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Delaying Onion Planting to Control Onion Maggot (Diptera: Anthomyiidae): Efficacy and Underlying Mechanisms

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ABSTRACT Onion maggot, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae), is an important pest of onion, *Allium cepa* L., in northern temperate areas, especially in the Great Lakes region of North America. Management of *D. antiqua* relies on insecticide use at planting, but insecticide resistance can cause control failures that threaten the long-term viability of this strategy. Delaying the time onions are planted was investigated as an alternative management approach for *D. antiqua* and the ecological and behavioral mechanisms underlying host age and insect relationships were examined in laboratory and field experiments. Delaying onion planting by two to four weeks reduced damage to onions by 35 and 90%, respectively. Onions planted later emerged later and this reduced the period overwintered flies had to oviposit on the plants. Moreover, flies tended to lay few to no eggs on these young, late-planted onions. As anticipated, *D. antiqua* laid 4–8 times more eggs on older onions than on young onions, and older onions were more resilient to injury caused by *D. antiqua* neonates compared with younger onions. However, the resiliency to maggot attack lessened as the density of *D. antiqua* increased from 2 to 10 eggs per plant, which probably explains why greater levels of maggot damage are typically observed in early onion plantings compared with later plantings. Delaying onion planting until mid-May reduced *D. antiqua* damage without jeopardizing the period required to produce marketable yield, but this cultural tactic must be combined with other management strategies to prevent economic loss.

KEY WORDS *Delia antiqua*, oviposition, *Allium cepa*, planting date, cultural control

Onion, *Allium cepa* L., is a high-value specialty crop grown throughout the Great Lakes region of North America. Onions grown in this region are long-day, globe types (Hoffmann et al. 1996) that mature between 90 and 115 d after planting in April and early May. Bulbs are harvested between July and October. In this region, onions are typically grown on high-organic muck soils, which are geographically isolated areas located in drained lake beds. Onion growers often do not rotate onion fields, and this lack of rotation exacerbates problems with plant pathogens and insects.

Onion maggot, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae), is one of the most serious pests of onion in the Great Lakes region. There are three generations of *D. antiqua* per year (Eckenrode et al. 1975), but the first generation causes the greatest economic loss because larvae kill young onion plants. Onion plant stands can be reduced by at least half when left unprotected (Taylor et al. 2001, Nault et al. 2006a). Second- and third-generation larvae cause very little damage to the onion crop relative to the first generation, but feeding injury can distort bulbs and allow entry by pathogens, both of which render onions unmarketable (Hoffmann et al. 1996). Management efforts primarily target the first generation.

Insecticide use continues to be the principal tactic for *D. antiqua* control (Eckenrode and Nyrop 1995, Nault et al. 2006a), primarily because it has been reliable, easy to implement, and is relatively inexpensive. For many years, growers have relied on only two insecticides, chlorpyrifos and cyromazine (Taylor et al. 2001). Chlorpyrifos is applied as a drench treatment in the furrow at planting, and onion seed is commercially treated with cyromazine. Control of *D. antiqua* populations with chlorpyrifos has become unpredictable because many populations have developed resistance to it (Nault et al. 2006b), leaving cyromazine as the only effective option. Recently, new seed treatments have been identified to control *D. antiqua* (Nault et al. 2006a), and two will become commercially available in 2011: the combination of clothianidin and imidacloprid (Sepresto 75WS, Bayer CropScience, Research Triangle Park, NC) and the combination of spinosad, thiamethoxam and several fungicides (FarMore FI500, Syngenta Crop Protection, Greensboro, NC). Long-term management of *D. antiqua* should not rely exclusively on use of these insecticides if they are to remain effective (Loosjes 1976).

Delaying onion planting into late spring has long been suggested as a method of cultural control for *D. antiqua* (Doane and Chapman 1952), but its efficacy

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has not been evaluated. Theoretically, this strategy would allow the onion crop to escape infestation by reducing the time plants would be exposed to oviposition in the spring. Yet, past research has shown that onions become more resilient to *D. antiqua* attack as they grow older. For example, Finch et al. (1986a) found that 37% of *D. antiqua* eggs placed onto early-bulbing onion plants survived to pupation, whereas no pupae were produced on plants that were 3–5 wk older. In contrast to the recommendation of planting late to avoid *D. antiqua* attack (Doane and Chapman 1952), these results suggest that it may be preferable for growers to plant onions early in the season so that onions are as old as possible, and thus maximally resilient, when *D. antiqua* emerge and oviposit.

Damage by *D. antiqua* tends to be greater in early-planted onion fields than in late-planted onion fields. Thus, some factor must cause the inherent resiliency of older plants to *D. antiqua* attack to break down. Early-planted onions are larger than late-planted onions at the time *D. antiqua* oviposition occurs. In laboratory experiments, female *D. antiqua* lay more eggs on larger plants when offered a choice between these and smaller plants (Harris et al. 1987). Although a laboratory choice test with single plants is not the same as comparing oviposition choices in fields with different aged onions, female *D. antiqua* may lay more eggs on larger, early-planted onions. Thus, densities of first-generation *D. antiqua* eggs might be greater on early- than on late-planted onions, providing a behavioral explanation for elevated damage.

The purpose of this research was to determine whether *D. antiqua* damage could be reduced by delaying onion planting. In addition, we aimed to identify the mechanisms that underlie variation in *D. antiqua* damage with planting date. To accomplish this, we used a combination of field and laboratory experiments. Field experiments focused on quantifying differences in *D. antiqua* damage between onions planted at different dates and relating differences to activity of ovipositing adults. Laboratory studies focused on determining 1) how oviposition might be affected by exposing flies to a range of plant ages for varying periods and 2) how the inherent resistance of different-aged plants interacts with *D. antiqua* larval densities. We hypothesized that 1) plant damage would be reduced by planting onions later in the spring; 2) damage reductions would occur because later plantings would escape oviposition and elicit less oviposition than older, larger plants; and 3) inherently greater resistance of older plants to *D. antiqua* attack would lessen under high densities, explaining why a greater resistance of early-planted onions does not translate into reduced damage. Feasibility of a delayed planting to produce an onion crop that yields well was also investigated.

