

OVIPOSITION PREFERENCE AND LARVAL HOST RANGE OF THE SUGARBEET ROOT

MAGGOT (DIPTERA: ULIDIIDAE)

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ABSTRACT

The sugarbeet root maggot, *Tetanops myopaeformis* Röder, is native to North America; however, its main crop host, sugarbeet, *Beta vulgaris* L., was introduced to the continent from Europe. This study involved an investigation of the attractiveness of cultivated crops and native North American weed species for oviposition by *T. myopaeformis* and the relative suitability of these potential host plant species for larval development, thus potentially shedding light on the native and current host range of this pest. Females preferred to oviposit near the following plant species: sugarbeet; spinach, *Spinacia oleracea* L.; palmer amaranth, *Amaranthus palmeri* S. Watts.; common lambsquarters, *Chenopodium album* L.; redroot pigweed, *Amaranthus retroflexus* L.; and spear saltbush, *Atriplex patula* L. Larval survival was highest on spinach, followed by sugarbeet, and spear saltbush (all belonging to the family Chenopodiaceae). This suggests that species within this family likely served as native host plants for *T. myopaeformis* before the introduction of sugarbeet to North America. Lower larval numbers on common lambsquarters, redroot pigweed, and Palmer amaranth suggest that these species are sub-optimal hosts, despite being attractive for oviposition. Additional findings showed a general lack of oviposition preference by *T. myopaeformis* females for sunflower, *Helianthus annuus* L., and common ragweed, *Ambrosia artemisiifolia* L. These results provide further insights into the rapidly successful host preference shift by this insect to sugarbeet.

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DEDICATION

To my late mother, Fella Msango, I am what I am because of you. Thanks for instilling in me the spirit of hardworking. Your advice that education is the gateway to success is the one that made me reach this far.

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GENERAL INTRODUCTION

Sugarbeet, *Beta vulgaris* L., was introduced to North America from the Mediterranean region in the mid-19th century (Lange 1987). It is a major crop in the Red River Valley of Minnesota (MN) and North Dakota (ND). The sugarbeet root maggot, *Tetanops myopaeformis* (Röder), is believed to be native to North America and is considered as the most serious insect pest of sugarbeet in much of beet-producing acreage in North America (Whitfield 1984). Considerable crop losses due to *T. myopaeformis* injury have been incurred in North Dakota since 1954 (Gojmerac 1956), and it is a perennial problem in Walsh and Pembina Counties in the northeastern part of the state. Yield reductions caused by the sugarbeet root maggot can result from stand loss, but damage occurs primarily from larval feeding injury to roots throughout the growing season (Campbell et al. 1998). Yield losses due to root maggot feeding injury can range from 10 to 100% (Cook 1993, Campbell et al. 1998, Boetel et al. 2010). Despite its economic significance, much information on the basic ecology of the sugarbeet root maggot is unclear. The lack of adequate understanding about the host range of *T. myopaeformis* could have potential management implications if it is found that this insect can exploit common regional weed species, especially, if one of those weed species were to become herbicide resistant. Therefore the objectives of this study were to: 1) assess the relative suitability of cultivated crops and selected native North American weed species as hosts for *T. myopaeformis* larval survival and development, and 2) determine oviposition preference of *T. myopaeformis* on these plant species. The overriding goal of this study was to develop a better understanding of the basic ecology of *T. myopaeformis* and provide useful information for developing long-term integrated pest management programs for this important insect pest.

LITERATURE REVIEW

Sugarbeet Production in North Dakota

Sugarbeet belongs to the family Chenopodiaceae. Accounts of sugarbeet production in the Red River Valley (RRV) of North Dakota point as far back as the late nineteenth century (Ali 2005). In 2008, the Red River Valley production area of North Dakota and Minnesota alone produced about 55% of the total sugarbeet production in the United States (Maung and Gustafson 2009).

Sugarbeet Root Maggot Taxonomy

Röder (1881) first described the sugarbeet root maggot as *Eurycephala myopaeformis* from male and female specimens collected near Sacramento, California. A detailed account of the taxonomic history of the insect was provided by Gojmerac (1956). The genus *Tetanops* was originally established by Fallen in 1820. In a subsequent taxonomic revision, Coquillett (1900) applied the scientific name *Tetanops polita* to the pest. Based on a specimen from Idaho, Hendel (1911) described the insect as *T. aldrichi*. The insect was then described by Essig (1926) as the ‘sugarbeet ortalid’ and classified as belonging to the family Ortalidae and subfamily Ulidiinae. Later, based on the original description by Röder (1881), it was reclassified under the subfamily Ortalinae by Aldrich (1931). In revising the order Diptera, Hennig (1973) maintained the insect within the genus *Tetanops* and also supported it being positioned within the subfamily Ulidiinae. Steyskal (1987) however, classified *Tetanops* as a member of the family Otitidae, which involved combining the subfamilies Otitinae and Ulidiinae. Recently, the older classification was revised and former members of the family Otitidae are now considered to belong to one of the following families: Richardiidae, Ulidiidae, and Platystomatidae. The sugarbeet root maggot is now classified as belonging to the family Ulidiidae (Steyskal 1987; Triplehorn and Johnson 2005).

Biology and Life Cycle

Early accounts on the basic biology of *T. myopaeformis* in the literature were provided by Hawley (1922), Knowlton (1934), and Harper (1962). A description of the insect's life cycle, along with observations on its growth requirements were provided by Whitfield and Grace (1985). The sugarbeet root maggot overwinters 24 to 40 cm below the soil surface as a third-instar larva for about six months (Bechinski et al. 1993). About 200 degree days are required for 50% adult emergence from overwintering sites at a base temperature of 8.6°C (Whitfield 1984). In the Red River Valley, adult flies of this pest generally emerge from mid-to late May, typically beginning two to four weeks after sugarbeets have been planted. Flies emerge from previous-year beet fields and move to current-year fields where they deposit eggs near the bases of sugarbeet seedlings (Callenbach et al. 1957). In North Dakota, Lundquist (1972) estimated the root maggot fly activity period to last about 43 days. In current-year beet fields in the RRV of North Dakota, peak fly activity usually occurs in early to mid-June, and the majority of larval feeding takes place in July (Campbell et al. 1998). Female flies ensure larval feeding and high survival by aggressive host-searching and oviposition activity adjacent to or directly below sugarbeet seedlings (Anderson et al. 1977). Ure (1966) indicated that the optimal temperature range for *T. myopaeformis* egg hatch is between 20 and 30°C.

Economic Impact

Accounts regarding the extent of injury and yield losses due to *T. myopaeformis* are available from published literature. Hawley (1922) was the first to recognize the sugarbeet root maggot as a pest of sugarbeet when crop losses of > 20% were observed near Amalga, UT in 1920. In the Red River Valley growing area, Gojmerac and Callenbach (1956) reported finding this insect in central Traill County, and northward to the Canadian border. Serious economic

damage to the sugarbeet crop from *T. myopaeformis* larvae was reported during the 1954-55 growing seasons in North Dakota (Gojmerac 1956). Whitfield (1984) reported *T. myopaeformis* as the key pest of sugarbeets in the western United States and two Canadian provinces (Manitoba and Alberta), with up to 100% crop losses being observed in certain areas of Canada; however, the crop is no longer grown in Manitoba, so the presence and incidence of *T. myopaeformis* in that province are currently unknown. Campbell et al. (1998) estimated that yield losses in unprotected plantings could reach 40% in portions of North Dakota and Minnesota without effective control. This estimate is supported by the work of Boetel et al. (2010), who indicated up to 45.2% (\$656/ha) losses in gross economic return as a result of *T. myopaeformis* injury.

Root Injury Rating Scales

A five-point scale for in-field visual rating of larval root feeding injury was developed by Blickenstaff et al. (1976). The authors suggested that such a rating scale for root injury was necessary since parameters such number of maggots per beet and percent infested beets alone were not reliable indicators of the level of injury in field settings. Campbell et al. (2000) proposed a ten-point (0 to 9) scale to rapidly quantify root scarring levels in the field. The 0 to 9 scale is now the most common index used by researchers for assessing *T. myopaeformis* injury to sugarbeet.

Sugarbeet Root Maggot Control Strategies

Sugarbeet root maggot damage to sugarbeet is only caused by the larval stage of the pest. Larvae inflict injury to the root by scraping the surface of sugarbeet root by using oral hooks, thereby creating slime tunnels where they feed. Heavy feeding can result in the tap root being completely severed, and such plants often wilt and die (Hein et al. 2009). Yield reduction can result from seedling death, especially if infestations occur early in the growing season; however,

significant yield loss also occurs from reduced root tonnage and sucrose content due to root maggot feeding throughout the growing season (Campbell et al. 1998).

Current sugarbeet root maggot control strategies fall under two broad categories: cultural and chemical (Armstrong et al. 1998). Sticky-stake traps are used to monitor *T. myopaeformis* fly activity and assist growers with the treatment decision-making process (Bechinski et al. 1990). Cultural control involves crop rotation. Cattanaach and Dexter (1990) reported that 55% of Red River Valley sugarbeet growers utilize a minimum three-year rotation with other crops to manage sugarbeet pests, while another 40% employ at least a four-year crop rotation. Only 5% were rotating sugarbeet on a two-year basis. Boetel et al. (2004) reported that two to three applications of insecticides are often used to manage high root maggot infestations, and that producer reliance on multiple applications is a cause of concern as it intensifies the selection pressure for insecticide resistance in *T. myopaeformis* populations. Alternative strategies for *T. myopaeformis* management such as resistant varieties and insect attractants could help reduce grower reliance on insecticides and, thus, reduce selection pressure for insecticide resistance development.

Host Plant Range and Food-Plant Range

Food-plant range of an insect can be defined as the diet breadth while host-plant range is the niche breadth of an herbivorous insect (Schoonhoven et al. 2005, Forister et al. 2009). Schoonhoven et al. (2009) indicated that as much as the two terms appear to be similar, the former is mostly associated with food for the larval stage while the latter refers to where the ovipositing adult chooses to deposit its eggs, and the areas that code for diet selection behavior in the larvae are different from those that govern host selection behavior by the ovipositing adult.

Oviposition site choice and larval performance are often the focus of host plant range investigations and the decision by the female on where to oviposit governs the fate of offspring during development (Forister et al. 2009). Maximizing offspring performance has been assumed to be a key motivator of female preference for specific host plants (Gratton and Welter 1998, Forister et al. 2009). Weckers et al. (2007) indicated that for cases where adults and immatures feed on different resources, changes in host use might culminate from behavior modifications that maximize fitness of adults, immatures, or both.

