Potential distribution and relative abundance of swede midge, *Contarinia nasturtii*, an invasive pest in Canada

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Abstract

The swede midge, *Contarinia nasturtii* (Kieffer) (Diptera: Cecidomyiidae), is a pest of most cultivated Brassicaceae such as broccoli, canola, cauliflower, cabbage, and Brussels sprouts. The species primarily has a Palearctic distribution and occurs throughout Europe and southwestern Asia to the Caucasus. Between 1996 and 1999, producers of cruciferous vegetables in Ontario, Canada, reported crop damage that was consistent with damage symptoms characteristic of *C. nasturtii* feeding and in 2000, field studies confirmed that this damage was caused by *C. nasturtii*. A bioclimatic model was developed to predict potential range and relative abundance of *C. nasturtii* in Canada in order to determine the impact of the establishment and spread of *C. nasturtii* populations. Model output indicated that *C. nasturtii* could potentially become established in all provinces of Canada, with the risk being greatest in southwestern British Columbia, southern Ontario and Quebec, New Brunswick, Nova Scotia, and Prince Edward Island. Results indicated that *C. nasturtii* population growth in the Prairie Ecozone of western Canada would be greatest in years with above average precipitation.

Introduction

Swede midge, *Contarinia nasturtii* (Kieffer) (Diptera: Cecidomyiidae), is a pest of cruciferous plants (Brassicaceae) (Barnes, 1946). This species primarily has a Palearctic distribution which includes Austria, Belgium, Britain, Bulgaria, Czech Republic, Denmark, France, Germany, Hungary, Ireland, Italy, Latvia, Lithuania, Norway, Poland, Portugal, Romania, Russia, Slovakia, Slovenia, Spain, Sweden, Switzerland, The Netherlands, Turkey, Ukraine, Yugoslavia, and southwestern Asia to the Caucasus (Skuhrava, 1986; Darvas et al., 2000; Garland, 2002; Fauna Europaea Web Service, 2004).

Plant hosts include cruciferous weeds and most cultivated crucifers such as broccoli, canola, cauliflower, cabbage, and Brussels sprouts (Stokes, 1953; Darvas et al., 2000). Plant damage is caused by larval feeding; symptoms include misshapen plants and the formation of galls on leaves and flowers (Bardner et al., 1971). The larval stage overwinters in the soil, adults emerge in May and females

lay eggs, in clusters of 2–50, on the surface of actively growing plants. Larvae feed on actively growing stems, leaves, and flowers, then drop to the soil to pupate. During the growing season, adults can emerge within 2 weeks or larvae enter diapause in autumn. Depending on temperature and soil moisture, *C. nasturtii* may have 2–5 generations (Readshaw, 1961, 1966; Rygg & Braekke, 1980; Hallett & Heal, 2001). Temperature and moisture have been identified to be the two most important factors responsible for population distribution, growth, and control. Population growth was greatest in warm, moist seasons and reduced in cool or dry seasons (Readshaw, 1961).

The recent introduction of *C. nasturtii* to North America presents a risk to widely grown cruciferous crops including broccoli, canola, and cabbage. As early as 1996, producers of cruciferous vegetables in southern Ontario, Canada, reported crop damage that was consistent with symptoms characteristic of *C. nasturtii*. Field studies in 2000 confirmed that this damage was caused by *C. nasturtii* (Hallett & Heal, 2001). In 2005, the Canadian Food Inspection Agency (CFIA) survey detected *C. nasturtii* in 15 counties in Ontario and 20 regulated areas in Quebec (CFIA, 2005).

Bioclimatic simulation models have been used successfully to predict the distribution and extent of insect

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establishment in new environments (McKenney et al., 2003; Olfert et al., 2004; Sutherst & Maywald, 2005). Bioclimatic modelling software, such as CLIMEX (Sutherst et al., 2004), enables the development of models that describe the potential distribution and relative abundance of a species based on climate (Sutherst, 2000). Inferential models infer a species response to climate, based on its geographic range, phenology, relative abundance, and empirical data. CLIMEX models allow researchers to develop an overview of climatic factors that affect species distribution and abundance and permit identification of non-climatic factors that limit species distribution (Sutherst & Maywald, 2005). Sensitivity analysis can be used to test hypotheses related to the effect of varying climate variables (i.e., warmer/cooler or wetter/drier than normal conditions) on the species distribution and abundance.