Materials and Methods

Planting Date and Maggot Damage in the Field. Field experiments were conducted on muck soil in commercial fields across the major onion producing regions of New York. Approximately 40% of the onions are grown in Orange County (southeast), 30% in Oswego, Wayne and Yates counties (central), and the remainder in Orleans and Genessee counties (west). Weed, disease, and *Thrips tabaci* Lindeman management were followed as recommended by Reiners and Petzoldt (2011). Insecticides targeting thrips rarely affect *D. antiqua* populations because they are applied at the end of the first *D. antiqua* generation and foliar insecticide sprays have minimal impact on fly mortality (Finch et al. 1986b).

The relationship between planting date and *D. antiqua* damage was investigated from 2003 through 2005 at field sites mentioned above. The 2004 experiment also compared plant damage levels between insecticide- and noninsecticide treated onions, whereas one of the 2005 experiments compared damage levels between early- and late-maturing, long-day onion cultivars.

2003 Planting Date Experiment. This experiment was conducted near Potter, NY, in Yates County. There were three planting dates considered as early (16 April), mid (6 May), and late (28 May) for the onion planting period in this region. 'Millennium' onion seeds were planted in single row plots that were 7.6 m in length and separated from other rows by 38 cm. Seeds were planted at a density of 30 per m by using a hand-pushed cone seeder equipped with a gravity-fed system for in-furrow drenches of pesticides, mounted onto a Planet Jr. frame. Each planting date treatment was arranged in a randomized complete block design replicated six times. Seeds were not treated with insecticides, but were treated with fungicides to manage seedling diseases. This was done using a solution containing a film-forming polymer (Disco, A1.018. Incotec Inc., Salinas, CA) that encapsulated the seed with a precise amount of thiram and carboxin (Pro-Gro) at a rate of 2.0 g (AI)/100 g (see Taylor 2003). Additional protection against diseases was afforded with a drench treatment of mancozeb (Dithane F-45, Dow AgroSciences, Indianapolis, IN) at a rate of 5.6 liters/ha.

The number of plants dead or dying from *D. antiqua* feeding was recorded one or two times per week beginning in late May and ending in July at the end of the first larval generation. Seedlings containing maggot larvae or those obviously dying from maggot feeding, but no larva present, were recorded as dead and then removed from the plot. Periodically, maggots were randomly collected from seedlings, reared to adult and then identified using a key by Brooks (1949) to ensure that maggots encountered were *D. antiqua* and not seedcorn maggot, *Delia platura* (Meigen). *D. antiqua* was the primary species found.

Onion seedlings may be killed by high winds and seedling diseases, factors that confound data analyses examining seedling mortality due to maggot feeding. Therefore, data were analyzed in the following manner. First, the cumulative number of seedlings killed by maggots was determined through the end of the first larval generation. Next, this total was divided by the sum of all maggot-killed plants plus the final plant stand count, which was taken in mid-July. This quotient was the final proportion of plants killed by *D. antiqua.* These data were analyzed using a mixed model (PROC MIXED), and treatment means were compared using LSMEANS at $P < 0.05$ (SAS Institute 2007). Treatment was considered as a categorical value (early, middle, or late planted) and a fixed variable in the model, whereas replication was considered random. Data were transformed using a square root $(x + 0.001)$ function before analysis to stabilize variance, but untransformed means are presented.

Activity of *D. antiqua* females was monitored on a weekly basis beginning at the estimated start of the first flight on 13 May. Five (15 by 15-cm) yellow sticky cards (Olson Products, Medina, OH) were clamped to stakes at an initial height of 13 cm above the ground. Thereafter, height was adjusted to keep card tops level with the onion canopy. Cards were equally spaced along the edge of the test site and replaced weekly. Numbers of *D. antiqua* females on both sides of each card were identified following the key of Brooks (1949) and recorded.

2004 Planting Date Experiment. This experiment was conducted near Pine Island (Orange County), Elba (Orleans County), and Sodus, NY (Wayne County). Millennium onion seeds were planted in eight-row plots that were either 9.1 m in length (Elba and Sodus) or 18.3 m in length (Pine Island), all at a density of 30 seeds per m. Seeds were planted as described in the 2003 experiment. There were three planting dates at each location, and plantings were spaced apart approximately every 2 wk. In Pine Island, plantings were 20 April and 5 and 19 May; in Elba, plantings were 29 April and 13 and 28 May; and in Sodus plantings were 21 April and 4 and 17 May. Half of each plot was planted with seeds that were not treated with insecticides, whereas the other half was planted with seeds treated with fipronil (Regent 6.2 TS; BASF, Research Triangle Park, NC) at a rate of 2.5 g (AI) / 100 g of seed for protection against maggots. All seeds were treated with Pro-Gro and Dithane F-45 as described previously. The experiment was a split-plot with planting date as the main plot factor and insecticide-treatment as the subplot factor. Treatments were not replicated within a site and location was considered as the replicate ($n = 3$).

Plants killed or dying from *D. antiqua* were recorded as described in the 2003 experiment. In addition, at the Elba and Sodus sites, 50 bulbs were inspected for maggot damage approximately every 2 wk beginning 20 July. Because damaged bulbs are culled during grading, they were considered equivalent to a dead plant. The percentage of bulbs damaged on each sampling date was added to the mean cumulative percent plants killed by maggots earlier in the season. Consequently, the response variable was mean cumulative percentage of plants killed and bulbs damaged by maggots. Data were analyzed as an analysis of variance (ANOVA) for a split-plot design (PROC GLM) (SAS Institute 2007). The replication by planting date interaction term was used as the mean square error for testing significance of planting date. Planting date was given a categorical value (early, middle, or late planted) in the model. Means were compared midseason ($n = 3$) and at harvest ($n = 2$) using LSMEANS at $P < 0.05$. Data were not taken between July and harvest at the Pine Island site.

