Seasonal development and natural enemies of an invasive exotic species, the swede midge *Contarinia nasturtii* (Kieffer), in Quebec

by

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Abstract

In Quebec, the swede midge (*Contarinia nasturtii*), a newly invasive pest, was found for the first time in 2003. During a two year study (2004-2005) I studied the seasonal development of the swede midge, the presence of natural enemies and tested entomopathogenic nematodes for its control. Results showed that the overwintering generation of the swede midge emerged during the second half of June. Based on adult captures and abundance of larvae in the field, there were three to four overlapping generations. Late transplants were more heavily attacked by the swede midge and broccoli and cauliflower were the most susceptible crops. No parasitoids were found in the experimental sites during either year of the study and two polyphagous coccinellid predators (*Harmonia axyridis* and *Coccinella septempunctata*) were field-collected for further evaluation under laboratory conditions. Although these two coccinellid species fed on swede midge larvae in plastic containers, further experiments demonstrated that *H. axyridis* was not able to prey on swede midge larvae on infested broccoli plants. The susceptibility of swede midge larvae to three species of entomopathogenic nematodes (*Steinernema feltiae*, *S. carpocapsae*, and *Heterorhabditis bacteriophora*) was also evaluated in laboratory assays. *Heterorhabditis bacteriophora* was the only species that caused significant mortality to swede midge larvae and, at a concentration of 1000 IJs/larva, caused 90-100% mortality in loam, sandy loam, clay and muck soil. This is the first study describing the seasonal development of the swede midge in Quebec. In addition, the potential use of entomopathogenic nematodes as biological control agents against the swede midge is demonstrated.

Résumé

Au Québec, un nouvel insecte ravageur, la cécidomyie du chou-fleur (*Contarinia nasturtii*), a été trouvé pour la première fois en 2003. Pendant 2 ans (2004-2005), j'ai étudié le développement saisonnier de cet insecte, évalué la présence d'ennemis naturels ainsi que testé des nématodes entomopathogènes pour des fins de contrôle biologique. Les résultats ont démontré que la population hivernante de la cécidomyie du chou-fleur émerge pendant la deuxième moitié du mois de juin. Selon les captures d'adultes et l'abondance des larves dans les sites expérimentaux, la cécidomyie effectue troi à quatre générations qui se surimposent par année. Les transplantations tardives ont été plus sévèrement attaquées par la cécidomyie et le brocoli ainsi que le chou-fleur sont les cultures qui ont été les plus susceptibles. Pendant les deux années de l'étude, aucun parasitoide n'a été trouvé dans les deux sites expérimentaux et deux prédateurs polyphages (les coccinelles *Harmonia axyridis* et *Coccinella septempunctata*) furent récoltés dans le champ pour être évalués en conditions de laboratoire. Bien que ces deux espèces de coccinelles se nourrissent des larves de la cécidomyie dans un milieu artificiel, dans des conditions plus naturelles (plants de brocoli infestés avec la cécidomyie), *H. axyridis* ne s'est pas attaquée aux larves de la cécidomyie. Lors d'essais en laboratoire, trois espèces de nématodes entomopathogènes (*Steinernema feltiae*, *S. carpocapsae*, et *Heterorhabditis bacteriophora*) ont été testées contre les larves de la cécidomyie dans le sol. *Heterorhabditis bacteriophora* a été la seule espèce causant une mortalité significative aux larves de la cécidomyie du chou-fleur, et à une concentration de 1000 IJs/larve, cette espèce de nématode a causée 90-100% de mortalité dans quatre types de sol: sable loameux, sol organique, loam sableux et argile. Il s'agit de la première étude décrivant le développement saisonnier de la cécidomyie du chou-fleur au Québec. De plus, le potentiel d'utilisation de nématodes entomopathogènes, comme agent de contrôle biologique contre la cécidomyie du chou-fleur, a été démontré.

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Contribution of Authors

Both manuscripts are co-authored by Dr. Guy Boivin who participated in the design and analysis of both studies. Dr. Guy Bélair provided his expertise in the experimental design and implementation of the experiments with entomopathogenic nematodes in Chapter 3. I participated in the experimental design of both studies, conducted all field and laboratory experiments, analyzed and interpreted the data, and wrote all the manuscripts. Dr. Guy Boivin and Dr. Guy Bélair revised, corrected and edited the manuscripts prior to submission to the journals Environmental Entomology (Chapter 2) and Biological Control (Chapter 3).

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Introduction

Biological invasions are the uncontrolled spread and proliferation of species including vertebrates, plants, arthropods, and pathogens from their native geographic ranges to new ranges (Mack et al. 2002). Paradoxically, while government agencies and society worry about the extinction of animal and plant species, agriculturalists are concerned about additions to the fauna and flora of their agroecosystems (Sailer 1983). The dispersal of organisms via human activity began when organized nomadic groups dispersed around the world (di Castri 1989). In North America, this dispersal accelerated when, with the arrival of Europeans, agriculture and commerce flourished, expanded, accelerating the arrival and spread of non-indigenous organisms (Sailer 1983, Mack et al. 2002).

The survival and growth of exotic organisms in their new environment are mostly regulated by three factors: 1) climatic and other abiotic factors, including temperature, humidity, precipitation; 2) biotic factors, including the presence of natural enemies competing organisms, and resources; and 3) the genetic plasticity of the exotic organism to adapt to the new set of physical and biological parameters (Scorza 1983).

One of the reasons why exotic species succeed in their new habitat is that they left behind the natural enemies present in their native region (Clay 2003); and these exotic species are unlikely to encounter natural enemies in the new habitat (Wolfe 2002) because these native natural enemies face host-specific limitations in adapting to new exotic species (Torchin et al. 2003). One of the first steps in integrated pest management or biological control programs is to survey and assess the presence of native natural enemies in the new region of invasion (DeBach and Bartlett 1964, Toepfer and Kuhlmann 2004). This assessment may lead to decisions on introductions of exotic natural enemies and also determine if introduced natural enemies will negatively affect native natural enemies (Wallace and Hain 2000).

However, the primary line of defense against exotic pests is to prevent their entry into a new region, and this is usually regulated by government agencies that monitor imported goods (Mack et al. 2002). The probability of exotic pests and diseases invading new ecosystems has increased rapidly in the last century as a result of globalization, agricultural trade, and other international connections (Sumner 2003).

In the horticultural industry, cole crops (*Brassica oleracea* L) are considered an important group of plants from the Brassicaceae family, a family among the 10 most economically important plant families in Canada (Warwick et al. 2003). Cole crops in Canada are attacked by a wide range of native and exotic insects (Finch and Thompson 1992, Howard et al. 1994, Capinera 2001).

Recently, Canadian producers of cole crops faced with a new problem, the introduction of an exotic invasive species, the swede midge *Contarinia nasturtii* Kieffer (Diptera: Cecidomyiidae). In the mid 90's, growers from Ontario noticed damage to their crops; this damage was first attributed to a bore deficiency and it was only in 2000, after scientists from University of Guelph conducted a survey on cole crop plantations in Ontario, that the presence of *C. nasturtii* was officially confirmed in Canada (Hallett and Heal 2001). Following the publication of the survey, the Canadian Food Inspection Agency (CFIA) implemented a Pest Risk Assessment (PRA) program and by 2002 the swede midge was declared a quarantine pest in Canada. Control measures were soon implemented and the following directive was established: "D-02-06: Interim phytosanitary requirements to prevent the entry and spread of swede midge (C*ontarinia nasturtii*)". This directive aimed to survey other parts of Canada, quarantine infested areas, restrict the movement of *Brassica* spp. plants out of the quarantine areas, and establish a swede midge certification program for growers (CFIA 2002). In 2003, the CFIA surveyed 94 vegetable farms in Quebec, and the swede midge was identified for the first time in Quebec in a vegetable farm in Laval (CFIA 2003). In 2006, according to the latest survey by the CFIA, the swede midge has spread to several counties in Ontario (22) and several MRC (Municipalité régionale de comté) in Quebec (26) (CFIA 2006).

The biology of the swede midge is known in Eurasia, its native region, but its seasonal development in Canada remains unknown. The larvae cause damage to the plants by actively feeding on the growing points and leaf stalks, causing malformations. In Canada the swede midge has damaged up to 80% of cole crops (Hallett and Heal 2001). In Eurasia, swede midge populations are strongly influenced by abiotic (weather conditions) and biotic factors (parasitoids) (Barnes 1946, Readshaw 1966). The host range of the swede midge includes not only cole crops but the entire Brassicaceae family (Barnes 1946, Stokes 1953). In Canada, with more than 200 plant species of the Brassicaceae family across the country (Warwick et al. 2003), the spread of this new invasive species is imminent.

When an exotic invasive insect is identified in a new region, it is crucial to understand its biology in the new environment and assess the presence of natural enemies in the new region. A good understanding of the biology of an invasive species plays an important role to develop efficient pest management programs. This research is the first to study this new invasive pest in Quebec.

Objectives:

1) Describe the seasonal development of the swede midge under the agro-climatic conditions of Quebec.

a) Monitor overwintering emergence of swede midge populations.
b) Evaluate the seasonal occurrence of adults and larvae, the number of generations and the flight period.
c) Evaluate the damage and susceptibility of different cole crops to the swede midge.

2) Survey and identify natural enemies of the swede midge in Quebec and test entomopathogenic nematodes against the swede midge.

Chapter 1. Literature Review

Cole crops

Origin and worldwide distribution

The Cruciferae includes 380 genera and 3,000 plant species. Native to Europe, the edible plants that belong to *Brassica oleracea* L are grouped together as brassica or cole crops (Nieuwhof 1969, Datta 1988, Coaker 1992, Decoteau 2000). Cole crops have been consumed by humans since the beginning of history with early reports from Europe (Allen 1904). Molecular genetic studies provide evidence that the species, from which modern cole crops originated, came from a single ancient progenitor that was similar to the wild *B. oleracea* found in the United Kingdom and European Atlantic coastline (Song et al. 1990). From there, these crops spread along the coasts of the Mediterranean and different forms evolved through selection and adaptation to various climates (Hodgkin 1995). Today, cole crops are cultivated from the northern hemisphere to the subtropics and at high altitudes in the tropics (FAO Statistical Databases 2005).

In this literature review, I will focus on the edible varieties of *B. oleracea* known as cole crops. These crops are known to have close taxonomic relationship, and similar cultural requirements and susceptibility to the same insect-diseases complex (Nieuwhof 1969, Yamaguchi 1983, Flint 1985, Peirce 1987). Finally, according to the International Code of Botanical Nomenclature Art. 18.5 (St Louis Code), both names Cruciferae and Brassicaceae are regarded as valid published names of the same family (Greuter 2000) and I will retain the name of the families as originally cited by the authors.

Cole crops in Canada

In Canada there are 223 plant species that belong to the Brassicaceae family (Warwick et al. 2003); the most important varieties of cole crops are: broccoli (*Brassica oleracea* var. *italica*), cauliflower (*B. oleracea* var. *botrytis*), brussels sprouts (*B. oleracea* var. *gemmifera*), and cabbage (*B. oleracea* var. *capitata*). In 2005, 11,282 hectares of cole crops were sown in Canada, with a farm gate value of CAN$ 94,100,000; in Quebec, 4,783 hectares of cole crops were sown generating a farm gate value of CAN$ 45,280,000 (Statistics Canada 2006).

Insect pests of cole crops

Insect pests of cole crops are widely distributed throughout the world and many of these pests are as cosmopolitan as the Brassicaceae family (Lamb 1989). In temperate regions, cole crops can be attacked by 50-60 insect species, of which about 20 are major pests, damaging all growth stages of the crop and all parts of the plants (Finch and Thompson 1992). According to Bonnemaison (1965), the most important insect species that attack these crops are in the orders Lepidoptera, Hemiptera, Hymenoptera, Coleoptera, and Diptera.

Non-dipteran insects

An important group of insects that attack cole crops worldwide are the Lepidoptera, including moths and butterflies (Capinera 2001). Among these are the large cabbage white butterfly (*Pieris brassicae* L.), small cabbage white butterfly or imported cabbage worm (*Pieris rapae* L.), cabbage looper (*Trichoplusia ni* Hübner); cabbage moth (*Mamestra brassicae* L.), diamond-back moth (*Plutella xylostella* L.), and the garden pebble moth (*Evergestis forficalis* L.) (Bonnemaison 1965, Jones and Jones 1984, Finch and Thompson 1992). Among these Lepidoptera, the diamondback moth is considered the most widespread species and also one of the most destructive for vegetable brassica crops (Finch and Thompson 1992, Talekar and Shelton 1993). With the exception of the garden pebble moth, all of the previously described species have been identified in Canada, (Howard et al. 1994).

Another important group of insects are the aphids (Hemiptera: Aphididae). Globally, there are six aphid species attacking cole crops (Blackman and Eastop 2000). The cabbage aphid (*Brevicoryne brassicae* L.), green peach aphid (*Myzus persicae*

Sulzer), turnip aphid (*Lipaphis erysimi* Kaltenbach), and turnip root aphid (*Pemphigus populitransversus* Riley) have been identified in Canada (Howard et al. 1994). Other sucking insects include stink bugs (*Murgantia histrionica* Hahn), whiteflies (*Aleyrodes proletella* L.) and the generalist onion thrips (*Thrips tabaci* Lindeman) which cause a disruption in the hormonal balance of plants promoting the leaves to curl and twist (Capinera 2001). The turnip sawfly larvae *Athalia rosae* L. (Hymenoptera: Tenthredinidae), a regular and sporadically serious pest in Europe, target the leaves, often leaving the midrib intact (Hill 1987).

Some species of Coleoptera also cause extensive damage to cole crops (Bonnemaison 1965). Overwintering adults of several species of flea beetles (*Psylliodes punctulata* Melsheimer, *Phyllotreta* spp.) have been reported attacking seedlings and leaving holes on the leaves of cole crops in Canada (Howard et al. 1994). Adults feed on cotyledons and young leaves making shot-hole damage, and some adults can transmit mosaic viruses (Hill 1987).

Dipteran pests

Harmful insect species of the order Diptera may be found in nearly all economically important groups of agricultural plants, including cole crops. According to Darvas et al. (2000), Diptera species recorded in the Palaearctic regions attacking cole crops are grouped in the following families and species: Agromyzidae: the faba bean leaf miner (*Liriomyza crucifericola* Hering), serpentine leaf-miner (*L. brassicae* Riley) and cabbage leaf-miner (*Phytomyza rufipes* Meigen); Anthomyiidae: radish fly (*Delia floralis* Fallen) and cabbage root fly or cabbage maggot (*D. radicum* L.); and Cecidomyiidae: brassica pod midge (*Dasineura brassicae* Winnertz), and the swede midge (*Contarinia nasturtii* Kieffer).

Members of the family Agromyzidae are small flies that make long winding tunnels (mines) in the leaf lamina of cole crops and they are considered minor pests in temperate regions (Hill 1987).

In the Anthomyiidae, *D. radicum* is considered a very serious pest of cole crops (Darvas et al. 2000). *Delia radicum* was first observed on the north-eastern coast of North America in the 19th century, and eventually spread westward to occupy available ecological niches (Biron et al. 2000). Females of *D. radicum* lay their eggs on the soil surface in cracks close to the stems of the plants. Soon after, larvae eat the lateral roots and the plants attacked wilt, the leaves turn bluish and the plants remain stunted and usually die (Hill 1987). *Delia floralis*, is widely distributed in Europe, Canada, USA, China and Japon and is restricted largely to the temperate zone of the Holarctic region (35-60° N) (Hill 1987, Finch 1989, Darvas et al. 2000). With a similar biology as *D. radicum*, adult females of *D. floralis* lay their eggs in large batches in the soil (100 eggs) close to the host plants. Soon after, the larvae hatch and feed in the roots (Hill 1987).

In the Cecidomyiidae, the brassica pod midge (*Dasineura brassicae*) an oligophagous species, attacks mostly *Brassica napus*, but is also found on *B. oleracea* and other species of *Brassica* (Darvas et al. 2000). The adults oviposit in the developing seed pods of the crop, and larval feeding results in swollen pods and seed loss (Ahman 1985). It has been observed that *D. brassicae* can use the damage caused by other phytophagous insects like the cabbage seed weevil (*Ceutorhynchus assimilis* Paykull) and Lygus bug (*Lygus rugulipennis* Poppius) for pod access (Hughes and Evans 2003). Finally, the swede midge (*Contarinia nasturtii*) has been described as a pest in its region of origin in Eurasia (Hill 1987, Darvas et al. 2000), and more recently, it has been of major concern in Canada and the USA where it was recently identified (Hallett and Heal 2001, Kikkert et al. 2006).

The swede midge (*Contarinia nasturtii* Kieffer)

Origin and distribution

The swede midge (*Contarinia nasturtii*) is part of a large group (Diptera: Cecidomyiidae: 5,451 species and 598 genera) of gall midges (Gagné 2004). The origin of this pest is Eurasia, where it was first described more than a century ago (Kieffer 1888, Darvas et al. 2000). Kieffer (1888) described adults, the larvae and the damage on swollen flowers of marsh watercress (*Nasturtium palustre* DC). Soon after, numerous reports described the damage, symptoms and biology of the swede midge in Europe (Taylor 1912, Dry 1915, Balachowsky and Mesnil 1936, Mesnil 1938, Barnes 1946). Currently, the swede midge is widespread in Europe and is also found in western Asia in Turkey (CFIA 2006).

In North America, in 1996, symptoms similar to those caused by the swede midge were found on broccoli plants in Ontario, Canada; but these symptoms were mistakenly attributed to nutrient deficiencies (Hallett and Heal 2001). In 2000, the first specimen of *C. nasturtii* was positively identified in Canada after a large survey on broccoli plantations in Ontario (Hallett and Heal 2001). Subsequently, in 2003, the swede midge was found in the province of Quebec in the MRC (Municipalité régionale de comté) of Laval, and in the summer of 2004 the swede midge was found in New York State in the United States (CFIA 2003, Kikkert et al. 2006). In 2005, the Canadian Food Inspection Agency found the swede midge in 20 counties in Ontario, and in 20 MRC of Quebec, whereas in the United States, in addition to the state of New York, the swede midge was found in Massachusetts (CFIA 2006). In Canada, based on a bioclimatic model developed by Olfert et al. (2006), there is a great concern that the swede midge could potentially establish in all provinces, with the risk being greatest in southwestern British Columbia, southern Ontario and Quebec, New Brunswick, Nova Scotia, and Prince Edward Island.

