treatment to protect onion from *D. antiqua*, the objectives of this study were to 1) determine if spinosad is taken up by onion plants under field conditions, 2) assess spinosad content in soil and aboveground and belowground plant tissue through time, 3) compare amounts of spinosad detected in plant tissue and soil to levels of spinosad necessary to cause mortality in larvae, and 4) evaluate the behavior of larvae when exposed to plants grown with spinosad-treated seeds. Understanding the mechanism for how spinosad protects onion seedlings from onion maggot will provide insight into future delivery tactics as well as future compatibility with other management strategies.

Methods & Materials

Spinosad detection in onion tissue and soil experiment. To evaluate the translocation and dissipation of spinosad in the soil and plant tissues in the field, spinosad-treated seeds were planted in a field with a history of onion production near Oswego, NY (GPS: 43^o 27’ 4.2876”, -76^o 23’ 55.9782”) in 2019. On May 16, dry bulb onion seeds, cultivar ‘Highlander’, were planted into muck soil with a hand-pushed cone-seeder at rates of 30 seeds/m. Two, 27 m rows spaced 25.4 cm apart were planted with spinosad-treated seeds. Seeds were commercially treated with Regard SC at the recommended 0.2 mg ai/ seed rate. A subset of plants was sampled from the two rows at five time points: 25, 40, 47, 54, and 61 days post planting (DPP). At each time point, 10 plants were collected including soil clinging to their roots and transported to the lab. Leaf stage of the sampled onions was recorded, and the soil was gently separated from the plants and roots. Aboveground tissue was separated from belowground material (seedling base and roots), and belowground tissue was rinsed with deionized water to remove any soil. Tissue samples from aboveground and belowground were each massed, placed into 50 mL Falcon tubes (Corning, Corning, NY, USA), and frozen at -20ºC until analysis. At the first time point, because the onions were very small, samples were bulked. Tissue of five plants was combined into a single sample (for belowground and aboveground tissue) for a total of 2 replicates. At the following sampling time points, tissue of two plants was combined into a sample for a total of 5 replicates. Soil collected from around the roots of each plant sample was homogenized by vigorously shaking the sample for one min. Soil surrounding roots of two plants was bulked together, for a total of 5 replicates at each time point. A 5 g aliquot of soil for each replicate was placed into a 50 mL Falcon Tube and frozen at -20ºC until analyzed. Another 5 g aliquot of soil was dried, and percent moisture was determined.

Spinosyn A and D are nearly identical in structure and typically found in an 85:15 ratio in commercial formulations (Kollman, 2002). Spinosyn A (for which we have better quantification) content of the belowground and aboveground tissue and soil was extracted using a modified QueChERS extraction method (Anastassiades et al., 2003) and quantified using liquid chromatography tandem mass spectroscopy (LC-MS/MS)

Onion maggot control with spinosad seed treatment experiment. Onion maggot control was evaluated in the same commercial onion field as described for the Spinosad detection in onion tissue and soil experiment. On 16 May 2019, dry bulb onion seeds, ‘Highlander’, were planted into muck soil with a hand-pushed cone-seeder at rates of 30 seeds/m. Each plot consisted of two 9.1 m rows spaced 25.4 cm apart, and plots were separated from each other within rows by a 0.91 m alley of bare soil. The treatments were spinosad-treated seed and no-insecticide treated seed. Spinosad-treated seeds were commercially treated with Regard SC (0.2 mg/seed), and both the spinosad-treated and untreated seeds were commercially treated with fungicides penflufen and thiram (EverGol Prime, Bayer CropScience, Research Triangle Park, NC) for seedling disease control. Treatments were replicated five times. Damage evaluations were initiated once damage was detected. The number of plants dead or damaged from onion maggot was recorded weekly at five time points: 39, 42, 46, 54, and 62 DPP. Damage by onion maggot was identified by plants with flaccid leaves; all damaged plants were removed and assessed for active feeding by larvae, or in the absence of larvae, entry or exit wounds. Subsamples of larvae were periodically sampled and identified as *D. antiqua*. Voucher specimens are kept at the Department of Entomology, Cornell AgriTech, Geneva, NY.

To account for seedling loss from factors other than *D. antiqua* damage (i.e. excessive rainfall, wind, and disease), the cumulative percentage of plants damaged by *D. antiqua* was assessed by dividing the cumulative number of plants damaged by the sum of plants damaged across all time points plus the final stand count for each replication. To compare cumulative damage in the untreated and spinosad-treated treatments over time, data were fit to a generalized linear mixed effects model using the *glmer* function of the lme4 package (Bates et al., 2015) in R (R Core Team, 2017). Cumulative plant damage (proportion of maggot damaged plants) modeled with a binomial distribution served as the response variable; treatment (spinosad-treated vs untreated), DPP, and their interaction were fixed effects, and block was included as a random effect to account for repeated measures across sampling points. An observation-level random effect was included to account for overdispersion. The model was simplified with stepwise backward elimination of non-significant parameters. Post-hoc contrasts were conducted using *emmeans* package with Tukey adjustment for multiple comparisons ($P \geq 0.05$(Lenth et al., 2020).