As in the 2003 experiment, female *D. antiqua* fly activity was monitored at each site. Three yellow sticky cards were collected and replaced on a weekly basis beginning at the estimated start of the first flight in May and continuing through the season as described previously.

2005 Planting Date and Cultivar Experiment. This experiment was conducted near Pine Island (Orange County), Elba (Orleans County), Sodus (Wayne County) and Oswego, NY (Oswego County). Cultivars planted were Millennium, which is a late-maturing, long-day onion (110 d after planting), and 'Sherman', which is an early-maturing, long-day onion (100 d after planting). Seeds were planted as described previously in eight-row plots that were either 9.1 m in length (Elba, Sodus and Oswego) or 18.3 m in length (Pine Island), all at a density of 30 seeds per m. There were three planting dates at each location and plantings were spaced apart approximately every 2 wk. In Pine Island, plantings were 14 and 29 April and 13 May; in Elba, plantings were 18 April and 4 and 16 May; in Sodus plantings were 15 and 29 April and 13 May; in Oswego plantings were 6 and 20 May and 2 June. Treatments were randomly assigned within each location, but treatments were not replicated within sites. Location was considered the replicate ($n = 4$). None of the seeds were treated with insecticides, but all were treated with Pro-Gro and supplemented with a drench treatment of Dithane F-45 at the rates described previously.

Plants killed or dying from *D. antiqua* were recorded as described in the 2003 experiment. In addition, 50 bulbs were inspected for maggot damage approximately every 2 wk beginning 20 July. The percentage of bulbs damaged on each sampling date was added to the mean cumulative percent plants killed by maggots earlier in the season. Consequently, the response variable was mean cumulative percentage of plants killed and bulbs damaged by maggots. These data were analyzed using a mixed model (PROC MIXED), and treatment means were compared using LSMEANS at $P < 0.05$ (SAS Institute 2007). Planting date (categorical value as early, middle, or late planted) and cultivar were considered as fixed variables, whereas location was considered random. Raw data were transformed using a square root function before analysis to stabilize variance; back transformed means are presented in the text.

Test Insects for Laboratory Experiments. *D. antiqua* eggs and flies used in laboratory experiments described below were obtained from colonies maintained in an environmental chamber (21°C, 60% RH, and a photoperiod of 16:8 [L:D] h) at Cornell University's New York State Agricultural Experiment Station in Geneva, NY. Colonies were established with larvae collected the previous year from onion fields in Yates County, NY. Colonies were maintained by providing flies ad libitum with water and a diet of brewer's yeast, powdered milk, sugar, and soy peptone (Ticheler 1971). Flies were allowed to oviposit in a dish containing sand and a peeled onion; eggs then were floated out of the sand by using water. Cohorts of similar-aged eggs were collected for experiments and for establishing subcolonies in which flies of a certain age could be obtained for ovipositional experiments in the laboratory.

Onion Plants for Laboratory Experiments. Millenium onion seeds were planted in plastic trays filled with muck soil collected from a nearby commercial farm. All seeds received a film-coating treatment of thiram and carboxin (Pro-Gro) at a rate of 2.0 g (AI) / 100 g of seed to protect against seedling diseases. Plants were allowed to germinate in an environmental chamber (21°C, 60% RH, and a photoperiod of 16:8 [L:D] h) after which time they were transferred to pots (15.2 by 15.2 cm) and maintained in the greenhouse (photoperiod of 16:8 [L:D] h) until plants reached the desired age for experimentation.

Ovipositional Experiments for Variously Aged Plants. Choice and no-choice ovipositional experiments were conducted in the laboratory by using flies and plants as described in the previously sections. We were interested to know whether *D. antiqua* would oviposit on larger, older onion plants than on younger, smaller onion plants when either given a choice or not given a choice between the two types of plants. Based on results suggesting that flies might wait to lay eggs until plants become larger, a second no-choice study was conducted that provided flies a much longer period to lay eggs on young and old plants. A third no-choice study was conducted to compare levels of damage to variously aged onion plants when infested with several densities of *D. antiqua* eggs.

Short-Duration Choice Experiment. *D. antiqua* ovipositional preference for onion plants varying in age was evaluated in a two-choice test in the laboratory. Onion seeds were planted four weeks apart to obtain plants that were 3 and 7 wk old. Sizes of these plants were similar to those encountered in a late (mid- to late May) and mid (late April to early May) planting of onions at the time flies from the overwintering generation would be ovipositing. At this time, the youngest plants had one to two leaves, whereas the older plants had three to four leaves. The experiment was conducted in a series of mesh cages (46 cm in length by 46 cm in width by 46 cm in height) that were kept in an environmental chamber (21°C, 60% RH, and a photoperiod of 16:8 [L:D] h). One 3-wk-old and one 7-wk-old plant were randomly assigned to each cage and exposed to seven female and three male *D. antiqua* flies. Flies were 7–10 d old and were offered water and the same food provided to the colonies within cages. Flies were allowed to oviposit on treatment plants for 48 h. Two runs were conducted, with six replicates in the first and four in the second, yielding a total of 10 replicates. The same cages and flies were used for both runs; however, treatments and cages were rerandomized before the second run. The rationale for using the same flies rather than new flies in the second run was because flies were still young (9–12 d old) and fecund. Dead flies were replaced with live flies, and new plants were placed in cages for the second run.

After the 48-h oviposition period, plants were removed and the numbers of eggs per pot counted. Most eggs were laid within the top one cm of soil around the base of the plants and only a few were laid on onion foliage. The majority of onion maggot eggs are typically laid within this soil depth (Havukkala et al. 1992). Soil was placed on a black surface, and eggs were sorted through with a paintbrush. *D. antiqua* eggs are white and clearly visible against a black background. Data were analyzed using a paired *t*-test implemented with PROC MEANS at $\alpha = 0.05$ (SAS Institute 2007).

