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ARTICLE

Modelling the tri-trophic population dynamics of a host crop (*Triticum aestivum*; Poaceae), a major pest insect (*Sitodiplosis mosellana*; Diptera: Cecidomyiidae), and a parasitoid of the pest species (*Macroglenes penetrans*; Hymenoptera: Pteromalidae): a cohort-based approach incorporating the effects of weather

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Abstract

This paper describes a tri-trophic analysis of the ecological dynamics of a crop, an insect pest, and a natural enemy of the insect pest. Worldwide wheat (*Triticum* Linnaeus) (Poaceae) production in 2018–2019 was estimated at over 700 million metric tons in 2018–2019. Wheat midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae), a serious insect pest of wheat, is widely distributed in many parts of the world where wheat production occurs. *Macroglenes penetrans* (Kirby) (Hymenoptera: Pteromalidae), a parasitoid of *S. mosellana*, has successfully established in most wheat midge-infested areas. Mechanistic, or process-based, population models were used in this study to assess the interactive population dynamics of the three species, based on their respective life cycles and meteorological factors. The models were validated with survey data from multiple sites over numerous years (1991–2016). These simulation models helped to detail our understanding of the tri-trophic population dynamics and will help guide pest management decisions both prior to the growing season and until wheat heading, when wheat is no longer susceptible to *S. mosellana*. The associated models also help identify gaps in system knowledge, provide a foundation for evaluating future innovative management options, and evaluate the potential impact of a changing climate.

Introduction

Worldwide wheat (*Triticum* Linnaeus) (Poaceae) production in 2018–2019 was estimated to be just over 700 million metric tonnes (Shahbandeh 2019). Wheat midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae), a serious insect pest of wheat, is widely distributed in many parts of the world where wheat production occurs, especially between 42°N and 62°N latitude (Affolter 1990). Although there are a number of natural enemies of *S. mosellana* worldwide (Affolter 1990), the parasitoid *Macroglenes penetrans* (Kirby) (Hymenoptera: Pteromalidae) is the predominant biological control agent in North America (Olfert *et al.* 2009).

There have been a number of studies related to forecasting *S. mosellana* population dynamics (Basedow and Gillich 1982; Basedow and Schütte 1982; Lamb *et al.* 1999; Doane and Olfert 2008; Elliott *et al.* 2009; Olfert *et al.* 2016). A recent study in Belgium assessed six published models and

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reported that none of the models produced consistent results for all regions over the four years of the study (Jacquemin *et al.* 2014). These models used degree-day accumulations and moisture to predict the phenology of *S. mosellana*. Olfert *et al.* (2016) developed a bioclimatic (or ecological niche) model to investigate how climate affected *S. mosellana* abundance and distribution. Their model, based on sensitivity analysis of precipitation changes, demonstrated that distribution and relative abundance of *S. mosellana* increased with wetter conditions and decreased during dryer than normal growing seasons. The authors suggested that, in addition to abiotic factors, a model should be developed to include biotic factors such as the host crop and the parasitoid, *M. penetrans*. Wheat emergence (and subsequent heading/flowering) has an impact on *S. mosellana* oviposition (Elliott and Mann 1996). For example, the North Dakota Agricultural Weather Network (Fargo, North Dakota, United States of America) developed a model that integrated seeding date of wheat, growing degree-day development, and degree-day development of *S. mosellana* to determine if the crop is susceptible, based on crop stage and emergence of female *S. mosellana* (North Dakota Agricultural Weather Network 2019). Timely pest management decisions require knowledge related to *S. mosellana, M. penetrans,* and host crop development. These components result in a complex agroecosystem that may require producers to make a number of decisions related to selection of wheat varieties, seeding dates, and application of insecticides that will minimise negative impacts on biological control agents. In some instances, decisions can be made well in advance of the growing season. Predictive, mechanistic, tri-trophic models can assist producers with making rapid, informed decisions.

Mechanistic, or process-based, population models have been used effectively to simulate fruit, crucifer (Brassicaceae), and soybean (*Glycine max* (Linnaeus) Merrill; Fabaceae) pest systems (Yonow and Sutherst 1998; Hallett *et al.* 2009, Bahlai *et al.* 2013; Li *et al.* 2016). In this paper, DYMEX 4.0 mechanistic modelling software (Hearne Scientific Software, Melbourne, Australia) was used to assess the population dynamics of the three species under study, based on their respective life cycles and climatic factors. The objective was to develop a tri-trophic bioclimatic model that included the host crop (*Triticum aestivum* Linnaeus), the insect pest (*S. mosellana*), and the parasitoid of the pest (*M. penetrans*) that would serve as a foundation to better understand interactive population dynamics and, in turn, guide management decisions that can be made before and during the crop growing season.

Methods

Data collection

Daily meteorological datasets from Environment and Climate Change Canada (2019) were developed for each location under study in western Canada for the period of 1991–2016 (1 March to 30 September for each year). Datasets included date, temperature (minimum and maximum), precipitation, and relative humidity.

Postharvest surveys for *S. mosellana* and *M. penetrans* populations have been conducted annually in Saskatchewan, Canada (September/October) since 1991 (Olfert *et al.* 2009). The overwintering larval cocoon of *S. mosellana* is the best stage for comparing populations from one year to the next because it is sessile and is present throughout the autumn and early spring, when sampling can be done to identify potentially damaging populations for the coming crop year. As a result, soil core samples provided the data required for population dynamics studies of *S. mosellana* and *M. penetrans* (Doane *et al.* 1987). Each fall, soil core samples are collected, washed, and sieved to determine *S. mosellana* larval cocoon densities (Doane *et al.* 1987). The larval cocoons are then dissected to determine parasitism rates by *M. penetrans*. The data from the survey are used to create a forecast map of risk related to *S. mosellana* for the following growing season. The forecast maps are released to wheat growers in a timely fashion by the Prairie Pest Monitoring Network (prairiepestmonitoring.blogspot.com) to help guide cropping decisions. Wheat midge cocoons

Table 1. Description of modules, inputs, and outputs for variables that are independent of the life cycle sub-models for the three species (wheat (*Triticum aestivum*), wheat midge (*Sitodiplosis mosellana*), and parasitoid (*Macroglenes penetrans*)).