Host plant range

In general, phytophagous insects are relatively specific and feed on a single plant family or subfamily (Bernays and Graham 1988). Although there are some polyphagous species in the Cecidomyiidae family, the species with a host range extending beyond one plant family are relatively rare (Yukawa and Rohfritsch 2005). Since the first report of the swede midge more than a century ago, all plants that have been described as host-plants are members of the Brassicaceae family. These include many important crops such as broccoli, cabbage, cauliflower, swedes, turnips, rape, cow cabbage, brussels sprouts kale, savoy, radish and canola; also, several species of weeds from the Brassicaceae family (Taylor 1912, Barnes 1946, Stokes 1953,Vincinaux and Biernaux 1973, Hallett and Callow 2004).

Damage and symptoms

Plant damage caused by phytophagous Cecidomyiidae is recognizable by the formation of galls on various parts of their host plants (Gagné 1989, Skuhravá 1997). The swede midge forms simple galls that distort the vegetative tissue that is affected. The typical symptoms of swede midge attack are when the stalks of the affected leaves become swollen and bend sharply inwards across the top of the plant (Taylor 1912). Barnes (1946) described that flowers became swollen, remained closed, and the heart leaves became crinkled and crumpled (crumpled-leaf and curly leaf disease). In addition, the feeding scars made by the larvae are prone to secondary bacterial soft rots resulting in unmarketable products. When the growing point of the plant is destroyed, secondary shots are enhanced which leads to the typical symptom known as "many neck" and "cabbage top" (Rogerson 1963). Baur and Rauscher (2003) found that when broccoli plants with 4 to 8 true leaves were attacked, no harvest occurred at all. Rygg and Braekke (1980) found that swede midge infestations caused a weight reduction in swedes and this was higher in late transplants. Bardner et al. (1971) found that early sown plants of swedes gave more tolerant plants and yielded more than late sown plants. Hallett and Callow (2004), when evaluating the host preference of the swede midge in cole crops and asian crucifers, found that the broccoli cultivar "Paragon", and the asian crucifers gai lan (*Brassica oleracea* L. var. *alboglabra*) and tsoi sim (*B. campestris* L. var. *parachinensis*) were more susceptible; whereas the broccoli (*B. oleracea* var. *italica*) cultivars "Everest", "Thriathlon", "Regal", and the asian crucifers tah tsai (*Brassica rapa* L. var. *rosularis*) and giant red mustard (*Brassica juncea* (L.) Czern) were the least susceptible to the attack of the swede midge.

Morphology

Eggs

Eggs measure 0.27 mm x 0.08 mm and have a pedicel measuring 0.06 mm (Barnes 1946). The eggs are transparent at oviposition, becoming creamy white just prior to hatching (Callow and Fraser 2003). They are laid in batches of 2 to 50, and arranged symmetrically when they are laid in small batches; whereas in large batches the eggs are closely packed in several layers (Readshaw 1966).

Larvae

Larvae of the Cecidomyiidae have three instars and are legless, flat-cylindrical, and tapered at both ends (Gagné 1989). The larval body comprises a head, three thoracic and nine abdominal segments. The head capsule is formed by a completely developed head capsule and a mouth apparatus, which consists of a labrum, labium, mandibles and maxillae (Mamaev and Krivosheina 1993). First instar larvae are colourless, have no spatula sternalis but do have a specialized respiratory system (Skuhravá 1997). Third instar larvae of *C. nasturtii* are 2 mm long, yellow in colour, have a spatula sternalis, and the terminal abdominal segment bears 4 pairs of unequal papillae (Darvas et al. 2000); they also have two salivary glands that produce secretions that dissolve the waxy cuticle and liquefy the underlying cells of the surrounding leaf surface of the plant where they feed (Readshaw 1966).

Pupae

The pupa is of the mummiform type, in which all the basic morphological structures of the future adult are to be found (Skuhravá 1997). Pupation takes place in oval or spherical cocoons previously made by the larvae in the soil (Readshaw 1966). *Contarinia nasturtii* pupae measure from 2 to 4 mm (Callow and Fraser 2003). As other gall midges, *C. nasturtii* pupae have a large, elongate prothoracic spiracle and short abdominal spiracles, and the antennal bases are the anteriormost parts of the pupa and they are usually strongly sclerotized to help escape from the soil (Gagné 1989).

Adults

As many members of the Cecidomyiidae family, swede midge adults are delicate small flies up to 2 mm long (Gagné 1989, Skuhravá 1997). Adults have reduced wing venation, with absence of cross veins. They have a radial vein straight or nearly so and a curbital fork in middle third of the wing. Mouthparts are haustellate, usually with a four-segmented palpus (Ellis 2005). Adults have long, filiform antennae, with 2 basal segments and 12 flagellomeres. Female antennal segments are cylindrical, and the male antenna is divided into two separate nodes surrounded by a threadlike looped sensillum (Ellis 2005). The swede midge has long legs, where the first tarsal segment is much smaller than the following segments, the abdomen has 8 segments, and the wing surface is covered with microtrichia (Skuhravá 1997).

Life history

The life history of the swede midge has been extensively described in Europe by several authors (Dry 1915, Barnes 1946, Readshaw 1966). Adults first appear in the spring emerging from the soil, take flight as soon as their wings are dry and they usually live up to 3 days. Males mate exclusively with virgin females, and once copulation has occurred, females remain inactive for up to two hours (Readshaw 1966). Soon after, oviposition takes place in adjacent plants and, according to Dry (1915), one female can oviposit enough eggs to cause the characteristic crumpled leaf symptoms. Each female can lay up to 95 eggs and the larvae hatch about 3 days after oviposition (Readshaw 1966). Larvae feed gregariously, destroying the surface of the host tissues; the feeding period varies from 7 to 21 days at temperatures ranging from 25 to 15 °C. Full grown larvae leave the plant by dropping to the ground where they burrow themselves in the upper 5 cm layer of the soil (Barnes 1946). In the soil, the larvae construct oval-shaped cocoons for pupation or spherical-shaped cocoons for dormancy. Dormancy may be due to the quiescence of the larvae due to the lack of water in the soil or diapause due to day-length and low temperatures (Readshaw 1966). Pupation can take from 6 to 21 days depending on the local and seasonal conditions, and adults emerge from the cocoons to go to the surface (Barnes 1946).

Population dynamics

The population of the swede midge can be variable in time and location. According to Barnes (1946), this species has several overlapping generations annually. In England, Taylor (1912) observed four generations: June, July, August and September. Olombel (1931) observed in northeast France that the first overwintering population of swede midge emerged on the first ten days of June with a maximum peak of emergence between 16-21 June; consecutive generations followed on 6-8 July and on 9-11 August. Mesnil (1938) observed that the first adults appeared on 15 May, and three generations were recorded during summer in the region of Saint-Omer, France. Rygg and Braekke (1980), in a three year study in Norway, observed that the earliest day of emergence was on 25 May in the first year of the study, but in consecutive years, most midges emerged after 10 June and the emergence continued throughout June, July and with a few individuals in August. In the Netherlands, the first adults were also observed from the end of May to the beginning of June and the population increased rapidly, 100 midges in the first generation gave rise to 80,000 adults in the third generation (Bouma 1996). The swede midge is typically trivoltine, but depending on local weather conditions, a fourth and a fifth generation are also possible as observed in Germany by Roesler (1937). In Ontario, Canada, Goodfellow (2005) observed that the swede midge may have 3 to 5 overlapping generations.

Natural enemies

Predators

There is little information on predators specific to the swede midge but some information is available on predators of gall midges (Cecidomyiidae) closely related to the swede midge. Predators of gall midges include vertebrates and arthropods (Gagné 1989). Birds can be important predators; for example, if a bird finds an internode full of larvae by pecking with its bill, it usually removes all larvae from that internode (Skuhravá and Skuhravý 1992). When mature gall midge larvae of *Dasineura oxycoccana* Johnson (Diptera: Cecidomyiidae) drop to the ground to pupate, they are preyed upon by red imported fire ants (*Solenopsis invicta* Buren) (Sampson et al. 2001). Three species of ants were found ripping apart the galls where the larvae of the gall maker *Eugeniamyia dispar* Maia (Diptera: Cecidomyiidae) reproduced (Mendonça and Romanowski 2002). Carabid predators (*Agonum*, *Amara*, *Bembidion* and *Pterostichus*) have been identified as having fed on wheat midge larvae *Sitodiplosis mosellana* Gehin (Diptera: Cecidomyiidae) in the field and on the soil, when the midge larvae ended their diapause during June and when they moved from the plant to the soil to pupate on August (Floate et al. 1990). Gall midges of *Contarinia* are also the target of various predators; for example, *Lestodiplosis pisi* Barnes (Diptera: Cecidomyiidae) consumes the larvae of the pea midge (*C. pisi* Winnertz); *C. tritici* Kirby is preyed upon by *Empis livida* L. (Diptera: Empididae) and by three species of *Platypalpus* (Diptera: Hybotidae) (Darvas et al. 2000). Dry (1915) mentioned the presence of an Empididae fly (unknown species) and small spiders (unknown species) feeding on swede midge flies *Contarinia nasturtii*. In Ontario, Canada, Goodfellow (2005) found *Medetera* sp. (Diptera: Dolichopodidae) preying on swede midge adults in broccoli-infested fields.

Parasitoids

Parasitoids attacking gall midges have been previously identified and studied at a population level (Brewer and Johnson 1977, Weis 1982, Hawkins 1988, Hawkins and

Gagné 1989). Gall formers from the Cecidomyiidae family are attacked by several species of parasitoids from different families, particularly from the order Hymenoptera; such families include Platygasteridae, Pteromalidae, Torymidae, Ceraphronidae, Encyrtidae, Eupelmidae, Eulophidae, Braconidae, Ichneumonidae and Eurytomidae (Gagné 1989, Yukawa and Rohfritsch 2005). Platygastrids, eupelmids and eurytomids are usually monophagous endoparasitoids attacking eggs and early instars of gall midge larvae, whereas torymids and braconids attack late instars and pupae of gall midges and they are usually multivoltine, polyphagous ectoparasitoids (Yukawa and Rohfritsch 2005). Some reports of parasitoids of *Contarinia* include a study on *Contarinia coloradensis* Felt, where two species of *Platygaster* (Hymenoptera: Platygasteridae) killed 50% of the population (Brewer and Johnson 1977). *Contarinia pisi* Winnertz is often parasitized by *Pirene chalybea* Haliday, *P. graminea* Haliday (Hymenoptera: Pteromalidae) and *Inostemma boscii* Jurine, *Leptacis tipulae* Kirby and *Sactogaster pisi* Förster (Hymenoptera: Platygasteridae) (Darvas et al. 2000).

There are several reports on parasitoids of the swede midge *Contarinia nasturtii.* Dry (1915) observed the presence of Proctotrupidae (Hymenoptera) (unknown species) parasitizing the larvae. Bovien and Knudsen (1950) observed that swede midge larvae from the second generation were parasitized (unknown rate of parasitism) by *Pirene eximia* Haliday (Hymenoptera: Chalcididae). Rogerson (1963) observed that female parasitoids of *Synopeas* sp. oviposited in swede midge larvae in the field, and Readshaw (1966) described and reared three species of parasitoids from full grown larvae of *C. nasturtii*; the parasitoids were *Platygaster* sp. and two species of *Synopeas* (Hymenoptera: Platygasteridae) all with similar life-cycles. The latter author described that adult females laid single eggs in feeding host larvae, and that eggs hatched only when the host was about to pupate. The parasitoid larvae consumed the host, preventing pupation. The adult parasitoids emerged from their host in the soil and crawled to the surface.

Nematodes

Entomopathogenic nematodes from the families Steinernematidae and Heterorhabditidae occur naturally in the soil and are obligate parasites of insects; the spectrum of nematode activity is well beyond that of any other microbial control agent (Poinar 1990, Kaya and Gaugler 1993, Boemare et al. 1996). The infection process starts when the invasive stage of the nematodes (3^{rd} instar infective juveniles) enters the host by natural openings (mouth, anus or spiracles) in *Steinernema* spp., or with the help of a dorsal tooth in *Heterorhabditis* spp. that breaks the outer cuticle of an insect. Once inside the host, nematodes release a bacteria (*Xenorhabdus* for *Steinernema* spp. and *Photorhabdus* for *Heterorhabditis* spp.), that causes septicaemia killing the insect within 24-48 hours (Poinar 1990, Boemare 2002). Members of the Cecidomyiidae have shown mixed results when entomopathogenic nematodes have been tried upon them. For example, Powell and Webster (2004) evaluated the potential of three species of entomopathogenic nematodes upon *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) when pupating in soil. They found that an application rate of 25 infective juveniles/cm^2 (IJs/cm^2) of *H. bacteriophora* Poinar and *S. carpocapsae* Weiser significantly reduced the emergence of adults *A. aphidimyza* from the soil, and in a separate experiment, cocoons of *A. aphidimyza* were targeted mainly by *H. bacteriophora*. In another study, Richardson (1987) reported that *Heterorhabditis heliothidis* (= *bacteriophora*) Khan, Brooks and Hirschmann was able to eradicate the gall midge *Heteropeza pygmaea* Winnertz (Diptera: Cecidomyiidae) when applied to compost containing larvae of the gall midge at an application rate of 100 000 IJs per beaker. In contrast to these positive results on cecidomyiids, Nielsen and Philipsen (2005) found that the brassica pod midge *Dasyneura brassicae* (Diptera: Cecidomyiidae) during pupation in the soil, was virtually unaffected by the nematodes *Steinernema bicornutum* Tallosi, *S. carpocapsae*, *S. feltiae* Filipjev and *Heterorhabditis bacteriophora* at a concentration of 250 nematodes per larva. The low susceptibility of *D. brassicae* was also observed in a study by Nielsen and Philipsen (2004) where it was rarely infected by entomopathogenic nematodes. There are no records on entomopathogenic nematodes for *Contarinia nasturtii*.

Pathogens

Pathogens may also cause mortality to several species of gall midges including the swede midge. Keller and Wilding (1985) described the presence of the fungal pathogen *Entomophthora brevinucleata* Keller and Wilding infecting three species of gall midges: the wheat blossom midge *Sitodiplisis mosellana* Gehin, *Mycodiplosis* sp. and *Contarinia tritici*. The larvae of two gall midge species, *Dasyneura canadensis* Felt and *D. rachiphaga* Tripp (Diptera: Cecidomyiidae), were very susceptible (100% mortality) to the entomopathogenic fungi *Beauveria bassiana* Balsamo and *Metarhizium anisopliae* Metsch after 48 hr of incubation (Timonin et al. 1980). Also, bioassays with strains of *Beauveria* spp. isolated from the field against the pine needle gall midge larva *Thecodiplosis japonensis* Uchida et Inouye (Diptera: Cecidomyiidae), resulted in 82.9% mortality of the gall midge (JongBok et al. 1995). The only report on pathogens of *Contarinia nasturtii* showed that *Bacillus thuringiensis* subsp. *israeliensis* significantly reduced larval population (52%) on broccoli plants (Wu et al. 2006).

Insect control

Chemical control

Chemical control has probably been the most efficient method to control swede midge infestations. Olombel (1931) observed that cauliflowers were attacked less when they were sown on soil treated with Sylvinite and Para-dichlorobenzene. Bovien and Knudsen (1950) successfully used DDT sprays on cauliflowers and cabbages in Denmark. Thomas (1960), by using Dieldrin, protected savoys from swede midge attack. Wu et al. (2006) tested the efficacy of 20 insecticides belonging to 12 different classes against swede midge larvae and adults on broccoli-infested plants. The results showed that the following rates (g[AI]/ha) of Lambda-cyhalothrin (33.6), Acephate (1,456), Acetamiprid (84), Chlorpyrifos (1,120) and Methomyl (1,008) were the most effective in reducing the larval population by 96.7-100% and, except for Acetamiprid, mortality of adults reached

100%. In Canada, Acetamiprid and Lambda-cyhalothrin are currently registered for use against the swede midge. However, the extensive use of insecticides could develop insect resistance in the swede midge.

Cultural control

Several cultural control methods have been suggested and used for managing swede midge infestations. Readshaw (1968) based on experiments on pupal depth and subsequent emergence of swede midge adults, suggested that by burying the pupae through shallow ploughing before transplanting the susceptible crops in spring, the emergence of the overwintering population of swede midges could be decreased or prevented. Early transplanting of susceptible crops and control of weeds from the Brassicaceae family have been also suggested for managing swede midge infestations (Stokes 1953, Bardner et al. 1971). Rotation of cole crops for host deprivation for the swede midge has been proven to be an effective way to control swede midge populations (Theunissen et al. 1997). Finally, using exclusion fences on infested fields significantly reduced the damage caused by the swede midge on broccoli (77.8 %) and kohlrabi (78.9 %) plantations (Wyss and Daniel 2004).

Biological control

Until now the only attempt to control the swede midge with biological control agents is the recent study by Wu et al. (2006) under laboratory conditions. Foliar applications with the bacteria *Bacillus thuringiensis* subsp. *israeliensis* at a rate of 241.5 (AI/ha) on infested broccoli plants with swede midge larvae, showed significant reduction of the larvae (52 %).

References

Ahman, I. 1985. Oviposition behaviour of *Dasineura brassicae* on a high-versus a low-quality *Brassica* host. Entomol. Exp. Appl. 39: 247-253

Allen, C. L. 1904. Cabbage cauliflower and allied vegetables from seed to harvest. Orange Judd Company, New York. 126pp.

Balachowsky, A. and L. Mesnil. 1936. Les insectes nuisibles aux plantes cultivées, leurs mœurs, leur destruction. Établissements Busson, Paris. pp. 1199-1203

Bardner, H. M., Edwards, C. A., Arnold, M. K. and J. P. Rogerson. 1971. The symptoms of attack by swede midge (*Contarinia nasturtii*) and effects on the yield of swedes. Entomol. Exp. Appl. 14: 223-233

Barnes, H. F. 1946. Gall midges of economic importance. Volume I. Gall midges of root and vegetable crops. Crosby Lockwood and Son Ltd., London. 104pp.

Baur, R. and S. Rauscher. 2003. Cécidomyie du chou: un grand ravageur de petite taille. Der Germüsebau/ Le Maraîcher 4: 8-9

Bernays, E. and M. Graham. 1988. On the evolution of host specificity in phytophagous arthropods. Ecology 69: 886-892

Biron, D. G., Landry, B. S., Nénon, J. P., Coderre, D. and G. Boivin. 2000. Geographical origin of an introduced pest species, *Delia radicum* (Diptera: Anthomyiidae), determined by RAPD analysis and egg micromorphology. Bull. Entomol. Res. 90: 23–32

Blackman, R. L. and V. F. Eastop. 2000. Aphids on the world's crops: an identification and information guide. 2nd ed. John Wiley and Sons, New York. 466pp.