Test Insects. First-generation *D. antiqua* larvae were collected from the commercial onion field described above in June 2018. Additional first-generation larvae were added to the lab colony from the same location in 2019. Larvae were reared in plastic containers (16.2 x 9.3 x 17.7 cm, Rubbermaid, Atlanta, GA, USA) lined with 3 cm of moistened, unwashed mason's sand and were fed halved yellow onions *ad libitum.* Pupae were removed from the sand and placed into nylon-screened cages (BugDorm®, 60 x 60 x 60 cm, MegaView Science, Co., Ltd., Taiwan) to emerge, feed, mate, and oviposit. Adults were provided dry diet (10:10:1:1, skimmed milk powder: sugar: brewer's yeast: soy peptone) (Ticheler, 1971), and an ovipositional dish consisting of a halved yellow onion placed on moistened sand. All life stages were placed in walk-in environmental chambers (photoperiod 16:8 [L:D] hr, 21°C, 40% RH). Approximately every 3 days, the ovipositional dish was removed and replaced, providing larval cohorts of similar age.

Larval Immersion Assay. Sensitivity to spinosad through contact was evaluated using a larval immersion assay modified from Nault et al. (2006). Larvae, in groups of five individuals (1-wk or 2-wk old), were submerged in a solution containing deionized water and spinosad (Regard SC, Syngenta, Greensboro, NC, USA) for 20 sec using a small wire mesh strainer. After immersion, larvae were placed into 30 ml plastic shot glasses (Polar Plastics, Inc., Mooresville, NC) and provided with a 0.5 x 0.5 cm piece of yellow onion. Five to six concentrations of spinosad plus a control (deionized water only) and a minimum of five replications for each concentration were included in each bioassay. Lids, ventilated with holes, were fitted to each cup, and assays were maintained at 21°C, 40% RH, and photoperiod of 16:8 (L:D) h. Mortality was assessed after 48 hours using a dissecting microscope, categorizing individuals as alive or dead. A larva was considered dead if it did not respond when probed with a paintbrush. Frequently, dead larvae were brown and shriveled.

Feeding Assay. Sensitivity to spinosad through feeding was evaluated using a diet-based concentration-response bioassay modified from Kain et al. (2004). Five to six concentrations of spinosad plus a control (deionized water only) and a minimum of five replications for each concentration were included in each bioassay. An aliquot of 0.2 ml spinosad solution was distributed evenly over 5 ml high wheat germ diet (~ 7 cm^2 surface area, Shorey and Hale 1965) in 30 ml plastic shot glasses. Once fully absorbed by the diet, five larvae (1-wk or 2-wk old), were added to each shot glass and covered with a ventilated lid, then held at 21°C, 40% RH, and photoperiod of 16:8 (L:D) h. The location of the larvae in the diet (on top of diet or feeding within diet) and mortality were assessed after 48 h.

Data from immersion and feeding assays were corrected with Abbott's formula (Abbott, 1925) accounting for mortality in the controls, which never exceeded 20%. Probit analysis of the concentration-dependent mortality response was used to generate LC_{50}s for the populations tested (source code available at github.com/JuanSilva89/Probit-analysis). Differences between LC_{50}s were considered significant if the 95% confidence intervals (CI) failed to overlap.

Plants for choice and no-choice assays. Onions, 'Highlander', were grown from untreated and spinosad-treated seeds in the greenhouse. Spinosad-treated seeds were commercially pelleted with the recommended 0.2 mg ai/seed Regard SC, and untreated seeds were pelleted with no active ingredients; neither treatment included fungicides. Seeds were sown into 5.7 cm pots in propagation mix (Sun Gro Horticulture, Agawam, MA, USA). Plantings were staggered to ensure that four and eight-week old plants were available for each assay. Plants were watered as needed and were not fertilized over their growing period. At the time of each assay, plants were carefully removed from their pots, and excess soil was shaken off the roots. The aboveground portion of the plant was removed and the roots were trimmed to 0.5 cm. The remaining belowground portion of the plant was rinsed with DI water to remove any excess soil and blotted dry with a paper towel.

Choice Assay. A choice assay was used to determine if larvae preferred to feed on untreated plants or those grown from spinosad-treated seed. Untreated and spinosad-treated belowground plant tissue were arranged in a 60 x 15 mm Falcon dish (Corning, Corning, NY, USA), lined with filter paper lightly moistened with deionized water. Onions were either four or eight-wks old. Location of the plants (left or right) in the dish was randomized for each replication. An individual two-wk old larva was place within the arena, and it's choice was recorded after 24 and 48 hrs. A larva was considered to have made a choice if it was actively feeding or had fed on one of the onions. Choice between treated and untreated four-wk old plants was replicated 23 times, and choice between treated and untreated eight-wk old plants was replicated 20 times. Chi-square tests were used to determine if choice was independent of plant age and whether larvae had a preference for untreated or spinosad-treated plants.

No-choice Assay. A no-choice assay was used to determine if *D. antiqua* larvae would feed on plants grown from spinosad-treated seed or would avoid them and not feed. A single two-wk old larva was placed into an arena (described in the choice assay) with a section of belowground tissue from either a four or eight-wk old plant. The same assay was done with untreated plants as a control. Each treatment was replicated 20 times. The presence of feeding and the mortality status of the larvae was recorded after 48 h. To determine if the presence or absence of feeding was affected by treatment (spinosad-treated vs untreated) after 48 h, data were modeled using a generalized linear mixed effects model. The presence of feeding was fitted to a binomial distribution, with plant age, treatment, and their interaction as fixed effects. Replication was included as a random effect to adjust for overdispersion. Mortality was low across all treatments (< 15%), so mortality data were not analyzed statistically.

Results

Spinosad detection in onion tissue and soil experiment. Spinosad was detected in both the aboveground and belowground plant tissue as well as the soil (Figure 3.1A). Minor translocation of spinosad to aboveground plant tissue was confirmed. Spinosad was detected in aboveground tissue in very low concentrations (<0.5 ppm) over all time points. Higher spinosad concentrations were detected in the belowground onion tissue, but concentrations never exceeded 2 ppm. Spinosad in both the aboveground and belowground onion tissue declined over time, with both tissues reaching levels below 0.05 ppm by 47 DPP, at which point, onions were at the 4-5th leaf stage. Across nearly all sampling points, the highest concentrations of spinosad were recovered from the soil. In addition to being the highest, spinosad content was also the most variable in the soil at the majority of time points evaluated. Unlike the onion tissue, spinosad content in the soil did not decline consistently across the timepoints evaluated, although an overall decline was observed.