Module	DYMEX Module	Inputs	Outputs	Description
Latitude and longitude	Query file	Weather data file	Latitude and longitude	The query file module is used to read latitude and longitude data from daily weather data files (for each location).
Metbase	Metbase	Simulation date	Temperature (minimum, maximum), precipitation, relative humidity (9 am and 3 pm)	The metbase module is used to produce daily meteorological data output
Daylength	Daylength	Simulation date, latitude	Day length, day length change	The daylength module calculates the number of hours between sunrise and sunset
Daily cycle	Circadian	daylength, minimum and maximum temperature (24 segments, composite (sine + exponential)	Hourly temperature	The circadian module calculates hourly temperature
30 day total rain	RunMean	Precipitation	Cumulative rain over 30 days	The runmean module calculates running total rainfall over 30-day intervals
Wheat				Table 2
Sitodiplosis mosellana				Table 3
Macroglenes penetrans				Table 4

sampled during annual surveys were destructively sampled to determine parasitism levels in the population. Therefore, voucher specimens were not available for preservation.

Model description

The tri-trophic model was developed using DYMEX 4.0 (Hearne Scientific Software, Melbourne, Australia). The model uses a one-day time-step to compute all outputs. The model consists of a number of modules that are used for data inputs, outputs, and to create new input and output variables (Table 1). The longitude and latitude module is used to read location values from each meteorological data file. The MetBase module is used to allow users to specify meteorological inputs that are used as inputs into the life cycle modules. The DayLength module, based on date and latitude, computes day length during the growing season. Inputs for the Circadian module (day length and daily maximum and minimum temperature data) are used to derive hourly temperatures. The model consists of sub-models, one for each life cycle of the three species: *Triticum aestivum*, *S. mosellana*, and *M. penetrans* (Fig. 1; Tables 2–4).

Host crop (*Triticum aestivum*)

The purpose of the wheat sub-model was to provide a substrate for *S. mosellana* oviposition. To ensure population survival, oviposition must coincide with wheat heading, and it has been

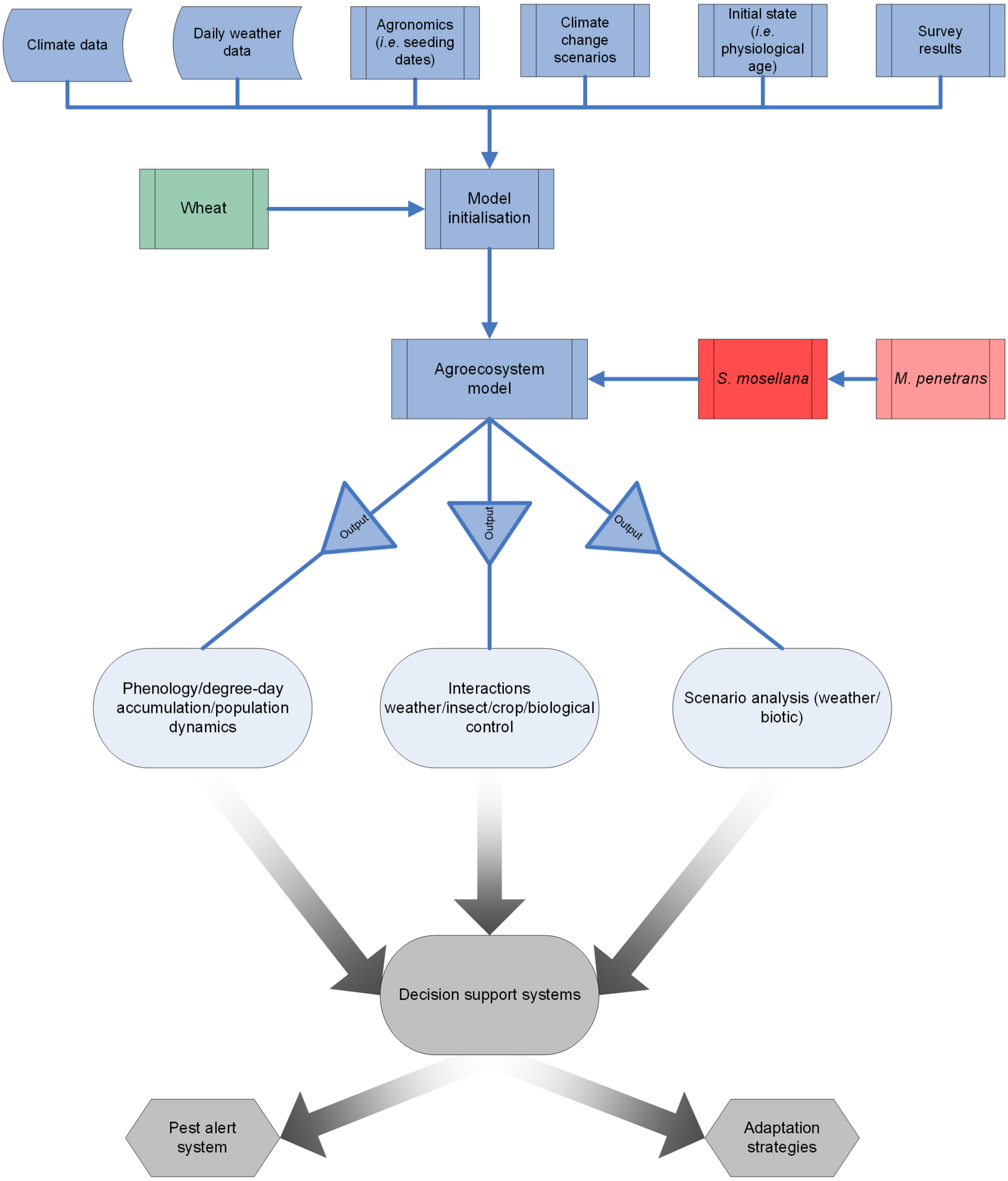

Fig. 1. Schematic overview of an agroecosystem control model and the components related to a tri-trophic system involving wheat, an insect pest of wheat, and its biological control agent.

reported that susceptibility declines significantly after anthesis begins (Elliott and Mann 1996). The wheat sub-model consists of 10 life stages that describe crop phenology during the growing season. Development parameters were based on values reported by Miller *et al.* (2001). Based on degree-day requirements for each specific life stage, the model computes when the wheat crop will transition from one phenological stage to the next. The step height (0–1) determines what proportion of the population will transfer to the next stage. For example, plants transition from the

Table 2. Description of processes, functions, independent variables, and parameters used for development of the wheat (*Triticum aestivum*) sub-model based on values obtained from Miller *et al.* (2001).