Boemare, N. 2002. Biology, taxonomy and systematics of *Photorhabdus* and *Xenorhabdus*. pp 35-36 *in* Gaugler, R. editor. Entomopathogenic Nematology. CABI Publishing NY, USA.

Boemare, N., Laumond, C. and H. Mauleon. 1996. The entomopathogenic nematode-bacterium complex: biology, life cycle and vertebrate safety. Biocontrol Sci. Technol. 6: 333-345

Bonnemaison, L. 1965. Insect pests of crucifers and their control. Annu. Rev. Entomol. 10: 233-256

Bouma, E. 1996. Contapré, prototype of a model of prediction of emerging of the swede midge (*Contarinia nasturtii*). Sp-report, Danish Institute of Plant and Soil Science. 15: 25-30

Bovien, P. and P. Knudsen. 1950. Krusesygegalmyggen (*Contarinia nasturtii* Kieff.), dens biologi og bekaempelse. Tid. Planteaul. 53: 235-257

Brewer, J. W. and P. R. Johnson. 1977. Biology and parasitoids of *Contarinia coloradensis* Felt a gall midge on ponderosa pine. Marcellia 39: 391-398

Callow, K. and H. Fraser. 2003. The swede midge, a new pest in crucifer crops in Ontario. Ontario Ministry of Agriculture and Food. Fact Sheet, 03-035.

Canadian Food Inspection Agency. 2003. Summary of plant quarantine pest and disease situations in Canada in 2003. http://www.inspection.gc.ca/english/sci/surv/sit2003e.shtml#connas. Accessed 20 August 2006

Canadian Food Inspection Agency. 2006. Lists of regulated countries and regulated areas within Canada for swede midge. http://www.inspection.gc.ca/english/plaveg/protect/dir/smidgee.shtml. Accessed 20 August 2006

Capinera, J. L. 2001. Handbook of vegetable pests. Academic Press, San Diego, Ca. 729pp.

Coaker, T. H. 1992. Classification, origins and production of vegetables. pp 1-27 *in* McKinlay, R. G., editor. Vegetable crop pests. CRC Press, Boca Raton, FL.

Darvas, B., Skuhravá, M. and A. Andersen. 2000. Agricultural dipteran pests of the Palaearctic region. pp 565-650 *in* Papp, L. and B. Darvas, editors. Contributions to a manual of Palaearctic Diptera, (with special reference to flies of economic importance). Vol. 1, General and Applied Dipterology. Science Herald, Budapest.

Datta, S. C. 1988. Systematic Botany. 4th ed. New Age Publishers, New Delhi. 468pp.

Decoteau, D. R. 2000. Vegetable crops. Prentice-Hall, Upper Saddle River, NJ. 464pp.

Dry, F. W. 1915. An attempt to measure the local and seasonal abundance of the swede midge in parts of Yorkshire over the years 1912 to 1914. Ann. Appl. Biol. 2: 81-108

Ellis, S. E. 2005. New Pest Response Guidelines: Swede Midge *Contarinia nasturtii* (Kieffer). USDA/APHIS/PPQ/PDMP, Riverdale, Maryland. http://www.aphis.usda.gov/ppq/manuals. Accessed 10 July 2006

FAO Statistical Database. 2005. Food and Agriculture Organization of the United Nations. http://faostat.fao.org/default.aspx?lang=en. Accessed 20 August 2006

Finch, S. 1989. Ecological considerations in the management of *Delia* pest species in vegetable crops. Annu. Rev. Entomol. 34: 117-37

Finch, S. and A. R. Thompson. 1992. Pests of cruciferous crops. pp 87-138 *in* McKinlay, R. G., editor. Vegetable crop pests. CRC Press, Boca Raton, Fl.

Flint, M. L. 1985. Integrated pest management for cole crops and lettuce. University of California Publication 3307, Oakland, CA. 112pp.

Floate, K. D., Doane, J. F and C. Gillott. 1990. Carabid predators of the wheat midge (Diptera: Cecidomyiidae) in Saskatchewan. Environ. Entomol. 19: 1503-1511

Gagné, R. J. 1989. The plant-feeding gall midges of North America. Cornell University Press, Ithaca, NY. 368pp.

Gagné, R. J. 2004. A catalog of the Cecidomyiidae (Diptera) of the world. Mem. Entomol. Soc. Wash. 25: 5-350

Goodfellow, S. A. 2005. Population dynamics and predictive modeling of the swede midge, *Contarinia nasturtii* Kieffer. M.Sc. Thesis, University of Guelph.

Greuter, W. 2000. International Code of Botanical Nomenclature (Saint Louis Code). Koeltz Scientific books, Germany. 474pp.

Hallett, R. H. and J. D. Heal. 2001. First Nearctic record of the swede midge (Diptera: Cecidomyiidae), a pest of cruciferous crops from Europe. Can. Entomol. 133: 713-715

Hallett, R. H. and K. Callow. 2004. Host preferences of the swede midge: cole crops, asian crucifers and cruciferous weeds. Ontario Fruit and Vegetable Convention and Trade Show, February 18-19, St. Catharines, Ontario.

Hawkins, B. A. 1988. Do galls protect endophytic herbivores from parasitoids? A comparison of galling and nongalling Diptera. Ecol. Entomol. 13: 473-477

Hawkins, B. A. and R. J. Gagné. 1989. Determinants of assemblage size for the parasitoids of Cecidomyiidae (Diptera). Oecologia 81: 75-88

Hill, D. S. 1987. Agricultural insect pests of temperate regions and their control. Cambridge University Press, London. 659pp.

Hodgkin, T. 1995. Cabbages, kales etc. *Brassica oleracea* (Cruciferae). pp 76-82 *in* Smartt, J. and N. W. Simmonds, editors. Evolution of crop plants. Longman, London.

Howard, R. J., Garland, J. A. and W. L. Seaman. 1994. Diseases and pests of vegetable crops in Canada. The Canadian Phytopathological Society and the Entomological Society of Canada. 554pp.

Hughes, J. M. and K. A. Evans. 2003. Lygid bug damage as a pod access mechanism for *Dasineura brassicae* (Dipt., Cecidomyiidae) oviposition. J. Appl. Entomol. 127: 116-118

Jones, F. G. W. and M. G. Jones. 1984. Pest of field crops. 3rd ed. Edward Arnold, London. 392pp.

JongBok, S., ByungRae, J., SangChul, S., HoYong, P., BumYoung, L., ChangKeun, L., and K. SeokKwon. 1995. Isolation of entomopathogenic fungi for infection to the pine gall midges, *Thecodiplosis japonensis* from the forest soil in Korea. Korean J. Appl. Entomol. 34: 368-372

Kaya, H. K. and R. Gaugler. 1993. Entomopathogenic nematodes. Annu. Rev. Entomol. 38: 181-206

Keller, S. and N. Wilding. 1985. *Entomophthora brevinucleata* sp. nov. (Zygomycetes, Entomophthoraceae), a pathogen of gall midges (Dipt.: Cecidomyiidae). Entomophaga. 30: 55-63

Kieffer, J. J. 1888. Beiträge zur Kenntnis der Gallmücken. Ent. Nachr. 14: 262-268

Kikkert, J. R., Hoepting, C. A., Wu, Q., Wang, P., Baur, R. and A. M. Shelton. 2006. Detection of *Contarinia nasturtii* (Diptera: Cecidomyiidae) in New York, a new pest of cruciferous plants in the United States. J. Econ. Entomol. 99: 1310-1315

Lamb, R. J. 1989. Entomology of oilseed *Brassica* crops. Annu. Rev. Entomol. 34: 211-29

Mamaev, B. M. and N. P. Krivosheina. 1993. The larvae of the gall midges (Diptera, Cecidomyiidae) comparative morphology, biology, keys. Balkema Publishers, Rotterdam, Brockfield. 350pp.

Mendonça, M. and H. P. Romanowski. 2002. Natural enemies of the gall-maker *Eugeniamyia dispar* (Diptera, Cecidomyiidae): predatory ants and parasitoids. Braz. J. Biol. 62: 269-275

Mesnil, L. 1938. La cécidomyie du chou-fleur dans la région de Saint-Omer. Ann. Épiphyt. Phyt. 4: 281-311

Nielsen, O. and H. Philipsen. 2004. Recycling of entomopathogenic nematodes in *Delia radicum* and in other insects from cruciferous crops. BioControl 49: 285–294

Nielsen, O. and H. Philipsen. 2005. Susceptibility of *Meligethes* spp. and *Dasyneura brassicae* to entomopathogenic nematodes during pupation in soil. BioControl 50: 623-624

Nieuwhof, M. 1969. Cole crops, botany, cultivation, and utilization. Leonard Hill Books, London. 353pp.

Olfert, O., Hallett, R., Weiss, R. M., Soroka, J. and S. Goodfellow. 2006. Potential distribution and relative abundance of swede midge, *Contarinia nasturtii*, an invasive pest in Canada. Entomol. Exp. Appl. 120: 221-228

Olombel, M. 1931. Note préliminaire sur la Cécidomyie du chou-fleur (*Contarinia torquens* de Meij.) C. R. Acad. Agric. France. 17: 178-182

Peirce, L. C. 1987. Vegetables: characteristics, production and marketing. John Wiley and Sons, New York. 433pp.

Pest Management Regulatory Agency. 2006. EDDENet, ELSE Label search. http://eddenet.pmra-arla.gc.ca/4.0/4.0.asp. Accessed 10 July 2006

Poinar, G. O. 1990. Biology and taxonomy of Steinernematidae and Heterorhabditidae. pp 23-61 *in* Gaugler, R. and H. Kaya, editors. Entomopathogenic nematodes in biological control. CRC Press, Boca Raton, Fl.

Powell, J. R. and J. M. Webster. 2004. Interguild antagonism between biological controls: impact of entomopathogenic nematode application on an aphid predator, *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). Biol. Control 30: 110-118

Readshaw, J. L. 1966. The ecology of the swede midge, *Contarinia nasturtii* (Kieff.) (Diptera, Cecidomyiidae). I. Life-history and influence of temperature and moisture on development. Bull. Entomol. Res. 56: 685-700

Readshaw, J. L. 1968. Damage to swedes by the swede midge, *Contarinia nasturtii* (Kieff.), and a possible method of cultural control. Bull. Entomol. Res. 58: 25-29

Richardson, P. N. 1987. Susceptibility of mushroom pests to the insect-parasitic nematodes *Steinernema feltiae* and *Heterorhabditis heliothidis*. Ann. Appl. Biol. 111: 433-438

Roesler, T. 1937. Drehherzkrankheit und Herzlosigkeit bei Kohl. Kranke Pflanze. 14: 124-129

Rogerson, J. P. 1963. Swede midge on two Northumberland farms, 1959-1961. Plant Pathol. 12: 161-171

Rygg, T. D. and H. P. Braekke. 1980. Swede midge (*Contarinia nasturtii* Kieffer) (Diptera Cecidomyiidae); Investigations on biology, symptoms of attack and effects on yield. Meldinger fra Norges Landbrukshoegskule. 59: 1-9

Sampson, B. J., Stringer, S. J. and M. J. Spiers. 2001. Integrated Pest Management for *Dasineura oxycoccana* (Diptera: Cecidomyiidae) in blueberry. Environ. Entomol. 31: 339–347

Skuhravá, M. 1997. Family Cecidomyiidae. pp 71-204 *in* Papp, L. and B. Darvas, editors. Contribution to a manual of Palaearctic Diptera. Vol. 2, Nematocera and lower Brachycera. Science Herald, Budapest, Hungary.

Skuhravá, M. and V. Skuhravý. 1992. Biology of gall midges on common reed in Czechoslovakia. pp 196-207 *in* Shorthouse, J. D. and O. Rohfritsch, editors. Biology of insect-induced galls. Oxford University Press, New York.

Song, K., Osborn, T. C. and P. H .Williams. 1990. *Brassica* taxonomy based on nuclear restriction fragment length polymorphisms (RFLPs). 3. Genome relationships in *Brassica* and related genera and the origin of *B. oleracea* and *B. rapa* (syn. *Campestris*). Theor. Appl. Genet. 79: 497-506

Statistics Canada. 2006. Fruit and vegetable production. February, 2006. Catalogue no. 22-003-XIB

Stokes, B. M. 1953. Biological investigations into the validity of *Contarinia* species living on the Cruciferae, with special reference to the swede midge, *Contarinia nasturtii* (Kieffer). Ann. Appl. Biol. 40: 726-741

Talekar, N. S. and A. M. Shelton. 1993. Biology, ecology, and management of the diamondback moth. Annu. Rev. Entomol. 38: 275-301

Taylor, T. H. 1912. Cabbage-top in Swedes. Univ. Leeds and York. Counc. Agric. Educ. 82: 1-21

Theunissen, J., Den Ouden, H. and G. Schelling. 1997. Can the cabbage gall midge, *Contarinia nasturtii* (Diptera, Cecidomyiidae) be controlled by host plant deprivation? Med. Fac. Ladbouww. Univ. Gent. 62/2b: 617-622

Thomas, P. R. 1960. Control of swede midge on savoys. Pl. Path. 9: 25-28

Timonin, M. I., Fogal, W. and S. Lopushanski. 1980. Possibility of using white and green muscardine fungi for control of cone and seed insect pests. Can. Entomol. 112: 849-854

Vincinaux, C. and J. Biernaux. 1973. Premières observations biologiques sur la cécidomyie du chou (*Contarinia nasturtii* kief.) déprédatrice des choux de Bruxelles. Mededelingen Fakulteit Landbouwwetenschappen Gent. 38: 1213-1224

Warwick, S. I., Francis, A. and G. A. Mulligan. 2003. Brassicaceae of Canada. Agriculture and Agri-Food Canada, Canadian Biodiversity Facility, Eastern Cereal and Oilseed Research Centre (ECORC). http://www.cbif.gc.ca/spp_pages/brass/index_e.php. Accessed 15 March 2006

Weis, A. E. 1982. Resource utilization patterns in a community of gall-attacking parasitoids. Environ. Entomol. 11: 809-815

Wu, Q., Zhao, J., Taylor, A. and A. M. Shelton. 2006. Evaluation of insecticides and application methods against *Contarinia nasturtii* (Diptera: Cecidomyiidae), a new invasive insect pest in the United States. J. Econ. Entomol. 99: 117-122

Wyss, E. and C. Daniel. 2004. The effect of exclusion fences on the colonization of broccoli and kohlrabi by the swede midge, *Contarinia nasturtii* (Diptera: Cecidomyiidae). Mitteilungen Deutschen Gesellshaft Allgemeine Angewandte Entomol. 14: 387-390.

Yamaguchi, M. 1983. World vegetables: principles, production and nutritive values. AVI Publishing Co. Inc. Wesport, Connecticut. 415pp.

Yukawa, J. and O. Rohfritsch. 2005. Biology and Ecology of gall-inducing Cecidomyiidae (Diptera). pp 273-304 *in* Raman, A., Schaefer, C. and T. Withers, editors. Biology, Ecology, and Evolution of gall-inducing arthropods. Science Publishers, Inc. Enfield, NH, USA.

Chapter 2, submitted to Environmental Entomology

Seasonal development of an invasive exotic species, the swede midge *Contarinia nasturtii* (Diptera: Cecidomyiidae), in Quebec

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Abstract

The seasonal development of the swede midge *Contarinia nasturtii* Kieffer (Diptera: Cecidomyiidae) was studied in Quebec in 2004 and 2005 using pheromone traps, emergence cages and visual inspection of plants. Overwintering population of the swede midge emerged in the second half of June. The swede midge had three to four overlapping generations in Quebec based on adult captures in pheromone traps and abundance of larvae in the field. There was a significant relationship between the number of adults captured in the pheromone traps and the subsequent abundance of larvae in the field during both years of the study. The level of infestation was higher in late transplants than in early transplants with cauliflower and broccoli being more susceptible to damage than white or red cabbage under high pest population.

Key words: Swede midge, seasonal development, cole crops

Introduction

The success of invasive species in their new region of introduction has been attributed to a variety of genetic, demographic, and ecological factors, and nowadays the identification and control of invasive species is at the forefront of many governmental agencies (Mack et al. 2002, Allendorf and Lundquist 2003). Kolar and Lodge (2001) described the process of invasion as a sequence of three steps involving introduction, initial establishment and subsequent spread in the new region. Once an invasive species is introduced, it will become a successful invader if the population is able to increase in abundance and spread from its point of entry (Mack et al. 2002). In addition, spread of these species will be in relation to the mechanisms of dispersal, the communities into which the organisms will spread, and the availability of suitable hosts, nutrients and other resources in the habitat (Mack et al. 2002).

In Eurasia, the swede midge *Contarinia nasturtii* Kieffer (Diptera: Cecidomyiidae) has been reported attacking cole crops (Barnes 1946, Darvas et al. 2000). In North America, there are over 60 species of *Contarinia* but none of them attack plants of the Brassicaceae family (Gagné 1989). In 2000, the swede midge was identified in Ontario, Canada, for the first time in broccoli plantations (Hallett and Heal 2001); and by 2003, its presence was detected in Quebec (CFIA 2003). In 2004, the swede midge was confirmed in the United States (Kikkert et al. 2006) and by 2005, the swede midge had spread into most areas where cole crops are grown in Ontario and Quebec (CFIA 2006). Based on a bioclimatic model, the swede midge has the potential to establish in all provinces of Canada (Olfert et al. 2006).

The swede midge overwinters as a late instar larva inside cocoons in the soil and pupation occurs when temperatures rise during the spring. However, emergence can be delayed when soil humidity is too low, the larva entering quiescence (Readshaw 1966). After a period of rain, the larva will resume its development and pupate. Soon after, adults emerge and oviposit in the apical meristem of plants, in the heart of the leaves, or leaf stalks (Barnes 1946). The host plants of the swede midge extend beyond cole crops

(*Brassica oleracea* L) to the entire Brassicaceae family including many weed species (Barnes 1946, Stokes 1953). Plants attacked show typical symptoms such as crumpled and twisted leaves, and when the central shoot is destroyed, secondary shoots appear causing the damage known as "many neck" or "cabbage top". In Eurasia there can be 2-5 generations depending on weather conditions (Barnes 1946, Darvas et al. 2000) whereas, in Ontario, there can be 3-5 overlapping generations (Goodfellow 2005). Several studies have shown that the swede midge has an unequal sex ratio, mostly female-biased (Barnes 1950, Rogerson 1963, Goodfellow 2005), and swede midge females often produce unisexual clutches of offspring (Barnes 1950, Stokes 1953).