Alternate host plants can play a significant role in the biology of a number of crop insect pests (Jones et al. 1992). In an investigation on host plants of *T. myopaeformis* in Idaho in field, greenhouse, and laboratory studies, Mahrt and Blickenstaff (1979) reported that only spinach, *Spinacia oleracea* L., sugarbeet, and a Canadian entry of *Atriplex hortensis* L. (i.e., all members of the family Chenopodiaceae) were suitable hosts for the sugarbeet root maggot. Spinach was 10 times as attractive as sugarbeet when flies were given a choice assay in field cage studies. The authors suggested that *T. myopaeformis* either preferred spinach for oviposition or the larval survival rate was that much greater on spinach than on sugarbeet. An examination of a commercial spinach field in Idaho showed a per-plant larvae infestation of about half that of surrounding beet fields. They also found that four *A. hortensis* entries (i.e., from Idaho, Canada, Poland, and Russia) were also infested with *T. myopaeformis* eggs. In greenhouse screening, Kruger (1986) reported that sugarbeet, spinach, and *A. subspicata* (Nutt.) were suitable hosts. Krueger also found that *A. heterosperma* Burge was a strong host candidate for *T. myopaeformis*. Some larvae were also collected from rough pigweed, *Amaranthus hybridus* L., creeping pigweed, *A. graecizans* L., curly dock, *Rumex crispus* L., and black nightshade, *Solanum nigrum* L., although recovery from those plants and root-associated soil was low. Kruger (1986) also

sampled numerous weed species growing within and along edges of sugarbeet fields and reported that *A. hybridus*, *A. graecizans*, and *A. subspicata* were the only species that showed scarring or presence of larvae. As a result of those findings and observations, it was suggested that all suitable and potential suitable host plants of the sugarbeet root maggot were in the family Chenopodiaceae; however, Kruger (1986) further stated that studies on potential native and introduced host plants need to be expanded, and that the genus *Atriplex* should be studied closely as both native and introduced species occur in North Dakota.

PAPER 1. SUGARBEET ROOT MAGGOT (DIPTERA: ULIDIIDAE) OVIPOSITION PREFERENCE AND HOST-RANGE FIELD EXPERIMENTS

ABSTRACT

Oviposition preference and larval survival of the sugarbeet root maggot, *Tetanops myopaeformis* (Röder), was evaluated on three cultivated plant species and five native North American weed species during the 2010 and 2011 growing seasons near St. Thomas, in northeastern North Dakota. Experiments were arranged in a randomized complete block design with eight replications. Treatments included the following: sugarbeet, *Beta vulgaris* L.; spinach, *Spinacia oleracea* L.; sunflower, *Helianthus annuus* L.; common lambsquarters, *Chenopodium album* L.; redroot pigweed, *Amaranthus retroflexus* L.; Palmer amaranth, *A. palmeri* S. Watts.; spear saltbush, *Atriplex patula* L.; and common ragweed, *Ambrosia artemisiifolia* L. Results from sticky-stake traps indicated adequate numbers of *T. myopaeformis* flies in treatment plots during both years of the study with higher numbers of flies in 2011 than that observed in the 2010 growing season. Palmer amaranth, sugarbeet, spinach, common lambsquarters, spear saltbush, and redroot pigweed were the preferred plant species for *T. myopaeformis* oviposition. Recovery of live third-instar larvae was highest on spinach, sugarbeet, and spear saltbush. Spear saltbush is considered to be native to central and northern latitudes of the continent, further indicating that this species could have served as a common or preferred host of *T. myopaeformis* before an apparent host preference shift to sugarbeet. Lower levels of survival were observed on common lambsquarters, redroot pigweed, and Palmer amaranth. Since sugarbeet and spinach are not native plant species, these findings suggest that the sugarbeet root maggot could have used the above-mentioned weed species as hosts. Lower survival on these weed species in this experiment suggest that *T. myopaeformis* populations have apparently made a significant preference shift to monocultures of the more suitable host, sugarbeet. However, oviposition and

larval survival on the aforementioned plant species suggests that these plant species can serve as alternate hosts. These findings could have important *T. myopaeformis* management implications, especially if one of these weeds were to become resistant to herbicides commonly used in sugarbeet production.

INTRODUCTION

The sugarbeet root maggot, *Tetanops myopaeformis* (Röder), has been a major economic pest of sugarbeet, *Beta vulgaris* L., in the Red River Valley of North Dakota and Minnesota since the early 1950s (Gojmerac and Callenbach 1956). It is particularly troublesome on sugarbeet grown in light, porous soils (Kruger 1986). General descriptions of the basic biology of *T. myopaeformis* are provided by Hawley (1922), Knowlton (1934), and Whitfield and Grace (1985). Sugarbeet root maggot flies begin emerging in late spring or early summer (i.e., usually May to early June in the Red River Valley of Minnesota and North Dakota) after overwintering and completing an obligate larval diapause. Flies leave the fields from which they overwintered as larvae, and move to newly planted sugarbeet fields to oviposit at or near the bases of young sugarbeet seedlings. Eggs usually hatch within seven to 10 d (Jarvi 1978), and the emerging larvae quickly begin feeding on roots by using paired oral hooks to scrape the root surface. High infestations of feeding larvae can sever small tap roots, causing seedlings to die early in the season. Plant mortality is most severe when plants are also under drought stress. After the seedling stage, yield reduction by the sugarbeet root maggot results from reduced root tonnage and sucrose content from larval feeding throughout the growing season (Campbell et al. 1998).

The sugarbeet root maggot is native to North America (Mahrt and Blickenstaff 1979). However, all current *B. vulgaris* cultivars are believed to be descendants of wild maritime beet, *B. vulgaris* (L.) spp.; *maritima* (L.), which is thought to have originated from the British Isles, north Atlantic European coast, Mediterranean Region, or Asia Minor (Ulbrich 1934, Coons 1936). These observations raise questions relating to the native host range that would have been exploited by *T. myopaeformis* before the introduction of sugarbeet to North America. There are conflicting and inconclusive accounts regarding this issue. Most accounts suggest that *T.*

myopaeformis larvae feed on plants in the Chenopodiaceae and Amaranthaceae families (Anderson et al. 1977). Hawley (1922) suggested that larvae of this pest had fed for many years on weeds such as common lambsquarters, *Chenopodium album* L.; (Chenopodiaceae) and redroot pigweed, *Amaranthus retroflexus* L., (Amaranthaceae). Knowlton (1934) and Jones et al. (1952) supported this suggestion by reporting *T. myopaeformis* oviposition and larvae feeding on a range of weed species, including black nightshade, *Solanum nigrum* L., and curly dock, *Rumex crispus* L., although larval development on these plants was not reported. Mahrt and Blickenstaff (1979) reported that support of larval development was limited to plants belonging to the genera *Beta*, *Spinacia*, and *Atriplex*. Those authors also indicated that none of the weed plants reported as hosts in the literature was suitable for sustaining the sugarbeet root maggot. However, that might not have been a true reflection of those weed species because their experimental units were very small i.e. single rows, 3 m long, one row caged and one uncaged. Thus, the extent of the native host range of this pest is unclear. Moreover, the limited amount of previous research on this topic lacked a focus on native North American plant species. This lack of a concrete understanding on *T. myopaeformis* host range could have implications for its management, especially if a weed host of this pest were to become herbicide resistant. The objective of this study was therefore, to assess the relative attractiveness for oviposition and suitability of selected cultivated crops and native North American weed species as hosts for *T. myopaeformis* larval survival and development. This information will advance knowledge about the ecology of *T. myopaeformis* and could aid in developing long-term management strategies for this important insect pest.

MATERIALS AND METHODS

A field experiment was conducted with natural infestations of *T. myopaeformis* during the 2010 and 2011 growing seasons near St. Thomas (Pembina County), in northeastern North Dakota, a site that regularly experiences heavy infestations of this pest. The experiment was arranged as a randomized complete block design with eight replications. Treatments included monoculture plots of crop and weed species as shown in Table 1.

Table 1. Treatment list of cultivated crop and weed species evaluated in the study

Treatment	Scientific name	Family	Status ^a
Sugarbeet	<i>Beta vulgaris</i> L.	Chenopodiaceae	Introduced
Spinach	<i>Spinacia oleracea</i> L.	Chenopodiaceae	Introduced
Sunflower	<i>Helianthus annuus</i> L.	Asteraceae	Native
Common lambsquarters	<i>Chenopodium album</i> L.	Chenopodiaceae	Native
Redroot pigweed	<i>Amaranthus retroflexus</i> L.	Amaranthaceae	Native
Palmer amaranth	<i>Amaranthus palmeri</i> S. Watts	Amaranthaceae	Native
Spear saltbush	<i>Atriplex patula</i> L.	Chenopodiaceae	Native
Common ragweed	<i>Ambrosia artemisiifolia</i> L.	Asteraceae	Native

^aStatus in the continent of North America

Sugarbeet was included as a control and spinach was also included for comparative purposes because *T. myopaeformis* is occasionally reported as damaging spinach in Colorado (M. Boetel, pers. Comm.). The other weed plants were selected based on previous research reports in the literature, and also that they are believed to be native to North America. Individual treatment plots were 7.6 m by 7.6 m, and all were separated by 4.6 m-wide weed-free alleys.

Treatment plots were planted on 19 May and 2 June in 2010 and 2011, respectively. Sugarbeet (Betaseed Inc., Shakope, MN), spinach (Agassiz Seed Supply, Fargo, ND), and

sunflower (Seeds 2000, Breckenridge, MN) were planted at a rate of one seed per 11.4 cm of row length using a commercial John DeereTM 71 Flex planter (Deere and Company, Moline, IL). Each row crop plot was 12 rows wide with rows spaced 55.8 cm apart. Common lambsquarters seed was from a local stock collection (Plant Sciences Department, North Dakota State University, Fargo). Redroot pigweed, palmer amaranth, and common ragweed were purchased from Azlin Seed Services (Leland, MS), and spear saltbush seed was obtained from S & S Seed, Inc. (Carpinteria, CA). Seed entries for all weed treatments (i.e., common lambsquarters, redroot pigweed, Palmer amaranth, spear saltbush, and common ragweed) were broadcast-sown at 400 seeds/m² using 125 ml plastic bottles with holes (2 to 4 mm diam.) in their lids for seed delivery. Seed was delivered evenly across each plot by inverting the seed-filled container and shaking it in a salt-shaker fashion while walking across the plot. A 2-m wide conventional harrow section, pulled by an all-terrain vehicle at about 9 kmh was used to incorporate the seeds into the upper 2 cm of soil. Seed-bearing portions of all plants in weed plots were removed and destroyed after final fly monitoring and soil sampling procedures to prevent weed infestation in subsequent years.

T. myopaeformis Fly Activity Monitoring

Adult *T. myopaeformis* flight activity was monitored in each plot using a modified version of the sticky-stake trap used by Blickenstaff and Peckenpaugh (1976). Each trap was composed of a wooden post (5 cm x 5 cm x 60 cm) that served as a base to which an orange garden stake (2.5 cm x 30 cm) was stapled. Trap deployment involved positioning each post such that the base of the orange garden stake was about 30cm above the ground, and applying a layer of TanglefootTM (The Tangle Foot Co, Grand Rapids, MI) to the orange garden stake portion. One trap was maintained in the center of each treatment plot throughout the *T. myopaeformis*

adult activity period (i.e. late-May through July), and traps were checked three times per week each year. TanglefootTM was reapplied regularly to ensure that a sufficiently adhesive surface was maintained on the stakes throughout the fly activity period each year.