The objective of the study was to develop a bioclimatic model to predict potential range and relative abundance of *C. nasturtii* in Canada, to identify areas in Canada that are at risk for establishment of the swede midge, and to use the model to develop a better understanding of how climate affects *C. nasturtii* populations.

Methods

The bioclimatic modeling process has been previously described (Vera et al., 2002; Mason et al., 2003; Olfert et al., 2004; Sutherst & Maywald, 2005). CLIMEX models derive Ecoclimatic Index (EI) values that describe the climatic suitability, in terms of insect survival and reproduction, of specific locations. The Growth Index (GI) is a function of weekly temperature – TI, diapause – DI, light – LI, and moisture – MI indices. Stress indices are related to factors that limit geographical distribution and include stress associated with temperature (heat stress – HS, cold stress – CS) and moisture (wet stress – WS, dry stress – DS). Each index value is derived from functions that are based on 2–5 parameters. Indices and related parameters are illustrated in Table 1. The EI value integrates annual growth with annual stress to produce a single value (between 1 and 100) for each location. EI values near 0 indicate that the location's climate is not suitable for long-term establishment of the species. An EI value greater than 30 indicates a very favourable climate.

Initial parameter values were based on published data that resulted from laboratory and field studies (Stokes, 1953; Readshaw, 1961, 1966; Bardner et al., 1971; Rygg & Braekke, 1980; Bouma, 1996) and are defined in Table 1. Climatic requirements were inferred from known distributions of swede midge in Europe. The model for *C. nasturtii*, using CLIMEX 2.0 (Sutherst et al., 2004), was

developed by iteratively adjusting parameter values to produce mapped results that closely approximated observed distribution for *C. nasturtii* in Europe. Model parameterization was conducted for Belgium, Britain, France, Germany, Switzerland, Norway, and The Netherlands. The remaining European countries were treated as an independent data set and used for model validation. Once the European distribution was defined, based on a visual comparison of model output with observed distribution, EI values were compared to reported data on relative abundance. Published results related to abundance were used to refine parameter values so that highest EI values occurred where *C. nasturtii* was known to cause damage and lower values occurred when the species was less prevalent.

The model was validated by comparing output to reported distributions and seasonal phenology and tested for consistency with empirical data. Three methods were used to validate the model first, the model was applied to predict the population distribution of *C. nasturtii* in eastern Europe (Bulgaria, Czech Republic, Hungary, Poland, Romania, Slovakia, Ukraine, and Yugoslavia), Asia, southern Ontario, and New York State. Model output for these regions was compared to known distributions as reported by Skuhrava (1986), Darvas et al. (2000), Garland (2002), Fauna Europaea Web Service (2004), and CFIA (2005). Second, model output for phenology and number of generations was compared to published reports for Europe (Readshaw, 1961, 1966; Rygg & Braekke, 1980; Bouma, 1996). Third, model results which related to insect phenology, based on southern Ontario weather data as input, were compared to field data collected by R. Hallett (unpubl.).

The CLIMEX model required five meteorological inputs: temperature (maximum and minimum), precipitation, and relative humidity (at 09:00 and 15:00 hours). The Compare Locations function required monthly long-term average climatic variables. Climate data from New et al. (1999) were used as an input for the Compare Locations function. The data set represents a splined 0.5° world grid data set. Models were run for Europe ($n = 6416$ grids) and Canada (south of 65°N latitude, $n = 4472$ grids). The moisture index (MI) is based on a calculated soil moisture value. CLIMEX used a hydrological submodel to compute a weekly soil moisture balance. Soil moisture balance was based on soil moisture from the previous week, and current week values for precipitation and evapotranspiration. CLIMEX used a degree-day model, based on the algorithm published by Baskerville & Emin (1969) to compute the temperature index (TI) and the potential number of generations per year.