The objective of this paper was to describe the seasonal development of the swede midge in its new region of invasion in Quebec during two consecutive years 2004-2005. The specific objectives were: a) monitor the pattern of emergence of the overwintering population throughout the season; b) evaluate the sex ratio of the overwintering population; c) monitor flight periods and number of generations; and d) evaluate the damage and susceptibility of different cole crops to the swede midge at different sowing dates.

Material and Methods

Experimental sites

The study was conducted at two experimental sites in southern Quebec (Laval island) in 2004 and 2005. The first site (9 x 40 m, N 45° 37' 14.3'', W 073° 42' 03.1'') was planted early (mid-May) with four different cole crops: white cabbage (*Brassica oleracea* var. *capitata* cv. Bronco), red cabbage (*B. oleracea* var. *capitata* cv. Super red 80), broccoli (*B. oleracea* var. *italica* cv. Windsor) and cauliflower (*B. oleracea* var. *botrytis* cv. Freemont). At the second site (22 x 40 m, N 45° 38' 14.0'', W 073° 40' 08.9''), early (mid-May) and late transplants (mid-late July) of broccoli (*B. oleracea* var. *italica* cv. Green Magic) were sown to provide suitable host plants for the swede midge for the entire season (May-October). Plants at both sites were transplanted with a density of 40 cm between plants and 40 cm between rows. No pesticides were applied at either site and commercial production practices were followed. Weather conditions were recorded from a nearby meteorological station (3.4 and 3.9 km away from site 1 and 2, respectively).

Monitoring overwintering emergence

The overwintering emergence of swede midge adults was monitored using standard emergence cages (Coutin 1952) made of wood (100 x 50 x 20 cm) painted white to avoid overheating. Two collecting tubes were placed on the side to capture swede midge adults that emerged from the soil, since they show positive phototropism (Coutin 1952). At each site in both years, three emergence cages were placed in the field in early May. The soil was watered once before installation of the emergence cages but no watering occurred during the season. In 2005 at Site 2, in addition to the three standard emergence cages, three modified emergence cages were also used. These cages had a removable top that permitted watering every other week (equivalent to 20 mm of rain), and were used to determine whether soil humidity had an effect on the pattern of emergence of the overwintering population (Readshaw 1966). Each emergence cage covered a soil surface of 0.50 m^2, and during both years of the study the collecting tubes were examined every other day for swede midge adults until late October. Identification of swede midges was based on morphological characters such as antenna and wing venation (Skuhravá 1997).

Monitoring flight periods and number of generations

A newly developed pheromone trap (Hillbur et al. 2005) was used to monitor flight periods and the number of generations of the swede midge in both years of the study. Pheromone traps were provided by PheroNet AB (Alnarp, Sweden) and they consisted of a delta type trap (brown waxed cardboard; 10 cm in height) with a pheromone lure and a sticky liner (15.5 x 9 cm) covered with a thin layer of Tangle Trap Insect Trap Coating (Tanglefoot, Grand Rapids, MI, USA). The traps were suspended 30 cm above the soil attached to a wooden stake with bull clips. Six traps were used per experimental site during both years of the study (from early May to early November), and were installed 10 m apart from each other. Pheromone lures and delta traps were changed every 30 and 60 days respectively and the sticky liners were replaced weekly. Swede midges captured in the traps were identified and recorded. Sticky liners containing swede midge captures were sent to Switzerland (Agroscope FAW Wädenswil) for confirmation of identification based on DNA analysis (Frey et al. 2004).

Monitoring larvae and damage to plants

Throughout both years of the study, cole crops were visually inspected to evaluate the abundance of larvae and the damage caused by the swede midge. At Site 1, five plants per crop were randomly inspected every two days, whereas at Site 2, 25 broccoli plants were inspected every two days. The damage for each plant inspected was noted according to a damage rating scale (Hallett 2007) (Table 2.1). Before the presence of side or lateral shoots on the plant, the number of larvae was recorded in the main growing point of the plant (apical meristem); once side shoots became visible, the whole plant was sub-divided into four sections and the mean number of larvae per side shoot and per subdivision was recorded. The level of infestation (percentage of plants attacked by the swede midge) was calculated based on these data only at Site 2, because only at this site were hosts available throughout the season (May-October) for both years of the study.

Statistical analyses

Differences from a 50:50 sex ratio in the overwintering population were tested with a χ^2 test for both years of the study. To test the differences between the total captures of overwintering swede midges in the modified vs standard emergence cages, a Student's t-test was conducted. Because the swede midge has the status of a quarantine pest in the region of the experiments (CFIA 2006), we had access only to two fields and therefore, each plant was sampled and considered as a replicate, although this design caused pseudo-replication (Hurlbert 1984). A regression analysis was carried out between the mean number of adults captured in pheromone traps and the mean number of larvae found in the plants a week later. This one week delay corresponds to the period between oviposition and the presence of mature larvae. Regression analyses were carried out exclusively for data obtained at Site 2, where hosts were available throughout the entire season (May-October) for both years of the study. To evaluate damage on different cole crops at Site 1, the data for plant damage 80-90 days after transplantation (which corresponded to the harvesting time for 2004 and 2005 respectively) was log10 (x+1) transformed; followed by an ANOVA and a multiple comparisons Tukey HSD test. Data are presented without transformation, and the statistical analyses were performed using SAS (SAS Institute 2001).

Results

Monitoring overwintering emergence

The overwintering population started to emerge late May in 2004 and early June in 2005 and peaked mid-late June in 2004 and late June to early July in 2005 (Fig. 2.1 A, B and C). The sex ratio of emerging adults was marginally not significantly different from 50:50 in 2004 (42 females and 26 males; $\chi^2 = 3.76$; df = 1; $P = 0.0524$), but it was in 2005 (235 females and 164 males; $\chi^2 = 12.63$; df = 1; $P = 0.0003$). In 2005, the patterns of emergence in both the modified and standard emergence cages were similar (Fig. 2.1 C), with peak emergence at the end of June to early July. The total numbers of swede midge captured during the entire season were not significantly different between the two types of emergence cages ($t = 0.012$; df = 122; $P = 0.990$).

Monitoring flight periods and number of generations

The earliest capture in the pheromone traps occurred mid- to late-May in 2004 and 2005 (Fig. 2.2); emergence continued throughout the season until late October in 2004 and 2005. The captures of swede midge males showed 3-4 peaks during both years of the study. In 2004 a total of 5487 and 9821 swede midge males were captured at Sites 1 and 2 respectively; whereas in 2005, 4051 and 7434 swede midge males were captured at Sites 1 and 2 respectively.

Monitoring larvae and damage to plants

The level of damage in cole crops varied between sites and between years during the study. The seasonal abundance of larvae for both years is presented only for site 2 (Fig. 2.3). In both years, the first observations of larvae occurred in mid-June when broccoli plants reached the 8-10 true leaves stage. Larvae were found on the growing tips (apical meristem) and on the leaves showing the typical symptoms of "crumpled leaves". Three to four peaks of abundance (early-July, late-July, mid-August and late-September early-October) were observed during the study.

At Site 2, the level of damage and the percentage of infested broccoli plants increased progressively during both seasons (Table 2.2). The percentage of infestation and the level of damage were higher on late transplants. Finally, there was a significant relationship between the number of captures in pheromone traps and the number of larvae found on broccoli plants one week later in both years of the study at Site 2 (Fig. 2.4).

The level of damage on the different cole crops at Site 1 differed in 2004 and 2005. In 2004, damage remained low (< 1 according to the damage rating scale) on all crops throughout the season (Fig. 2.5 A), and there was no significant difference among them 80 days after being transplanted in the field ($F = 1.82$; df = 3; $P = 0.1609$). In 2005, the level of damage progressively increased with time (Fig. 2.5 B), and there was a significant difference among cole crops ($F = 75.8$; df = 3; $P < 0.0001$). Cauliflower and broccoli showed the highest damage while white cabbage had the lowest. The cumulative number of larvae and the highest damage found in each crop for both years of the study are presented in Table 2.3. The population density of larvae was higher in 2005 and in both years the highest number of larvae was found on broccoli.

Discussion

The swede midge was first identified in Canada in 2000 and has since spread to most crucifer growing areas of Ontario and Quebec (CFIA 2006) suggesting that this species has the capacity to adapt to local conditions. Invasive species often show an increase in population growth in a newly invaded habitat after adapting to local environmental conditions and native hosts (Allendorf and Lundquist 2003).

In Quebec and under the experimental conditions, overwintering swede midges emerged in a single peak. In Europe, it has been observed that the overwintering swede midges emerge mostly in spring (late May and June) and that a second peak can occur (Olombel 1931, Mesnil 1938, Barnes 1950, Rogerson, 1963); part of the population may also remain in diapause for an additional year (Rygg and Braekke 1980). In Ontario, two to three peaks of overwintering emergence (early June, late June and early-mid August) were observed when using emergence tents (Goodfellow 2005). In general, insects show different emergence strategies to increase survival when facing variation in environmental conditions, food shortage and host synchronization (Yukawa 2000, Biron et al. 2003, Fournet et al. 2004). Examples of this characteristic have been clearly observed in the Diptera (Anthomyiidae) *Delia radicum* L and *Delia floralis* Fallen (Biron et al. 2003, Fournet et al. 2004) and in gall midges (Cecidomyiidae) such as *Asteralobia sasakii* Monzen (Tabuchi and Amano 2003), and *Daphnephila machililoca* Yukawa (Maeda et al. 1982). Previous studies have shown that a combination of increased temperature and humidity in the soil are crucial factors for the swede midge to emerge in the spring, and low soil humidity can delay the emergence of overwintering individuals (Readshaw 1961, Readshaw 1966, Rygg and Braekke 1980, Bouma 1996). As the swede midge is strongly influenced by soil humidity to complete its life cycle, the multiple events observed in Ontario were probably the result of weather conditions where a period of low humidity in the soil delayed the emergence of part of the population of swede midges. This study used an emergence tent that allowed humidity to be the same inside and outside the tent as precipitation occurred (Goodfellow 2005). When using wooden emergence cages, a high humidity level was maintained inside the cages after watering them early in the season, and this allowed the overwintering swede midges to complete the pupal stage and the subsequent adult emergence on a single event. The fact that a similar emergence pattern, and a similar number of overwintering individuals emerged from the two types of emergence cages, suggest that a single watering in spring provided enough humidity for swede midge emergence throughout the season.

In both years of the study, the sex-ratio of the overwintering population was female-biased although not significantly so in 2004. Similar female-biased sex ratios have been previously observed for both overwintering and summer generations of the swede midge (Barnes 1950, Rogerson 1963, Goodfellow 2005). Although the adaptive significance of such female-biased sex ratios has not been clearly determined in the swede midge (Goodfellow 2005), it is known that females of several cecidomyiid species, including the swede midge (Barnes 1950, Stokes 1953, Readshaw 1966), primarily or exclusively produce unisexual broods throughout their lifetime (Dorchin and Freidberg 2004).

Both adult captures in pheromone traps and visual counts of larvae on plants indicated that the swede midge has three to four overlapping generations in Quebec. The number of generations reported for this species varies from two in Norway (Rygg and Braekke 1980), three in France (Olombel 1931, Mesnil 1938); three to four in England (Taylor 1912, Dry 1915, Readshaw 1961), four in the Netherlands (Bouma 1996), and up to five in Germany (Roesler 1937). In Ontario, three to five overlapping generations were recorded (Goodfellow 2005). Differences in the number of generations found in Quebec, Ontario and Europe are the result of regional weather conditions in each region, where temperature and humidity are the most important factors (Readshaw 1961, Readshaw 1966). In addition, fluctuations in numbers and sporadic outbreaks of the swede midge can be influenced by a combination of factors such as environmental conditions, the presence of available hosts, and agricultural practices from each particular region (Readshaw 1966, Readshaw 1968, Theunissen et al. 1997). Nonetheless, according to a bioclimatic model in Canada, the conditions prevailing in southern Ontario and southern Quebec are ideal for swede midge development (Olfert et al. 2006).

Late transplants suffered higher infestation and higher level of damage as the season progressed, probably because early transplants were attacked by the overwintering generation which was lower in density compared to the summer generations. In England, it was observed that early sown plants can escape from swede midge damage since plants have a larger leaf area at the time of arrival of the first summer generation (Bardner et al. 1971). Baur and Rauscher (2003) found a relationship between the phenological stage of broccoli plants and the level of damage and infestation caused by the swede midge; young plants (4-8 true leaves) showed 90% damage with no yield while only 50% of older plants (1-3 cm head formed) were damaged.

Weather conditions differed in 2004 and 2005 resulting in differences in the population of swede midge larvae, adults and the damage on cole crops. Summer 2004 was cooler and dryer (1747 DD (based on a base temperature for the swede midge of 7.2 °C [Noll 1959]) with an accumulation of 471.6 mm of rain between April and October) than the summer of 2005, (accumulation of 1966 DD and 887 mm of precipitation during the same period). Temperature and humidity play an important role in the development of the swede midge (Readshaw 1961, Readshaw 1966), and these conditions influenced its seasonal development. In 2004, low numbers of overwintering swede midges were captured in the emergence cages and although pheromone captures of adults were higher than in 2005, the subsequent population of larvae throughout the season remained low as did the level of damage to cole crops. However, in 2005 there were higher captures of overwintering swede midges in the emergence cages, a higher population of larvae and higher damage on all cole crops evaluated with broccoli and cauliflower being the most susceptible to the swede midge. Dry (1915) and Readshaw (1961) observed that swede midge populations increased in warm and moist seasons, whereas in dry and cold seasons populations remained low and the larvae became scarce.

References

Allendorf, F. W. and L. Lundquist. 2003. Introduction: population biology, evolution, and control of invasive species. Conserv. Biol. 17: 24-30

Bardner, H. M., Edwards, C. A., Arnold, M. K. and J. P. Rogerson. 1971. The symptoms of attack by swede midge (*Contarinia nasturtii*) and effects on the yield of swedes. Entomol. Exp. Appl. 14: 223-233

Barnes, H. F. 1946. Gall midges of economic importance. Volume I. Gall midges of root and vegetable crops. Crosby Lockwood and Son Ltd., London. 104pp.

Barnes, H. F. 1950. The identity of the swede midge, with notes on its biology. Ann. Appl. Biol. 37: 241-248

Baur, R. and S. Rauscher. 2003. Cécidomyie du chou: un grand ravageur de petite taille. Der Germüsebau/ Le Maraîcher 4: 8-9

Biron, D. G., Brunel, E., Tiilikkala, K., Hellqvist, S. and P. L. Dixon. 2003. Expression of a bimodal emergence pattern in diapausing and non-diapausing *Delia floralis*: a phenological survival strategy. Entomol. Exp. Appl. 107: 163-166

Bouma, E. 1996. Contapré, prototype of a model of prediction of emerging of the swede midge (*Contarinia nasturtii*). Sp-report, Danish Institute of Plant and Soil Science. 15: 25-30

Canadian Food Inspection Agency. 2003. Summary of plant quarantine pest and disease situations in Canada in 2003. http://www.inspection.gc.ca/english/sci/surv/sit2003e.shtml#connas. Accessed 20 August 2006

Canadian Food Inspection Agency. 2006. Lists of regulated countries and regulated areas within Canada for swede midge. http://www.inspection.gc.ca/english/plaveg/protect/dir/smidgee.shtml. Accessed 20 August 2006

Coutin, R. 1952. Bases scientifiques et organisation d'un avertissement sur la cécidomyie du chou-fleur aux Pays-Bas. Phytoma 39: 11-12

Darvas, B., Skuhravá, M. and A. Andersen. 2000. Agricultural dipteran pests of the Palaearctic region. pp 565-650 *in* Papp, L. and B. Darvas, editors. Contributions to a manual of Palaearctic Diptera, (with special reference to flies of economic importance). Vol. 1, General and Applied Dipterology. Science Herald, Budapest.

Dorchin, N. and A. Freidberg. 2004. Sex ratio in relation to season and host plant quality in a monogenous stem-galling midge (Diptera: Cecidomyiidae). Ecol. Entomol. 29: 677-684

Dry, F. W. 1915. An attempt to measure the local and seasonal abundance of the swede midge in parts of Yorkshire over the years 1912 to 1914. Ann. Appl. Biol. 2: 81-108

Fournet, S., Astier, N. A., Cortesero, M. and D. G. Biron. 2004. Influence of a bimodal emergence strategy of a dipteran host on life-history traits of its main parasitoids. Ecol. Entomol. 29: 685-691

Frey, J. E., Frey, B. and R. Baur. 2004. Molecular identification of the swede midge (Diptera: Cecidomyiidae). Can. Entomol. 136: 771-780

Gagné, R. J. 1989. The plant-feeding gall midges of North America. Cornell University Press, Ithaca, NY. 368pp.

Goodfellow, S. A. 2005. Population dynamics and predictive modeling of the swede midge, *Contarinia nasturtii* Kieffer. M.Sc. Thesis. University of Guelph.

Hallett, R. H. 2007. Host plant susceptibility to the swede midge, *Contarinia nasturtii* (Diptera: Cecidomyiidae). J. Econ. Entomol. (submitted)

Hallett, R. H. and J. D. Heal. 2001. First Nearctic record of the swede midge (Diptera: Cecidomyiidae), a pest of cruciferous crops from Europe. Can. Entomol. 133: 713-715

Hillbur, Y., Celander, M., Baur, R., Rauscher, S., Haftmann, J., Franke, S. and W. Francke. 2005. Identification of the sex pheromone of the swede midge, *Contarinia nasturtii*. J. Chem. Ecol. 31: 1807-1828

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187-211

Kikkert, J. R., Hoepting, C. A., Wu, Q., Wang, P., Baur, R. and A. M. Shelton. 2006. Detection of *Contarinia nasturtii* (Diptera: Cecidomyiidae) in New York, a new pest of cruciferous plants in the United States. J. Econ. Entomol. 99: 1310-1315

Kolar, C. S. and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends Ecol. Evol. 16: 199-204

Mack, R. N., Barrett, S. C. H., DeFur, P. L., MacDonald, W. L., Madden, L. V., Marshall, D. S., McCullough, D. G., McEnvoy, P. B., Nyrop, J. P., Reichard, S. E. H., Rice, K. J. and S. A. Tolin. 2002. Predicting invasions of nonindigenous plants and plant pests. National Academy Press, Washington, DC. 194pp.