Soil Core Sampling

Soil core sampling was carried out each year to determine *T. myopaeformis* oviposition preference and measure larval establishment and survival rates among treatments. Soil samples were collected at four developmental levels per year with timing of the collections aimed at coinciding with peak presence of eggs and specific larval stadia. Sampling for eggs was conducted on 8 and 20 June in 2010 and 2011, respectively. This was about 10 to 11 d after fly activity had begun and within 1 d of peak fly activity each year. Core sampling efforts for first-, second-, and third instar larvae were carried out on 15 June, 7 July, and 26 July, respectively. In 2011, the procedures for recovery of the same respective larval stadia were conducted on 30 June, 15 July, and 28 July, respectively. At each sampling, the tops of four randomly selected plants from each treatment plot were removed, and a stainless steel soil core sampler (5-cm diam.) was used to collect all soil surrounding the base and root of each plant. Soil cores were collected by driving the core sampler to a depth of 3 cm and removing all the soil in the cup. This depth was chosen to minimize the volume of unneeded soil because *T. myopaeformis* flies typically deposits nearly all eggs within the upper 0.5 to 1 cm of soil (Jarvi 1978). All collected samples were placed in ZiplocTM re-sealable plastic bags (SC Johnson & Son, Racine, WI) and placed into a plastic cooler at room temperature (i.e., 25°C) for transport to the laboratory. Samples were subsequently placed into laboratory storage and maintained at 5°C pending processing. The same collection procedures were followed for first-instar larvae. Sampling for second- and third-instars involved a similar procedure; however, a larger (i.e. 10 cm diam. X 15

cm) golf cup cutter was used to collect the samples, and the sampler was driven into the ground to a depth of 15 cm. The larger core sampler was employed to increase the likelihood of recovering all larvae present for two reasons: 1) later-season plants were larger and roots were deeper than those present during egg sampling; and 2) later-instar larvae have increased propensity to “stray” from the immediate rhizosphere, especially if several larvae are present. All larval soil samples were handled as described above for those collected during soil sampling for eggs.

Soil Sample Processing

Processing soil samples for the presence of eggs was carried out by initially placing each soil core on a plastic tray and visually examining it for the presence of eggs. All soil from the sample was then floatation-washed by running tap water through a column made of Plexiglas (8cm diam. by 27cm high, with a 5-cm outlet spout) and successively passing the sample through No. 45 (355 μ m) and 60 (250 μ m) sieves (Newark Wire Cloth Co., Newark, NJ). The sieves were then suspended in a rectangular stainless steel dish (30 cm x 25 cm x 9.5 cm) (National Sanitation Foundation, Dallas, TX) which was filled to about 50% with clean tap water, and any remaining eggs were recovered using a small, damp artist’s brush (Jack Richeson-series 9000, Artist’s Materials and Farming, Saint Paul, MN) with the aid of a 10X magnifying glass. All eggs were individually placed on a petri plate covered with a black cotton cloth, which was dampened with distilled water. Eggs were then counted under a microscope at 10X magnification.

To quantify larval presence in soil samples, individual soil cores were examined by sifting through and visually inspecting soil. Second and third-instars were placed into ZiplocTM

plastic bags (SC Johnson Co) filled with moist silica sand (Unimin Corporation) and stored at 5°C pending laboratory rearing to adult stage.

Data Analysis

Data collected on fly activity, egg counts, and larval samplings were analyzed with the general linear models procedure in SAS (SAS Institute, 2008). Means were separated using Fisher's Protected Least Significant Difference at $P \leq 0.05$.

RESULTS

Sugarbeet Root Maggot Fly Activity

Sugarbeet root maggot fly activity in 2010 was first detected on 28 May and lasted four weeks. Peaks in fly activity were observed on 1 and 7 June, and activity had ceased by 8 July. Weekly fly counts from sticky-stake traps did not generate differences among the plant species during the 2010 growing season (Table 2); however, these data substantiated the presence of an adequate number of flies throughout the plots for the experiment. Fly densities were higher in 2011, and emergence was later due to extended periods of cool spring weather; however, fly activity followed similar patterns to those observed in the first year of the experiment. In 2011, fly captures on sticky-stakes began on 10 June. Activity peaks occurred on 20 and 27 June, and 4 July, and ceased by 13 July. Similar to 2010, there were no significant differences in weekly fly counts from sticky-stake traps among the treatments in 2011 (Table 3).

Table 2. Weekly captures of *T. myopaeformis* flies on orange sticky-stake traps in monoculture crop and weed plant habitats, St. Thomas, ND, 2010

Plant species	Trapping period (Mean \pm se)			
	Week 1	Week 2	Week 3	Week 4
Sugarbeet	189 \pm 7	171 \pm 7	97 \pm 9	32 \pm 5
Spinach	186 \pm 11	151 \pm 18	72 \pm 13	35 \pm 4
Sunflower	167 \pm 10	159 \pm 12	77 \pm 6	30 \pm 4
Common lambsquarters	187 \pm 12	142 \pm 14	72 \pm 10	32 \pm 3
Redroot pigweed	178 \pm 15	161 \pm 6	70 \pm 12	30 \pm 4
Palmer amaranth	178 \pm 10	158 \pm 12	87 \pm 9	28 \pm 5
Spear saltbush	180 \pm 9	156 \pm 10	68 \pm 16	31 \pm 4
Common ragweed	173 \pm 16	153 \pm 21	70 \pm 13	28 \pm 3

Fly numbers were not significantly different across plant species on each of the sampling periods at $P = 0.05$.

Table 3. Weekly captures of *T. myopaeformis* flies on orange sticky-stake traps monoculture crop and weed plant habitats, St. Thomas, ND, 2011

Plant species	Trapping period (Mean \pm se)			
	Week 1	Week 2	Week 3	Week 4
Sugarbeet	4 \pm 0.9	351 \pm 19	359 \pm 22	58 \pm 6
Spinach	4 \pm 0.4	339 \pm 18	300 \pm 22	47 \pm 7
Sunflower	4 \pm 0.5	334 \pm 19	298 \pm 20	62 \pm 6
Common lambsquarters	5 \pm 0.7	347 \pm 23	303 \pm 30	47 \pm 3
Redroot pigweed	3 \pm 0.6	361 \pm 17	300 \pm 20	52 \pm 3
Palmer amaranth	4 \pm 0.9	366 \pm 22	281 \pm 14	49 \pm 3
Common ragweed	4 \pm 0.8	351 \pm 23	350 \pm 40	48 \pm 6

Fly numbers were not significantly different across plant species on each of the sampling periods at $P = 0.05$.

Oviposition Preference

Results from soil sampling procedures in 2010 (Figure 1) indicated that females deposited significantly more eggs in sugarbeet, spinach, and Palmer amaranth than any of the other plant habitats tested ($F = 6.51$; $df = 7, 49$; $P < 0.0001$), and none of these apparent preferred treatments differed significantly from each other. Common ragweed and sunflower habitats appeared to be least preferred for oviposition; however, numbers of eggs recovered from these treatments did not differ significantly from those of lambsquarters, redroot pigweed, or spear saltbush.

Oviposition preference in 2011 varied significantly ($F = 10.76$; $df = 6, 42$; $P < 0.0001$) among plant species. The largest numbers of eggs were recovered from redroot pigweed and

common lambsquarters habitats, and these plant species incurred significantly greater rates of oviposition than sugarbeet, sunflower, Palmer amaranth, and common ragweed (Figure 2).

Relatively large numbers of eggs were also recovered from soil samples collected in spinach and sugarbeet. Those plant species had significantly more eggs per sample than sunflower and common ragweed. Similar to the results from 2010, the lowest numbers of eggs in 2011 were recovered from sunflower and common ragweed habitats.

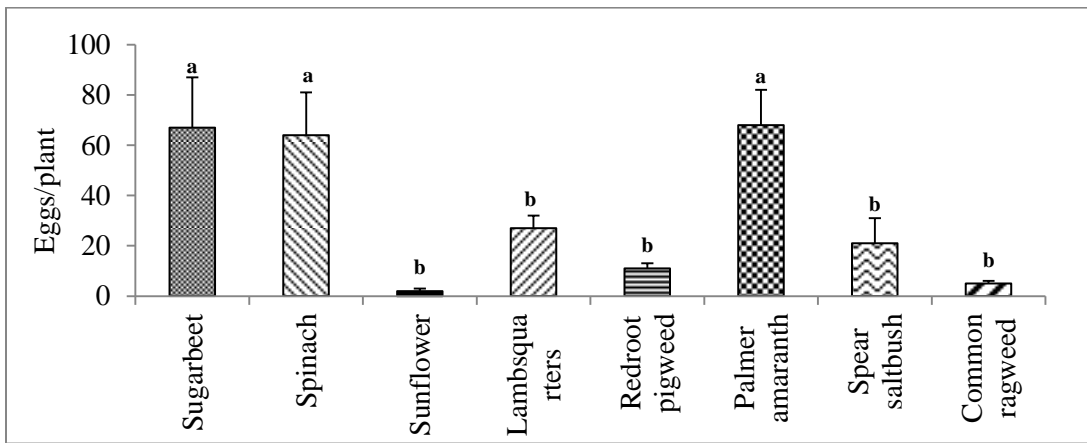


Fig. 1. Mean number of sugarbeet root maggot eggs collected from crop and weed plant habitats at St. Thomas, ND in 2010. Bars sharing a letter are not significantly different at $P= 0.05$ (Fisher's Protected Least Significant Difference test).

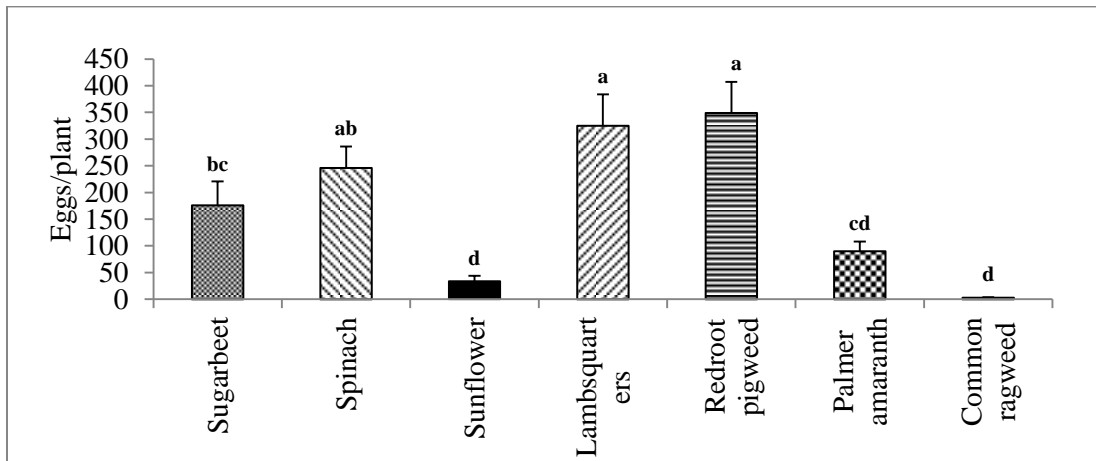


Fig. 2. Mean number of sugarbeet root maggot eggs collected from crop and weed plant habitats at St. Thomas, ND in 2011. Bars sharing a letter are not significantly different at $P= 0.05$ (Fisher's Protected Least Significant Difference test).