Process	Life stage	Function	Independent variable	Unit	Parameters*
Development	Emergence	LAT	Daily cycle	°C	Thr = 0, m = 1
	Leaf development	LAT	Daily cycle	°C	Thr = 0, m = 1
	Tillering	LAT	Daily cycle	°C	Thr = 0, m = 1
	Stem elongation	LAT	Daily cycle	°C	Thr = 0, m = 1
	Heading	LAT	Daily cycle	°C	Thr = 0, m = 1
	Anthesis	LAT	Daily cycle	°C	Thr = 0, m = 1
	Seed fill	LAT	Daily cycle	°C	Thr = 0, m = 1
	Dough	LAT	Daily cycle	°C	Thr = 0, m = 1
	Mature	LAT	Daily cycle	°C	Thr = 0, m = 1
	Harvest	LAT	Daily cycle	°C	Thr = 0, m = 1
Stage transfer	Emergence	Step	Physiological age	DD	Thr = 142, SH = 0.25
	Leaf development	Step	Physiological age	DD	Thr = 47, SH = 0.5
	Tillering	Step	Physiological age	DD	Thr = 206, SH = 0.5
	Stem elongation	Step	Physiological age	DD	Thr = 125, SH = 0.5
	Heading	Step	Physiological age	DD	Thr = 105, SH = 0.5
	Anthesis	Step	Physiological age	DD	Thr = 228, SH = 0.85
	Seed fill	Step	Physiological age	DD	Thr = 267, SH = 0.75
	Dough	Step	Physiological age	DD	Thr = 374, SH = 0.75
	Mature	Step	Physiological age	DD	Thr = 107, SH = 0.75

*Abbreviations: LAT, linear above threshold; Step, step function; Daily cycle, daily temperature cycle; DD, degree days; Thr, threshold; m, slope; SH, step height

emergence stage to leaf development after accumulation of 142 degree days. The step height is 0.25, indicating that each day, after accumulation of 142 degree days, 25% of the population will transition to the leaf development stage. The results are variable, in that not all wheat plants transition to the next stage on the same day. The software groups individuals into cohorts. Cohorts share similar properties including life stage, age based on the date of initial occurrence, and occupy the same space. All individuals that are in the same cohort experience the same abiotic and biotic conditions. Each life stage may have multiple cohorts. Cohort properties include number, stage, development, reproduction, mortality, and stress accumulation. Cohort properties have been used to account for a range of stage-specific responses to different biotic and abiotic conditions (Yonow *et al.* 2004). This method was applied to a number of stages in the three life cycle sub-models (Tables 2–4).

Pest (*Sitodiplosis mosellana*)

The *S. mosellana* sub-model consists of six life stages (Table 3) and describes processes that include development, mortality, and reproduction. The life cycle of *S. mosellana* has been described in western Canada (Doane and Olfert 2008), the United States of America (Reeher 1945), the United Kingdom (Oakley *et al.* 1998), Germany (Basedow 1977), and Switzerland (Affolter 1990). In western Canada, the species overwinters in the soil as a larval cocoon (*S. mosellana* third-instar cocoon).

Table 3. Description of processes, functions, independent variables, parameters, and citations used for development of the wheat midge (*Sitodiplosis mosellana*) sub-model.

Process	Life stage	Function	Independent variable	Unit	Parameters*	Relevant citations and notes
Development	Egg	LAT	Daily cycle	°C	Thr = 11.7, m = 1	Oakley *et al.* (1998)
	L3 cocoon	LAT	Daily cycle	°C	Thr = 3, m = 1	Basedow (1977), Oakley *et al.* (1998), Doane and Olfert (2008)
	L3 soil surface	LAT	Daily cycle	°C	Thr = 6, m = 1	Doane and Olfert (2008)
	Pupa	LAT	Daily cycle	°C	Thr = 6, m = 1	Doane and Olfert (2008)
Stage transfer	Egg	Step	Physiological age	DD	Thr = 33.3, SH = 0.75	Oakley *et al.* (1998), Doane *et al.* (2000)
	L1, L2[†]	Step	Chronological age	Days	Thr = 14 days, SH = 0.25	No temperature related development available; Doane *et al.* (2000)
	L3 cocoon[‡]	Step	Physiological age	DD	Thr = 222, SH = 0.25	Oakley *et al.* (1998), Doane and Olfert (2008)
		FR	30 day total rain	mm	25, 75, 100,150	Elliott *et al.* (2009)
		FR	Day of year	Days	128, 140, 150, 196	Function used to simulate diapause termination (third instar) based on the day of the year (128 = May 8, 140 = May 20, 150 = May 30, 196 = July 15)
		Step	Chronological age	Days	60	Basedow (1977); an interpolated value of 60 days was used for April 1 initialisation
	L3 soil surface[§]	Step	Physiological age	DD	Thr = 155, SH = 0.25	Doane and Olfert (2008); Note that they reported development relative to soil temperature
L3 transfer to pupa		FR	30 day total rain	mm	25, 75, 100,150	Elliott *et al.* (2009); combine with product rule
	Pupa	Step	Physiological age	DD	Thr = 125, SH = 0.25	Doane and Olfert (2008)
Mortality – *M. penetrans*	L3 cocoon	Parameter		%	30	Per cent parasitism based on survey results (third-instar cocoons) from the preceding fall
Mortality – predation	L3 soil surface	Parameter		%	20	Doane and Olfert (2008) noted 40% population reduction between stages, likely due to predation (Reeher 1945; Barnes 1956; Floate *et al.* 1990)
	Pupa	Parameter		%	31.5	See note for third-instar soil surface larvae (directly above)

(*Continued*)

Table 3. (*Continued*)

Process	Life stage	Function	Independent variable	Unit	Parameters*	Relevant citations and notes
Mortality[‖]	Adult	Step	Chronological age	Days	Thr = 1, SH = 0.15	Pivnick and Labbé (1993)
		Step	Rainfall	mm	Thr = 10, SH = 0.5	Rainfall results in adult mortality
Fecundity	Adult	Parameter		Total eggs	60	Default set to 60 eggs per female with expected 50:50 sex ratio
Progeny production[#]	Adult	LAT	Chronological age	Days	Thr = 1, m = 17.2	Pivnick and Labbé (1993). Note that oviposition started one day after female emergence
	Adult	Step	Wheat stem heading and anthesis	Total plants	Thr = 25, SH = 0.1	Default set to 25 plants at flowering (anthesis)
	Adult	FR	Rainfall	mm	0, 0.05, 5, 15	Excessive rainfall limits progeny production

*Abbreviations. LAT = linear above threshold; Step = step function; FR = favourability range; Daily cycle = daily temperature cycle; DD, degree days; Thr = threshold; m = slope; SH = step height.

[†] L1, L2 = first and second instars.

[‡] Third-instar cocoon stage transfer functions ($n = 4$) were combined with the product combination rule.