Maeda, N., Sato, S. and J. Yukawa. 1982. Polymodal emergence pattern of the machilus leaf gall midge *Daphnephila machililoca* Yukawa (Diptera: Cecidomyiidae). Konchu 50: 44-50

Mesnil, L. 1938. La cécidomyie du chou-fleur dans la région de Saint-Omer. Ann. Épiphyt. Phyt. 4: 281-311

Noll, J. 1959. Über den Einfluss von Temperatur und Bodenfeuchtigkeit auf die larven und Puppen der Kohldrehherzmücke (*Contarinia nasturtii* Kieffer) als Grundlage für die Vorausberechnung des ersten Schlüpftermins im Frühjahr, Archiv für Gartenbau. 7, S. 362-415

Olfert, O., Hallett, R., Weiss, R. M., Soroka, J. and S. Goodfellow. 2006. Potential distribution and relative abundance of swede midge, *Contarinia nasturtii*, an invasive pest in Canada. Entomol. Exp. Appl. 120: 221-228

Olombel, M. 1931. Note préliminaire sur la Cécidomyie du chou-fleur (*Contarinia torquens* de Meij.) C. R. Acad. Agric. France. 17: 178-182

Readshaw, J. L. 1961. The biology and ecology of the swede midge, *Contarinia nasturtii* (Kieffer) (Diptera: Cecidomyiidae). Ph.D Thesis. University of Durham, Durham, UK.

Readshaw, J. L. 1966. The ecology of the swede midge, *Contarinia nasturtii* (Kieff.) (Diptera, Cecidomyiidae). I. Life-history and influence of temperature and moisture on development. Bull. Entomol. Res. 56: 685-700

Readshaw, J. L. 1968. Damage to swedes by the swede midge, *Contarinia nasturtii* (Kieff.), and a possible method of cultural control. Bull. Entomol. Res. 58: 25-29

Roesler, T. 1937. Drehherzkrankheit und Herzlosigkeit bei Kohl. Kranke Pflanze. 14: 124-129

Rogerson, J. P. 1963. Swede midge on two Northumberland farms, 1959-1961. Plant Pathol. 12: 161-171

Rygg, T. D. and H. P. Braekke. 1980. Swede midge (*Contarinia nasturtii* Kieffer) (Diptera Cecidomyiidae); investigations on biology, symptoms of attack and effects on yield. Meldinger fra Norges Landbrukshoegskule. 59: 1-9

SAS Institute. 2001. SAS/STAT User's guide, version 8. Cary, NC.

Skuhravá, M. 1997. Family Cecidomyiidae. pp 71-204 *in* Papp, L. and B. Darvas, editors. Contribution to a manual of Palaearctic Diptera, vol. 2. Nematocera and lower Brachycera. Science Herald, Budapest, Hungary.

Stokes, B. M. 1953. Biological investigations into the validity of *Contarinia* species living on the Cruciferae, with special reference to the swede midge, *Contarinia nasturtii* (Kieffer). Ann. Appl. Biol. 40: 726-741

Tabuchi, K. and H. Amano. 2003. Polymodal emergence pattern and parasitoid composition of *Asteralobia sasakii* (Monzen) (Diptera: Cecidomyiidae) on *Ilex crenata* and *I. integra* (Aquifoliaceae). Appl. Entomol. Zool. 38: 493-500

Taylor, T. H. 1912. Cabbage-top in Swedes. Univ. Leeds and York. Counc. Agric. Educ. 82: 1-21

Theunissen, J., Den Ouden, H. and G. Schelling. 1997. Can the cabbage gall midge, *Contarinia nasturtii* (Diptera, Cecidomyiidae) be controlled by host plant deprivation? Med. Fac. Ladbouww. Univ. Gent. 62/2b: 617-622

Yukawa, J. 2000. Synchronization of gallers with host plant phenology. Popul. Ecol. 42: 105-113

Table 2.1. Swede midge damage rating scale for cole crops.

Rating scale [*]	Button stage before side shots	Heading with side shoots
0	No damage	No damage
1	Mild crumpling of leaves	Mild crumpling of leaves
2	Severe crumpling of leaves	Severe crumpling of leaves, side shoots twisting or head scarring
3	Blind growth /no head formation	No head formation

[*] Rating scale according to Hallett (2007).

Table 2.2. Percentage of broccoli plants attacked by swede midge larvae ± 95 % CL with the corresponding level of damage according to a rating scale (0-3) at Site 2.

Weeks after transplant	2004		2005	
	1st transplant % damage (rate)*	2nd transplant % damage (rate)	1st transplant % damage (rate)	2nd transplant % damage (rate)
2	0 (0)	0 (0)	0 (0)	0 (0)
4	0 (0)	56.00 ± 19.85 (0.56 ± 0.10)	12.00 ± 9.09 (0.12 ± 0.04)	78.66± 9.33 (1.10 ± 0.08)
6	18.66 ± 8.87 (0.18 ± 0.04)	96.00 ± 7.83 (2.08 ± 0.15)	57.33 ± 11.26 (0.73 ± 0.08)	100.00 ± 0.00 (2.72 ± 0.09)
10	61.30 ± 11.00 (1.10 ± 0.11)	96.00 ± 7.83 (2.00 ± 0.14)	94.66 ± 5.11 (1.80 ± 0.09)	100.00 ± 0.00 (3.00 ± 0.00)

* Numbers in parentheses are the mean damage rating (0 = no damage, 1 = mild crumpling of leaves, 2 = severe crumpling of leaves, 3 = no head formation) ± S.E.

Table 2.3. Cumulative number of swede midge larvae and highest level of damage found on different cole crops for both years of the study at Site 1.

	2004		2005	
Crop	Cumulative Larvae	Highest damage [1]	Cumulative larvae	Highest damage [1]
White cabbage	0.46	0.40	2.33	0.66
Red cabbage	1.06	0.46	19.2	1.80
Broccoli	4.30	0.60	57.2	2.33
Cauliflower	0.46	0.53	17.53	3.00

[1] Based on a rating scale (0 = no damage, 1 = mild crumpling of leaves, 2 = severe crumpling of leaves, 3 = no head formation)

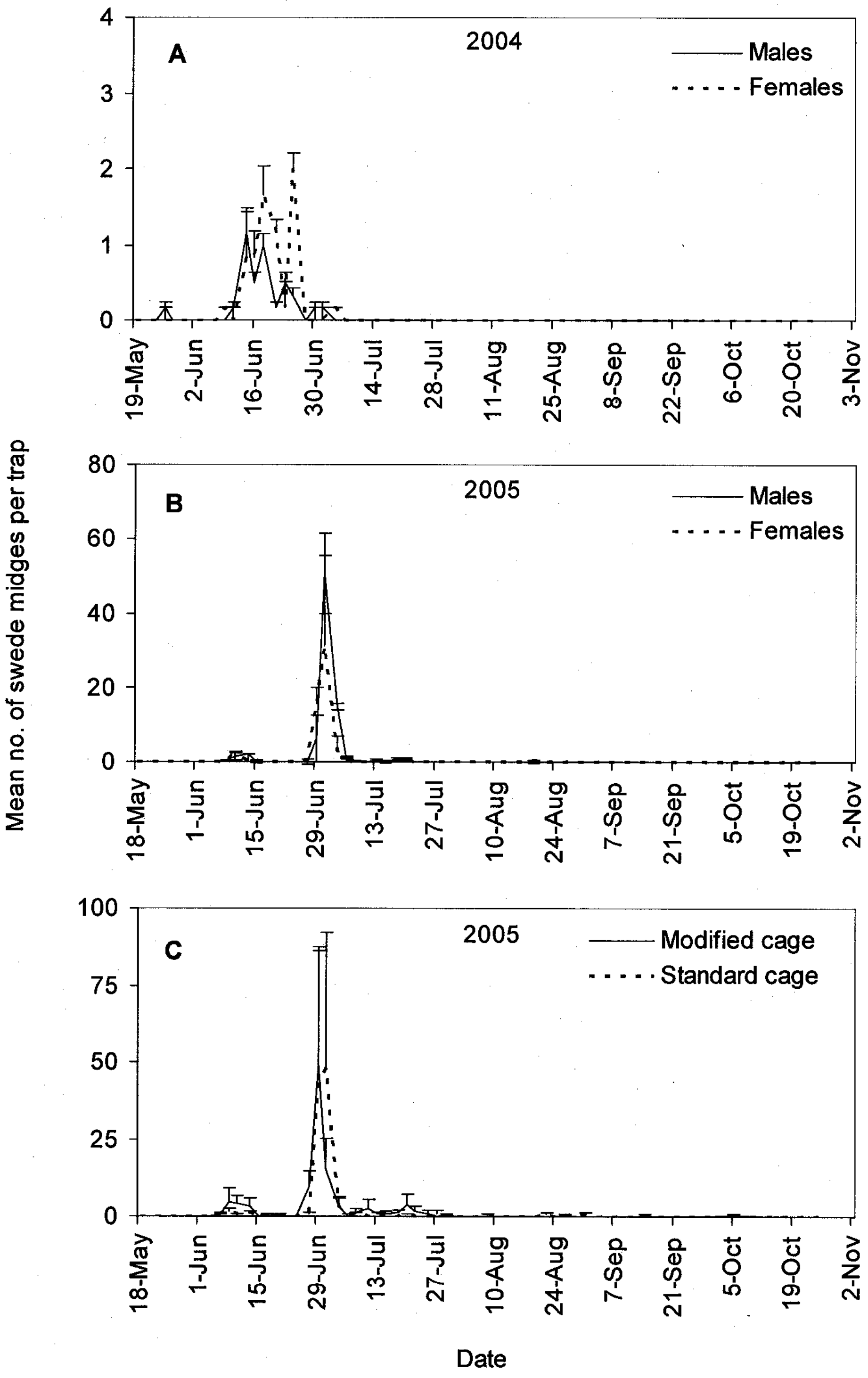

Figure 2.1. Overwintering emergence of the swede midge adults (mean ± S.E.). (A) Site 1 in 2004; (B) Site 1 in 2005; (C) Site 2 for both standard and modified emergence cages.

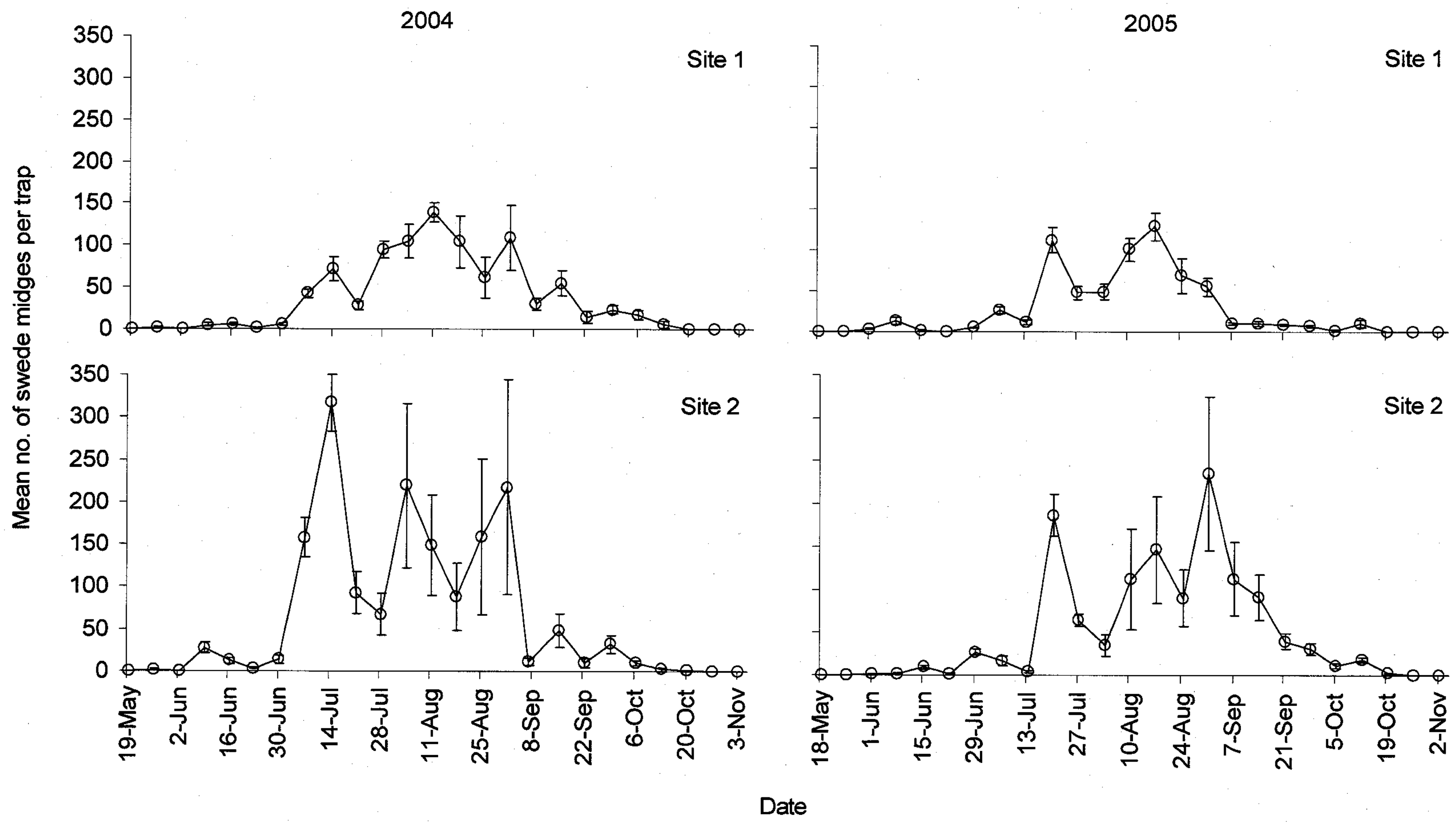

Figure 2.2. Captures of swede midge males (mean ± S.E.) in pheromone traps during 2004 and 2005.

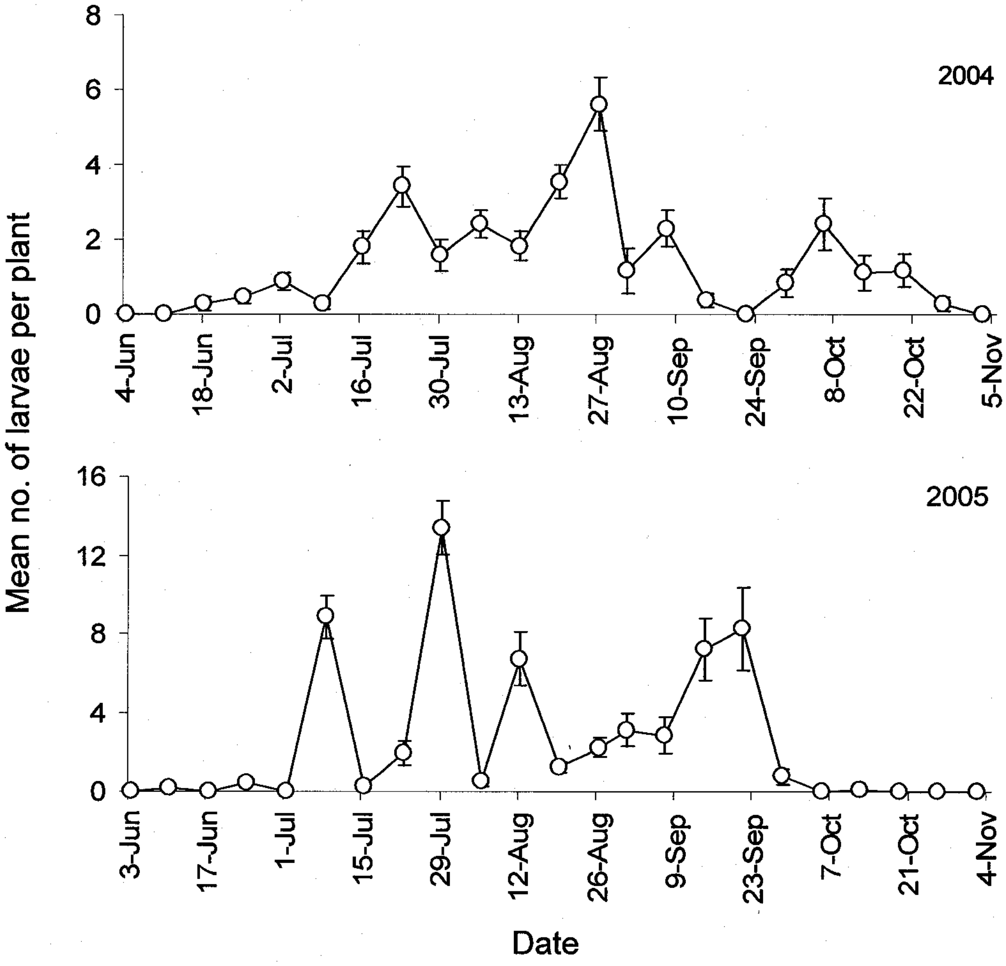

Figure 2.3. Seasonal abundance of swede midge larvae (mean ± S.E.) in broccoli plantations (Site 2) in 2004 and 2005.

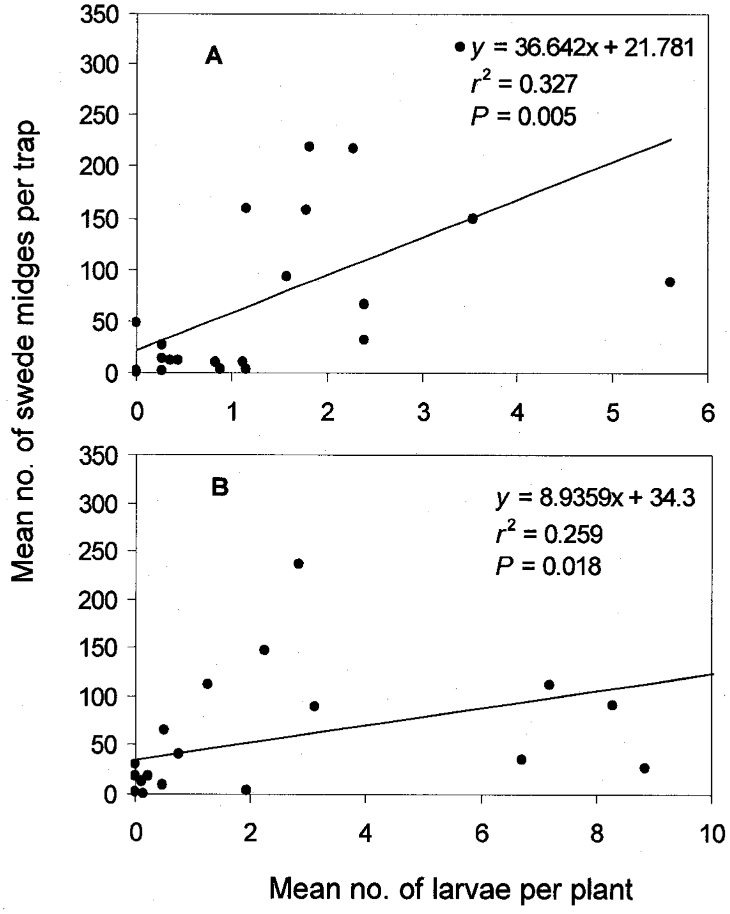

Figure 2.4. Relationship between the mean number of swede midge males captured in pheromone traps, and the mean number of swede midge larvae in broccoli plants a week later at Site 2, in (A) 2004 and (B) 2005.