Plant damage. In the field trial comparing damage to plants grown with spinosad-treated seeds and untreated seeds, damage was first recorded 39 DPP (24 June) (Figure 3.1B). At each time point assessed, cumulative damage in the untreated plots was significantly greater than in spinosad-treated ones ($P < 0.05$); however, there was no treatment by time effect, indicating that the change in damage for each treatment was similar over time. Damage in the untreated controls indicated severe pest pressure at the field site. On the final sampling date (15 July), average cumulative damage in the untreated plots was 79%, while average cumulative damage in spinosad-treated plants was 48%. The spinosad seed treatment provided ~30% control.

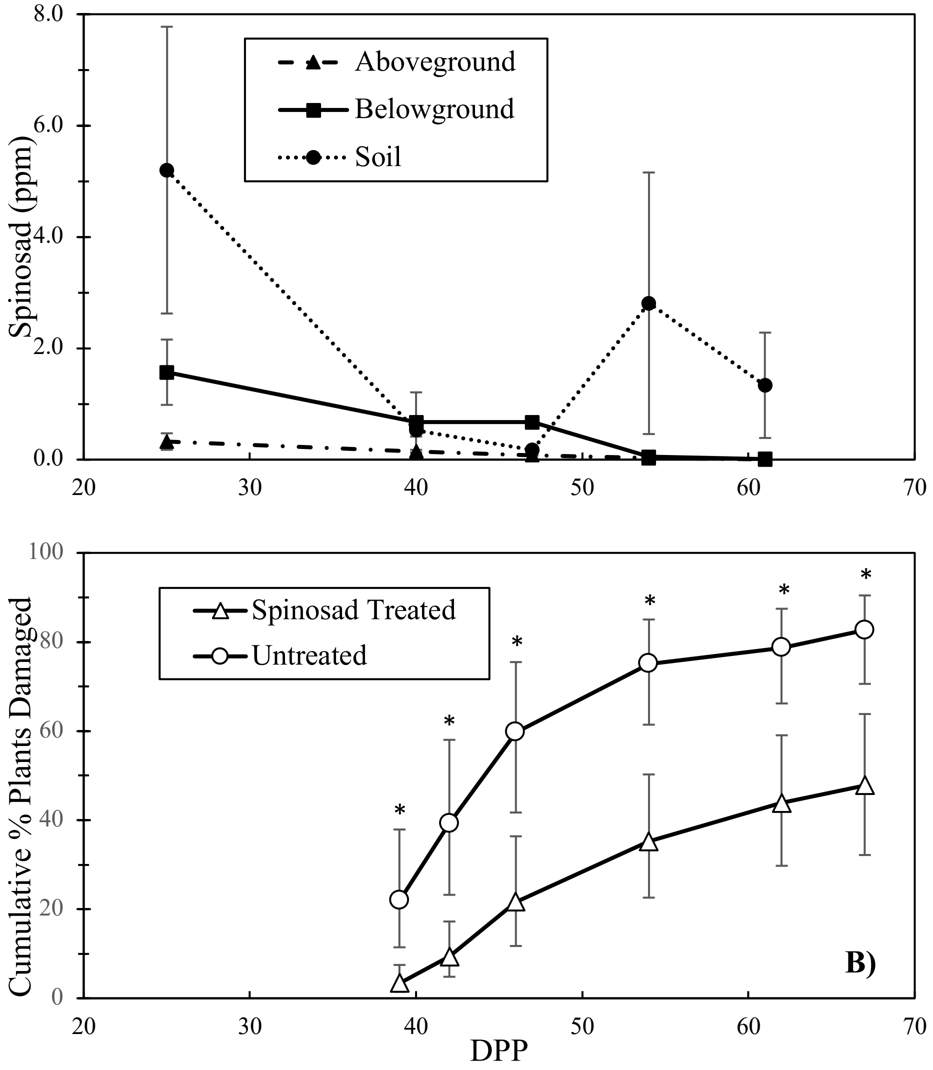

Figure 3.1. Concentration of spinosad (spinosyn A, ppm) in onion plant tissue (µg spinosad/kg plant tissue) and soil (µg spinosad/g dry soil) ±SEM (A), and plant damage by first-generation *D. antiqua* (± 95% CL) (B) in a New York onion field at time points measured days post planting (DPP). In damage evaluations (B), asterisks (*) indicate significant differences between treatments (Tukey, $P < 0.05$).

Immersion and ingestion assays. LC_{50}s for both contact (immersion) and feeding (ingestion) assays exceeded the concentrations found in plant tissue and the soil (Table 3.1). In immersion assays, susceptibility of one and two-wk old larvae was similar. In contrast, younger larvae were more susceptible than older larvae when fed a spinosad-treated diet. Spinosad was more toxic to one-wk old larvae though ingestion than through contact, but LC_{50}s from the two modes of exposure were similar for two-wk old larvae.

Table 3.1. Susceptibility of *Delia antiqua* larvae to spinosad (Regard SC) in immersion and feeding assays.