[§] Third-instar soil surface stage transfer functions ($n = 2$) were combined with the product combination rule.

[‖] Adult mortality functions ($n = 2$) were combined with the compliment product combination rule.

[#] Adult progeny production functions ($n = 3$) were combined with the product combination rule.

Table 4. Description of processes, functions, independent variables, parameters, and citations used for the development of *Macroglenes penetrans* sub-model (Mp = *Macroglenes penetrans*; Sm = *Sitodiplosis mosellana*).

Process	Life stage	Function	Independent variable	Unit	Parameters*	Relevant citations and notes
Development	Egg	LAT	Daily cycle	°C	Thr = 7, m = 1	Elliott *et al.* (2011)
	Larva (post diapause)	LAT	Daily cycle	°C	Thr = 5, m = 1	Elliott *et al.* (2011)
Stage transfer	Egg	Step	Physiological age	DD	Thr = 81, SH = 0.5	Doane (1988); Note that if a threshold of 5 °C is used and hatch occurs in 4.5 days, then 81 DD were required for egg development.
	L1, L2	Step	Chronological age	Days	Thr = 30, SH = 0.5	Doane (1988)
Mortality	Adult	Step	Chronological age	Days	Thr = 1, SH = 0.2	Doane (1988); This variable models oviposition (females).
Fecundity	Adult	Parameter			20	Doane (1988); Note that field values may be lower than 25 eggs/female
Progeny production[‡]	Adult	LAT	Chronological age	Days	Thr = 1, m = 8.8	Doane (1988)
	Adult	Step	*S. mosellana* eggs	Total eggs	Thr = 10, SH = 0.5	Note that Mp oviposits in Sm eggs, thus Sm eggs must be present for Mp oviposition to occur.

*Abbreviations. LAT = linear above threshold; Step = step function; FR = favourability range; Daily cycle = daily temperature cycle; DD, degree days; Thr = threshold; m = slope; SH = step height.

[†] L1, L2 = first and second instars

[‡] Adult progeny production functions ($n = 2$) were combined with the product combination rule

(i) Larval cocoons (*S. mosellana* third-instar cocoon). One mortality factory, related to parasitism by *M. penetrans* was programmed to affect third-instar cocoon survival. Doane and Olfert (2008) reported that *M. penetrans* completes larval development in the spring and that adults emerge from their third-instar cocoon hosts. Parasitism occurs during the previous year. Fall surveys provide accurate estimates of parasitism rates. A function was parameterised to the parasitism rate, based on fall survey data. Diapause suspension occurred once 220 degree days, above the 3 °C threshold, was accumulated after 1 January (Oakley *et al.* 1998). A cold period (below 10 °C) of 120 days was required to terminate diapause (Basedow 1977), and Doane and Olfert (2008) reported that 219–224 degree days (calculated with a threshold of 3 °C) was required to complete diapause. Diapause termination is related to increasing temperatures and moist conditions. The model used four functions to specify when third instars transition from larval cocoons to the soil surface stage (Table 3). A product combination (Maywald *et al.* 2007) rule was used to ensure that all four factors must be met before third-instar cocoon populations can develop to the third-instar soil surface stage.

a. Rain. Elliott *et al.* (2009) reported that larval development and emergence of adults was enhanced with 20–30 mm of rainfall in May. Rainfall amounts greater than 145 mm resulted in delayed larval development (Elliott *et al.* 2009). The favourability range (Maywald *et al.* 2007) uses four values to define the lower and upper thresholds and lower and upper optimal ranges of rainfall. The lower limit was set to 50 mm, and the upper threshold was 250 mm. The lower and upper optimal values were parameterised to 125 and 150 mm, respectively.

b. Physiological age. Larval development was complete after accumulation of 225 degree days (development threshold of 3 °C for degree-day calculation) (Doane and Olfert 2008). In order to extend appearance of third-instar soil surface larvae, the step height was set to 0.25.
c. Date. Day of year was used to specify the period over which rainfall accumulation would affect third-instar cocoon development. Transition from the cocoon stage to the soil surface stage occurs over an extended period of time (May to July). A favourability range function was parameterised with an upper and lower threshold of 121 and 196 Julian days, respectively, with an optimal range of 135 and 172 Julian days.
d. Chronological age. A step function, based on larval age in days, was used to best reflect any additional delays of the transition process from larval cocoons to third-instar soil surface larvae.

(ii) Larvae at soil surface (*S. mosellana* third instars). Third instars transition to the third-instar soil surface stage (Gagné and Doane 1999). Based on a report by Doane and Olfert (2008), there was an approximate reduction of 40% of larvae at the soil surface from the larval cocoon stage. A parameter function, with a default of 20% mortality was used for this stage. Larval development was based on a threshold temperature of 6 °C and a requirement of 155 degree days (Doane and Olfert 2008).

(iii) Pupae (*S. mosellana* pupae). The parameter to explain pupal mortality was similar to that used for the third-instar soil surface life stage. Doane and Olfert (2008) reported that the first pupae occurred on June 15 (139 degree days, base threshold of 6 °C) and June 10 (125 degree days, base threshold of 6 °C) in 1984 and 1985, respectively.

(iv) Adults (*S. mosellana* adults). In western Canada, adults emerge during July (Elliott *et al.* 2009). Two mortality factors, attributed to chronological age and rainfall, were used to explain adult survival. Based on growth cabinet studies (21 °C), continuous mortality occurred over a period of 11 days and 50% mortality occurred on day eight (Pivnick and Labbé 1993). A step function, based on chronological age, was used to simulate adult mortality. Adult mortality, related to significant rainfall events, was parameterised with a default rainfall value of 10 mm. A complement product rule (Maywald *et al.* 2007) was used to combine the two factors (chronological age and rainfall). Mean total fecundity was 83.6 ± 10.9 (± standard error) eggs (Pivnick and Labbé 1993). The default parameter for fecundity was set to 60 eggs per female. Oviposition is dependent on host plant phenology. Females lay eggs (*S. mosellana* eggs) under glumes or palea (Mukerji *et al.* 1988). It was observed that oviposition takes place throughout heading (including after anthesis) but declines during anthesis (Elliott and Mann 1996; Ding and Lamb 1999). The *S. mosellana* sub-model used three factors to simulate progeny production using a product combination rule: chronological age, crop phenology, and rainfall. Pivnick and Labbé (1993) observed that eggs were produced over a period of eight days at 21 °C in a growth cabinet study and that oviposition began one day after female emergence. In order to account for the effects of wheat phenology, a step function was used to allow oviposition when wheat had at least 25% of the crop in the heading stage. Finally, it was assumed that rainfall may limit female flight and oviposition. A favourability range function was parameterised with a lower and upper threshold of 0 and 15 mm daily rainfall, respectively, and with an optimal range of 0.05 and 5.0 mm daily rainfall.