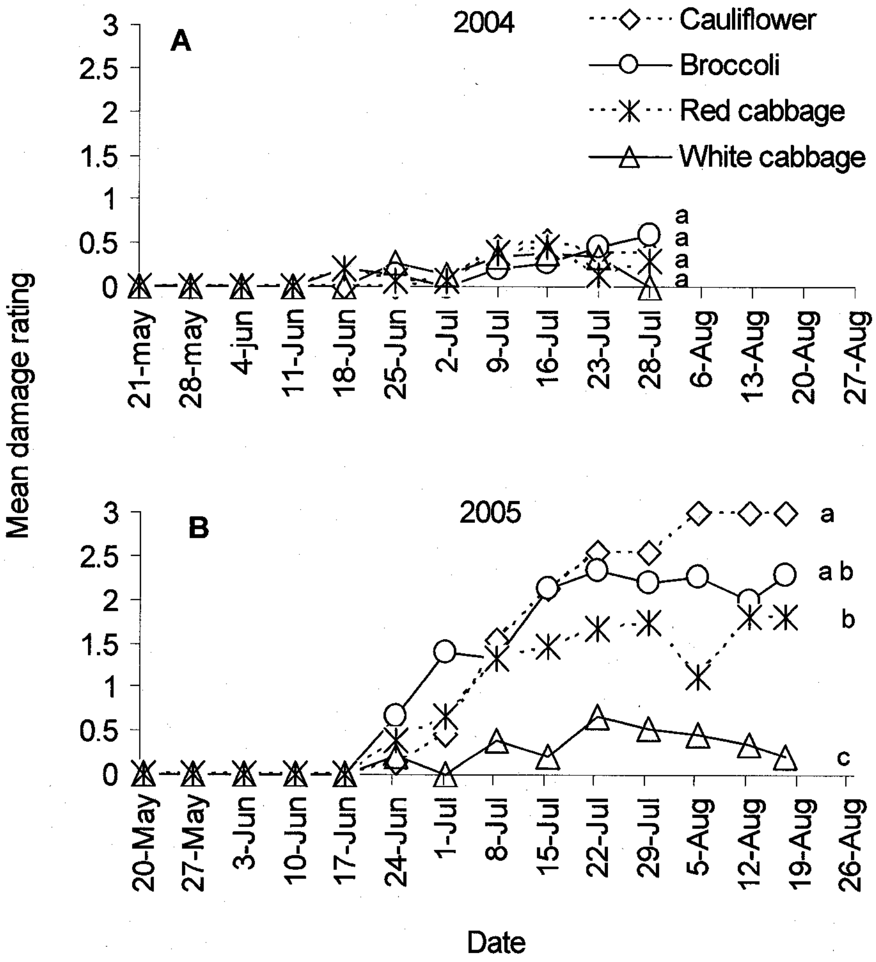

Figure 2.5. Level of damage to cole crops caused by swede midge larvae according to a rating scale (0-3) at Site 1, for (A) 2004 and (B) 2005. Damage levels followed by the same letter are not significantly different (Tukey HSD, $P \leq 0.05$).

Connecting text

In Chapter 2, the seasonal development of the swede midge, a newly invasive exotic species, was studied under the agro-climatic conditions prevailing in Quebec. The swede midge was present during the entire productive season (May-October) attacking cole crops during both years of the study, showing the capacity of the swede midge to develop under the local weather conditions in the new region of invasion. For newly invasive pest species, it is also important to investigate the presence of natural enemies in the new region of invasion, as they may play an important role in regulating pest populations. Therefore, the objective in Chapter 3 was to identify the presence of natural enemies in infested cole crops fields, and also to test commercially available biological control agents (entomopathogenic nematodes) against the swede midge in the soil.

Chapter 3, submitted to Biological Control

Efficiency of natural enemies against the swede midge, *Contarinia nasturtii* (Diptera: Cecidomyiidae), a new invasive species in North America

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Abstract

The swede midge, *Contarinia nasturtii* Kieffer (Diptera: Cecidomyiidae), a widespread pest of cruciferous crops in Europe, has been recently found in Canada. A two-year survey in Quebec yielded no specialized natural enemies. Two polyphagous coccinellid predators (*Harmonia axyridis* and *Coccinella septempunctata*) were field collected for further evaluation. In laboratory experiments, these two coccinellid species fed on swede midge larvae, and *H. axyridis* showed a higher voracity than *C. septempunctata*. Late larvae and adults of *H. axyridis* were shown to consume more swede midge larvae than young larvae, while the adults of *H. axyridis* showed no preference between swede midge larvae and the green peach aphid *Myzus persicae*. However, *H. axyridis* adults were not able to prey on swede midge larvae on potted infested broccoli plants. The susceptibility of swede midge larvae to three species of entomopathogenic nematodes (*Steinernema feltiae*, *S. carpocapsae*, and *Heterorhabditis bacteriophora*) was also evaluated. *Heterorhabditis bacteriophora* was the only species that caused significant mortality to swede midge larvae. At a concentration of 1000 IJs/larva, *H. bacteriophora* caused 90-100% mortality to swede midge larvae in loam, sandy loam, clay and muck soils.

Key words: Swede midge, *Contarinia nasturtii*, natural enemies, entomopathogenic nematodes, Coccinellidae

Introduction

The enemy-release hypothesis states that invasive species are more successful in the new region of invasion than in their native region due to the absence of coevolved natural enemies, resulting in higher population growth rates of the invasive species (Drake 2003). Parasitoid attack rate is generally lower in invasive hosts than in native hosts, and invasive hosts have a larger proportion of generalist parasitoids compared to native hosts (Cornell and Hawkins 1993). This trend is found across several plant and animal taxa supporting the enemy-release hypothesis (Clay 2003, Mitchell and Power 2003, Torchin et al. 2003, Torchin and Mitchell 2004). The low number of parasitoids attacking exotic species could be explained by the fact that generally only a few individuals invade a new habitat thus decreasing the probabilities that their natural enemies are introduced simultaneously (Clay 2003). When natural enemies arrive in the new habitat, they face several constraints for their establishment including complex life cycles requiring more than one host, presence of suitable hosts, and host population bottlenecks after introduction that may break transmission of those parasites present in the founder population (Torchin et al. 2003).

Many biological invasions go unnoticed until either ecological or economic impacts are recognized. This was the case with the swede midge, *Contarinia nasturtii* Kieffer (Diptera: Cecidomyiidae), whose symptoms of attack on host plants were first observed in broccoli plantations in Ontario, Canada, during the mid 1990s, but were mistakenly attributed to nutrient deficiencies (Hallett and Heal 2001). This damage was attributed to *C. nasturtii* several years later, and by then this pest was causing up to 85 % losses in broccoli plantations (Hallett and Heal 2001). The swede midge has since been found in Quebec in 2003 and in the United States in 2004 (CFIA 2003, Kikkert et al. 2006).

In its region of origin, swede midge larvae are parasitized by *Pirene eximia* Haliday (Hymenoptera: Chalcididae) (Bovien and Knudsen 1950), *Synopeas* sp. (Hymenoptera: Platygasteridae) (Rogerson 1963, Readshaw 1966, Readshaw 1968), and

Platygaster sp. (Hymenoptera: Platygasteridae) (Readshaw 1966). In North America, cecidomyiids are attacked by several natural enemies, mostly parasitoids, from nine Hymenoptera families (Gagné 1989). Recent studies showed the presence of *Medetera* sp. (Diptera: Dolichopodidae) preying on swede midge adults in Ontario (Goodfellow 2005), and in laboratory experiments, Wu et al. (2006) observed that *Bacillus thuringiensis* subsp. *israeliensis* caused significant mortality (52%) to swede midge larvae in infested broccoli plants.

Because the swede midge spends part of its life cycle in the soil, entomopathogenic nematodes could be potential natural enemies. The entomopathogenic nematodes *Steinernema* and *Heterorhabditis* have been successfully used in managing pests in horticulture and greenhouse productions; they are commercially mass-produced, and several species are readily available against soil-dwelling insects (Ehlers 1996, Ehlers and Shapiro-Ilan 2005). Furthermore, entomopathogenic nematodes are safe to the environment and consumers (Ehlers and Hokkanen 1996).

The objectives of this paper were to: a) search for and identify natural enemies of the swede midge in Quebec; b) test two species of coccinellid predators (*Harmonia axyridis* Pallas and *Coccinella septempunctata* L) against swede midge larvae under laboratory conditions; c) test three species of entomopathogenic nematodes (*Steinernema carpocapsae* Weiser, *S. feltiae* Filipjev, and *Heterorhabditis bacteriophora* Poinar) on swede midge larvae in the soil; and d) evaluate the mortality of swede midge larvae to a high concentration of *H. bacteriophora* in different types of soil.

Material and Methods

Survey for natural enemies of swede midge in infested fields

Field surveys were conducted at two experimental sites on the Island of Laval in Quebec, Canada, where previous infestations of the swede midge were recorded. At site #1 (Plot: 360 m^2, N 45° 37' 14.3''; W 073° 42' 03.1''), early transplants (mid-May) of broccoli, cauliflower, and red and white cabbages were used as host plants for the swede midge, whereas at site #2 (Plot: 880 m^2, N 45° 38' 14.0''; W 073° 40' 08.9'') both early (mid-May) and late transplants (mid-late July) of broccoli were used. Plants (5 plants per crop at site #1, and 25 plants at site #2) were randomly inspected in the field every two days throughout the season for the presence of predators, and infested material (infested growing tips and crumpled leaves with the presence of swede midge larvae), was brought to the laboratory. The infested material was placed in containers (55 cm^3 covered with a lid with a fine mesh at the top) with pasteurized humid soil in incubators (25 °C; 16:8 L:D; 60% RH for a maximum of 30 days) to let the immature swede midges complete their cycle and to observe the presence of parasitoids.

Insect material

The two predator species found (*Harmonia axyridis* and *Coccinella septempunctata*) were field-collected to evaluate their voracity against swede midge larvae. Both species were reared under controlled conditions (20 ± 2°C, 16:8 L:D; 60% RH) on an artificial diet (Firlej et al. 2006) and aphids (*Acyrthosiphon pisum* Harris), Lepidoptera eggs (*Ephestia kuehniella* Keller) and mixed pollen as a food source. Field-collected adults were regularly added to the culture. The green peach aphid (*Myzus persicae* Sulzer) came from a culture of sweet pepper plants (*Capsicum annuum* L.) maintained at 20 ± 2°C, 50% RH and 16:8 L:D. Apterous aphid adults were used in the host choice experiments.

The initial population of swede midge came from crucifer plots at Laval, Quebec. Infested tips of broccoli plants with third-instar larvae were placed in small pots (55 cm^3 covered with a lid with a fine mesh at the top) containing a mixture of sand and organic soil (50:50) previously humidified. The pots containing the infested material were then placed in incubators (25 °C; 16:8 L:D; 60% RH for a maximum of 30 days) to allow the immatures to complete their life cycle in the soil. When emergence was noticed (10-12 days after placement of the infested material), adult swede midges were placed into a cage (50 × 50 × 50 cm) covered with a fine mesh screen containing 10 host plants (broccoli *Brassica oleracea* var. *italica*, cv. Captain at the eight-true-leaf stage and grown in pairs in 15 cm diameter pots). Cages were watered from the outside through the mesh with a spray to provide water to the adults every 24 h for 3 days. After infestation of plants (10-12 days), infested tips with visible swede midge larvae were cut and the cycle repeated. Third-instar larvae from the rearing were used in the predation experiments.

Laboratory experiments

a) Predation experiments

These experiments were performed under laboratory conditions (20 ± 2°C; 16:8 L:D; 60% RH). Coccinellid predators were starved for 24h in plastic Solo cups (30 cm^3) with access to a water-soaked piece of cotton before each experiment. Four different experiments were performed with coccinellid predators.

Voracity of two species of coccinellid predators. Adults of both species (*H. axyridis* and *C. septempunctata*) (n=15) were placed individually in plastic Solo cups (30 cm^3) with 35 third-instar swede midge larvae. After 1h, the number of swede midge larvae consumed was recorded.

Voracity of different instars of *Harmonia axyridis*. Second-instar, fourth-instar larvae and adults of *H. axyridis* (n=15) were placed individually in plastic solo cups along with 35 third-instar swede midge larvae. After 1h, the number of swede midge larvae consumed was recorded.

Prey choice by *Harmonia axyridis* adults. Fifteen adult aphids and 15 third-instar swede midge larvae were simultaneously offered to an *H. axyridis* adult in a plastic solo cup; after 1h, the number of prey consumed was recorded. A total of 15 *H. axyridis* were tested during this experiment.

Predatory efficiency of *Harmonia axyridis* on broccoli. Two different experiments were performed:

- Artificially infested broccoli plants. Eight-true-leaf broccoli in 15 cm diameter pots were artificially infested with 10 third-instar swede midge larvae placed inside the growing tips (apical meristem) 24 h before the experiments.

- Naturally infested broccoli plants. Infested broccoli plants (8-10 true leaves) with swede midge larvae (2-40 per infested growing tip) were taken from the rearing for the experiments.

In both experiments, infested plants were placed in a cylindrical plastic cage (37 x 18 cm diameter) with the top covered with fine mesh and the bottom covered with tissue paper to collect the larvae that left the plant by jumping to the ground (Barnes 1946). The number of swede midge larvae was recorded before releasing the coccinellid predators. In a first series of tests we used one adult of *H. axydiris* per cage. Because no predation was obtained at this density (see results), we also tested a higher density with five adults per cage. After 24 h, the number of swede midge larvae remaining was recorded.

b) Entomopathogenic nematode experiments

Source of entomopathogenic nematodes and swede midge larvae. Initial infective juvenile (IJs) populations of the entomopathogenic nematodes (EPN) *Steinernema feltiae*, *S. carpocapsae*, and *Heterorhabditis bacteriophora*, were supplied by Plant Products, Nic Inc., and Koppert Biological Systems respectively. The EPN were reared on larvae of *Galleria mellonella* L. prior to the experiments using the methodology of Dutky et al. (1964). Third-instar swede midge larvae were field-collected for the experiments. This instar was chosen because it is the larval stage that leaves the plant to complete its life cycle in the soil (Readshaw 1966).

Susceptibility of swede midge to three species of EPN. Plastic solo cups (30 cm^3) were filled with 15 cm^3 of pasteurized loamy sand (82% sand, 11% silt, 7% clay and 15% humidity). One swede midge larva was transferred to each cup and placed 1 cm deep into the soil using a fine brush. Cups were incubated at 22 °C in the dark for 24 h before inoculation with EPN. *Steinernema carpocapsae*, *S. feltiae* and *H. bacteriophora* were applied at concentrations of 0, 50, 500 and 1000 IJs per cup in 1 ml of water (with < 1µl of the surfactant Triton X-100). After inoculation, cups were incubated at 22 °C (obscurity; 80% RH) for twelve days. The emergence of swede midge adults from the solo cups was recorded during a 30-day post-treatment period which is twice as long as the normal duration of pupation (Readshaw 1966) after which each cup was carefully inspected for the remains of cocoons or larvae in the soil. The trial was repeated twice at separate times, and each trial consisted of 4 replicates (each replicate of 10 solo cups per concentration and per species).

Influence of four types of soil on the efficiency of *H. bacteriophora* against the swede midge. To evaluate the influence of soil type on the efficiency of *H. bacteriophora*, four different soil types were tested: loamy sand (82% sand, 11% silt, 7% clay), sandy loam (74% sand, 13% silt, 13% clay), clay (26% sand, 33% silt, 41% clay); and muck soil (organic matter 81 %). Each soil type was pasteurized prior to the experiments. Soil moisture was set to the point empirically referred as good for seed bed germination and estimated as the following moisture content (w/w): 15% for loamy sand, 9.8% for sandy loam, 12.8% for clay and 61.6 % for muck soil. Plastic cups (30 cm^3) were filled with 15 cm^3 of soil and swede midge larvae were individually placed in the cups at a 1-cm soil depth. After 24 h of incubation at 22 °C in the dark all cups were inoculated with 1000 *H. bacteriophora* IJs in 1 ml of water (with < 1µl of the surfactant Triton X-100). Twelve days after inoculation, emerging adults were recorded during a 30-day period after which the soil was carefully inspected for the presence of remains of cocoons or larvae. The trial was repeated twice at separate times, the first trial with 4 replicates, and the second with 3 (each replicate of 10 solo cups per soil type and per concentration).

Statistical analyses

Coccinellid predators

The voracity of the two species of coccinellid predators was compared using a Student's *t* test after square root transformation of the data. For the voracity of different instars of *H. axyridis*, the data were log10 (x+1) transformed and an ANOVA was used followed by a multiple comparison test by Tukey HSD. Finally, data for the choice test were analyzed using pairwise comparisons with a Wilcoxon's signed ranks test (data not normally distributed). The alpha level was set at $P = 0.05$ and the statistical analyses were conducted using the Statistical Analysis System (SAS Institute 2001).

Entomopathogenic nematodes

Data were arcsine transformed before statistical analyses with the following formula: arcsine $\sqrt{[(x+3/8)/(n+3/4)]}$ to handle heteroscedasticity (Anscombe 1948, Zar 1996). Comparisons between treatments were performed using a two-way ANOVA (factors: species and concentration, or soil type and nematodes) and one-way ANOVA (concentrations within species) respectively. When significant differences were found, multiple comparisons were performed using the least significance difference (LSD) mean comparison procedure. The variances and normality were checked by the univariate procedure and a residual plot respectively. The alpha level was set at $P = 0.05$ and the statistical analyses were performed using the Statistical Analysis System (SAS Institute 2001).

Results

Survey for natural enemies of swede midge in infested fields

The total numbers of swede midge larvae inspected for the presence of parasitoids were 1830 in 2004 and 3312 in 2005. For both years of the study, no parasitoids emerged from the incubated swede midge larvae. During the first year of the study, two species of coccinellid predators (*H. axyridis* and *C. septempunctata*) were found in mid-July at both experimental sites and further research was conducted under laboratory conditions to evaluate the potential of these predators on the swede midge (see next section).