Larval age	*N*	Slope (SE)	LC_{50} (ppm)	95% CL	X^2(df)[a]
Immersion Bioassay					
1 wk-old	216	1.66 (0.17)	21.6	17.3-27.0	4.67 (4)*
2 wk-old	241	1.34 (0.17)	32.6	24.3-43.6	3.85 (4)*
Feeding Bioassay					
1 wk-old	126	2.70 (0.41)	9.8	7.6-12.5	3.67 (3)*
2 wk-old	194	1.94 (0.17)	20.9	17.8-24.6	1.47 (3)*

[a] The X^2 values followed by "*" indicate good fit of the data to the probit model ($P > 0.05$).

Larval choice and no-choice assays. In choice tests, larval choice was independent of plant age (four vs eight wks), at 24 (X^2= 0.046, df=1, P=0.83) and 48 h (X^2= 0.042, df=1, P=0.84). At 24 h, 64% of larvae that made a choice fed on untreated rather than spinosad-treated onions, but this was not statistically significant (X^2= 3.10, df=1, P=0.08). At 48 h, however, 75% of larvae chose untreated onions, displaying a significant preference for untreated rather than spinosad-treated onions (X^2= 8.0, df=1, *P*=0.005). In no-choice tests in which larvae were presented with either a single spinosad-treated or untreated four-wk old or eight-wk old onion, there was no difference in feeding based on plant age ($F_{1,75}$ = 0.15, *P* = 0.73), treatment ($F_{1,75}$ = 0.12, *P* = 0.73) or their interaction ($F_{1,75}$ = 0.10, *P* = 0.75) after 48 h. Without a choice, the majority (>85%) of larvae fed on the plant they were presented, regardless of plant age or treatment. Mortality was low across all of the treatments, with fewer than three individuals (3/20) perishing in each treatment. Results indicated that older larvae will feed on spinosad-treated onion and a majority would survive.

Discussion

Spinosad is registered for use as a foliar spray to manage insect pests in many cropping systems. However, it is only used at-planting to control maggot pests in onion. In this case, its only permitted application at planting is in the form of a seed treatment, and its use as an onion seed treatment has been highly effective for managing *D. antiqua* for nearly a decade (Nault et al. 2006a, Hoepting and Nault 2012, Wilson et al. 2015). Despite this success, little was known regarding the mechanisms responsible for its effectiveness, its translocation within onion plants, its longevity in the environment after planting, or how it effects the feeding behavior of *D. antiqua*. We identified that spinosad is found in soil around roots and in onion tissue, with both dissipating over time. Larvae were susceptible to spinosad through both contact and feeding, suggesting that exposure could occur in either the soil or through feeding on belowground tissue. We also documented that larvae will avoid spinosad-treated onion plants when given a choice, but readily feed on treated plants when a choice is not offered.

Spinosad applied as a foliar spray has translaminar activity in plant tissue, but its physical properties suggest that systemic activity is limited (Bret et al., 1997). Spinosad is a large molecule (732 g/mol, spinosyn A) with relatively low water solubility (290 ppm at 20^{o}C, pH = 5), qualities which do not favor uptake and movement through xylem and phloem (Kollman, 2002; Salgado and Sparks, 2005). In our study, spinosad was detected in the aboveground tissue (i.e., leaves) of onions, confirming some translocation of the product in onion (Figure 3.1A). This is not the first example documenting that spinosad can be systemic in plants. For example, spinosad applied to the base of tomato plants grown in rockwool successfully managed foliar feeding pests including two-spotted spider mite, whiteflies, and cotton leaf worm (Van Leeuwen et al., 2006; van Leeuwen et al., 2005).

In both plant tissue and surrounding soil, spinosad content declined over the sampling period from 25 to 61 DPP (Figure 3.1A). Spinosad is known to dissipate rapidly; in many vegetable crops, including cabbage and cauliflower (Mandal et al., 2009; Sharma et al., 2007), tomato (Adak and Mukherjee, 2016; Kashyap et al., 2015), eggplant (Zhao et al., 2007), and zucchini (Liu et al., 2013), spinosad half-lives applied as a foliar spray are less than 4 d. In onion, the half-life of spinosad has been reported at fewer than 1.5 d (Dasenaki et al., 2016; Srinivas P. et al., 2012). The primary route of spinosad degradation is photolysis (Cleveland et al., 2002; Kollman, 2002). When applied as a foliar spray on the plant canopy, spinosad readily degrades in sunlight. In contrast, when spinosad is delivered as a seed treatment buried in the soil without direct sunlight, photodegradation is reduced considerably. Although it is also broken down through microbial degradation, in the absence of sunlight, spinosad's persistence in the soil may be extended (Hale and Portwood, 1996; Kollman, 2002). While dissipation kinetics of spinosad delivered as a seed treatment were not evaluated in our study, this information would provide key insight into the window of protection offered by seed treatments (Alford and Krupke, 2017).

The greatest amount of spinosad was recovered from the soil; however, it is unclear whether it was biologically active. Previous studies have shown that spinosad applied as a soil drench does not provide control equal to application as a seed treatment (Wilson et al. 2015, Nault unpublished data). Strong adsorption of pesticides to soil particles can render them biologically unavailable (Sims et al., 1991), but few studies have evaluated spinosad sorption to soils. Among those that have, adsorption was relatively strong but was assessed only in mineral soils (Hedia and El-Aswad, 2016; Kollman, 2002). Sorption is strongly influenced by soil type and pH as well as the amount of organic matter present (Sims et al., 1991). In the Great Lakes region, onions are commercially produced almost exclusively on muck soil, high organic matter histosols derived from drained wetlands (Lucas, 1982). Organic matter in these fields can range from 20-80%, which could have a dramatic effect on soil adsorption. Generally, increased organic matter is associated with increased adsorption; as a consequence, muck soils have the potential to strongly bind insecticides, which may reduce their efficacy.