Contour maps were generated by importing CLIMEX output into ARCVIEW 8.1 (ESRI Inc., 2001). EI values

Table 1 Descriptions of CLIMEX parameters and parameter values used to predict the potential distribution and relative abundance of *Contarinia nasturtii* in Canada

Index	Parameter	Description	Value
Temperature	DV0	Limiting low temperature	10.0 °C
	DV1	Lower optimal temperature	16.0 °C
	DV2	Upper optimal temperature	25.0 °C
	DV3	Limiting high temperature	32.5 °C
Moisture	SM0	Limiting low soil moisture	0.15
	SM1	Lower optimal soil moisture	0.40
	SM2	Upper optimal soil moisture	1.40
	SM3	Limiting high moisture	1.50
Diapause	DPD0	Diapause induction day length	14 h
	DPT0	Diapause induction temperature	10 °C
	DPT1	Diapause termination temperature	6 °C
	DPD	Diapause development days	150
Cold stress	DPSW	Diapause indicator for winter diapause	0
	TTCS	Cold stress threshold	-18 °C
	THCS	Cold stress temperature rate	-0.0008
	TTHS	Heat stress temperature threshold	35 °C
Heat stress	THHS	Heat stress temperature rate	0.005
	SMDS	Dry stress threshold	0.10
Dry stress	HDS	Dry stress rate	-0.01
	SMWS	Wet stress threshold	1.50
Wet stress	HWS	Wet stress rate	0.0005
Day-degree accumulation above DV0	DV0		10
	DV3		35
	DV3		35
Day-degree accumulation above DV3	DV3		35
	DV4		100
Day-degree accumulation above DVCS	DVCS		6.50
	DV4		100
Degree-days per generation	PDD	Minimum degree days above DV0 to complete generation	200

were displayed in four categories: 'unfavourable' (0–10), 'suitable' (10–20), 'favourable' (20–30), and 'very favourable' (>30). The 'suitable' and higher categories represent areas that may experience pest outbreaks of *C. nasturtii*. Actual densities will be dependent on meteorological conditions that differ from climate normals. The 'favourable' and 'very favourable' categories describe meteorological conditions, similar to climate normals, in which outbreaks resulting in crop damage may occur.

Sensitivity analysis was conducted to quantify the response of *C. nasturtii* to changes in precipitation and temperature. Incremental scenarios were developed to reflect the possible range of temperature and precipitation values that could be expected to occur in Europe and Canada, based on current climate. Scenarios were selected, based on potential variation of present climate. EI values,

based on current climate, were compared to scenarios that differed by -2, -1, +1, and +2 °C from current temperatures (maximum and minimum monthly values) and precipitation values (monthly total) that were -40, -20, +20, and +40% of current values. The comparison was conducted for Toronto and four European locations (Table 2). The locations were selected to provide a range of EI values (22–36).

Results and discussion

Model development

Initial temperature threshold values for DV0, DV1, DV2, and DV3 were based on Readshaw (1961, 1966). Developmental thresholds for eggs, larvae, and pupae were 9.5, 11.5, and 6.5 °C, respectively. Egg development was

Table 2 Effect of changes in mean annual temperature and precipitation from current values on ecoclimatic indices for *Contarinia nasturtii* at four European and one Canadian location

Location	Latitude	Longitude	Current	Ecoclimatic indices under different climatic conditions					
				Change in mean temperature (°C)				Change in mean precipitation (%)	
				−1	−2	+1	+2	−20	−40
Stuttgart, BRD	N 48°48′	W 09°11′	36	26	32	39	41	29	15
Rotterdam, NL	N 51°55′	W 04°30′	36	25	31	41	46	35	21
Tynemouth, UK	N 55°01′	W 01°26′	22	10	15	29	36	22	22
Oslo, NOR	N 59°54′	W 10°43′	26	19	23	26	28	18	8
Toronto, CAN	N 43°39′	W 79°20′	32	26	30	32	32	25	14

most rapid at 30 °C, development ceased at 32.5 °C, and greatest viability occurred at 25 °C. Larval development was linear between 15 and 25 °C. Pupal development ceased at 32.5 °C. Adult emergence occurred at all temperatures between 10 and 30 °C, and oviposition occurred between 16 and 26 °C, with the most favourable temperature being 22 °C (Stokes, 1953). DV0 values, between 6 and 14 °C, were iteratively tested in simulation runs and a value of 10.0 °C provided the best fit to the European distribution (Table 1). Similar iterations were conducted to assign values for DV1, DV2, and DV3 (Table 1).