Recovery of Sugarbeet Root Maggot Larvae

First Instars. In 2010, significantly ($F = 7.00$; $df = 6, 42$; $P < 0.0001$) greater numbers of first-instar larvae were recovered from common lambsquarters habitats than all other treatments except sugarbeet (Figure 3). Other habitats in which the number of first instars was not significantly different from sugarbeet included spinach, redroot pigweed, Palmer amaranth, and spear saltbush. Numbers of first-instar larvae recovered from sunflower and common ragweed habitats were statistically lower than those of all other treatments in in 2010.

In 2011, significantly ($F = 7.00$; $df = 6, 42$; $P < 0.0001$) more first instars were recovered from common lambsquarters than any other plant species habitat. Similar to the results of 2010, significantly ($F = 7.00$; $df = 6, 42$; $P < 0.0001$) more first-instar larvae were collected per core sample in sugarbeet, spinach, and redroot pigweed habitats than in sunflower and common ragweed treatments (Figure 4).

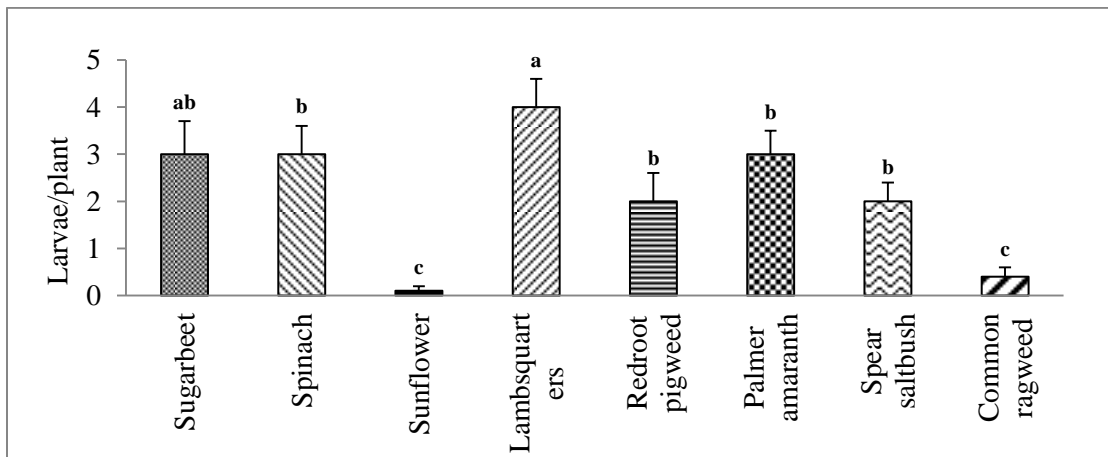


Fig. 3. Number of first instars collected from crop and weed plant habitats at St. Thomas, ND in 2010. Bars sharing a letter are not significantly different at $P = 0.05$ (Fisher's Protected List Significant Difference).

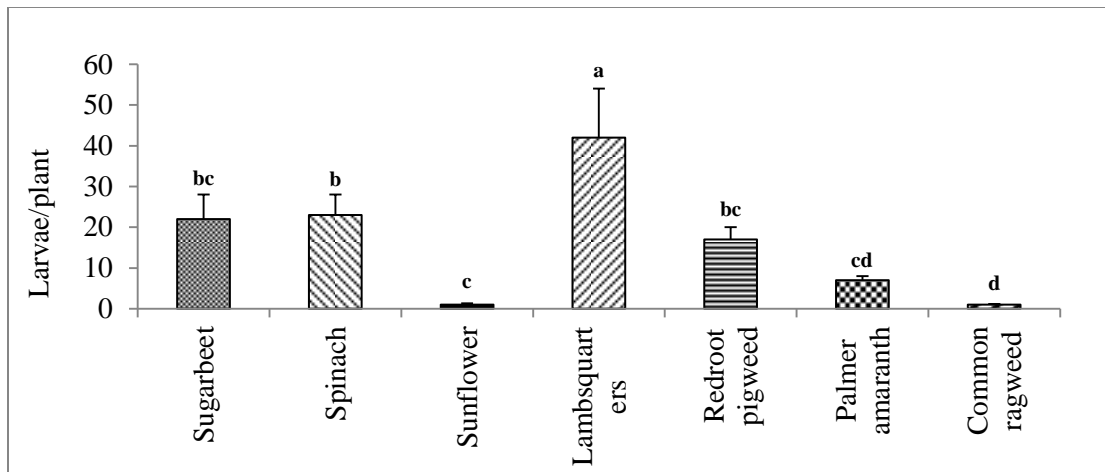


Fig. 4. Number of first instars collected from crop and weed plant habitats at St. Thomas, ND in 2011. Bars sharing a letter are not significantly different at $P = 0.05$ (Fisher's Protected List Significant Difference).

Second Instars. Soil sampling results from 2010 indicated that significantly ($F = 4.97$; $df = 7, 49$; $P = 0.0003$) more second-instar larvae were collected from spinach plots than from any other plant habitat (Figure 5). Additionally, sugarbeet and spear saltbush plots had significantly greater numbers of surviving second-instar larvae than all remaining treatments except spinach.

Similar to the 2010 findings, significantly more ($F = 43.95$; $df = 6, 42$; $P < 0.0001$) second-instars were recovered from spinach plots than from any other plant species habitat during the 2011 growing season. More second-instar larvae were collected from sugarbeet habitats than those of any other treatment in 2011 (Figure 6). No second instars were detected in sunflower in either year of the experiment. Similarly, second-instar larvae were at very low densities per plant in common ragweed in 2010 and none were recovered from common ragweed in 2011.

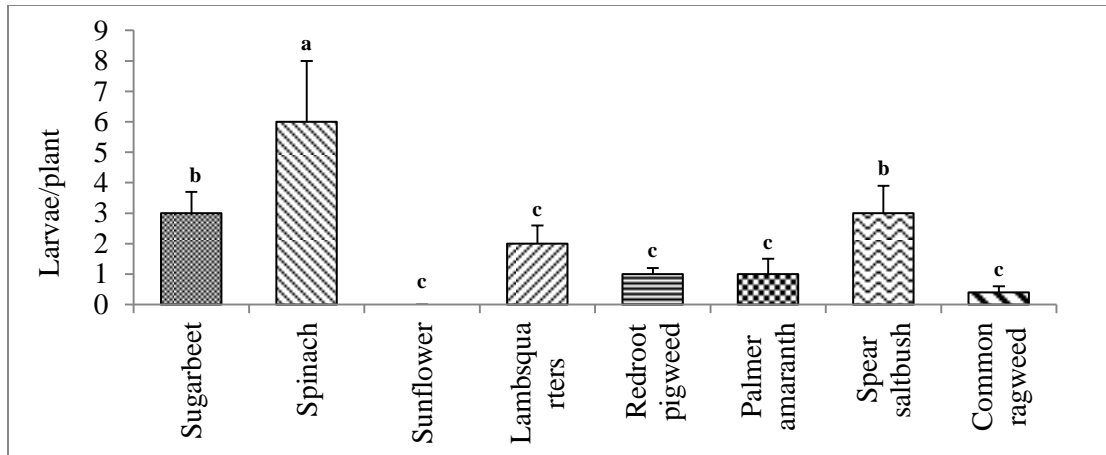


Fig. 5. Number of second instars collected from crop and weed plant habitats at St. Thomas, ND in 2010. Bars sharing a letter are not significantly different at $P = 0.05$ (Fisher's Protected List Significant Difference).

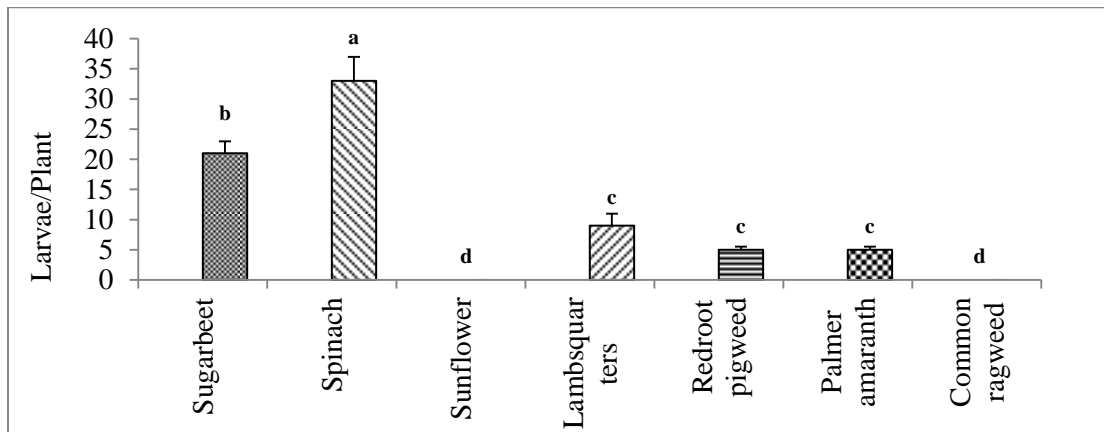


Fig. 6. Number of second instars collected from crop and weed plant habitats at St. Thomas, ND in 2011. Bars sharing a letter are not significantly different at $P = 0.05$ (Fisher's Protected List Significant Difference).

Third Instars. Numbers of third instars recovered from spinach were significantly ($F = 16.85$; $df = 7, 49$; $P < 0.0001$) greater than any other plant species in 2010. The second-highest densities of third instars were detected in sugarbeet; however, the mean number of larvae recovered from sugarbeet plots was not significantly different from that in spear saltbush, common lambsquarters, and redroot pigweed. Plants in which larval to the third instar was significantly lower than sugarbeet in 2010 included sunflower, Palmer amaranth, and common ragweed (Figure 7). Soil sampling for third-instar *T. myopaeformis* larvae during the 2011

growing season produced similar results to those observed in 2010, but with fewer differences among treatments. More larvae developed to the third instar on spinach than on any other plant species (Figure 8). Also, with the exception of spinach, sugarbeet allowed significant development of *T. myopaeformis* to the third-instar than all other plant species. Also reflective of the 2010 results, monocultures of sunflower or common ragweed did not support larval development to third-instar (Figure 8).