(v) Eggs (*S. mosellana* eggs). In Saskatchewan, *S. mosellana* eggs took four to seven days to hatch (Doane *et al.* 2000). Oakley *et al.* (1998) reported that the threshold was 11.7 °C and 33.3 degree days were required to complete egg development.

(vi) First and second instars (*S. mosellana,* instars 1–2). Larvae hatch in four to seven days and feed on developing wheat kernels. Larval development is completed in approximately three weeks (Doane and Olfert 2008). Once larval development is complete, the larvae drop to the soil and spin a larval cocoon in the soil (third-instar cocoons). We assumed that larval mortality could occur after instars 1–2 dropped to the ground. A mortality parameter similar to that used for third-instar soil surface and pupal mortality was used to explain instars 1–2 mortality. The effect of temperature on development of instars 1–2 is not known. Doane *et al.* (2000) reported that larvae mature to third instars in 2–3 weeks. A step function, based on chronological age, was parameterised to 14 days with 25% of the population transitioning to the third-instar cocoon stage on a daily basis.

Parasitoid (*Macroglenes penetrans*)

The *M. penetrans* sub-model consists of four life stages. The purpose of this sub-model was to incorporate the phenology and fecundity of *M. penetrans* and *S. mosellana* populations to understand and predict *M. penetrans* population dynamics and the impact of parasitism on *S. mosellana*.

(i) Eggs (*M. penetrans* eggs). Female *M. penetrans* (*M. penetrans* adults) deposit their eggs (*M. penetrans* eggs) into the eggs of *S. mosellana* (*S. mosellana* eggs). The threshold temperature for *M. penetrans* egg development was reported as 5 °C with a requirement of 81 degree days (Elliott *et al.* 2011).

(ii) First and second instars (*M. penetrans* instars 1–2). Development of instars 1–2, as a function of temperature, has not been reported. First instars reach full size by late August through early September, then moult to second instars to enter diapause for the winter (Doane 1988).

(iii) Post-diapause late instars and pupae (*M. penetrans* post-diapause instar). In spring, instars 1–2 complete development and transfer to the post-diapause larval/pupal stage (post-diapause instar). Temperature-based development data for *M. penetrans* at this stage of development were not available. Furthermore, there were no data that reported when pupation occurred. For this reason, third instars and pupae were grouped together in the model. A simplified function, based on chronological age, was used to model transition from the pupal stage to the adult stage of the parasitoid. A step function, based on a threshold of 30 days, was used to model transition for the post-diapause stage to the adult stage.

(iv) *Macroglenes penetrans* adults (*M. penetrans* adults). Doane (1988) reported that *M. penetrans* males live up to eight days and females live between one and 16 days. In growth cabinet studies, Doane (1988) reported that on average females produced 178 eggs, with a range of 139–220 eggs. Assuming that the sex ratio of eggs is 50:50, we estimated fecundity to be 50% of 180 eggs. Field values may be lower than 25 eggs/female. Progeny production was based on chronological age of females and the presence of *S. mosellana* eggs. A linear above threshold function was used to model female progeny production. Oviposition was parameterised to begin on day one, and 90 eggs could be oviposited in 10 days (Doane 1988). A step function, with *S. mosellana* eggs being the independent variable, was used to limit *M. penetrans* oviposition to occur only in the presence of a suitable host. The default threshold value was 10 *S. mosellana* eggs.

Model initialisation

Model runs were conducted for an area ± 0.5 (latitude and longitude) around four locations in Saskatchewan. The centred coordinates of these locations were Melfort (52.85°N, 104.61°W), Saskatoon (52.14°N, 106.69°W), Wynyard (51.77°N, 104.18°W), and Yorkton (51.21°N, 102.46°W). Location selection was based on sites that had long-term average densities of *S. mosellana* that were similar to the four major infestation categories (<600 larvae/m^2, $600 \leq 1200$ larvae/m^2, $1200 \leq 1800$ larvae/m^2, and > 1800 larvae/m^2). Annual average *S. mosellana* densities and per cent parasitism were calculated by determining the mean density of larval cocoons from fall surveys.

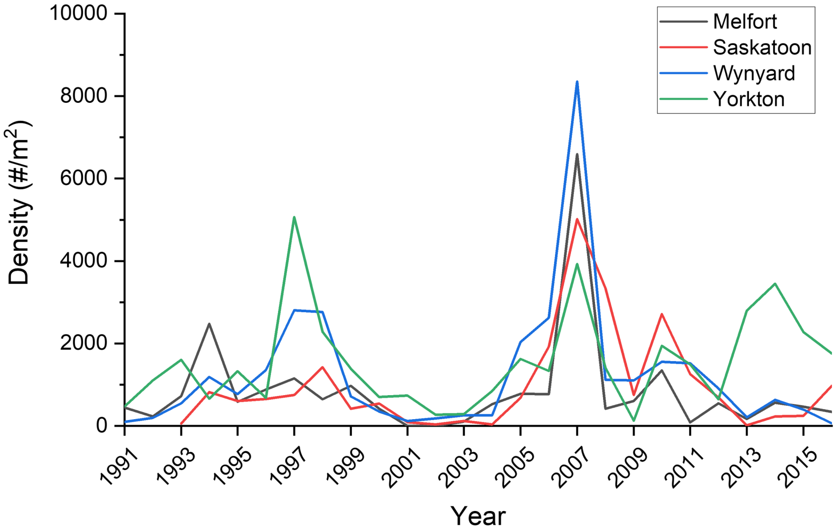

Fig. 2. Annual average number of larval cocoons per m^2 of *Sitodiplosis mosellana* observed in soil cores collected in late September at four locations in Saskatchewan between 1991 and 2016.

These data were based on average values from soil core samples that were collected from areas around each of the four locations.

A model framework, the agro-ecosystem model was designed to provide an overview of our tri-trophic model. The agro-ecosystem model can be initialised in a number of ways (Fig. 1). The pest, *S. mosellana*, was initialised with third-instar (L3) cocoons on 1 April, and densities were based on larval densities from the survey that was conducted during the previous fall. Parasitism, related to *M. penetrans*, was initialised by setting the third-instar mortality parameter to the per cent parasitism value that was obtained from the same survey that was used to determine *S. mosellana* larval cocoon densities. This value was initialised on 1 April. The wheat sub-model was initialised with 250 seedlings that emerged on 21 May, which was based on the optimal seeding rate for hard red spring wheat of 250 seeds/m^2 (Alberta Agriculture and Forestry 2019).