Soil moisture indices (SM0, SM1, SM2, and SM3) reflected the assumption that soil moisture is a major factor affecting plant moisture content and microclimatic conditions (Sutherst et al., 2004). Readshaw (1961) reported that eggs hatched between 95 and 100% r.h., but did not between 75 and 85% r.h. Dry soil conditions resulted in pupae entering a dormant state and the dormancy was terminated in response to thorough wetting of the soil, due to either rain or irrigation. Adult emergence was found to be a function of soil moisture and soil type (Readshaw, 1966). Emergence in sandy loam did not occur at 7.9% soil moisture, very low emergence did occur at 14.9%, and higher emergence occurred at 21–31% soil moisture. Adult emergence in clay soils increased at a linear rate between 40 and 90% soil moisture. The value for SM0 was set to reflect swede midge emergence in sandy loam soils, and SM1 was based on optimal adult emergence values for clay soils (Table 1). Values for SM2 and SM3 reflected conditions for clay soils and allowed for irrigation where soil may become saturated. Field studies indicated that saturation of soil was required to permit adequate soil moisture at the 2.5 cm depth in order to terminate dormancy that results from dry soil conditions (R Hallett, unpubl.).

CLIMEX uses both photoperiod and temperature as inputs for determination of induction and temperature for termination of diapause. Diapause induction was related

to time of pupation and temperature. In Britain, the incidence of diapause increased from summer to winter and also increased with lower temperatures (Readshaw, 1961). Day length was shown to be a more important factor in diapause than temperature (Readshaw, 1966). Diapause induction occurred with day lengths between 10 and 16.6 h. In field conditions, diapause induction occurred at day lengths of 16.5 h (2%) and the rate of induction increased at a linear rate to 100% for a 10-h day length. Simulations indicated that an induction day length of 14 h provided the best fit to Readshaw's data (1966) (Table 1). This value is very similar to bioclimatic models for other species that occur in central Europe (Dosdall et al., 2002; Mason et al., 2003; Olfert et al., 2004). The induction temperature was set at 10 °C so that diapause was initiated during August and September in locations where *C. nasturtii* occurs. Similarly, the diapause termination temperature was defined as 6 °C in order to allow for spring activity in May. In Britain, completion of diapause occurred when the species had spent 100 days between 2 and 5 °C and an additional 30 days at 20–25 °C. Termination of diapause was shown to be related not only to spring temperatures, but also to soil moisture (Readshaw, 1961). Post-diapause development was delayed until the soil was thoroughly wet. Model parameterization resulted in a best fit, in terms of visual comparison of observed European distribution and model output, with a value of 150 diapause development days (DPD) (Table 1).

CLIMEX includes abiotic stress indices (heat, cold, wet, dry, and interactions) to place limits on potential range of the species to survive during unfavourable conditions. Stress values were parameterized to delimit the range of *C. nasturtii* in northern and southern regions of Europe. With respect to temperature, the European distribution of *C. nasturtii* is a result of both cold winter temperatures and suboptimal summer temperatures. Results indicated that suboptimal growing season temperatures north of 60°N were responsible for limiting potential population growth

during the summer months. Pupae overwinter in the soil and may be exposed to temperatures that are substantially different from observed air temperatures, depending on snow depth, soil type, soil moisture, and crop residue. Since *C. nasturtii* has been reported from southern Norway and Sweden, but not Finland, cold stress values for threshold (TTCS) and rate of cold stress accumulation (THCS) (Table 1) were set to limit *C. nasturtii* range to southern locations in Norway, Sweden, and Finland. The threshold for dry stress (SMDS) and rate of dry stress accumulation (HDS) resulted in dry stress accumulation in Portugal, Spain, Italy, Greece, Armenia, Azerbaijan, and southern Russia. Heat stress occurred in southern regions of Turkey.

Model validation

Modeled distribution and relative abundance of *C. nasturtii* in Europe, Asia, southern Ontario, and New York State agreed with published reports (Skuhrava, 1986; Darvas et al., 2000; Fauna Europaea Web Service, 2004; NAPIS, 2004; CFIA, 2005). Swede midge has been reported to be a major pest in Germany, Switzerland, Belgium, The Netherlands, and Slovenia (Readshaw, 1966; Bouma, 1996). It is a minor pest in Poland, Austria, Norway, and Sweden. It is a sporadic pest in Great Britain and France.