Short-Duration No-Choice Experiment. In the spring, *D. antiqua* flies typically emerge from the soil into nonrotated, relatively large fields of onions. Therefore, females probably make ovipositional decisions in a no-choice setting where plants are all of relatively similar age. Consequently, we used no-choice tests to compare oviposition of *D. antiqua* on 2- and 8-wk-old plants. Plant size treatments, flies and cages were obtained as described in the short-duration choice experiment. A single plant from one of the age classes mentioned above was randomly assigned to its own cage containing 20 7-d-old *D. antiqua* flies, half of each sex. Each treatment was replicated three times ($n = 3$), and there was a total of six cages. Flies were allowed to oviposit for 6 d, after which time plants were removed and the numbers of eggs per pot counted as described in the short-duration choice experiment. Few eggs hatched before 6 d; in the few instances when eggs did hatch, either larvae or chorions were counted.

This experiment was repeated with the same cohort of plants and flies that were used in the first run. The second run was 1 wk later, so plant age treatments were then 3 and 9 wk old and flies were 13 d old. Cages that received the treatments were randomly chosen so that the same cage did not always receive plants of the same relative age in the two runs. Numbers of eggs laid per pot were recorded 6 d later. Because there was a one-wk age difference between plants and flies used in the two runs, data were analyzed separately for each run using ANOVA (PROC GLM), and means were compared using a single-degree-of-freedom F-test at $\alpha = 0.05$ (SAS Institute 2007).

Long-Duration No-Choice Experiment. Results from the short-duration no-choice experiment suggested that *D. antiqua* adults might delay oviposition when plants are young, waiting until they are older to deposit eggs. To address this possibility, *D. antiqua* flies were restricted to onion plants that were initially either 3 or 9 wk old and permitted to oviposit on these plants until they died. Plant size treatments, flies and cages were obtained as described previously; the study was conducted in the laboratory. A single plant of each age was randomly assigned to its own cage containing 10 female and 10 male *D. antiqua* flies, all of which were 7 d old. Each treatment was replicated ten times. Plants were removed from cages after 1 wk, and the number of eggs per pot was counted as described in short-duration choice experiment. Plants were imme-

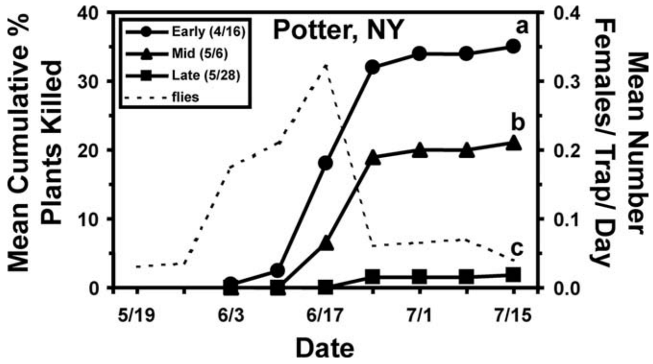

Fig. 1. Mean cumulative percentage of plants killed by first-generation *D. antiqua* larvae through time (solid line) in field plots of onion (Millennium) planted early, mid, or late spring in Potter, NY, in 2003 ($n = 6$). On 15 July, means followed by different letters indicate a significant difference ($P < 0.05$; LSMEANS). Mean number of female *D. antiqua* captured per yellow sticky card per day (dashed line) at the test site ($n = 5$).

diately replaced with new plants from the same cohort (now 1 wk older), which were maintained in the greenhouse. The experiment was conducted for 1 mo, so the ages of plants in the two treatments at the end of this experiment were 7 and 13 wk old. Total numbers of eggs laid per pot over the four sampling dates for each treatment were analyzed using ANOVA (PROC GLM), and means were compared using a single-degree-of-freedom F-test at $P < 0.05$ (SAS Institute 2007).

Plant Age and Insect Density No-Choice Experiment. This laboratory experiment tested whether older onion plants were inherently more resilient against *D. antiqua* larvae across a range of larval densities compared with younger plants. Plant size treatments, flies, and cages were obtained as described previously. One difference from the other laboratory experiments was that plants were grown in 5.1- by 5.1-cm pots. When an onion plant was 2, 4, 6, or 8 wk old, it was infested a single time with two, five, or 10 *D. antiqua* eggs. These plants were subsequently maintained in an environmental chamber for the duration of the experiment (21°C, 60% RH, and a photoperiod of 16:8 [L:D] h). The experiment was a factorial and included all combinations of seedling ages (four levels) and egg densities (three levels). These treatments were arranged in a completely randomized design replicated 20 times. After 9 d, each plant was recorded as either damaged by *D. antiqua* or not damaged. Plants were considered damaged if they were dead, flaccid, or fed upon by larvae but not flaccid. The binomial data were analyzed using PROC GENMOD at $P < 0.05$ (SAS Institute 2007). Data were represented as the percentage of plants damaged by *D. antiqua* in each plant age by egg density combination.

Planting Date Impact on Bulb Yield Experiment. This experiment was conducted adjacent to each of the four locations described in the 2005 planting date field experiment. Sherman onion seeds, protected with fipronil seed treatment (Regent 6.2 TS) as described in the 2004 field experiment, were planted at the same densities and in plots with the same dimensions as described previously ($n = 4$). All plantings were made on the same dates as in the planting date field experiment. All seeds were treated with Pro-Gro and supplemented with a drench treatment of Dithane F-45 at the rates described previously.

Marketable yield was determined by harvesting all onion bulbs within one of the center rows in each plot in early to late August. Only marketable U.S. No. 1 grade bulbs (>3.8 cm in diameter) were harvested. Data were analyzed using a mixed model (PROC MIXED), and treatment means were compared using LSMEANS at $P < 0.05$ (SAS Institute 2007). Planting date was considered as a fixed variable, whereas location was considered random.