The overall model was initiated on 15 March, with daily meteorological data and terminated on 30 September. Model output was produced for each day of the growing season. Daily outputs indicated the phenological stage for each species and changes in density. Annual comparisons were based on larval-cocoon values for 30 September. This stage/date was chosen to compare with survey data that were collected annually in late September and early October.

Model validation

Model outputs were validated by comparing them with historic annual surveys and *S. mosellana* phenology data from the four locations in Saskatchewan that were used to initialise the model. Melfort, Saskatoon, Wynyard, and Yorkton represent a range of *S. mosellana* larval cocoon densities (Fig. 2, Table 5), where the risk of economic damage is greatest and is similar to the infestation categories described on maps produced with annual survey data (Olfert *et al.* 2009, 2016). Fall densities of *S. mosellana* less than 1200 larval cocoons per m^2 are considered sub-economic. Based on long-term averages for 1991–2016, cocoon densities near Melfort and Saskatoon were rated as sub-economic and densities in the Wynyard and Yorkton regions were economic.

To verify model accuracy, we assessed the ability of the model to predict sub-economic versus economic densities by comparing modelled populations to field observed populations. Populations were rated as sub-economic (< 1200 larval cocoons/core) or economic (> 1200 larval cocoons/core) and scored as a binary value of 0 or 1, respectively. Based on binary values,

Table 5. Comparisons between observed *Sitodiplosis mosellana* larval cocoon densities (#/m^2) and modelled output for third-instar cocoon estimates at four locations in Saskatchewan. Observed and modelled values represent averages for 1991–2016.

Location	Observed (#/m^2)	Modelled (#/m^2)	Difference (#/m^2)
Melfort	841	976	116.1
Saskatoon	975	1057	108.4
Wynyard	1236	1463	118.4
Yorkton	1547	2347	151.7

Table 6. Comparison of model outputs to field observations (larval cocoons of *Sitodiplosis mosellana* between 1991 and 2016) for Melfort ($n = 25$ years), Saskatoon ($n = 23$ years), Yorkton ($n = 25$ years), and Wynyard ($n = 25$ years), where values represent the number of years that model output was categorised as an underestimate, overestimate, or correct estimate of the survey results, relative to the economic threshold of 1200 cocoons per m^2. Per cent values represent the per cent of the total within each row.

Location	Underestimate	Overestimate	Correct	Total
Melfort	2 (8%)	5 (20%)	18 (72%)	25 (100%)
Saskatoon	2 (8.7%)	5 (21.7%)	16 (69.6%)	23 (100%)
Yorkton	4 (16%)	3 (12%)	18 (72%)	25 (100%)
Wynyard	4 (16%)	3 (12%)	18 (72%)	25 (100%)
Total	**12 (12.2%)**	**16 (16.3%)**	**70 (71.4%)**	**98 (100%)**

modelled populations and observed populations were rated as underestimates, overestimates, or correct (Table 6). Underestimates indicate that the model predicted < 1200 when observed value was greater than 1200, and overestimates indicate that the model predicted > 1200 when observed value was less than 1200. Comparisons were rated as correct when model prediction agreed with the value observed in the field. Analysis was based on all available data site-years ($n = 98$) for the four locations chosen for model initialisation.

Results and discussion

Model initialisation and validation based on *Sitodiplosis mosellana* population densities

The model was initialised and validated for four locations in Saskatchewan (Fig. 2), where Melfort had the lowest long-term density (841 cocoons/m^2) and densities near Saskatoon were 975 cocoons/m^2. Densities near Wynyard were 1236 cocoons/m^2, and the highest value was reported for fields near Yorkton (1547 cocoons/m^2). Based on averages for 1991–2016, model estimates of third-instar cocoon populations were greater than observed in the field for all four locations. Across the four locations, model estimates exceeded observed densities by 23.6% (Table 4). *Sitodiplosis mosellana* larval cocoon densities vary spatially and temporally, thus it is reasonable to expect variation in model outputs compared to observed values over the same scales.

Although the model frequently overestimated larval cocoon densities, it correctly predicted economic populations in 73 of 98 site-years (71.4%). For Saskatoon, the model underestimated the population in two of 23 years, overestimated populations in five years, and was correct for 16 years (Table 6). Across the four sites, the model predicted sub-economic populations that were actually economic in 12 of the 98 site-years (12.2%) and predicted economic populations that were actually sub-economic in 16 of the 98 site-years (16.3%) (Table 6). From a pest management perspective, the field survey results provide producers with an estimate of pest risk in the following growing season. The tri-trophic model confirms that field survey data provide an accurate estimate of risk between growing seasons.

Sitodiplosis mosellana phenology

Model validations were conducted to test modelled phenology against observed seasonal phenology of *S. mosellana*. At Melfort, larvae were observed on the soil surface in mid-May in 1984 (Doane and Olfert 2008), but model output predicted that larvae would appear on the soil surface in late May. The discrepancy between observed and modelled values is most likely due to the fact that occurrence of larvae at the soil surface is affected by soil temperatures, and the model is based on air temperature. Soil moisture also plays a role in diapause termination and subsequent infestation (Hinks and Doane 1988; Elliott *et al.* 2009), such that larvae terminate diapause and move to the soil surface for a few days before pupating when accumulated rainfall exceeds 20 mm in May (Doane and Olfert 2008). Inadequate soil moisture can result in erratic larval emergence or extended diapause (Smith and Lamb 2004) when soil moisture is less than 12% (Basedow and Schütte 1982). Based on 30-day rainfall, larval movement to the soil surface was accurately modelled with rainfall parameter values between 25–150 mm.

Occurrence of *S. mosellana* adults is critical to *S. mosellana* control and development of economic populations. Emergence of *S. mosellana* was evaluated at 19 sites in Saskatchewan in 1991–2000, and average dates of 10%, 50%, and 90% emergence were 11 July, 18 July, and 25 July, respectively (Elliott *et al.* 2009). Model runs were conducted for each year and each location to compare model output for third-instar cocoons with observed densities (Fig. 3). Model output was similar to published observations in that the model predicted occurrence of adults between the end of June and early August (Doane and Olfert 2008). Trends between observed and model densities of larval cocoons were similar, with especially close agreement near Saskatoon. Between 2007 and 2009, field populations declined from 5020 to 748 larval cocoons/m^2. Dry soil conditions may result in reduced emergence of larvae from larval cocoons, due to prolonged diapause (Basedow and Schütte 1971; Smith and Lamb 2004). Population carry-over between years was reported from populations in northeastern Saskatchewan (Doane and Olfert 2008). Post-diapause development was shown to be related to temperature and soil moisture; soil moisture was shown to significantly influence prolonged diapause (Cheng *et al.* 2017). Examination of output suggested that low rainfall amounts in May and June limited emergence of larval cocoons, resulting in larval cocoons remaining in the soil. In 2009, May rainfall was 11 mm, and model output indicated that only 48% of the larval population emerged and pupated.