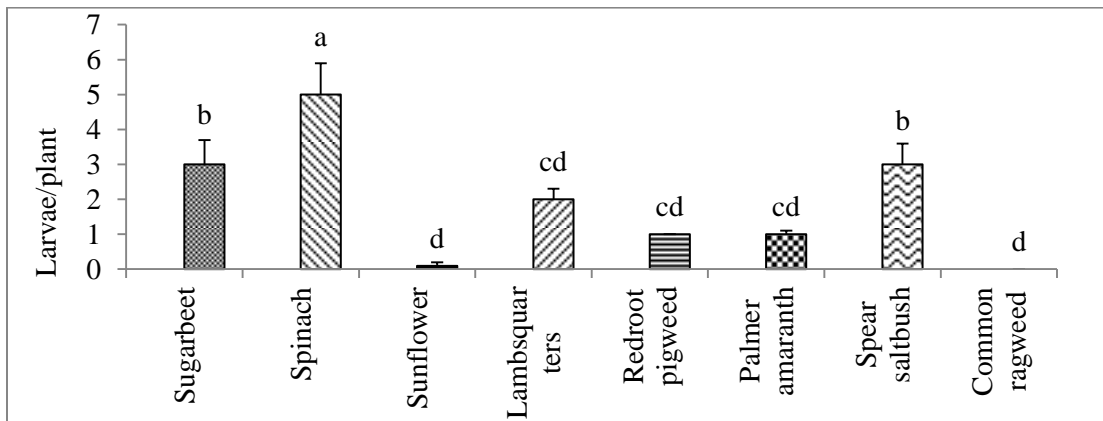


Fig. 7. Number of third instars collected from crop and weed plant habitats at St. Thomas, ND in 2010. Bars sharing a letter are not significantly different at $P= 0.05$ (Fisher's Protected List Significant Difference).

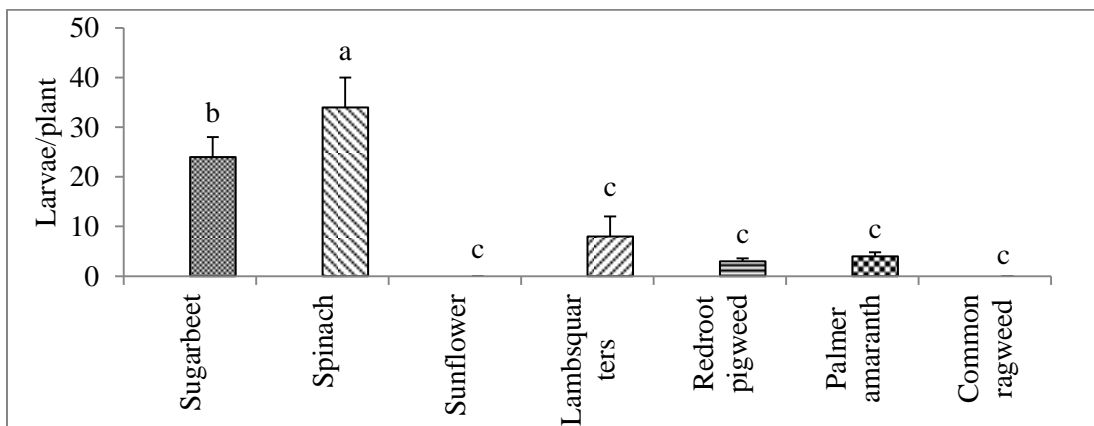


Fig. 8. Number of third instars collected from crop and weed plant habitats at St. Thomas, ND in 2011. Bars sharing a letter are not significantly different at $P= 0.05$ (Fisher's Protected List Significant Difference).

DISCUSSION

Results from sugarbeet root maggot fly monitoring efforts during this experiment indicated that adult activity followed similar patterns during the 2010 and 2011 growing seasons, despite the occurrence of much higher fly densities during the second year. The first series of soil core samples, collected during the first two weeks of fly activity were to compare *T.*

myopaeformis egg densities and determine oviposition preference in this study. There were no statistical differences in fly activity levels between plant treatments during this time in either year of the experiment; however, egg densities were highest in sugarbeet, spinach, and Palmer amaranth in 2010 and in spinach, common lambsquarters, redroot pigweed, and sugarbeet in 2011. This suggests that, although *T. myopaeformis* adults apparently visit multiple plant species during adulthood, potentially for foraging, mate selection, and copulation, or in host searching efforts, they prefer ovipositing in microhabitats provided by plant species belonging to specific families. All plant species that appeared to be attractive for oviposition by *T. myopaeformis* females in this experiment belong to the families Chenopodiaceae and Amaranthaceae, which are both classified within the plant order Caryophyllales. Another consistent finding across years was that the lowest egg densities in this experiment were observed in common ragweed and sunflower, which both belong to the family Asteraceae, thus indicating that microhabitats at the bases of these plant species are not preferred for oviposition by *T. myopaeformis* females.

Mahrt and Blickenstaff (1979) reported that *T. myopaeformis* females are not selective in their oviposition when in the vicinity of a suitable host plant. This behavior was not apparent in the present study. Our results suggest that females are discriminate when selecting an oviposition site. In this study, females selectively oviposited in spinach, sugarbeet, and to a lesser extent,

common lambsquarters, redroot pigweed, Palmer amaranth, and spear saltbush, but avoided common ragweed and sunflower.

Another behavior observed in other insect species is that females will mark a host plant after oviposition to alert conspecifics that the plant has already been utilized (Stelinski et al. 2009). This behavior was not observed with *T. myopaeformis* in the present study. Individual sugarbeet root maggot females can oviposit up to 200 eggs (Hein et al. 2009). In the present study, it was common to find on average 300 or more eggs per single-plant soil sample, thus suggesting that microsites surrounding individual plants were frequently exploited for oviposition by more than one female. Therefore, host marking does not appear to occur in *T. myopaeformis*.

Results on larval development from first to third instar were somewhat similar across the plant species during the 2010 and 2011 growing seasons. Larval progression through instars appeared to be best on spinach, sugarbeet, and spear saltbush in both years of the study. Despite finding higher egg numbers on common lambsquarters, redroot pigweed, and Palmer amaranth, larval survival to the third instar on the aforementioned plant species was poor. These results suggest that, although some survival to later instars is possible by feeding on these species, they appear to be sub-optimal hosts for larval development when compared to spinach, sugarbeet, and spear saltbush.

Evolutionary theories on the relationship between oviposition preference of herbivorous insects and the survival of offspring suggest that females of some species prefer to oviposit on substrates that will sustain feeding and survival of their offspring (Harris et al. 2001, Schoonhoven et al. 2005). This appeared to be the case in our study, as flies appeared to preferentially oviposit near the bases of spinach, sugarbeet, and spear saltbush plants; however,

the theory did not hold true with other plant species. For example, sugarbeet root maggot larval survival was relatively low on common lambsquarters, Palmer amaranth, and redroot pigweed, despite relatively high numbers of eggs being found in soil collected from the bases of these plant species. One theory proposed to explain such inconsistencies is the chemical similarity model (Forister et al. 2009), which suggests that a female will deposit eggs on or near an alternative plant because it has similar physicochemical cues to those of the principal host, regardless of whether the alternatively chosen host plant is a suitable resource for offspring survival. Oviposition preference data from the present study suggest that common lambsquarters, redroot pigweed, and Palmer amaranth could have produced similar morphological and/or chemical cues to those of sugarbeet that accordingly stimulated sugarbeet root maggot flies to oviposit on these plants. Kourtney and Kibota (1990) and Leather (1994) indicated that there are no exceptional factors for a positive relationship between female oviposition and offspring performance, and that host use patterns are governed by a range of factors other than plant chemistry alone.

Hawley (1922), Knowlton (1934), and Jones et al. (1952) reported observing sugarbeet root maggot eggs and feeding activity on common lambsquarters and redroot pigweed. Their reports however, did not indicate whether the insect completed larval development on these weed species. The present study demonstrated that sugarbeet root maggot adults will oviposit on common lambsquarters and redroot pigweed, and that the larvae are able to develop on these plants (Figure 9). The sugarbeet root maggot is believed to be native to North America. Hence, our observations of oviposition preference and larval survival on common lambsquarters, redroot pigweed, Palmer amaranth, and spear saltbush suggest that these weed species or similar plants belonging to the same genera or families could have served as native host plants for this insect

before the introduction of sugarbeet to North America. Additionally, the relatively lower survival on these plants, when compared to that in sugarbeet in this study, probably explains why the sugarbeet root maggot preferred the more suitable and abundant sugarbeet when it was introduced and planted in monocultures in North America. These results are in contrast with those of Mahrt and Blickenstaff (1979) who reported that only plants in the genera *Beta*, *Spinacia*, and *Atriplex* were found to support larval development. The difference between their results and those from the present study could be associated with different experimental methodology. For example, their plot size was smaller (i.e., single rows, 3 m long, one row caged and one uncaged), whereas our plots were larger monoculture field plots (i.e., 7.6 m by 7.6 m) for each host.

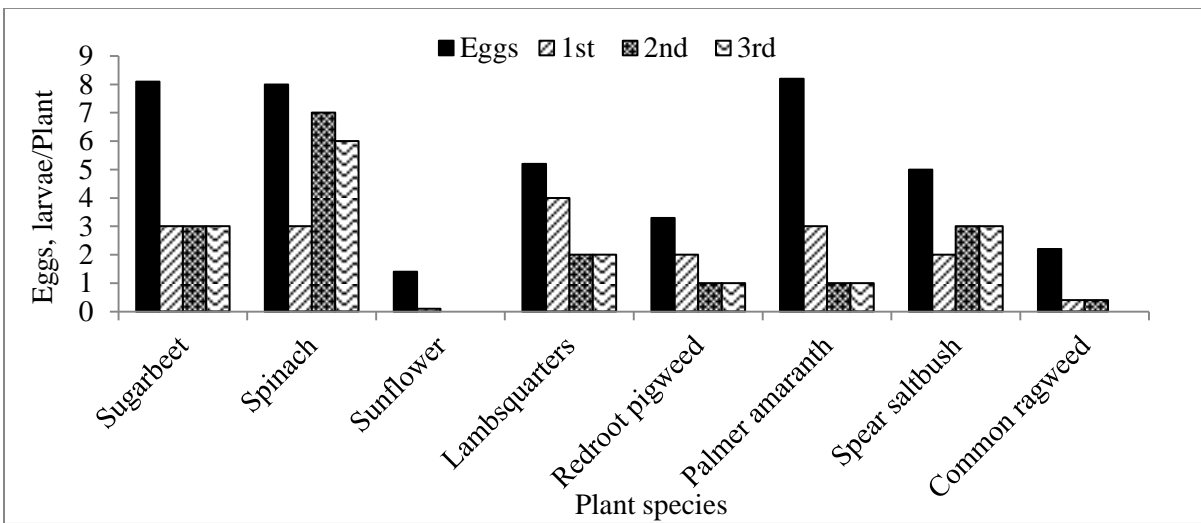


Fig. 9. Sugarbeet root maggot development progression from eggs to the 3rd instar across plant species, St. Thomas, ND, 2010-2011. Egg values are square roots of the original means.

Results on larval development indicated that spinach, an introduced cultivated crop species, was superior to sugarbeet in relation to suitability for sustaining sugarbeet root maggot larvae. This finding supports those of Mahrt and Blickenstaff (1979) who found spinach to be equally suitable as a sugarbeet root maggot larval host. These results could pose significant

implications regarding sugarbeet root maggot management in some areas because farmers have reported sugarbeet root maggot damage to spinach in sugarbeet-producing states such as Colorado (M. Boetel, pers. comm.). Spinach is widely distributed and cultivated as a vegetable crop (Mahrt and Blickenstaff 1979). As such, spinach could be contributing significantly to sugarbeet maggot infestations in areas where both crops are grown.