The decline in spinosad content observed over the course of the study corresponded to an increase in damage in spinosad-treated plants (Figure 3.1B). While spinosad appeared to reduce plant damage by first-generation *D. antiqua* relative to untreated plants, damage in the treated plants was still considered unacceptable (> 10%), and damage in the untreated and treated plants increased at nearly the same rate after 42 DPP. This suggests that spinosad protected seedlings earlier in the growing season but was no longer effective as its concentration declined. Larval immersion and feeding assays revealed that the concentration of spinosad necessary to cause mortality in larvae far exceeded amounts detected in the belowground tissue and soil, where larvae may come into contact with the insecticide. Smaller larvae were more sensitive to spinosad through ingestion, indicating that neonates are most susceptible to the insecticide and likely explains why this seed treatment is so effective earlier in the growing season. Other studies reported that younger, compared to older, *D. antiqua* instars are more susceptible to some insecticides used in their management, including cyromazine (Yildirim and Hoy, 2003) and chlorpyrifos (Nault et al. 2006b). Larger larvae were less susceptible to spinosad through ingestion, and although they exhibited a preference for untreated onions, without a choice they fed upon spinosad-treated onions and did not experience mortality. This indicates that spinosad in plants may have a deterrent effect on larger larvae but does not inhibit feeding or cause mortality. A deterrent effect could be effective at reducing *D. antiqua* pressure by forcing larvae to move within the soil matrix in search of another host plant. Thus, larval mortality also could be caused by an extended period of movement through the soil, especially if conditions in the soil are inhospitable for dispersal, for example hot or dry (Ellington, 1963; Workman, 1958).

Overall, despite providing excellent control of onion maggot in previous studies (Nault et al. 2006a, Wilson et al. 2015), spinosad provided poor control of onion maggot in this field trial with cumulative damage reaching nearly 50% in treated plants. The poor performance of the seed treatment could be the result of excessive pressure from the pest, overwhelming the ability of the insecticide to protect the seedlings. The field where this experiment took place has a history of high onion maggot pressure and perennial use of spinosad seed treatment since 2011. This information, together with the larval immersion and feeding assays results, which demonstrated that levels of spinosad detected in plants should not have been high enough to cause mortality, may indicate that the population is no longer susceptible to spinosad.

Spinosad's limited use as a seed treatment for agricultural crops has resulted in very few assessments of its activity and mechanism of control. Despite being available for nearly a decade as an onion seed treatment, this was the first study to evaluate spinosad uptake in onions planted with treated seeds and to establish a dose-response relationship for larvae exposed to spinosad through both ingestion and contact. The results from this study establish a framework that highlights areas in need of further study. Specifically, it is clear that more research is needed regarding adsorption in high organic matter soils, dissipation rates, and larval susceptibility.

REFERENCES

Abbott, W.S., 1925. A Method of Computing the Effectiveness of an Insecticide. J Econ Entomol 18, 265–267. https://doi.org/10.1093/jee/18.2.265a

Adak, T., Mukherjee, I., 2016. Dissipation kinetics of spinosad from tomato under sub-tropical agro-climatic conditions. Environ Monit Assess 188, 299. https://doi.org/10.1007/s10661-016-5291-6

Alford, A., Krupke, C.H., 2017. Translocation of the neonicotinoid seed treatment clothianidin in maize. PLOS ONE 12, e0173836. https://doi.org/10.1371/journal.pone.0173836

Anastassiades, M., Lehotay, S.J., Stajnbaher, D., Schenck, F.J., 2003. Fast and easy multiresidue method employing acetonitrile extraction/partitioning and "dispersive solid-phase extraction" for the determination of pesticide residues in produce. J AOAC Int 86, 412–431.

Bates, D., Maechler, M., Bolker, B.M., Walker, S.C., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67, 1–48.

Biondi, A., Mommaerts, V., Smagghe, G., Vinuela, E., Zappala, L., Desneux, N., 2012. The non-target impact of spinosyns on beneficial arthropods. Pest Manag. Sci. 68, 1523–1536. https://doi.org/10.1002/ps.3396

Bret, B.L., Larson, L.L., Schoonover, J.R., Sparks, T.C., Thompson, G.D., 1997. Biological properties of spinosad. Down to Earth 52, 6–14.

Cleveland, C.B., Bormett, G.A., Saunders, D.G., Powers, F.L., McGibbon, A.S., Reeves, G.L., Rutherford, L., Balcer, J.L., 2002. Environmental Fate of Spinosad. 1. Dissipation and Degradation in Aqueous Systems. J. Agric. Food Chem. 50, 3244–3256. https://doi.org/10.1021/jf011663i

Dasenaki, M.E., Bletsou, A.A., Hanafi, A.H., Thomaidis, N.S., 2016. Liquid chromatography–tandem mass spectrometric methods for the determination of spinosad, thiacloprid and pyridalyl in spring onions and estimation of their pre-harvest interval values. Food Chemistry 213, 395–401. https://doi.org/10.1016/j.foodchem.2016.06.099

Dripps, J.E., Boucher, R.E., Chloridis, A., Cleveland, C.B., DeAmicis, C.V., Gomez, L.E., Paroonagian, D.L., Pavan, L.A., Sparks, T.C., Watson, G.B., 2011. CHAPTER 5. The Spinosyn Insecticides, in: López, Ó., Fernández-Bolaños, J.G. (Eds.), RSC Green

Chemistry. Royal Society of Chemistry, Cambridge, pp. 163–212. https://doi.org/10.1039/9781849732901-00163

Eckenrode, C., Vea, E., Stone, K., 1975. Population Trends of Onion Maggots Correlated with Air Thermal Units Accumulations. Environ. Entomol. 4, 785–789.