Sitodiplosis mosellana mortality and synchrony with *Macroglenes penetrans*

Populations of *S. mosellana* are affected by a number of abiotic and biotic mortality factors that were included in the model as parameters or functions. Per cent mortality values were set as a constant (parameter) over the duration of each life stage in the model. Mortality of *S. mosellana* adults was attributed to two factors: chronological age and excessive rain, based on results presented by Pivnick and Labbé (1993), where 10% of the adult population died each day. Model outputs best agreed with observed values when the step function explaining mortality was parameterised with adult mortality occurring on day one and with 15% of the population dying each day. A second mortality factor was used to interpolate adult mortality as a function of excessive daily rain, such that adult mortality increased in the model when daily rainfall amounts exceeded 10 mm.

Larval and pupal mortality occurs at the soil surface, with the population of *S. mosellana* reduced by approximately 40% between the larval cocoon stage and pupation (Doane and Olfert 2008). Additional mortality could be due to predation by spiders (Araneae) and mites (Acari) (Reeher 1945; Barnes 1956), or Carabidae (Coleoptera) and Staphylinidae (Coleoptera)

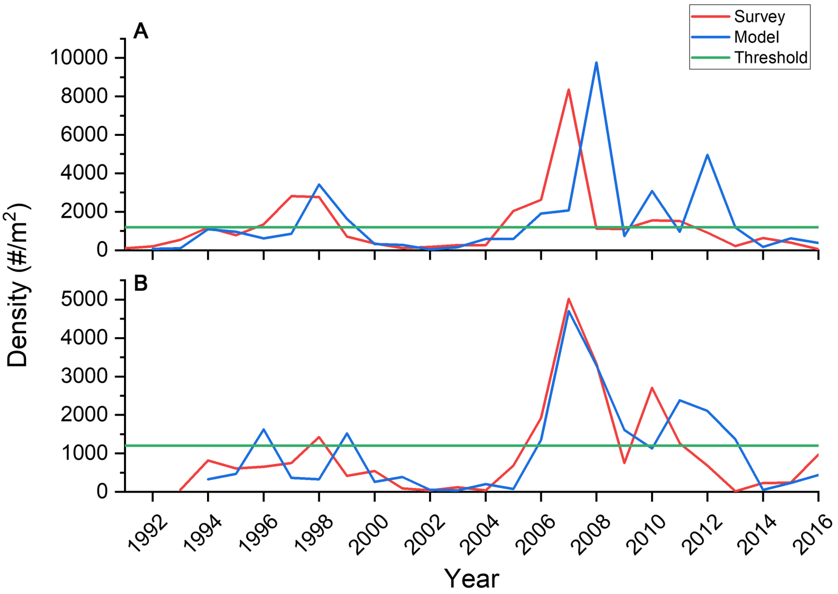

Fig. 3. Comparison of the average number of *Sitodiplosis mosellana* cocoons per m^2 observed in the soil in late September (field survey data 1991–2016). **A**, Model outputs for Saskatoon, Saskatchewan; **B**, model outputs for Wynyard, Saskatchewan.

(Basedow and Schütte 1973; Floate *et al.* 1990). Doane and Olfert (2008) reported that *M. penetrans* completed larval development in the spring before emerging from their third-instar cocoon hosts. Third-instar cocoon mortality was set as a parameter function, based on per cent parasitism from the previous year. The *M. penetrans* sub-model was used to investigate the importance of synchrony of *M. penetrans* adults with *S mosellana* larvae, based on parasitoid eggs found in the host (Fig. 4). This procedure resulted in model output that could be used to analyse interactions between the two species during years of high and low parasitism in the field. Model output suggested that synchrony between *S. mosellana* eggs and *M. penetrans* adults had a significant impact on parasitism rates. Model runs were initialised on 1 April with 600 *S. mosellana* larval cocoons and 10 *M. penetrans*. In 1994, parasitism at Melfort was 57.5%, compared to 12% at Wynyard in 2007. At Melfort in 1994, *M. penetrans* females were predicted to occur when *S. mosellana* egg populations were peaking (Fig. 4 A). At Wynyard in 2007, *S. mosellana* oviposition was bimodal and peak *M. penetrans* oviposition occurred after the first peak of *S. mosellana*, suggesting that larvae emerging from the first oviposition event avoided parasitoid attack (Fig. 4B).

Impact of wheat phenology on *Sitodiplosis mosellana* oviposition

Wheat emergence (and subsequent heading/flowering) has an impact on *S. mosellana* oviposition. Wheat heads are most susceptible to damage when oviposition occurs during heading (51–59 Zadoks code) (Zadocks *et al.* 1974; Elliott and Mann 1996). Seeding dates and subsequent crop development were analysed in the model to estimate the impact of crop development on *S. mosellana* populations by initialising the model with various wheat emergence dates. Populations were compared for five seeding dates for Wynyard during the 2007 growing season by initialising the model with values from the 2006 survey (2620 larval cocoons and a parasitism rate of 20%). The model run, conducted from 1 April to 30 September, generated different number of third-instar cocoons (Fig. 5) that varied, based on initialisation date. The earliest wheat emergence date (14 May) resulted in the lowest number of third-instar cocoons (1449), which was 51.5% fewer cocoons than observed when wheat emerged on 4 June (2975 cocoons). Thus, the