Results from this study also suggest that weed species belonging to the families Chenopodiaceae and Amaranthaceae can serve as alternative hosts that support survival of the sugarbeet root maggot. Larval survival on these weed species suggests that this insect has a wider host range than previously thought (Mahrt and Blickenstaff 1979) and that these weed species could be currently contributing to localized infestations of this insect in sugarbeet-producing areas. The ability of the sugarbeet root maggot to survive on these weed species could pose serious implications regarding the management of this pest in the future, especially if any of the weed species that support larval development were to develop herbicide resistance in sugarbeet production areas. This is especially important, given that glyphosate-resistant sugarbeet and associated glyphosate applications have been highly adopted in recent years by growers in the United States. As of 2009, about 95% of the entire U.S. sugarbeet acreage was sown to glyphosate-resistant varieties (Wilson and Sbatella 2011). Uncontrolled weed escapes in other non-sugarbeet cropping habitats could provide additional harborage and potentially contribute to increased root maggot densities in localized areas. Thus, it will be important for growers and others associated with weed management in the known range of the sugarbeet root maggot to closely monitor these weed species for potential herbicide resistance.

This study also indicated that the sugarbeet root maggot readily oviposited in common lambsquarters, Palmer amaranth, and redroot pigweed; however, survival on these species was

very low. This lack of preference-performance relationship was unexpected, and suggests areas for future research such as investigating the physiological impacts of these weed species on development of sugarbeet root maggot as well as investigating potential visual or chemical cues that may stimulate sugarbeet root maggot adults to oviposit in these weed host habitats. An understanding of how sugarbeet root maggot flies find these host plants could be an invaluable tool in devising effective control measures for this pest, either through direct application of plant volatiles, or through plant breeding for improved sugarbeet varieties that are less attractive to ovipositing females.

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**PAPER 2. SUGARBEET ROOT MAGGOT (DIPTERA: ULIDIIDAE) OVIPOSITION
PREFERENCE AND LARVAL SURVIVAL IN CHOICE AND NO-CHOICE
GREENHOUSE ASSAYS**

ABSTRACT

Choice and no-choice tests were conducted in the greenhouse during the winter and fall of 2011 to determine oviposition preference and larval survival of the sugarbeet root maggot, *Tetanops myopaeformis* Röder. Results from free-choice tests indicated that the sugarbeet root maggot flies preferred ovipositing on sugarbeet, spinach, common lambsquarters, spear saltbush, redroot pigweed, and Palmer amaranth, and avoided sunflower and bare soil. In the no-choice test, females oviposited on all treatments, including the bare-soil control. However, significantly more eggs were deposited on sugarbeet, spinach, spear saltbush, and lambsquarters. Results on larval survival and development from the no-choice test indicated that the greatest larval survival, in descending order, was found on spinach, sugarbeet, and spear saltbush. Larvae developed faster on these plant species. However, significantly lower larval survival was observed in common lambsquarters, redroot pigweed, and Palmer amaranth. This reduced survival indicates that these plants species are suboptimal for sugarbeet root maggot larvae. However, the overall findings from this study suggest that these species could be used as alternate hosts in the absence of the preferred host, sugarbeet.

INTRODUCTION

Oviposition site preference is one of the life-history traits that define oviparous insects (Resetarits 1996). Oviposition site selection involves the female choosing a habitat for her offspring; and the resulting choice determines larval performance and adult fitness (Blaustein 1999, Smith et al. 2003). Variation in host plant quality is presumed to affect host selection behavior, and optimality models in evolutionary ecology suggest a close correlation between oviposition preference and offspring performance (Smith et al. 2003). Anulewicz et al. (2008) indicated that adaptation of an insect to its host plants involve two major characters: 1) insect behavior that influences choice of plant for oviposition or feeding; and 2) physiological traits that affect the insect's growth and reproduction. Oviposition choice is critical for insects that have a larval stage whose mobility is limited. In such circumstances, offspring survival is driven by host suitability rather than host preference, because larvae must feed and develop on the host chosen by the adult female (Anulewicz et al. 2008).

The sugarbeet root maggot, *Tetanops myopaeformis* (Röder), is believed to be native to North America (Jarvi 1978), and it is a major economic pest of sugarbeet, *Beta vulgaris* L. (Whitfield 1984). However, sugarbeet is an introduced crop from Europe. This raises a key biological question about the pest: Did the sugarbeet root maggot undergo a shift from its native North American hosts to sugarbeet? Many aspects of the sugarbeet root maggot basic biology have been described by previous authors (Hawley 1922, Whitefield and Grace 1985); however, very little is known about the extent of its host plant range. A more thorough understanding of the sugarbeet root maggot host range could have beneficial implications for its management, especially if an alternate host plant of the pest were to become herbicide resistant. A proper and more precise understanding of its host range also could be helpful in maximizing utility of

current control efforts. This is especially important, given that glyphosate-resistant sugarbeet and associated glyphosate applications have been highly adopted in recent years by growers in the United States. As of 2009, about 95% of the entire U.S. sugarbeet acreage was sown to glyphosate-resistant varieties (Wilson and Sbatella 2011). This series of experiments evaluated oviposition preference and larval performance of the sugarbeet root maggot in greenhouse choice and no-choice tests to gain a better understanding of this insect's basic ecology. Greenhouse tests are suited for such experiments because they make it easier to manipulate treatments and assess behaviors such as oviposition in choice and no-choice settings that are difficult to test in field settings.

MATERIALS AND METHODS

Plants

Attempts to rear the sugarbeet root maggot through its entire life cycle on artificial diets or using artificial growth media in the laboratory have been largely unsuccessful due to low rates of larval survival past the first instar (Jarvi 1978). Previous research suggested that the sugarbeet root maggot benefits nutritionally from microbial associations, which are probably lacking in laboratory diets (Jarvi 1978) and, in all likelihood, commercially available potting soil used in laboratory settings. Therefore, field collected-soil obtained from areas that consistently support relatively high root maggot infestations was used to raise plants for the greenhouse experiments to increase the likelihood of microbes being present to aid larval survival and development throughout the duration of the experiments.

Table 4. Treatment list of cultivated crop and weed species evaluated in the study

Treatment	Scientific name	Family	Status ^a
Sugarbeet	<i>Beta vulgaris</i> L.	Chenopodiaceae	Introduced
Spinach	<i>Spinacia oleracea</i> L.	Chenopodiaceae	Introduced
Sunflower	<i>Heliunthus annuus</i> L.	Asteraceae	Native
Common lambsquarters	<i>Chenopodium album</i> L.	Chenopodiaceae	Native
Redroot pigweed	<i>Amaranthus retroflexus</i> L.	Amaranthaceae	Native
Palmer amaranth	<i>Amaranthus palmeri</i> S. Watts	Amaranthaceae	Native
Spear saltbush	<i>Atriplex patula</i> L.	Chenopodiaceae	Native
Bare soil-control	-	-	-

^aStatus in the continent of North America

Individual plants were grown in pots consisting of a PVC pipe section (11 cm diam. x 25.5 cm high) with the bottom capped, and four 3-mm holes drilled in the cap for drainage.

Plants were maintained under greenhouse conditions ($25 \pm 2^{\circ}\text{C}$, 60 to 80% R.H., and a photoperiod of L15:D9). Each potted plant was supplied with 3 g of multipurpose controlled-release fertilizer (Multicote 4TM14-14-16 + minors; Sungro Horticulture, Bellevue, WA), and all plants were watered on an as-needed basis.

Insects

Choice and no-choice tests were conducted on *T. myopaeformis* adult flies reared from third-instar larvae that had been field-collected in northeastern North Dakota in September of 2009. After being returned to the laboratory, larvae were maintained in cold storage at 5°C for a minimum of 10 months to break diapause. To obtain adult flies for oviposition preference screening, post-diapausal larvae were placed into plastic containers containing silica sand moistened with distilled water, then placed in a rearing chamber and maintained at a temperature of $22 \pm 1^{\circ}\text{C}$ for pupation. Pupae were removed from the plastic pupation containers and placed into petri dishes (9 cm x 1.5 cm) on moistened filter paper, and then returned to the rearing chamber at $22 \pm 1^{\circ}\text{C}$ for emergence. Newly emerged flies were used for all testing.

Eggs for the no-choice larval survival test were obtained from flies that were held in plastic containers (9 cm in diam. base x 14 cm high x 10 cm in diam. on the top) with a screw-top lid. About 6 holes (1.5 cm diam.) were cut onto the wall of each container and covered with nylon screens (0.5 mm diam.) for ventilation, and an additional hole on the lid was used to hold a distilled-water containing vial that was plugged with a cotton dental wick to provide moisture. A petri dish (9 cm diam. x 2.5 cm) filled with a mixture (2:1) of plaster of paris to one part of black soil was placed below the screened base of each oviposition container. A cotton cloth (dampened with distilled water) was placed on the surface of each oviposition plate. This provided a surface on which females could oviposit, with eggs ultimately being deposited below the cloth onto the

oviposition dish. Flies were provided with a diet mixture of honey (20g), yeast (5g), cholesterol (0.063 g), and distilled water (2ml). Eggs for use in infesting plants in the greenhouse were removed from oviposition plates with a small moistened artist's brush (Jack Richeson-series 9000, Artist's Materials and Farming, Saint Paul, MN). Egg infestations were staggered over time, with one to two replicates being infested at a time to allow for an adequate supply of eggs to infest all treatments within individual replicates at the same time.

Choice Test: Sugarbeet Root Maggot Oviposition Preference

A choice test was carried out twice (i.e., Choice Tests 1 and 2) in the greenhouse to determine oviposition preference of sugarbeet root maggot flies. Pots containing plants at the three- to five- leaf stage (i.e., the typical stage at which *T. myopaeformis* fly activity and oviposition begin in the field) were placed in 60 cm x 60 cm x60 cm aluminum-framed cages fashioned with white nylon mesh (American Biological Supply Co, Baltimore, MD). Two pots were used for each plant species, and each pot contained an individual plant. The experiment was arranged as a randomized complete block design containing four replications of the treatments, and each cage was considered a replicate. A 60 cm x 60 cm sheet of flat black foam rubber, prepared with eight holes (11 cm diam.) equally spaced and cut to fit tightly around each pot, was positioned over the block of pots inside the arena to simulate a flat soil surface around the pots. Sugarbeet root maggot flies were then released from a central location in the cage such that all had an equal chance of choosing a plant on which to lay eggs. Ten females and 10 male flies, all less than 24 h old, were maintained in the arenas and allowed to mate and oviposit for five days, after which the soil in the top 2.5 cm of each pot was collected and stored at 5°C pending sample processing.