Ellington, J.J., 1963. Field and laboratory observations on the life history of the onion maggot ylemyia antiqua (Meigen). Cornell University.

Ester, A., de Putter, H., van Bilsen, J.G.P.M., 2003. Filmcoating the seed of cabbage (Brassica oleracea L. convar. Capitata L.) and cauliflower (Brassica oleracea L. var. Botrytis L.) with imidacloprid and spinosad to control insect pests. Crop Protection 22, 761–768. https://doi.org/10.1016/S0261-2194(03)00042-5

Finch, S., Eckenrode, C.J., Cadoux, M.E., 1986. Behavior of onion maggot (Diptera: Anthomyiidae) in commercial onion fields treated regularly with parathion sprays. Journal of economic entomology 79, 107–113.

Hale, K.A., Portwood, D.E., 1996. The aerobic soil degradation of spinosad - a novel natural insect control agent. Journal of Environmental Science and Health, Part B 31, 477–484. https://doi.org/10.1080/03601239609373010

Hedia, R.M., El-Aswad, A.F., 2016. Spinosad Adsorption on Humic and Clay Constituents of Lacustrine Egyptian Soils and Its Leaching Potential. Alexandria Science Exchange 37, 458.

Hessney, M.L., Eckenrode, C.J., 2000. Onion maggot resistance to Lorsban 1999. Arthropod Manag Tests 25. https://doi.org/10.1093/amt/25.1.L9

Hoepting, C.A., Nault, B.A., 2012. New developments for managing onion maggot. Cornell Cooperative Extension. VegEdge 8, 10–13.

Jeschke, P., Nauen, R., 2019. Nicotinic acetylcholine receptor competitive modulators and channel blockers: Target and selectivity aspects, in: Modern Crop Protection Compounds. John Wiley & Sons, Ltd, pp. 1223–1265. https://doi.org/10.1002/9783527699261.ch33

Kain, W.C., Zhao, J.-Z., Janmaat, A.F., Myers, J., Shelton, A.M., Wang, P., 2004. Inheritance of Resistance to Bacillus thuringiensis Cry1Ac Toxin in a Greenhouse-Derived Strain of Cabbage Looper (Lepidoptera: Noctuidae). JOURNAL OF ECONOMIC ENTOMOLOGY 97, 6.

Kashyap, L., Sharma, D.C., Anil, 2015. Dissipation behaviour of spinosad in polyhouse grown tomato under mid-hill conditions of Himachal Pradesh, India. Environmental

Monitoring and Assessment; Dordrecht 187, 1–6. http://dx.doi.org/10.1007/s10661-014-4210-y

Kollman, W.S., 2002. Environmental Fate of Spinosad.

Lenth, R.V., Love, J., Buerkner, P., Herve, M., 2020. Estimated Marginal Means, aka Lest-Squares Means. R Package Version 1.4.5.

Liu, Y., Sun, H., Wang, S., 2013. Dissipation and Residue of Spinosad in Zucchini Under Field Conditions. Bulletin of Environmental Contamination and Toxicology; New York 91, 256–9. http://dx.doi.org/10.1007/s00128-013-1050-3

Lucas, R., E., 1982. Organic Soils (Histosols): Formation, Distribution, Physical and Chemical Properties and Management for Crop Production. Michigan State University, Agricultural Experiment Station.

Mandal, K., Jyot, G., Singh, B., 2009. Dissipation Kinetics of Spinosad on Cauliflower (Brassica oleracea var. botrytis. L.) Under Subtropical Conditions of Punjab, India. Bulletin of Environmental Contamination and Toxicology; New York 83, 808–11. http://dx.doi.org/10.1007/s00128-009-9844-z

Moretti, E., Nault, B., Hoepting, C., 2019. Seed treatment recommendations for onion maggot control in 2020. VegEdge 15, 4–5.

Moretti, E., Nault, B.A., 2020. Onion Maggot Control in Onion, 2019. Arthropod Manag Tests 45. https://doi.org/10.1093/amt/tsaa007

Nault, B. A., Straub, R.W., Taylor, A.G., 2006. Performance of novel insecticide seed treatments for managing onion maggot (Diptera : Anthomyiidae) in onion fields. Crop Prot. 25, 58–65. https://doi.org/10.1016/j.cropro.2005.03.020

Nault, Brian A., Zhao, J.-Z., Straub, R.W., Nyrop, J.P., Hessney, M.L., 2006. Onion maggot (Diptera : Anthomyiidae) resistance to chlorpyrifos in New York onion fields. J. Econ. Entomol. 99, 1375–1380.

Orr, N., Shaffner, A.J., Richey, K., Crouse, G.D., 2009. Novel mode of action of spinosad: Receptor binding studies demonstrating lack of interaction with known insecticidal target sites. Pesticide Biochemistry and Physiology 95, 1–5. https://doi.org/10.1016/j.pestbp.2009.04.009

Pesticide Fact Sheet: Spinosad, 1999.

Reiners, S., Curtis, P.D., Helms, M., McGrath, M.T., Nault, B.A., Seaman, A., 2019. Cornell integrated crop and pest management guidelines for commercial vegetable production, in: N.Y. State Integ. Pest Manag. Progr. Cornell University, Geneva, NY.