Results

Planting Date and Maggot Damage in the Field

2003 Field Experiment. Fewer onion plants were killed by maggots in plantings made later in the spring (Fig. 1). Onions planted in mid-April were more likely to be killed than those planted in either early or late May, whereas onions planted in early May were more likely to be killed than those planted in late May ($F = 42.0$; df = 2, 10; $P < 0.0001$). The first plants infested with maggots were detected on 3, 17, and 24 June in early, mid, and late plantings, respectively (Fig. 1). Few onion plants were killed in all treatments after 24 June. *D. antiqua* females were active from before mid-May through late July, and their activity peaked on 17 June. As a result, later plantings were exposed to a much smaller portion of first-generation flies than early plantings. During this period, the earliest planted onions had more leaves and were larger than those planted later (B.A.N., unpublished data).

2004 Field Experiment. *Mid-Season Evaluation.* Delaying planting reduced *D. antiqua* damage to onions (Figs. 2A–C, and 3A). Onions planted in late April (=early) and early May (=middle) were significantly more likely to be killed than those planted in late May (=late) ($F = 41.2$; df = 2, 4; $P = 0.0021$) (Fig. 3A). Onions grown from insecticide-treated seed were significantly less likely to be killed compared with those

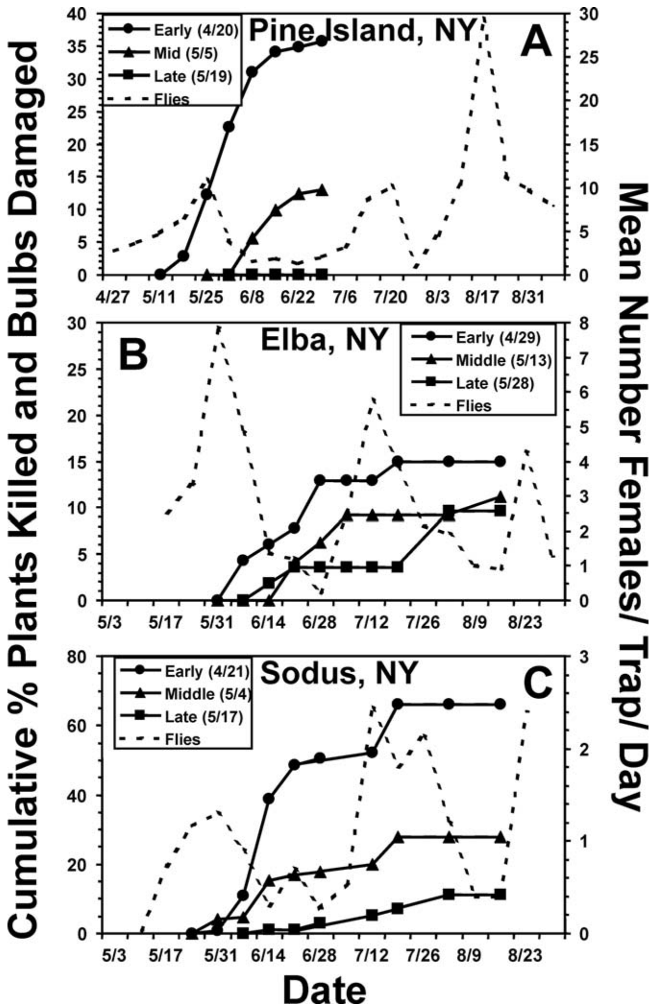

Fig. 2. Cumulative percentage of plants killed by *D. antiqua* larvae through time (solid lines) in noninsecticide treated field plots of onion (Millennium) planted early, mid, or late spring in Pine Island, NY (A); Elba, NY (B); and Sodus, NY (C), in 2004 (n = 1 at each test site). Mean number of female *D. antiqua* captured per yellow sticky card per day (dashed line) (n = 3 at each test site). Note that the scales on the y-axes differ among subfigures.

not treated with an insecticide (F = 49.7; df = 1, 6; P = 0.0004) (Fig. 3A). Onions killed by maggots were not significantly affected by a planting date by insecticide treatment interaction ($P > 0.05$).

In Pine Island, plants infested with maggots were first detected on 19 May and 8 June in early and mid plantings, respectively (Fig. 2A). No maggot damage was observed in the latest planting. In Elba, maggots were first detected on 7, 13, and 20 June in early, mid, and late plantings, respectively (Fig. 2B). In Sodus, maggots were first detected on 1, 1, and 14 June in early, mid, and late plantings, respectively (Fig. 2C). *D. antiqua* females were active in late April and early May and peaked on or a week before maggots were first seen at each site (Fig. 2A–C). As in the 2003 field experiment, late plantings at all sites were exposed to a much smaller portion of first-generation flies than early plantings. During the time these females were most active, earlier planted onions had more leaves and were larger than those planted later (B.A.N., unpublished data).

In most plantings at all sites, the percentage of plants killed by maggots did not increase much beyond early July. One notable exception was the late planting in Elba (Fig. 2B), where an increase in damage in late July and August was caused by second-generation maggots. In this case, late-planted onions were probably attractive to second-generation flies and vulnerable to attack by maggots.

Harvest Evaluation. Results at harvest were similar to those during mid-season because damage to bulbs beyond mid-July was relatively minimal for most treatments (Fig. 2B and C). Onions planted in late April (=early) were significantly more likely to be killed or to have bulbs damaged than those planted in late May (=late) (F = 23.4; df = 2, 4; P = 0.0409) (Fig. 3B). Plantings in early May (=middle) had similar numbers of dead plants and bulbs damaged as the other

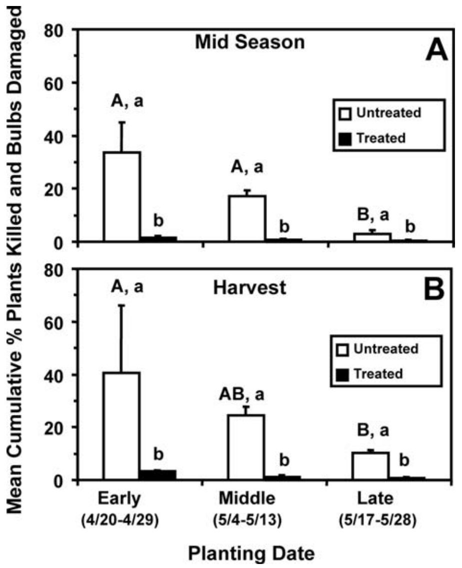

Fig. 3. (A) Mean (±SEM) cumulative percentage of plants killed by *D. antiqua* larvae in the middle of the season in insecticide-treated or noninsecticide treated onions (Millennium) planted early, mid, or late spring 2004 (n = 3 locations). (B) Mean (±SEM) cumulative percentage of plants killed plus bulbs damaged by *D. antiqua* larvae in the same treatments at harvest (n = 2 locations). Means followed by different uppercase letters signify a significant difference among planting dates, whereas means followed by different lowercase letters indicate significant differences between treated and untreated onions within each planting date ($P <$ 0.05; LSMEANS).