Predation experiments

Voracity of two species of coccinellid predators. After 1h contact, adults of *H. axyridis* consumed significantly more swede midge larvae than adults of *C. septempunctata* (*H. axyridis* 20.2 ± 2.2 larvae; *C. septempunctata* 11. 4 ± 1.6 larvae; t = 3.18; df = 28; $P \leq 0.05$).

Voracity of different instars of *H. axyridis.* The total number of prey consumed differed significantly according to predator instars ($F = 25.58$; df = 2; $P \leq 0.05$). Fourth instar larvae and adults of *H. axyridis* consumed significantly more swede midge larvae than did second instar larvae (Fig. 3.1).

Prey choice by *H. axyridis* adults. In choice tests, *H. axyridis* consumed on average 7.7 ± 1 swede midge larvae and 9.4 ± 0.6 aphids, which was not significantly different (*z-value* = -1.534; $P = 0.125$).

Predatory efficiency of *H. axyridis* on broccoli. In both artificially and naturally infested broccoli plants, and with either low or high predator density, no predation occurred as all swede midge larvae were still present 24 h after the release of the coccinellid predators. With the artificially infested broccoli plants, the larvae did not form a gall, however 60% of the larvae remained at the site where they were deposited (apical meristem); the remaining 40% were found on the tissue paper at the bottom of the plant. In the second experiment with naturally infested plants, gall formation occurred, and 100 % of the larvae were found in the growing tips. These results show that even at five adults per cage, the coccinellids had no impact on swede midge larvae on broccoli plants.

Entomopathogenic nematode experiments

Susceptibility of swede midge to three species of EPN. When the effect of EPN species and concentration on the percentage of swede midges emerging was analyzed by a two-way ANOVA, EPN species, concentrations and interactions were statistically significant in trial #1 (species: $F = 6.78$, df = 2, $P = 0.0032$; concentration: $F = 8.76$, df = 3, $P = 0.0002$; interaction: $F = 3.82$, df = 6, $P = 0.0048$), and trial #2 (species: $F = 32.50$, df = 2, $P < 0.0001$; concentration: $F = 8.71$, df = 3, $P = 0.0002$; interaction: $F = 8.45$, df = 6, $P < 0.0001$). The only EPN species that caused a mortality higher than the control was *H. bacteriophora* in both trials (trial #1: $F = 15.94$, df = 3, $P = 0.0002$; Trial #2: $F = 44.70$, df = 3, $P < 0.0001$), and this species caused 80-87 % mortality at concentrations above 500 IJs per swede midge larvae (Table 3.1).

Influence of four types of soil on the efficiency of *H. bacteriophora* against swede midge. The nematode *H. bacteriophora*, when applied at a rate of 1000 IJs, caused mortality above 90 % to swede midge larvae in the four different soil types (Fig. 3.2). This mortality was significantly higher than in the control for all soil types but there was no significant differences between soil types in trial #1 (soil type: $F = 1.11$, df = 3, $P = 0.3637$; nematodes: $F = 186.21$, df = 1 $P < 0.0001$; interaction: $F = 2.28$, df = 3, $P = 0.1049$) or trial #2 (soil type: $F = 2.28$, df = 3, $P = 0.1188$; nematodes: $F = 512.01$, df = 1, $P < 0.0001$; interactions: $F = 1.89$, df = 3, $P = 0.1726$).

Discussion

Four years after the presence of the swede midge was reported in Canada (Hallett and Heal 2001), no specialized natural enemies (parasitoids) were found in Quebec. Although gall midges (Diptera: Cecidomyiidae), including *Contarinia* species, are attacked by several parasitoid species in North America, mainly from Platygasteridae, Pteromalidae, and Torymidae (Gagné 1989), no transfer of such parasitoids to the new invasive species has yet been demonstrated. The fact that the native *Contarinia* species occupy ecological niches different than those occupied by the swede midge (R.J. Gagné 2004 personal communication), that attacks exclusively members of the Brassicaceae family (Barnes 1946, Stokes 1953), could be one of the reasons explaining why parasitoids attacking other *Contarinia* species have not switched to the swede midge. The data from this study confirms that the swede midge has arrived in North America without its associated natural enemies reported from its region of origin (Eurasia) (Bovien and Knudsen 1950, Rogerson 1963, Readshaw 1966, Readshaw 1968) as it is often the case with invasive species (Scorza 1983). The only record of a natural enemy in North America is a generalist polyphagous predator, *Medetera* sp. (Diptera: Dolichopodidae), which was found preying on swede midge adults in Ontario (Goodfellow 2005). In general, *Medetera* species are generalist predators of bark beetles, aphids and mites (Nagel and Fitzgerald 1975, Rathman et al. 1988, Wermelinger 2002) as are the two polyphagous coccinellids that were tested in this study.

Laboratory experiments showed the acceptance of swede midge larvae by *H. axyridis* and *C. septempunctata* in small containers and confirmed the polyphagous nature of these two coccinellid species (Kring et al. 1985, McClure 1986, Lucas et al. 1997, Koch 2003, Koch et al. 2003, Lucas et al. 2004). The higher voracity of *H. axyridis* compared to *C. septempunctata* has also been previously demonstrated on other prey (Lucas et al. 1997). Voracity increases with successive instars of *H. axyridis* (Miura and Nishimura 1980), and in the laboratory experiments, fourth-instar larvae and adults consumed on average more swede midge larvae than did second instars. Under natural conditions, *H. axyridis* uses a series of visual and olfactory clues to locate its prey (Koch

2003) and the absence of such clues probably resulted in the lack of predation observed here with both artificially and naturally infested broccoli. In these tests, the predators were not able to find the swede midge larvae, contrary to the experiments in the small containers where predation was observed. However, other species of predators could be more efficient against late instar swede midge larvae just before pupation when these larvae move into the soil. For instance, carabid predators *Agonum*, *Amara*, *Bembidion* and *Pterostichus* prey on wheat midge larvae *Sitodiplosis mosellana* Gehin (Diptera: Cecidomyiidae) on the soil (Floate et al. 1990). Similarly, Holland and Thomas (2000) showed that polyphagous predators such as Carabidae, Staphylinidae and Araneae reduced the numbers of *S. mosellana* in the soil.

Among the EPN tested, *H. bacteriophora* was the only species that caused a significant mortality to swede midge larvae. This could be explained by the searching strategy (cruiser) of this nematode (Kaya and Gaugler 1993) that actively seeks hosts through the soil (Hominick et al. 1996, Griffin et al. 2005). Similar results were observed in another gall midge species where *Heterorhabditis heliothidis* (= *bacteriophora*) was observed to eradicate gall midge larvae *Heteropeza pygmaea* Winnertz (Diptera: Cecidomyiidae) in beakers filled with spawned compost using a high concentration of nematodes per beaker of 100 000 IJs (Richardson, 1987). Powell and Webster (2004) evaluated the potential of three species of entomopathogenic nematodes upon *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) when pupating in soil. They found that at an application rate of 25 IJs/cm^2, *H. bacteriophora* and *S. carpocapsae* were the only species that significantly reduced the emergence of adults from the soil. Nielsen and Philipsen (2005) found that *Dasineura brassicae* Winnertz (Diptera: Cecidomyiidae) during pupation in the soil were almost unaffected by the nematodes *S. bicornutum* Tallosi, *S. carpocapsae*, *S. feltiae* and *H. bacteriophora* at a concentration of 250 IJs/larva, this lack of effect in the host was probably the result of the low concentration of nematodes tested. For the swede midge, a high concentration (up to 1000 IJs/larva) is needed in order to have a significant mortality of the larvae in the soil.

In the second experiment with EPN using a high concentration (1000 IJs per swede midge larva), *H. bacteriophora* caused high mortality (90-100%) on swede midge larvae in all soils tested. Although soil texture may affect mobility of EPN (Georgis and Poinar 1983, Choo and Kaya 1991), compaction of the soil is probably an important factor that interacts with soil texture to significantly reduce the movement of EPN (Portillo-Aguilar et al. 1999). In all experiments, because soil was not compacted and a high rate of nematodes was used, there was a rapid distribution of the nematodes in the container resulting in no differences in the mortality of the swede midge by *H. bacteriophora* among soils. However, at lower rates of nematodes, differences could appear between soil types.

While this study indicates that specialized natural enemies of the swede midge are absent from cruciferous crops in Quebec and that generalist predators are unlikely to control the swede midge, EPN hold promises and should be considered for additional testing. Furthermore, because the only currently available method to control swede midge in Ontario and Quebec is through pesticide applications, the use of EPN could represent a valuable tool for an Integrated Pest Management approach, and even more so for organic productions where chemical products are not used.

References

Anscombe, F. J. 1948. The transformation of poisson, binomial, and negative binomial data. Biometrika 35: 246-254

Barnes, H. F. 1946. Gall midges of economic importance. Volume I. Gall midges of root and vegetable crops. Crosby Lockwood and Son Ltd., London. 104pp.

Bovien, P. and P. Knudsen. 1950. Krusesygegalmyggen (*Contarinia nasturtii* Kieff.), dens biologi og bekaempelse. Tid. Planteaul. 53: 235-257

Canadian Food Inspection Agency. 2003. Summary of plant quarantine pest and disease situations in Canada in 2003. http://www.inspection.gc.ca/english/sci/surv/sit2003e.shtml#connas. Accessed 20 August 2006

Choo, H. Y. and H. K. Kaya. 1991. Influence of soil texture and presence of roots on host finding by *Heterorhabditis bacteriophora*. J. Invertebr. Pathol. 58: 279-280

Clay, K. 2003. Parasites lost. Nature 421: 585-586

Cornell, H. V. and B. A. Hawkins. 1993. Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. Am. Nat. 141: 847–65

Drake, J. M. 2003. The paradox of the parasites: implications for biological invasion. Proc. R. Soc. Lond. Series B, supplement (Biology Letters). 270: S133-S135

Dutky, S. R., Thompson, J. V. and G. E. Cantwell. 1964. A technique for the mass propagation of the DD-136 nematode. J. Insect Pathol. 6: 417-422

Ehlers, R. 1996. Current and future use of nematodes in biocontrol: practice and commercial aspects with regard to regulatory policy issues. Biocontrol Sci. Technol. 6: 303-316

Ehlers, R. and H. M. T. Hokkanen. 1996. Insect biocontrol with non-endemic entomopathogenic nematodes (*Steinernema* and *Heterorhabditis* spp.): conclusions and recommendations of a combined OECD and COST workshop on scientific and regulatory policy issues. Biocontrol Sci. Technol. 6: 295-302

Ehlers, R. and D. I. Shapiro-Ilan. 2005. Mass production. pp 68-75 *in* Grewal, P. S., Ehlers, R. and D. I. Shapiro-Ilan, editors. Nematodes as biocontrol agents. CABI Publishing international, Wallingford, Oxfordshire, UK.

Firlej, A., Chouinard, G. and D. Coderre. 2006. A meridic diet for the rearing of *Hyaliodes vitripennis* (Hemiptera: Miridae), a predator of mites in apple orchards. Biocontrol Sci. Technol. 16: 743-751

Floate, K. D., Doane, J. F. and C. Gillott. 1990. Carabid predators of the wheat midge (Diptera, Cecidomyiidae) in Saskatchewan. Environ. Entomol. 19: 1503-1511

Gagné, R. J. 1989. The plant-feeding gall midges of North America. Cornell University Press, Ithaca, NY. 368pp.

Georgis, R. and G. O. Poinar. 1983. Effect of soil texture on the distribution and infectivity of *Neoaplectana carpocapsae* (Nematoda: Steinernematidae). J. Nematol. 15: 308-311

Goodfellow, S. A. 2005. Population dynamics and predictive modeling of the swede midge, *Contarinia nasturtii* Kieffer. M.Sc. Thesis, University of Guelph.

Griffin, C. T., Boemare, N. E. and E. E. Lewis. 2005. Biology and behaviour. pp 47-64 *in* Grewal, P. S., Ehlers, R. and D. I. Shapiro-Ilan, editors. Nematodes as biocontrol agents. CABI Publishing international. Wallingford, Oxfordshire, UK.

Hallett, R. H. and J. D. Heal. 2001. First Nearctic record of the swede midge (Diptera: Cecidomyiidae), a pest of cruciferous crops from Europe. Can. Entomol. 133: 713-715

Holland, J. M. and S. R. Thomas. 2000. Do polyphagous predators help control orange wheat blossom midge, *Sitodiplosis mosellana* Géhin (Dipt., Cecidomyiidae) in winter wheat? J. Appl. Entomol. 124: 325-329

Hominick, W. M., Reid, A. P., Bohan, D. A. and B. R. Briscoe. 1996. Entomopathogenic nematodes: biodiversity, geographical distribution and the convention on biological diversity. Biocontrol Sci. Technol. 6: 317-331

Kaya, H. K. and R. Gaugler. 1993. Entomopathogenic nematodes. Annu. Rev. Entomol. 38: 181-206

Kikkert, J. R., Hoepting, C. A., Wu, Q., Wang, P., Baur, R. and A. M. Shelton. 2006. Detection of *Contarinia nasturtii* (Diptera: Cecidomyiidae) in New York, a new pest of cruciferous plants in the United States. J. Econ. Entomol. 99: 1310-1315

Koch, R. L. 2003. The multicolored asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. J. Insect Sci. 3: 1-16

Koch, R. L., Hutchison, W. D., Venette, R. C. and G. E. Heimpel. 2003. Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). Biol. Control. 28: 265-270

Kring, T. G., Gilstrap, F. E. and G. J. Michels. 1985. Role of indigenous coccinellids in regulating greenbugs (Homoptera: Aphididae) on Texas grain sorghum. J. Econ. Entomol. 78: 269-273

Lucas, E., Coderre, D. and C. Vincent. 1997. Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. Entomol. Exp. Appl. 85: 151-159

Lucas, E., Demougeot, S., Vincent, C. and D. Coderre. 2004. Predation upon the oblique-banded leafroller, *Choristoneura rosaceana* (Lepidoptera: Tortricidae), by two aphidophagous coccinellids (Coleoptera: Coccinellidae) in the presence and absence of aphids. Eur. J. Entomol. 101: 37-41

McClure, M. S. 1986. Role of predators in regulation of endemic populations of *Matsucoccus matsumarae* (Homoptera: Margarodidae) in Japan. Environ. Entomol. 15: 976–983

Miura, T. and S. Nishimura. 1980. The larval period and predacious activity of an aphidophagous coccinellid, *Harmonia axyridis* Pallas. Bull. Fac. Agri., Shimane University. 14: 144-148

Mitchell, C. E. and A. G. Power. 2003. Release of invasive plants from fungal and viral pathogens. Nature 421: 625–27

Nagel, W. P. and T. D. Fitzgerald. 1975. *Medetera aldrichii* larval feeding behavior and prey consumption (Dipt.: Dolichopodidae). Entomophaga 20: 121-127

Nielsen, O. and H. Philipsen. 2005. Susceptibility of *Meligethes* spp. and *Dasyneura brassicae* to entomopathogenic nematodes during pupation in soil. BioControl 50: 623-624

Portillo-Aguilar, C., Villani, M. G., Tauber, M. J., Tauber, C. A. and J. P. Nyrop. 1999. Entomopathogenic nematode (Rhabditida: Heterorhabditidae and Steinernematidae) response to soil texture and bulk density. Environ. Entomol. 28: 1021-1035

Powell, J. R. and J. M. Webster. 2004. Interguild antagonism between biological controls: impact of entomopathogenic nematode application on an aphid predator, *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). Biol. Control 30: 110-118

Rathman, R. J., Brunner J. F. and S. J. Hulbert. 1988. Feeding by *Medetera* species (Diptera: Dolichopodidae) on aphids and eriophyid mites on apple, *Malus domestica* (Rosaceae). Proc. Entomol. Soc. Washington 90: 510-512

Readshaw, J. L. 1966. The ecology of the swede midge, *Contarinia nasturtii* (Kieff.) (Diptera, Cecidomyiidae). I. Life-history and influence of temperature and moisture on development. Bull. Entomol. Res. 56: 685-700

Readshaw, J. L. 1968. Damage to swedes by the swede midge, *Contarinia nasturtii* (Kieff.), and a possible method of cultural control. Bull. Entomol. Res. 58: 25-29

Richardson, P. N. 1987. Susceptibility of mushroom pests to the insect-parasitic nematodes *Steinernema feltiae* and *Heterorhabditis heliothidis*. Ann. Appl. Biol. 111: 433-438

Rogerson, J. P. 1963. Swede midge on two Northumberland farms, 1959-1961. Plant Pathol. 12: 161-171

SAS Institue. 2001. SAS/STAT User's guide, version 8. Cary, NC.

Scorza, R. 1983. Ecology and genetics of exotics. pp 219-238 *in* Wilson, C. L. and C. L. Graham, editors. Exotic plant pests and North American agriculture. Academic Press, New York.

Stokes, B. M. 1953. Biological investigations into the validity of *Contarinia* species living on the Cruciferae, with special reference to the swede midge, *Contarinia nasturtii* (Kieffer). Ann. Appl. Biol. 40: 726-741

Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J. and A. M. Kuris. 2003. Introduced species and their missing parasites. Nature 421: 628-630

Torchin, M. E. and C. E. Mitchell. 2004. Parasites, pathogens, and invasions by plants and animals. Front. Ecol. Environ. 2: 183-190

Wermelinger, B. 2002. Development and distribution of predators and parasitoids during two consecutive years of an *Ips typographus* (Col., Scolytidae) infestation. J. Appl. Entomol. 126: 521-527

Wu, Q., Zhao, J., Taylor, A. and A. M. Shelton. 2006. Evaluation of insecticides and application methods against *Contarinia nasturtii* (Diptera: Cecidomyiidae), a new invasive insect pest in the United States. J. Econ. Entomol. 99: 117-122

Zar, J. H. 1996. Biostatistical analysis. 3rd ed. Prentice Hall, Upper Saddle River, NJ New Jersey. 662pp.

Table 3.1. Percent mortality (mean ± S.E.) of the swede midge when treated with different concentrations of *Steinernema carpocapsae*, *Steinernema feltiae*, and *Heterorhabditis bacteriophora*.