Salgado, V.L., Sparks, T.C., 2005. The Spinosyns: Chemistry, Biochemistry, Mode of Action, and Resistance, in: Comprehensive Molecular Insect Science. Elsevier, pp. 137–173. https://doi.org/10.1016/B0-44-451924-6/00078-8

Schoonover, J.R., Larson, L.L., 1995. Laboratory Activity of Spinosad on Non-Target Beneficial Arthropods, 1994. Arthropod Manag Tests 20, 357–357. https://doi.org/10.1093/amt/20.1.357

Sharma, A., Srivastava, A., Ram, B., Srivastava, P.C., 2007. Dissipation behaviour of spinosad insecticide in soil, cabbage and cauliflower under subtropical conditions. Pest Management Science 63, 1141–1145. https://doi.org/10.1002/ps.1437

Shorey, H.H., Hale, R.L., 1965. Mass-Rearing of the Larvae of Nine Noctuid Species on a Simple Artificial Medium. J Econ Entomol 58, 522–524. https://doi.org/10.1093/jee/58.3.522

Sims, G.K., Radosevich, M., He, X.T., Traina, S.J., 1991. The effects of soprtion on the bioavailability of pesticides, in: Biodegradation: Nautral and Synthetic Materials. Springer London, London, pp. 119–139.

Sparks, T.C., Crouse, G.D., Durst, G., 2001. Natural products as insecticides: the biology, biochemistry and quantitative structure–activity relationships of spinosyns and spinosoids. Pest. Manag. Sci. 57, 896–905. https://doi.org/10.1002/ps.358

Srinivas P., S., Banerjee, K., Jadhav, M.R., Ghaste, M.S., Lawande, K.E., 2012. Bioefficacy, dissipation kinetics and safety evaluation of selected insecticides in *Allium cepa* L. Journal of Environmental Science and Health, Part B 47, 700–709. https://doi.org/10.1080/03601234.2012.669262

Thompson, G.D., Dutton, R., Sparks, T.C., 2000. Spinosad – a case study: an example from a natural products discovery programme. Pest Management Science 56, 696–702. https://doi.org/10.1002/1526-4998(200008)56:8<696::AID-PS182>3.0.CO;2-5

Thompson, G.D., Michel, K.H., Yao, R.C., Mynderse, J.S., Mosburg, C.T., Worden, T.V., Chio, E.H., Sparks, T.C., Hutchins, S.H., 1997. The discovery of Saccharopolyspora spinosa and a new class of insect control products. Down to Earth 52, 1–5.

van Leeuwen, T., Dermauw, W., Van De Veire, M., Tirry, L., 2005. Systemic Use of Spinosad to Control the Two-spotted Spider Mite (Acari: Tetranychidae) on Tomatoes Grown in Rockwool. Experimental and Applied Acarology 37, 93–105. https://doi.org/10.1007/s10493-005-0139-8

Van Leeuwen, T., Van de Veire, M., Dermauw, W., Tirry, L., 2006. Systemic toxicity of spinosad to the greenhouse whiteflyTrialeurodes vaporariorum and to the cotton leaf wormSpodoptera littoralis. Phytoparasitica 34, 102–108. https://doi.org/10.1007/BF02981345

Watson, G.B., Chouinard, S.W., Cook, K.R., Geng, C., Gifford, J.M., Gustafson, G.D., Hasler, J.M., Larrinua, I.M., Letherer, T.J., Mitchell, J.C., Pak, W.L., Salgado, V.L., Sparks, T.C., Stilwell, G.E., 2010. A spinosyn-sensitive Drosophila melanogaster nicotinic acetylcholine receptor identified through chemically induced target site resistance, resistance gene identification, and heterologous expression. Insect Biochemistry and Molecular Biology 40, 376–384. https://doi.org/10.1016/j.ibmb.2009.11.004

Weintraub, P.G., Mujica, N., 2006. Note: Systemic effects of a spinosad insecticide onLiriomyza huidobrensis Larvae. Phytoparasitica 34, 21–24. https://doi.org/10.1007/BF02981335

Whitfield, G.H., Carruthers, R.I., Haynes, D.L., 1985. Phenology and control of the onion maggot (Diptera: Anthomyiidae) in Michigan onion production. Agriculture, Ecosystems & Environment 12, 189–200. https://doi.org/10.1016/0167-8809(85)90110-0

Wilson, R.G., Orloff, S.B., Taylor, A.G., 2015. Evaluation of insecticides and application methods to protect onions from onion maggot, Delia antiqua, and seedcorn maggot, Delia platura, damage. Crop Prot. 67, 102–108. https://doi.org/10.1016/j.cropro.2014.10.002

Workman, R.B., 1958. The biology of the onion maggot, Hylemyia antiqua (Meigen), under field and greenhouse conditions. Oregon State College.

Yildirim, E., Hoy, C.W., 2003. Cyromazine Seed Treatments to Control Onion Maggot, Delia antiqua, on Green Onions. JOURNAL OF ECONOMIC ENTOMOLOGY 96, 6.

Zhao, E., Xu, Y., Dong, M., Jiang, S., Zhou, Z., Han, L., 2007. Dissipation and Residues of Spinosad in Eggplant and Soil. Bull Environ Contam Toxicol 78, 222–225. https://doi.org/10.1007/s00128-007-9133-7

CONCLUSION

Onion maggot, *Delia antiqua*, is a widespread threat to onion production in northern temperature regions worldwide. The work described above addresses some basic questions about its distribution and damage in onion fields and how it is controlled with spinosad seed treatments. The results from this research will be used to improve management of this important pest and have motivated new research questions regarding the biology and management of *D. antiqua* as well as the chemistry of spinosad. Collectively, these projects have provided me with strong laboratory and field research skills as well as improved communication, that I hope to continue to implement in grower-motivated research.