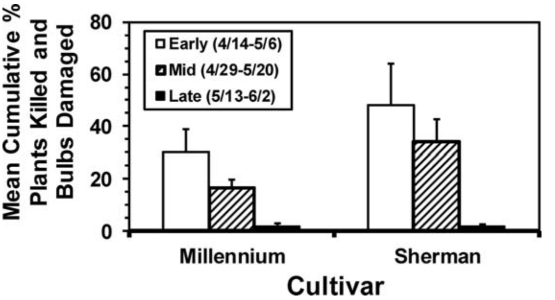

Fig. 4. Mean cumulative percentage of plants killed and bulbs damaged by *D. antiqua* for an early-maturing, long-day onion (Sherman, 100 d from planting to harvest) and a late-maturing, long-day onion (Millennium, 110 d from planting to harvest), grown from noninsecticide treated seed planted early, mid, and late spring in New York in 2005 (n = 4 locations).

plantings (Fig. 3B). Onions grown from insecticide-treated seed were significantly less likely to be killed or to have bulbs damaged compared with those not treated with an insecticide (F = 81.7; df = 1, 6; P = 0.0029) (Fig. 3B). Onions killed and damaged by maggots were not significantly affected by a planting date by insecticide treatment interaction ($P > 0.05$).

2005 Field Experiment. Delaying planting reduced *D. antiqua* damage to plants and bulbs for both Millennium and Sherman onions (F = 40.1; df = 2, 15; $P <$ 0.0001) (Fig. 4). Averaged across all planting dates, Sherman plants were more likely to be killed or to have bulbs damaged than Millennium (F = 4.5; df = 1, 15; P = 0.05) (Fig. 4). Sherman plants grew larger and produced more leaves early in the season compared with Millennium plants (data not shown). Based on results from our lab assays that indicated an oviposition preference for larger onion plants, flies may have been more likely to oviposit on Sherman than Millennium onions, and this would explain differences in maggot damage. Damage was not affected by an interaction between cultivar and planting date ($P >$ 0.05).

For both cultivars, plant growth in the mid plantings caught up quickly (late June) to plant growth in the early plantings in Sodus and Elba (Fig. 5). In contrast, plant growth in the late plantings did not catch up to the early plantings until mid- to late July in Sodus and Elba. Plant growth of both cultivars in the mid and late plantings in Oswego was much further behind the early plantings by late July because they were planted extraordinarily late (Fig. 5). These results indicate that a delay in planting both early and late-maturing onion cultivars beyond mid-May will result in smaller onions that have fewer leaves during the time first-generation flies are searching for hosts.

Ovipositional Experiments for Variously Aged Plants

Short-Duration Choice Experiment. Females laid significantly more eggs on 7-wk-old onion plants than on 3-wk-old plants when given a choice (t = 2.39, df = 9, P = 0.0094). Nearly four times more eggs were laid per 7-wk-old onion plant (37.6 ± 8.3) compared with a 3-wk-old onion plant (10.3 ± 3.6), indicating that *D. antiqua* prefer to lay eggs on older plants.

Short-Duration No-Choice Experiment. Females laid significantly more eggs on 8- and 9-wk-old onion plants than on 2- and 3-wk-old onions when confined to these plants for 6 d (8- versus 2-d-old plants: F = 91.0; df = 1, 4; P = 0.0007; 9- versus 3-d-old plants: F = 14.1; df = 1, 4; P = 0.0199). No eggs were laid on 2-wk-old plants, whereas 30.3 ± 3.2 eggs were laid on 8-wk-old plants. Less than a third as many eggs were laid on 3-wk-old plants (45.6 ± 11.5) compared with 9-wk-old plants (167 ± 30.3). These results indicate that if onion plants are too young, females will not lay eggs or will not lay as many as they would on larger plants.

Long-Duration No-Choice Experiment. Females laid significantly more eggs on older onion plants than on younger onion plants when confined to these plants for a month (F = 16.3; df = 1, 17; P = 0.0009) (Fig. 6). Females laid more eggs on older plants than on younger plants each week for 3 wk, but none were laid between 3 and 4 wk. Most eggs were laid within 7 d in both plant age treatments, but then declined substantially thereafter (Fig. 6). These results indicate that sexually mature females will lay more eggs on onion