The preferred range of this pest species is within the Atlantic and Continental biogeographical regions of Europe (Fauna Europaea Web Service, 2004). These regions are associated with a temperate, humid climate that is characterized by mild temperatures and frequent precipitation. As a result, the distribution is limited by dry, warm conditions in the south and dry, cool conditions in the northern limits. Model output agreed with these observations and analysis suggested that potential range and relative abundance of *C. nasturtii* was most affected by temperature and moisture. In addition to the climatic influences on the pest status of *C. nasturtii*, there are likely a number of non-climatic constraints that limit population build-up throughout Europe. Factors such as fragmentation of suitable habitat, physical barriers, competing species, natural enemies, and intensive control of pests in horticultural production tend to dampen infestation levels (Sutherst & Maywald, 2005).

Observed life history events were compared to model predictions, based on output for weekly GI and DI values and number of generations. Predictions were based on long-term climatic averages rather than site-specific weather data. In Europe, *C. nasturtii* has 2–4 overlapping generations, with three generations in central Europe, the first generation reported to emerge in May and June (Darvas et al., 2000). In Norway, first emergence occurred in June during the 1973 growing season (Rygg & Braekke,

1980). The model predicted that diapause should terminate in late May to early June. In Britain in 1959, first generation adults were collected from fields in the first week of June (Readshaw, 1966). Model output indicated that midge development would begin in mid to late May. Bardner et al. (1971) reported that in 1960, adults were collected from fields in north-eastern England in late September. The model agreed with these observations in that it predicted that *C. nasturtii* should cease activity in late September.

Ecoclimatic Index values indicated that *C. nasturtii* would be most abundant in Germany, Switzerland, Belgium, The Netherlands, Slovenia, France, and Italy (Figure 1A, Table 2). Areas with greatest EI were associated with high TI and MI values and longer growing seasons (Figure 1B,C). Results suggested that areas with high EI values, and a greater number of generations, may have a higher risk than areas with low EI and fewer generations. Regions with optimal TI, MI, and longer growing seasons were predicted to support four generations of *C. nasturtii* per season. Regions that have had pest outbreaks of *C. nasturtii* are associated with climates that have 18 or more weeks with positive values of GI. The longer growing season would be expected to result in the potential for additional generations. The model predicted that the climate in Stuttgart, Germany, has the potential to produce four generations per season. The model predicted that *C. nasturtii* would complete two generations in Norway, three in northern Britain, and three to four in The Netherlands. This agrees with findings of Rygg & Braekke (1980) for Norway, Readshaw (1961) in Britain, and Bouma (1996) for The Netherlands.

Model output, when compared with actual *C. nasturtii* distributions in Canada and New York State, agreed with recent surveys of *C. nasturtii* in Ontario, Quebec, and New York (Hallett & Heal, 2001; NAPIS, 2004; CFIA, 2005). In 2005, CFIA confirmed that there were 15 counties in Ontario and 20 in Quebec that had *C. nasturtii*. The species had been collected in locations that were in close proximity to the St. Lawrence River and crop losses occurred in Ontario (CFIA, 2005; Hallett & Heal, 2001). Model output predicted that, not only could *C. nasturtii* become established in Canada, EI values were large enough to indicate that significant crop loss could result, particularly in agricultural areas bordering the St. Lawrence River (Figure 1D). The climate in this region had temperature and moisture conditions favourable for *C. nasturtii* development and reports confirmed that crop damage, related to *C. nasturtii*, occurred in southern Ontario (Hallett & Heal, 2001; CFIA, 2005). The EI for Toronto (EI = 32) was very similar to areas in Europe where *C. nasturtii* is currently a serious pest including Stuttgart

Figure 1 CLIMEX output for Europe and Canada. EI, ecoclimatic index; TI, diapause index; MI, moisture index.

(EI = 36) (Table 2). Model output, which predicted that *C. nasturtii* activity in southern Ontario would begin in mid to late May, was validated by observations in this region (Hallett & Heal, 2001).

Sensitivity analysis

Results indicated that EI values in scenarios where moisture conditions were above normal were not different than under current conditions. This result was due to the

fact that current moisture levels result in MI values that are between the lower (SM1) and upper (SM2) optimal moisture levels. Values for SM2 were set to permit the occurrence of *C. nasturtii* in irrigated fields. As a result, EI was negatively affected by dryer than normal conditions. A 20% reduction in precipitation resulted in a decrease of EI by 31% in Oslo, while those in Tynemouth did not change (Table 2). Reduced precipitation scenarios in Oslo resulted in lower than optimal soil moisture. When precipitation was reduced by 40%, EI values were 69 and 56% lower for Oslo and Toronto, respectively.