Factors influencing* D. antiqua *damage

Environmental and management factors and their association with *D. antiqua* damage were evaluated in commercial onion fields in New York. This was the first study to evaluate multiple factors known to influence *D. antiqua* in the field. This research was largely initiated in response to a question that many onion growers in the region had, specifically, why do some growers have a problem with onion maggot while others do not? Many anecdotal reports from growers claim that cooler, wetter conditions favor *D. antiqua* and that this explains the disparities in damage observed from field to field. This claim is commonly found in many extension factsheets from reputable institutions, and associations between humidity and temperature can be found in the literature from laboratory studies; however, no field study had formally substantiated the association.

In response to this lack of information, we sought to expand on existing research indicating that environmental factors and management can influence *D. antiqua* damage. We identified several factors from the literature, including temperature, precipitation, soil organic matter, surrounding landscape, planting date, and plant size at peak fly activity. The studies which implicated these factors were often limited in scope; they were either done exclusively under laboratory conditions or evaluated only a single factor. Studies such as these are important, as they control for variation caused by many other interacting factors, but outcomes from studies conducted in the laboratory or under controlled conditions do not always translate to field conditions. We wanted to assess all of these factors in the field to determine if they were associated with the distribution of damage and could explain the variation in damage that was observed.

Field conditions present an intersection of many factors, where abiotic and biotic effects of the environment occur alongside management tactics imposed by growers. Working with multiple factors in the field presents a multitude of challenges, principal among them the difficulty of correctly attributing effects to the factors that cause them and the need for statistical power in the form of large sample sizes to accommodate many factors in a model. Nevertheless, studies such as the one presented here reveal interesting relationships that may not otherwise be detected. For example, we observed consistent effects of both planting date and surrounding landscape on *D. antiqua* damage (later planting dates and more forest in the landscape were associated with greater damage), but the effects of soil temperature and soil organic matter varied based on within-year conditions. These results suggested that rather than existing on a continuum, some relationships were more threshold-based (e.g. soil temperature), and some relationships depended on extraneous factors, for example, the relationship between damage and soil organic matter depended on seasonal precipitation. This has important implications for model development as well as management recommendations.

The study also importantly refuted current planting date recommendations. Although many growers don't use delayed planting to manage *D. antiqua* because the length of the growing season discourages late planting, delayed planting is frequently cited as a way to reduce *D. antiqua* damage. Despite the rigor of the previous study that came to this conclusion, the results of our study found that fields planted later had more damage than those planted earlier. The difference in outcomes of these two studies highlights the importance of research that follows up on adoption of practices and efficacy once implemented. Unfortunately, studies that evaluate efficacy of recommendations executed by growers are seldom conducted but can clearly show limitations of management recommendations.

Collectively, the results of the study identified that environmental factors have an important role influencing *D. antiqua* populations and damage. The results from the study improve our understanding of the biology and dynamics of an important pest of onion, and can be used to inform management decisions. For instance, identifying surrounding landscape as an important factor influencing *D. antiqua* populations may help growers select fields that are candidates for more intensive management tactics, such as rotation, or can be exploited with the strategic deployment of insecticides.

Spinosad seed treatments

Insecticide seed treatments can considerably reduce the amount of insecticide applied to manage a pest relative to drench applications. Broadly, despite the widespread use of seed treatments to manage insect pests, aside from true systemic insecticides, very little research has focused on how insects come into contact with an insecticide when applied in this way. Spinosad seed treatments have been adopted widely by onion growers to manage *D. antiqua* since its registration nearly a decade ago. Spinosad is used as a foliar spray to manage many insect pests but is registered for use as a seed treatment only in onion. As a consequence, very little research has focused on how this product works to manage onion maggot. Understanding how a product works, for instance, where it is found in a plant, how much is present, and how fast it dissipates, is important for determining the window of protection offered by a product. Importantly, this information may also help identify why a product may fail to protect plants against damage.

We evaluated spinosad uptake in onion plants and soil, evaluated larval susceptibility to spinosad through contact and oral ingestion, and assessed behavior of larvae when exposed to plants grown from spinosad-treated seeds. This research established basic information about the product and its effects on the target pest *D. antiqua*. Recovery of spinosad from aboveground tissue indicated that spinosad has some minor systemic activity in onion plants. We established concentration-response curves for a population of *D. antiqua* and observed that spinosad has a deterrent effect on larger (two-wk old) larvae but did not fully dissuade feeding and did not cause direct mortality in behavioral assays. Overall, this research established a basic understanding of where spinosad is found when applied as a seed treatment and how larvae respond when exposed to it. Importantly, it highlighted areas in need of future research to fully understand its mechanism of control.

The majority of spinosad was recovered from the soil surrounding plant roots. However, it was unclear if the product remained biologically active at this point. Spinosad can bind to soils, but it is not known how strongly spinosad binds to muck soils in which onions are primarily grown or whether the product remains biologically available once bound to the soil. Future research should focus on spinosad sorption to high organic matter soils and how this may influence efficacy against target pests.

Additionally, at the location where the field research took place, a field with a history of high *D. antiqua* and annual use of spinosad seed treatments, spinosad did reduce larval feeding relative to untreated controls but did not maintain damage below an economically damaging level (~10%). Spinosad levels declined over the course of the study, and the decline was associated with an increase in larval damage. However, the amounts of spinosad detected in both the plant tissue and soil across all timepoints assessed were well below the concentrations needed to cause mortality in larvae. It is unclear whether the control failure was the result of the seed treatment wearing off, so larvae escaped the window or protection, or if larvae in the field were no longer susceptible to the product. Assessing the susceptibility of larvae from fields that are successfully controlled with spinosad and establishing clear dissipation kinetics of the product when applied as a seed treatment will be important in discerning which is responsible in control failures moving forward.