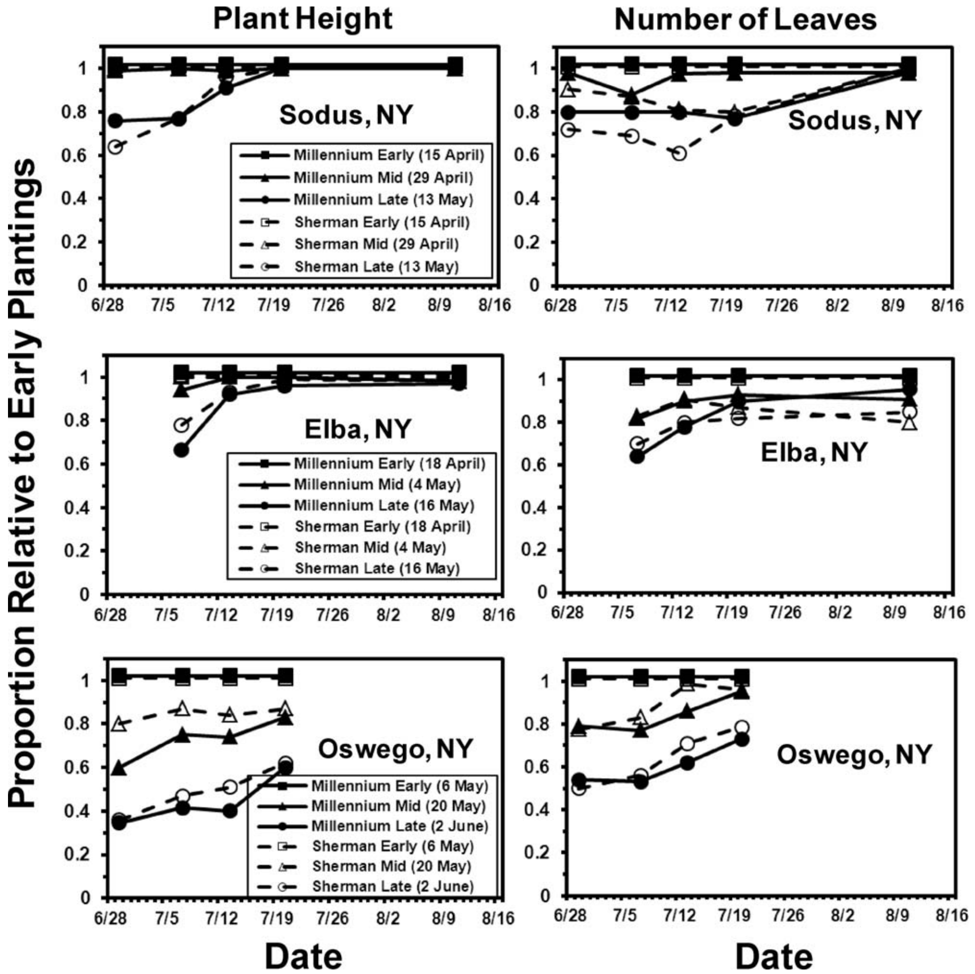

Fig. 5. Proportion of the height and leaves per plant relative to the earliest planted onions at each of three locations in New York in 2005. All early planted onions had a proportion of 1.0. Sherman (100 d to maturity) and Millennium onions (110 d to maturity) were planted in early, mid, or late spring (n = 10 plants per observation).

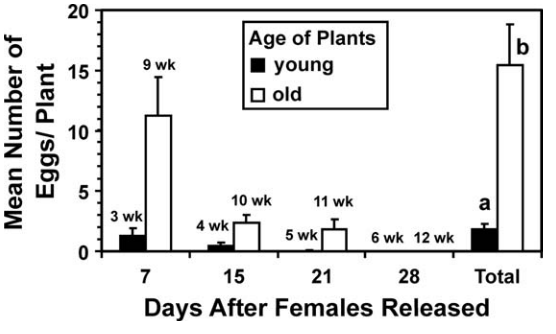

Fig. 6. Mean (±SEM) number of *D. antiqua* eggs laid per plant each week for a month when restricted to onions varying in age (n = 3 for each treatment). Plants were initially 3 or 9 wk old when placed in groups of four in cages that initially contained 20 10-d-old flies (10 of each sex) in the laboratory. Eggs were counted, and plants were replaced each week. Mean total number of eggs per plant with different letters indicate a significant difference (P < 0.05; LSMEANS).

plants if plants are an appropriate age and size when first encountering them compared with those that are too young and small. Females are not likely to wait until plants get older and larger to lay eggs.

Plant Age and Insect Density No-Choice Experiment. Plant age and egg density interacted to affect damage in differently aged onion plants (Fig. 7). Plant damage was significantly affected by an interaction between plant age and egg density (χ^2 = 5.5, df = 1, P = 0.0189) (Fig. 7). Percentages of 2- and 4-wk-old onion plants with maggot damage tended to be high regardless of egg density, whereas 6-wk-old onion plants had more maggot damage at densities of five to 10 eggs per plant than at two eggs per plant, and 8-wk-old plants had more damage at a density of 10 eggs per plant than at the other densities. These results indicate that as onion plants get older, they become more resilient to attack by *D. antiqua* larvae but that this resiliency breaks down under high maggot densities.

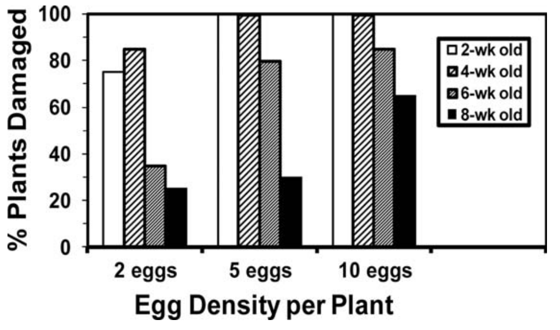

Fig. 7. Mean percentage of onion plants damaged by *D. antiqua* after 1 wk of exposure to treatments that varied in plant age and infestation densities in the laboratory.

Planting Date Impact on Bulb Yield Experiment

Marketable bulb yield did not differ significantly among plantings of Sherman onions ($P > 0.05$). Bulb yield was 51.7 ± 5.7, 47.7 ± 10.4, and 43.4 ± 8.5 T/ ha for early, mid, and late plantings, respectively. These results indicate that planting an early-maturing, long-day onion late in the season to reduce maggot damage should produce a marketable onion crop.

Discussion

D. antiqua damage to plants and bulbs was consistently lower in later plantings of onions. Onions planted later emerged later and this reduced the period that overwintered flies had to oviposit on the plants. Moreover, flies tended to lay few to no eggs on these young, late-planted onions. This suggests that planting onions later in the spring reduces damage by allowing plants to "escape in time" and by taking advantage of *D. antiqua* ovipositional behavior. We also discovered that resistance of older plants to *D. antiqua* larvae broke down under high densities. This finding suggests that during the first generation any benefits of increased resistance in older plantings will be offset by increased egg densities, explaining why greater maggot damage was observed in early onion plantings compared with later plantings.