Egg counting

Processing soil samples for the presence of eggs was carried out by initially placing each soil core on a plastic tray and visually examining it for the presence of eggs. All soil from the sample was then floatation-washed by running tap water through a column made of Plexiglas (8cm diam. by 27cm high, with a 5-cm outlet spout) and successively passing the sample through No. 45 (355 μ m) and 60 (250 μ m) sieves (Newark Wire Cloth Co., Newark, NJ). The sieves were then suspended in a rectangular stainless steel dish (30 cm x 25 cm x 9.5 cm) (National Sanitation Foundation, Dallas, TX) which was filled to about 50% with clean tap water, and any remaining eggs were recovered using a small, damp artist's brush (Jack Richeson-series 9000, Artist's Materials and Farming, Saint Paul, MN) with the aid of a 10X magnifying glass. All eggs were individually placed on a petri plate covered with a black cotton cloth, which was dampened with distilled water. Eggs were then counted under a microscope at 10X magnification.

No-Choice Test: Sugarbeet Root Maggot Oviposition

A no-choice oviposition test was conducted twice in the greenhouse during 2011 to determine the attractiveness of the aforementioned plant treatments for oviposition by *T. myopaeformis* flies when no other host options are available. Treatments were arranged in a randomized complete block design with four replications. Experimental units were two individual plants grown using pots similar to those described in the choice preference study; however, the cages consisted of 2-liter beverage containers with the bottom removed and six 2.5-cm holes in the walls that were covered with nylon screen for ventilation. The tests were conducted under the same conditions as described for the choice test, except that two males and two female flies were introduced into each cage, which contained one test plant at the three- to

five-leaf developmental stage. The flies were allowed to mate and oviposit for five days, after which all soil in the top 2.5 cm of each pot was collected and examined for the presence of *T. myopaeformis* eggs by using the previously described technique.

Larval Survival

A larval survival test was conducted twice in the spring and fall of 2011 by infesting potted crop and weed species with sugarbeet root maggot eggs to assess the relative suitability of the plants for larval survival and development. Potted plants were grown under the same conditions as described for the choice experiment on oviposition preference. The treatments were single pots, containing an individual plant, that were arranged in a randomized complete block design with six replications. Each potted plant was infested with 50 eggs (test 1) and 100 eggs (test 2) at the three- to five-leaf stage (i.e., typical stage at which most infestation occurs in the field). Infestation consisted of placing the eggs near (i.e., within 0.5 cm) the bases of individual plants, just beneath (i.e., 0.4 cm) the soil surface. The eggs were left to hatch, and resulting larvae were allowed to feed and develop for six weeks, after which the pots were examined for surviving larvae.

Data Analysis

All data from choice and no-choice experiments were analyzed by using the general linear models procedure (SAS Institute 2008), and means were separated by using Fisher's protected least significant difference (LSD) test at $\alpha = 0.05$. A folded F-test (SAS Institute 2008) indicated no significant differences between the data sets of test 1 and 2. As a result, a combined analysis was performed on the no-choice oviposition sets.

RESULTS

Oviposition Preference – Choice Test

Results from choice test 1 indicated that oviposition preference varied significantly ($F = 2.75$, $df = 7, 21$, $P = 0.0344$) among the plant species. Sugarbeet root maggot flies deposited significantly more eggs at the bases of sugarbeet plants than on sunflower, Palmer amaranth, and the bare-soil control (Fig. 10). Entries in which oviposition rates did not differ significantly from that of sugarbeet included spinach, common lambsquarters, redroot pigweed, and spear saltbush. Low to moderate numbers of sugarbeet root maggot eggs were found at the bases of redroot pigweed and Palmer amaranth; however, oviposition in those treatments was not significantly different from sunflower and the bare-soil control, which received the lowest levels of oviposition in the experiment.

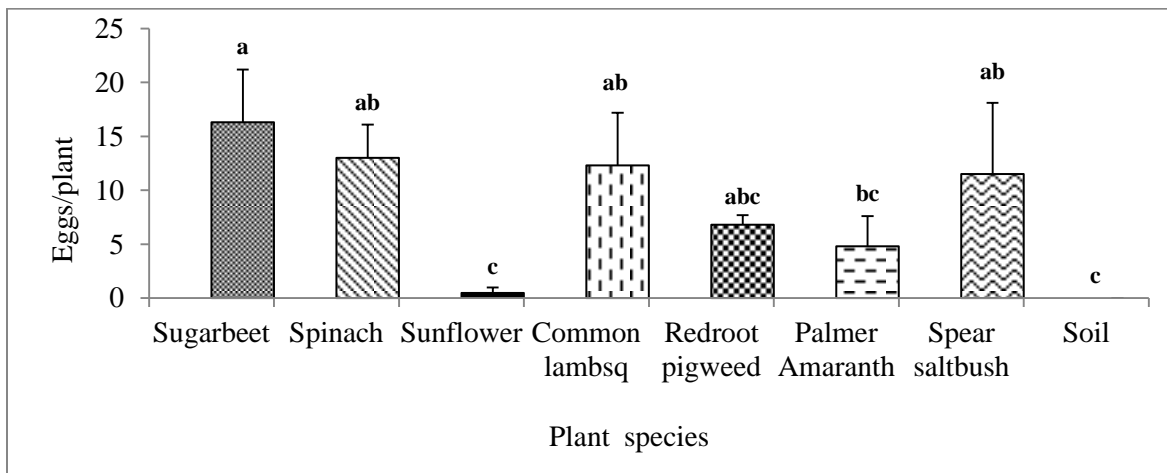


Fig.10. *T. myopaeformis* oviposition preference on different plant species in greenhouse choice test 1.

In the second choice experiment, significantly ($F = 4.29$, $df = 7, 21$, $P = 0.0044$) more sugarbeet root maggot eggs were deposited in Palmer amaranth than in sugarbeet, spinach, redroot pigweed, sunflower, and the bare-soil control (Fig. 11). Relatively high rates of oviposition occurred in spear saltbush and common lambsquarters, and the numbers of eggs

recovered in these treatments were not significantly different from Palmer amaranth, sugarbeet, spinach, or redroot pigweed. Similar to the results of choice experiment 1, sugarbeet root maggot flies had a very low oviposition preference for sunflower and bare soil habitats.

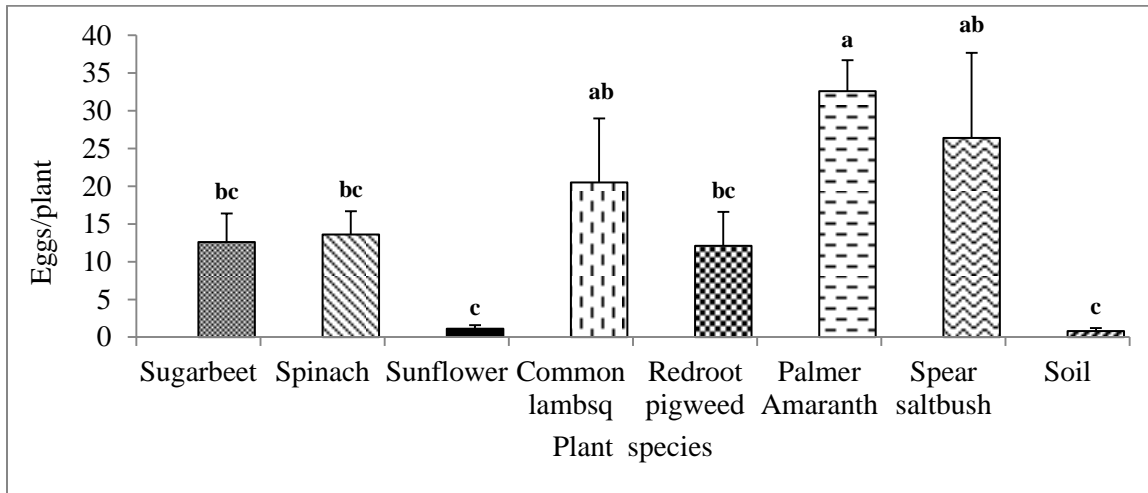


Fig.11. *T. myopaeformis* oviposition preference on different plant species in greenhouse choice test 2.

No-choice Test: Oviposition

A folded *F*-test indicated that the results of no-choice tests 1 and 2 could be combined because there was no test by treatment interaction ($F = 1.78$, $df = 31, 31$; $P = 0.1142$) between the two data sets. The resulting combined analysis indicated that, despite being presented with no-choice monoculture settings for egg deposition, oviposition rates varied significantly ($F = 2.22$, $df = 7, 49$, $P=0.0488$) among plant species. Significantly greater numbers of sugarbeet root maggot eggs were deposited in spinach, sugarbeet, and spear saltbush than in pots containing sunflowers, and these were not statistically different from each other (Fig. 12). Other treatments that were not statistically different from sugarbeet included common lambsquarters, Palmer amaranth, and redroot pigweed. Contrary to the results of the choice oviposition experiment, low

to moderate numbers of sugarbeet root maggot eggs were found in all treatments in the no-choice test, including the bare-soil entry.

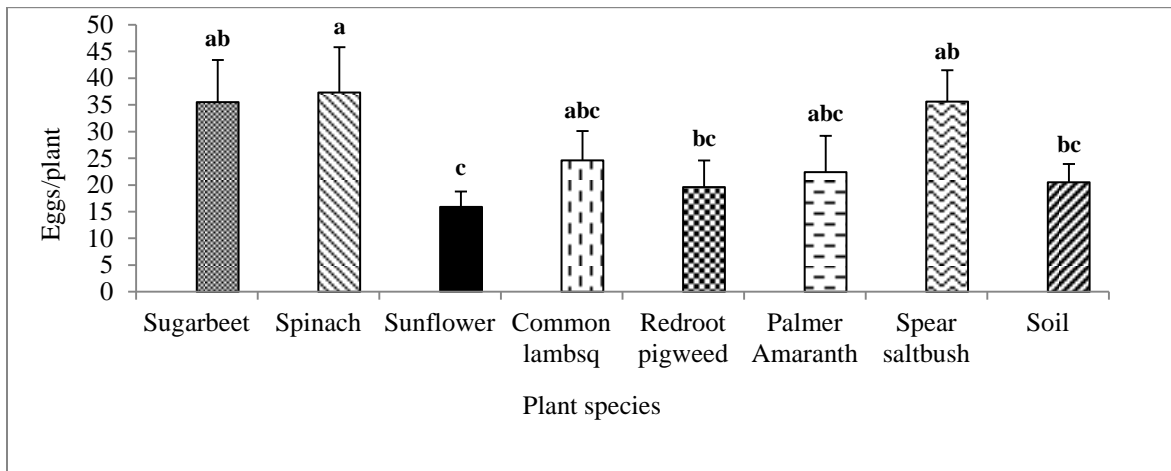


Fig. 12. *T. myopaeformis* oviposition on different plant species in greenhouse no-choice test.

Larval Test

No-choice larval survival tests indicated that there were significant ($F = 11.08$, $df = 6, 30$, $P < 0.0001$) differences among the plant species. Significantly greater numbers of live sugarbeet root maggot larvae were recovered from sugarbeet and spear saltbush than any other plant species tested (Fig. 13). Low levels of survival were also observed in spinach, common lambsquarters, redroot pigweed, and Palmer amaranth; however, survival rates on these plants were not statistically different from sunflower, which was unsuitable as a host to sugarbeet root maggot larvae.