Temperature variation also affected EI, number of generations, and length of growing season (Table 2). Reduced temperatures resulted in lower EI values. The largest differences were observed in Tynemouth, where mean temperatures of 1 and 2 °C lower than average decreased EI values by 32 and 55%, respectively. Stuttgart and Toronto were least sensitive to reduced temperatures. For both locations, lower temperatures resulted in shorter growing seasons and reduced number of generations for *C. nasturtii*. Results indicated that a decrease of 1 °C would result in one less generation and a shorter growing season than for average temperatures. The model predicted that *C. nasturtii* populations in Tynemouth would have 1–2 generations per season, compared to three under average temperature conditions. However, if temperatures were to increase by 1 °C above average, model output predicted that the growing season in Tynemouth would lengthen by about 2 weeks and allow for an additional generation of *C. nasturtii*. A 2 °C increase resulted in two additional generations.

Populations are more sensitive to variations in temperature and precipitation when they occur in regions that are near the limits of their geographic range (Sutherst, 2000). Model output reflected this, in that the population growth of *C. nasturtii* was predicted to be greatest in warm, moist seasons and lowest in cool, dry seasons. For example, *C. nasturtii* populations in Toronto and Stuttgart were predicted to be less likely affected by annual changes in temperature and precipitation than Oslo or Tynemouth, both of which are near the outer limits of this species range. Regions with higher sensitivity are more likely to have low population levels in most years, but will quickly respond to both optimal and suboptimal conditions. The model indicated that relative abundance in southern Ontario would be more similar to central Germany than England or Norway.

Risk in Canada

Model output indicated that *C. nasturtii* could potentially become established in all provinces of Canada (Figure 1D). Results from Europe indicated that pest outbreaks of *C. nasturtii* occur in regions with 18 or more weeks of

positive GI. In Canada, based on climate data, this region is limited to areas in southern Ontario and southern Quebec, along the St. Lawrence River valley. The model predicted that the most significant risk would occur in southern Ontario with a lesser risk in the lower mainland of British Columbia, Quebec, New Brunswick, Nova Scotia, and Prince Edward Island. Southern regions of British Columbia also had isolated areas that were categorized as 'favourable'. Temperatures in these regions were less than those in southern Ontario, resulting in EI = 24–29, suggesting that relative abundance of *C. nasturtii* would be slightly less than in southern Ontario. Results indicated that *C. nasturtii* population growth in the Prairie Ecozone of western Canada may be limited by lack of growing season precipitation and cold stress during the winter. Growing season temperatures (TI) in this region were very similar to values for southern Ontario (Figure 1E). Low MI values, associated with low precipitation values during the growing season, limited EI values (Figure 1F). Due to higher precipitation in July and August, EI values near Edmonton, Alberta, were higher than other regions of the Prairie Ecozone. Further analysis suggested that EI values in this region could double with increased summer rainfall. Simulation runs with increased rainfall in June, July, and August increased EI values from EI = 8–12 to EI = 16–20. As a result, in years when rainfall on the Prairie Ecozone is well above normal, as occurred in 2005 at Saskatoon (60% above normal), the model indicated that the EI would increase from 8 to 18, which would significantly increase the risk of pest establishment.

Establishment of *C. nasturtii* poses a significant risk to cruciferous crops in Canada. Our model indicates that *C. nasturtii* has a high potential to become established in many regions of Canada, if introduced. The species will potentially cause significant damage to crops and economic losses to producers in the event that a population becomes established in canola-growing areas in western Canada. The total value of cruciferous vegetable crops produced in Canada is approximately \$ 120 million annually (Warwick et al., 2005). Canola has a value of \$ 2.2 billion (Canola Council of Canada, 2005) and in the Prairie Ecozone of western Canada 4–5 million ha of summer canola (*Brassica napus* L. and *Brassica rapa* L.) are grown annually (DeClercq, 2004). Results of this study emphasize the need for continued monitoring of swede midge distribution and development of management strategies to minimize the economic and environmental impact of this new pest in Canada.

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