	S. carpocapsae		*S. feltiae*		*H. bacteriophora*	
IJs/larva	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2
0	32.5 ± 2.5 a*	20.0 ± 5.7 a	40.0 ± 7.0 a	42.5 ± 2.5 a	35.0 ± 9.5 a	42.5 ± 4.7 a
50	65.0 ± 5.0 a	20.0 ± 10.8a	45.0 ± 6.4 a	50.0 ± 4.0 a	57.5 ± 2.5 b	30.0 ± 4.0 a
500	57.5 ±16.0a	37.5 ± 8.5 a	60.0 ± 5.7 a	35.0 ± 8.6 a	80.0 ± 7.0 c	87.5 ± 4.7 b
1000	40.0 ± 4.0 a	20.0 ± 9.1 a	47.5 ± 9.4 a	47.5 ± 10.3a	85.0 ± 5.0 c	85.0 ± 2.8 b

* Means followed by the same letter within column are not significantly different between concentrations (IJs/larva) (LSD, $P \leq 0.05$).

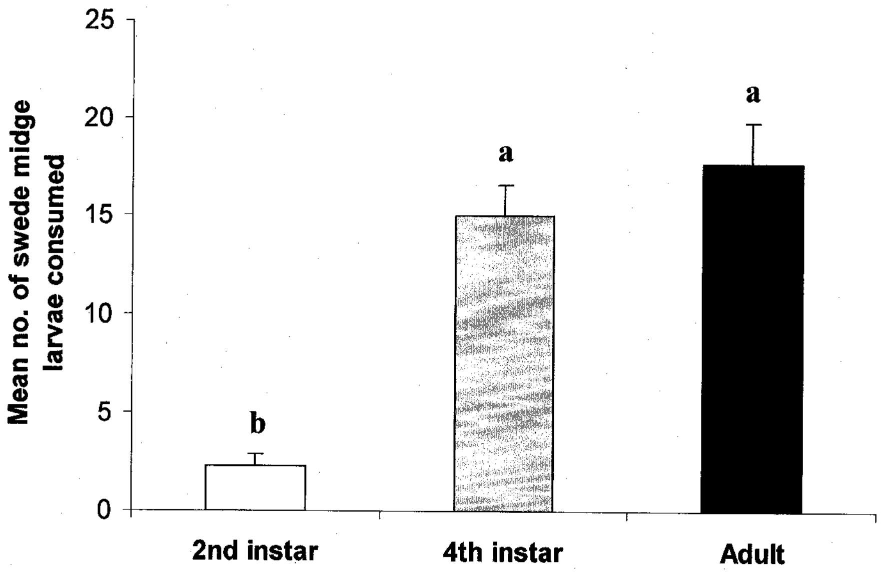

Figure 3.1. Voracity (mean ± S.E.) of different instars of *Harmonia axyridis* against swede midge larvae in 1h experiments. Different letters indicate significant difference between instars (Tukey HSD, $P \leq 0.05$).

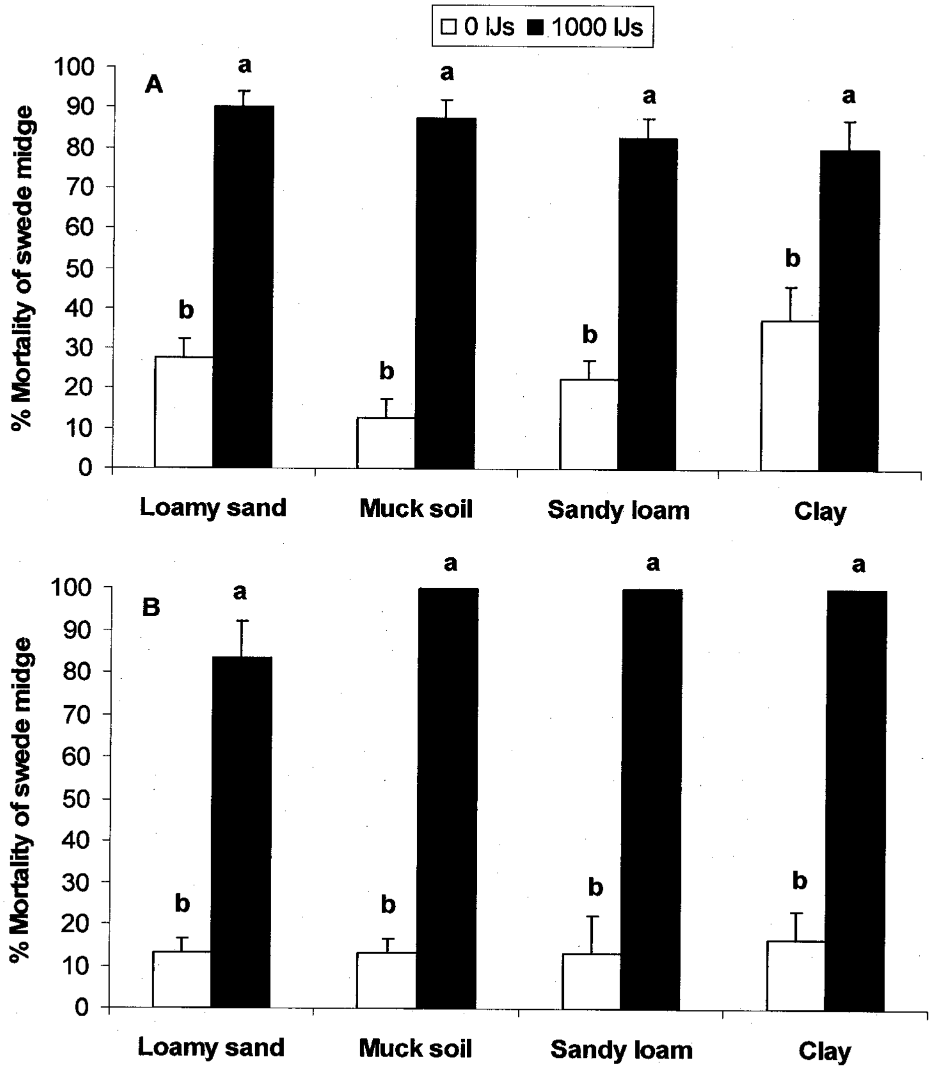

Figure 3.2. Percentage (mean ± S.E.) of swede midge mortality in different soil types, after application of 1000 IJs of *H. bacteriophora* in trial #1 (A) and #2 (B). Bars with the same letters are not significantly different (LSD, $P \leq 0.05$).

Chapter 4. General Discussion and Conclusion

Ever since the swede midge was identified in Ontario and Quebec the Canadian Food Inspection Agency gave it the status of a quarantine pest. In infested regions, producers have to comply with phytosanitary requirements to prevent the spread of swede midge (CFIA 2002). In Quebec, this study provides the first description of the seasonal development of this species; a survey of natural enemies on infested cole crops fields, and finally the evaluation of the susceptibility of the swede midge to commercially available entomopathogenic nematodes.

With three to four overlapping generations during the two-year study, the swede midge was present during the entire production season (May-October). As previously observed in Europe by Bardner et al. (1971), and during these experiments, late transplants are usually more heavily attacked compared to early transplants. Based on this observation, fields should be planted as early as possible to avoid damage due to swede midge summer generations. This study also suggests that cole crops have different susceptibility to the swede midge, as previously observed in Ontario (Hallett and Callow 2004), with broccoli and cauliflower being the most susceptible crops. If at all possible, fields with previous swede midge infestations should not be planted with these crops in successive years.

Natural enemies are organisms that kill and decrease the reproductive potential of another organism, and in pest management, they constitute an important factor in the mortality of pest populations (DeBach and Rosen 1991, Flint and Dreistadt 1998). During the survey of natural enemies of swede midge in Quebec, no specific natural enemies, such as parasitoids, were found. The swede midge thus did not arrive with its native natural enemies, as predicted by the enemy release hypothesis. The new enemy-free environment has facilitated the establishment of this invasive pest. *Medetera* sp. (Diptera: Dolichopodidae), a polyphagous predator consuming swede midge adults (Goodfellow 2005) has been reported in Ontario, however its potential as a biological control agent remains unclear. In addition, it was shown that two polyphagous predators, *Harmonia* *axyridis* and *Coccinella septempunctata*, although they preyed on swede midge larvae in plastic containers, were unable to prey on swede midge larvae on infested broccoli plants. While native generalist polyphagous predators, such as *Medetera* sp., could prey on the swede midge, further studies are necessary to evaluate their potential as biocontrol agent. As most of the natural enemies for the swede midge in its native region of origin are hymenopteran parasitoids of Platygasteridae and Chalcididae (Bovien and Knudsen 1950, Rogerson 1963, Readshaw 1966, Readshaw 1968), the swede midge could be an ideal candidate for classical biological control through importation of these native parasitoids into the region of invasion.

The results with entomopathogenic nematodes showed that *Heterorhabditis bacteriophora* can kill swede midge larvae in the soil. It was observed that mortality on the swede midge increased with the concentration of *H. bacteriophora* (IJs/larvae) and that, regardless of soil type; at a concentration of 1000 (IJs/larva) *H. bacteriophora* was able to cause 90-100% mortality. This is the first report of an entomopathogenic nematode causing mortality to the swede midge. However these are laboratory results and further investigation is necessary to develop effective technology to use this biological control agent. Further research could use field trials targeting overwintering populations that remain in the soil thus preventing subsequent summer generations, evaluate optimum applications, or carry out a cost-benefit analysis when using nematodes. The only effective method to control swede midge infestations in Canada at this moment is the use of the four insecticides currently registered (Pest Management Regulatory Agency 2006). However, there is concern that the swede midge could develop resistance to these products. Therefore, the use of alternative methods of control, including biological control agents such as entomopathogenic nematodes, could represent an important approach to be incorporated into an IPM program.

Monitoring plays an important role in pest identification and management by providing growers and consultants the necessary information to be implemented in IPM programs (Binns et al. 2000). According to Harris and Foster (1999) some of the problems when dealing with cecidomyiid pests is that they are difficult to detect because all life stages are extremely small, adults have a short life span and are thus present during a short period of time, the larval stage typically feeds in sheltered places causing gall formations and damage is usually detected when the larvae have already left the plant. In addition, cecidomyiid pests occur sporadically and outbreaks may appear after the populations have build up in consecutive years (Barnes 1956, Harris and Foster 1999), a phenomenon observed during my experiments. As IPM programs rely on the periodic examination of crops to determine if pest populations are reaching damaging levels, the use of pheromone traps constitutes an important tool for monitoring pests; and when combined with visual inspection of the pest in the field, it gives an insight of the situation in the field. During my experiments, when combining the newly developed pheromone trap for the swede midge (Hillbur et al. 2005), emergence cages and visual inspection of larvae on the plants, I was able to monitor the seasonal development of swede midge population. Furthermore, by using the pheromone traps in combination with visual inspection I was able to find a relationship between adult swede midge captures and the number of larvae present on infested plants. However, the practical use of the emergence cages is questionable. First of all, due to its cumbersome nature it is impractical to use on commercial farms because it is labor intensive and requires qualified personal to identify the swede midges. Pheromone traps proved to be the best monitoring tool together with visual inspection of the plants. The pheromone trap is currently being used by the Canadian Food Inspection agency to detect new outbreaks in regions in Canada, and there is ongoing research to establish economic thresholds based on adult captures and timing of insecticides.

Overall, the results of this study increased the understanding of the biology of the swede midge under agro-climatic conditions in the new region of invasion, and also demonstrated the lack of specific natural enemies. Furthermore, it demonstrates the potential use of entomopathogenic nematodes as biological control agents. However, in order to manage swede midge infestations, it is important to consider several methods that include effective monitoring techniques, rotation of crops when swede midge has been found previously in infested areas, agricultural practices and the use of insecticides only when needed. An IPM program combining all these methods would be the most effective strategy to be used against the swede midge.

Chapter 5. References

Bardner, H. M., Edwards, C. A., Arnold, M. K. and J. P. Rogerson. 1971. The symptoms of attack by swede midge (*Contarinia nasturtii*) and effects on the yield of swedes. Entomol. Exp. Appl. 14: 223-233

Barnes, H. F. 1946. Gall midges of economic importance. Volume I. Gall midges of root and vegetable crops. Crosby Lockwood and Son Ltd., London. 104pp.

Barnes, H. F. 1956. Gall midges of economic importance. Vol. VII. Gall midges of cereal crops. Crosby Lockwood and Son Ltd, London. 261pp.

Binns, M. R., Nyrop, J. P. and W. Van Der Werf. 2000. Sampling and monitoring in crop protection. CAB International, Wallingford, Oxon, UK. 284pp.

Bovien, P. and P. Knudsen. 1950. Krusesygegalmyggen (*Contarinia nasturtii* Kieff.), dens biologi og bekaempelse. Tid. Planteaul. 53: 235-257

Canadian Food Inspection Agency. 2002. Interim phytosanitary requirements to prevent the entry and spread of swede midge (*Contarinia nasturtii*). http://www.inspection.gc.ca/english/plaveg/protect/dir/d-02-06e.pdf. Accessed 10 December 2005

Canadian Food Inspection Agency. 2003. Summary of plant quarantine pest and disease situations in Canada in 2003. http://www.inspection.gc.ca/english/sci/surv/sit2003e.shtml#connas. Accessed 20 August 2006

Canadian Food Inspection Agency. 2006. Lists of regulated countries and regulated areas within Canada for swede midge. http://www.inspection.gc.ca/english/plaveg/protect/dir/smidgee.shtml. Accessed 20 August 2006

Capinera, J. L. 2001. Handbook of vegetable pests. Academic Press, San Diego, Ca. 729pp.

Clay, K. 2003. Parasites lost. Nature 421: 585-586

DeBach, P. and B. R. Bartlett. 1964. Methods of colonization, recovery, and evaluation. pp 402-426 *in* DeBach, P. and E. I. Schlinger, editors. Biological control of insect pests and weeds. Reinhold Publishing Corp., New York.

DeBach, P. and D. Rosen 1991. Biological control by natural enemies. 2nd ed. Cambridge University Press, New York. 440pp.

di Castri, F. 1989. History of biological invasion with special emphasis on the old world. pp 1-30 *in* Drake, J. A., Mooney, H. A., di Castri, F., Groves, R. H., Kruger, F. J., Rejmanek, M. and M. Williamson, editors. Biological invasions: a global perspective. John Wiley and Sons, New York.

Finch, S. and A. R. Thompson. 1992. Pests of cruciferous crops. pp 87-138 *in* McKinlay, R. G., editor. Vegetable crop pests. CRC Press, Boca Raton, Fl.

Flint, M. L. and S. H. Dreistadt. 1998. Natural enemies handbook: the illustrated guide to biological pest control. Publ. 3386. University of California Press, Berkeley.

Goodfellow, S. A. 2005. Population dynamics and predictive modeling of the swede midge, *Contarinia nasturtii* Kieffer. M.Sc. Thesis. University of Guelph.

Hallett, R. H. and J. D. Heal. 2001. First Nearctic record of the swede midge (Diptera: Cecidomyiidae), a pest of cruciferous crops from Europe. Can. Entomol. 133: 713-715

Hallett, R. H. and K. Callow. 2004. Host preferences of the swede midge: cole crops, asian crucifers and cruciferous weeds. Ontario Fruit and Vegetable Convention and trade show, February 18-19, St. Catharines, Ontario.

Harris, M. O. and S. P. Foster. 1999. Gall midges. pp 27-49 *in* Hardie, J. and A. K. Minks, editors. Pheromones of non-lepidopteran insects associated with agricultural plants. CAB International, Oxford, UK.

Hillbur, Y., Celander, M., Baur, R., Rauscher, S., Haftmann, J., Franke, S. and W. Francke. 2005. Identification of the sex pheromone of the swede midge, *Contarinia nasturtii*. J. Chem. Ecol. 31: 1807-1828.

Howard, R. J., Garland, J. A. and W. L. Seaman. 1994. Diseases and pests of vegetable crops in Canada. The Canadian Phytopathological Society and the Entomological Society of Canada. 554pp.

Mack, R. N., Barrett, S. C. H., DeFur, P. L., MacDonald, W. L., Madden, L. V., Marshall, D. S., McCullough, D. G., McEnvoy, P. B., Nyrop, J. P., Reichard, S. E. H., Rice, K. J. and S. A. Tolin. 2002. Predicting invasions of nonindigenous plants and plant pests. National Academy Press, Washington, DC. 194pp.

Pest Management Regulatory Agency. 2006. EDDENet, ELSE Label search. http://eddenet.pmra-arla.gc.ca/4.0/4.0.asp. Accessed 10 July 2006

Readshaw, J. L. 1966. The ecology of the swede midge, *Contarinia nasturtii* (Kieff.) (Diptera, Cecidomyiidae). I. Life-history and influence of temperature and moisture on development. Bull. Entomol. Res. 56: 685-700

Readshaw, J. L. 1968. Damage to swedes by the swede midge, *Contarinia nasturtii* (Kieff.), and a possible method of cultural control. Bull. Entomol. Res. 58: 25-29

Rogerson, J. P. 1963. Swede midge on two Northumberland farms, 1959-1961. Plant Pathol. 12: 161-171

Sailer, R. I. 1983. History of insect introductions. pp 15-38 *in* Wilson, C. L. and C. L. Graham, editors. Exotic plant pests and North American agriculture. Academic Press, New York.

Scorza, R. 1983. Ecology and genetics of exotics. pp 219-238 *in* Wilson, C. L. and C. L. Graham, editors. Exotic plant pests and North American agriculture. Academic Press, New York.

Stokes, B. M. 1953. Biological investigations into the validity of *Contarinia* species living on the Cruciferae, with special reference to the swede midge, *Contarinia nasturtii* (Kieffer). Ann. Appl. Biol. 40: 726-741

Sumner, D. A. 2003. Exotic pests and public policy for biosecurity: an introduction and overview. pp 3-6 *in* Sumner, D. A., editor. Exotic pests and diseases, biology and economics for biosecurity. Iowa State Press, Ames, Iowa.

Toepfer, S. and U. Kuhlmann. 2004. Survey for natural enemies of the invasive alien chrysomelid, *Diabrotica virgifera virgifera*, in central Europe. BioControl 49: 385-395

Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J. and A. M. Kuris. 2003. Introduced species and their missing parasites. Nature 421: 628-630

Wallace, M. S. and F. P. Hain. 2000. Field surveys and evaluation of native and established predators of the hemlock woolly adelgid (Homoptera: Adelgidae) in the southeastern United States. Environ. Entomol. 29: 638-644

Warwick, S. I., Francis, A. and G. A. Mulligan. 2003. Brassicaceae of Canada. Agriculture and Agri-Food Canada, Canadian Biodiversity Facility, Eastern Cereal and Oilseed Research Centre (ECORC). http://www.cbif.gc.ca/spp_pages/brass/index_e.php. Accessed 15 March 2006

Wolfe, L. M. 2002. Why alien invaders succeed: support for the escape-from-enemy hypothesis. Am. Nat. 160: 705-711