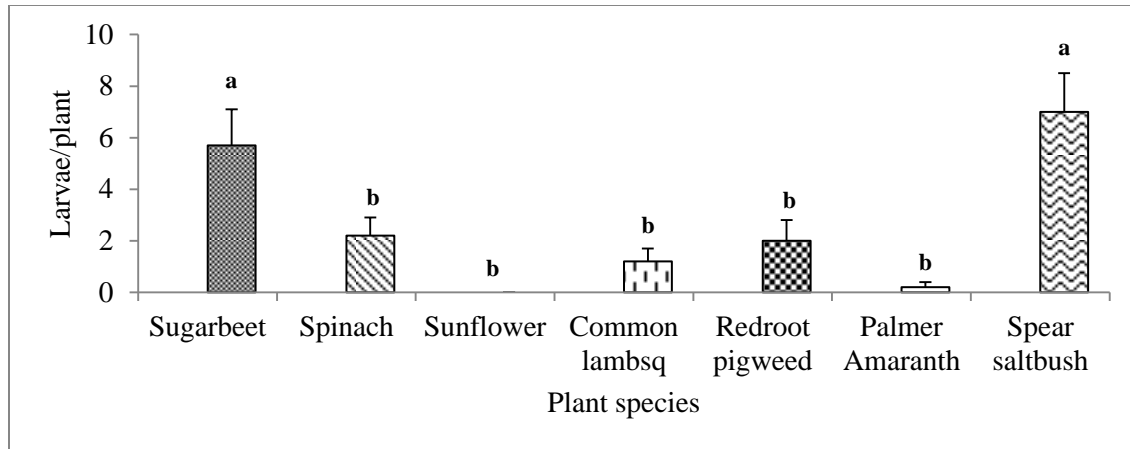


Fig.13. *T. myopaeformis* larval survival on different plant species in greenhouse no-choice test 1.

In the second no-choice test, there were significant differences among the plant species in relative suitability to support larval development ($F = 9.22$, $df = 6, 30$, $P < 0.0001$). Larval survival responses were similar to those in no-choice larval test 1. For example, the highest larval survival to the third instar occurred on spear saltbush, spinach, and sugarbeet. Survival on common lambsquarters and redroot pigweed was significantly lower than that on sugarbeet, spinach, and spear saltbush, and no surviving larvae were recovered from Palmer amaranth or sunflower (Fig. 14).

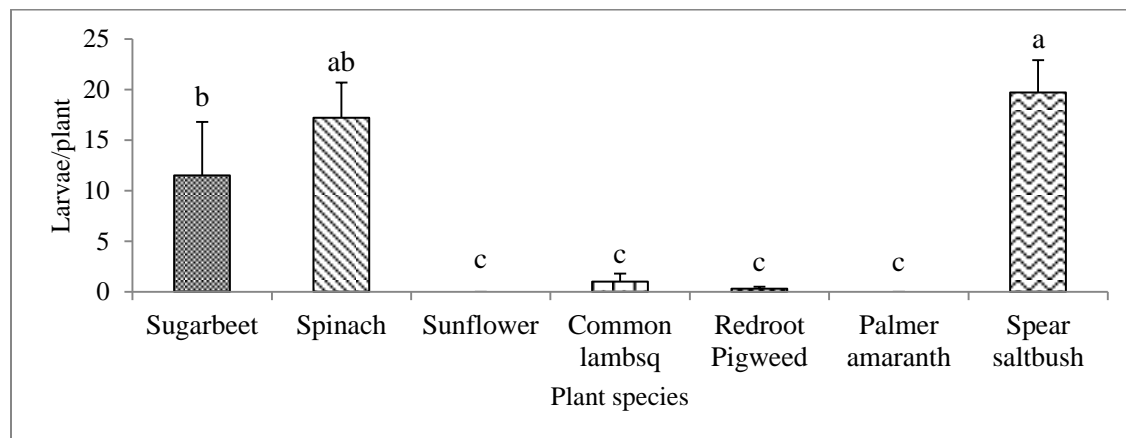


Fig.14. *T. myopaeformis* larval survival on different plant species in greenhouse no-choice test 2.

DISCUSSION

Results from the oviposition tests indicated that female sugarbeet root maggot flies behaved differently in the choice and no-choice tests. In the choice test, females preferred sugarbeet, spinach, common lambsquarters, spear saltbush, and Palmer amaranth for oviposition, and avoided sunflower and bare soil habitats. This behavior suggests that females were able to discriminate host plants from non-hosts. However, in the no-choice test, eggs were deposited in all treatments including sunflower and bare soil, which were avoided in the choice test. This apparent willingness by females to oviposit at the bases of otherwise non-preferred hosts and bare soil could be related to the rather short lifespan (i.e., about 8 d of the adult stage) (K.R.M., pers. observation) of the sugarbeet root maggot. This apparent indiscriminant oviposition behavior is not uncommon in other short-lived insects (Rosenheim et al. 2008).

Rosenheim et al. (2008) indicated that oviposition behavior appears to be governed by both egg load and time or host limitation which are balanced against reproductive advantages when an oviparous insect makes reproductive decisions such as host choice. However, oviposition behavior optimality models predict that a host-limited female is less discriminating on where on where to deposit its eggs (Rosenheim et al. 2008). This phenomenon could have been a factor in the apparent sugarbeet root maggot oviposition on plants that were not otherwise accepted by the females in the choice oviposition preference test. Although this occurred under greenhouse conditions in a no-choice scenario, it suggests that female sugarbeet root maggot flies would oviposit at the bases of less-preferred host plants if they were unable to locate more suitable hosts. It further suggests that females of this species will proceed with oviposition rather than retaining and or resorbing eggs if no preferred host habitat is located.

The results of no-choice assays on larvae indicated that survival across all plant species was generally low, especially considering the number of eggs used in each test (i.e., 50 and 100 eggs/plant for tests 1 and 2, respectively). Larval survival on spear saltbush (i.e., larval no-choice tests 1 and 2) and spinach (i.e., test 2) was comparable to that on sugarbeet. The relatively low survival across all treatments, relative to the high egg infestation rates, could have been caused by an inadequate titer of live microbial symbionts in the field-collected soil used in the assays. Jarvi (1978) indicated that the sugarbeet root maggot appear to benefit nutritionally from association with bacteria of the Pseudomonadaceae and Enterobacteriaceae families, especially during early stages of larval development. Regardless of those potential environmental impacts on larvae in the present study, all treatments involved the same soil source and the various plant species evaluated demonstrated clear differences in their relative suitability to support sugarbeet root maggot larval development.

The relatively low larval survival on spinach (no-choice larval test 1) may not be a true indicator of its potential as a larval host because the maggots killed most of the young spinach plants within three weeks after egg infestation. Thus, the undeveloped larvae probably died due to starvation. This contention is supported by the findings of no-choice larval test 2 where spinach plants were not killed within three weeks and larval survival was not significantly different from sugarbeet or spear saltbush. These results corroborate those of Kruger (1986) who also found spinach and two other species of *Atriplex* (i.e., *A. heterosperma* and *A. subspicata*) to be suitable host plants for larvae of this insect. Spinach is a garden plant and is widely distributed (Mahrt and Blickenstaff 1979), whereas spear saltbush is a native North American weed species that is common throughout the western United States (USDA 2012). The fact that the sugarbeet root maggot is able to survive and develop on these plant species at comparable levels to those

observed on the pest's key crop host, sugarbeet, suggests two important points. First, it is plausible that the sugarbeet root maggot could have exploited plants in the genus *Atriplex* or other species within the order Caryophyllales, which includes Chenopodiaceae and Amaranthaceae, before sugarbeet was introduced to the continent. Second, it is further possible that plants in this genus or related genera could be contributing to sugarbeet root maggot infestations in current production systems.

Although sugarbeet root maggot adults readily oviposited in common lambsquarters, redroot pigweed, and Palmer amaranth in choice and no-choice oviposition tests, these plants were not strongly conducive to sugarbeet root maggot larval survival and development following direct infestation with root maggot eggs. Common lambsquarters belongs to the same family (i.e., Chenopodiaceae) as sugarbeet, spinach, and spear saltbush, while redroot pigweed and Palmer amaranth belong to Amaranthaceae, a family that is considered closely related to the Chenopodiaceae. The fact that the sugarbeet root maggot preferred to oviposit on all of the aforementioned species suggests that plants in those genera may possess physical or phytochemical elements that are similar to sugarbeet. However, low larval survival on these plant species is an indication that they are less sufficient as hosts for this pest. The lack of larval performance on these weed hosts could be explained by the "Novel Superiority model", which predicts that a new host that is not initially preferred by the female but is suitable for offspring development could result in the insect evolving to prefer the new host over its native host (Forister et al. 2009). Such a host-shift scenario could have been the case with the sugarbeet root maggot when sugarbeet was introduced to North America. Common lambsquarters, redroot pigweed, and Palmer amaranth have very wide distributions in North America. Although

sugarbeet root maggot survival on these weed species was found to be low, it should not be assumed that they are not currently being used by this pest as host plants. Thus, infestations of these weed species could still serve as reservoirs for root maggot populations, and could be contributing to localized infestations, albeit, at currently undetermined levels.

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GENERAL CONCLUSIONS

This series of field and greenhouse studies indicated that *T. myopaeformis* larvae are capable of utilizing a wider range of host plants than previously thought. The results of choice assays demonstrated that females prefer to oviposit around plant species in the Chenopodiaceae and Amaranthaceae families. In field experiments, females were discriminatory regarding the plant species they chose for depositing eggs; however, they accepted less-suitable plant species in no-choice oviposition assays in the greenhouse. These results suggest that sugarbeet root maggot flies become less choosy and are willing to oviposit on less-preferred plants if a preferred host plant is not available. Host suitability findings indicated that larval survival was greatest on spinach, sugarbeet, and spear saltbush. However, larval survival was low on common lambsquarters, redroot pigweed, and palmer amaranth, despite these plant species being preferred oviposition microhabitats in both field and greenhouse experiments. The overall results of this investigation suggest that these weed species can be utilized as alternate hosts by root maggot larvae, and that uncontrolled escapes of these weeds could be contributing at undetermined levels to localized maggot infestations. Additionally, the lower rates of larval survival observed on the aforementioned weed species provide insight into the host preference shift to sugarbeet after the crop was introduced and grown in large monocultures in North America.

The ability of an insect to locate and successfully exploit a suitable host plant will have a strong influence on its fitness. This study indicated that weed species such as common lambsquarters and redroot pigweed express similar physical or phytochemical cues to those of sugarbeet that attract *T. myopaeformis* flies, and resultingly stimulate them to lay eggs around such plants. However, it was interesting to note that larval survival on these weed species was very low, thus suggesting that they possess other characteristics that prevent or impair larval

development. Future research, aimed at identifying and incorporating such traits into sugarbeet germplasm, could lead to the development of varieties that are resistant or less attractive to this pest. In addition, further research is needed to determine the mechanism of host plant finding by the sugarbeet root maggot. This information could be pivotal in designing alternative root maggot management strategies such as attract-and-kill tactics or the use of less-attractive varieties.

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