D. antiqua laid more eggs on older onion plants than on young plants, regardless of whether flies were given a choice between the two age categories of plants. When given a choice, flies laid 4 times more eggs on older plants than on young plants. When flies were not given a choice, flies laid four to 7 times more eggs on older plants. Moreover, when flies were exposed to onions for a month beginning when plants were young and small, flies laid fewer eggs compared with those that were initially offered older and larger plants. These results suggest that oviposition cues are elicited when flies are young. Harris et al. (1987) demonstrated that *D. antiqua* oviposition increased with an increase in onion stem diameter and may likewise explain why *D. antiqua* laid more eggs on larger plants, which happened to be older and planted earlier. In our long-duration no-choice experiment, we confined flies to cages containing small onion plants that were unlikely to be attractive to ovipositing flies. However, these plants grew for 4 wk and were certainly large enough to be attractive to ovipositing flies. Yet, few eggs were laid. Results from past research have shown that there is a deterministic sequence of postalighting oviposition behaviors required for *D. antiqua* to lay eggs on onion plants (Mowry et al. 1989). Based on our results, onion plants did not grow quickly enough to reach a size necessary for the preovipositing behaviors to engage and for flies to lay many eggs.

Onion plants became more resilient to attack by *D. antiqua* larvae as they aged, but this resiliency broke down under high maggot densities. Finch et al. (1986a) conducted a greenhouse experiment to measure the effects of onion plant age on *D. antiqua* survival to pupation. Onion plants were collected from the field in New York on 19 July and 10 and 24 August, and each plant was infested with 40 eggs. Thirty-seven percent of *D. antiqua* eggs survived to pupation when fed plants collected on 19 July, whereas 1.6 and 0% survived to pupation on the older plants. They concluded that bulbs become inherently more resistant to penetration by *D. antiqua* as onions mature. In our study, plants were much younger (e.g., prebulbing stages) than the plants used in the Finch et al. (1986a) study. Despite this difference, we observed the same results: older plants had less damage by maggots than younger plants. We also found that older onion plants became less impervious to maggot damage as maggot densities increased. Plants that were 6- to 8-wk old had ≈2.5 times more damage when infested with 10 eggs compared with two eggs.

A delay in onion planting reduced *D. antiqua* damage. Based on results from our field experiments (2003–2005), numbers of onion plants killed or bulbs damaged by *D. antiqua* were reduced on average by 35 and 90% when onions were planted 2–3 wk and 4–6 wk later than the earliest planted onions in that region, respectively. A delay in planting 2–3 wk after the earliest planting, which typically occurred between 29 April to 20 May (=mid planting date treatment), did not reduce damage to an acceptable level (mean = 24%). In contrast, planting 4–6 wk after the earliest planting, which typically occurred between 13 May and 2 June (=late planting date treatment), did reduce damage to an acceptable level (mean = 4%). A delay in planting by only 2–3 wk would not be a stand alone management tactic for *D. antiqua*, whereas it could be for onions planted 4–6 wk later than normal.

The reduction in damage caused by *D. antiqua* in fields planted later in the season was probably due to temporal asynchrony between female flies and onion plants of sufficient size to elicit oviposition. Later plantings of onions escaped in time from the period females were most active and likely ovipositing (Figs. 1 and 2), and these plants were small and unlikely to be attractive to ovipositing flies (Fig. 7). Planting onions in late May to early June in New York rarely occurs because it constitutes an economic risk to growers. Onion growers usually plant fields as early as soil moisture conditions permit to maximize the amount of time available for plants to produce foliage before a photoperiod threshold is exceeded to induce plants to initiate bulbing (Brewster 1994). In the Great Lakes region, long-day onions initiate bulb development when photoperiod is 14.5:9.5 (L:D) h (Hoffmann et al. 1996). Younger plants exposed to this photoperiod may not produce a bulb or produce smaller bulbs (Brewster 1994). Typically, onion growers receive premium prices for large bulbs. Early-maturing cultivars grow rapidly and often produce bulbs as large as later-maturing cultivars, but in less time. Thus, it is feasible to plant an early-maturing cultivar late in the spring and not compromise its yield potential. Based on our 2005 field study, bulb yields from the early-maturing Sherman onions did not differ significantly between early and late plantings, indicating that the threat of yield reduction in a late planting could be minimized by planting an early-maturing cultivar.

Management Implications. Our results indicate how altering crop phenology in relation to pest phenology and behavior can effectively manage a target pest. This form of cultural control is easy for growers to implement because it does not require modifying how onions are grown, only when they are planted. For many logistical and economic reasons, there will not be a fundamental shift toward planting all onion fields late in the season to avoid *D. antiqua.* However, there are scenarios where this cultural control tactic could be used effectively to manage this pest.

Planting onions late (e.g., beyond mid-May) resulted in the greatest reduction in maggot damage. However, the most serious limitation of planting onions late is the increased risk for producing undersized bulbs, even for early-maturing cultivars. Nevertheless, this option might be worthwhile to implement in fields with a chronic history of high *D. antiqua* infestations. These fields could be the last fields planted on the farm and they could be planted with an early-maturing cultivar. Organic onion growers, who have no effective chemical options available to them for *D. antiqua* control, may benefit most from planting late.

Planting onions midway through the onion planting period (e.g., late April and early May) also significantly reduced maggot damage, but not to subeconomic levels. Management tactics like an insecticide seed treatment at planting or crop rotation, or both, would need to compliment such a moderate delay in planting. In contrast to planting onions late, there is little threat of truncating the growing season to a point where undersized onions would be produced in a mid-spring planting. For these reasons, a moderate delay in planting would be a conservative and effective option for growers to reduce maggot damage and could be adopted on most farms.

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