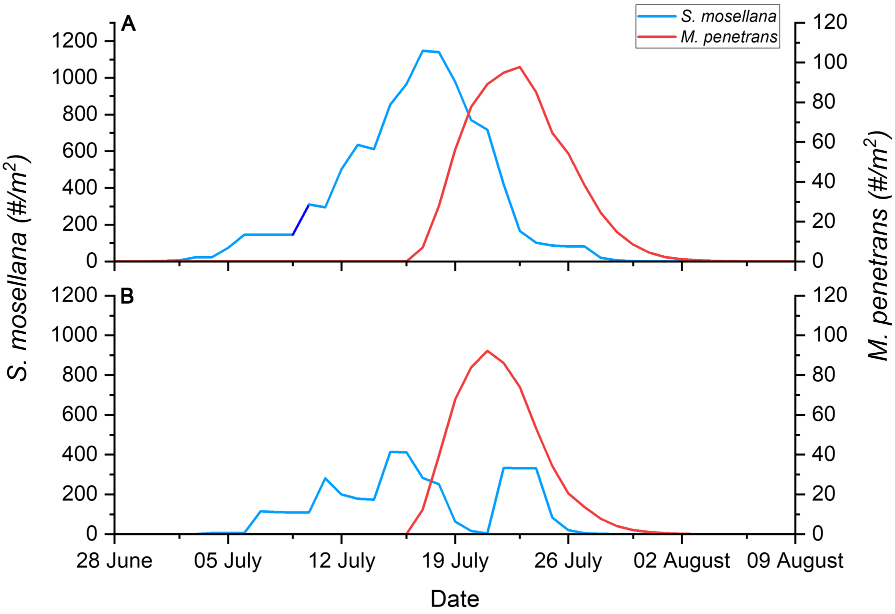

Fig. 4. Synchrony of *Sitodiplosis mosellana* and *Macroglenes penetrans* populations. **A**, Under conditions with high parasitism rates predicted by the tri-trophic model (*i.e.*, Melfort 1994); **B**, under conditions with low parasitism rates predicted by the tri-trophic model (*i.e.*, Wynyard 2007).

model predicted that *S. mosellana* populations would be reduced if adult midge emerged when wheat crop phenology was too advanced, which occurred when wheat emerged early in the growing season. The model output agrees with field observations demonstrating that oviposition occurs throughout heading (including after anthesis) and declines during anthesis (Elliott and Mann 1996; Ding and Lamb 1999). Model predictions suggest that earlier seeding dates could reduce larval feeding and subsequent yield losses. At a regional scale, earlier seeding dates may result in lower *S. mosellana* population levels.

Conclusions and implications for *Sitodiplosis mosellana* management

The tri-trophic model developed in this study consisted of three sub-models, the pest (*S. mosellana*), its parasitoid (*M. penetrans*), and its host crop (*Triticum aestivum*). It was parameterised using published phenology and population data based on annual surveys that have been conducted in Saskatchewan since 1991 and published as risk maps by the Prairie Pest Monitoring Network. The surveys, conducted in September and October, use soil cores to estimate larval cocoon populations and *M. penetrans* parasitism rates (Olfert *et al.* 2009). To validate the tri-trophic model, we selected four locations in Saskatchewan that represented a wide range of average densities of *S. mosellana* larval cocoons in the soil and initialised the model with *S. mosellana* densities and *M. penetrans* parasitism based on fall survey data from the previous year. Across all year-location combinations ($n = 98$), the model predicted economic and sub-economic populations correctly 71.4% of the time. During the growing season, there are two significant events associated with *S. mosellana* phenology: appearance of larvae on the soil surface and emergence of adults. Compared to field data from 1984 and 1985, our model predicted appearance of soil surface larvae would occur approximately two weeks later than observed (Doane and Olfert 2008). The difference in emergence was attributed to extensive availability of air temperature data, rather than soil temperature data for running the model, and the fact that soil temperature is a more powerful driver of *S. mosellana* development. The model predicted adult emergence that agreed with results reported by Elliott *et al.* (2009). In agreement with the existing literature,

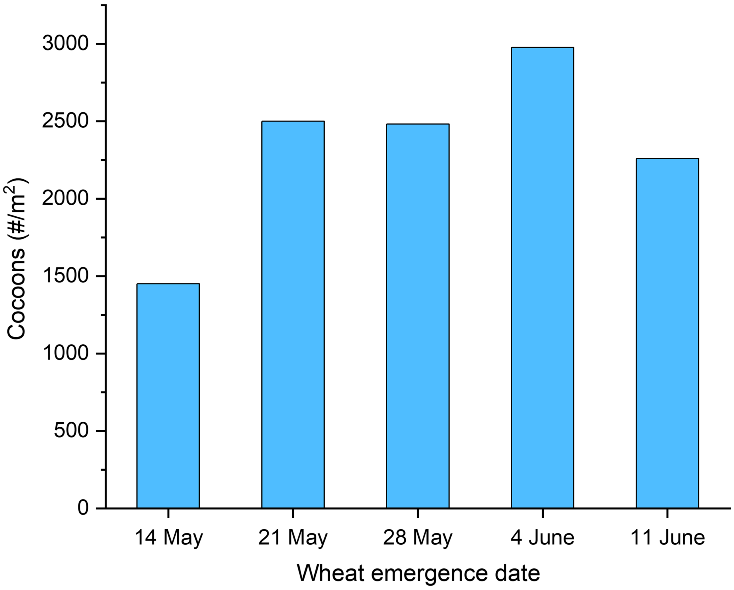

Fig. 5. The effect of the timing of wheat emergence on *Sitodiplosis mosellana* populations, represented by the number of larval cocoons per m^2 at Wynyard, Saskatchewan in 2007.

our model demonstrated that precipitation, specifically 30 days cumulative rain, had an impact on movement of larvae to the soil surface. It also demonstrated that dry periods in May and June affected larval transition from the cocoon stage to the larval stage that moved to the soil surface and that dry conditions delay or reduce emergence of adults.

This model is unique in that it overlays the effect of host plant phenology and parasitism on a pest population. It clearly demonstrates, as expected, that synchrony between the host plant and pest is required for pest population growth, and that synchrony between *S. mosellana* and *M. penetrans* affects parasitism levels. The tri-trophic model can be used to guide a number of management decisions that could help to prevent yield loss associated with *S. mosellana*. The model allows for management decisions to begin before the growing season and can be used to produce continuous predictions based on current conditions until wheat heading, when host plants are less vulnerable to damage by *S. mosellana* larvae. Model outputs will contribute to two dominant factors in the decision-making process to support *S. mosellana* management, as it quantifies crop risk and the time frame of the expected risk. For example, (i) high risk – long-term time frame may require use of resistant *S. mosellana* 1 gene varieties. This decision is made during the winter; (ii) high risk – short-term time frame will likely require insecticide application. In this instance, insecticide selection and application should be implemented so as to minimise impact on *M. penetrans*; (iii) low risk – long-term time frame may be used to minimise loss of crop resistance (*S. mosellana* 1 gene) by the use of conventional varieties; and (iv) low risk – short-term time frame would not support insecticide use under most situations.

Selection of early maturing varieties and early spring seeding dates were shown to be an effective tool for management of *S. mosellana* in western Canada, as these methods interrupt synchrony in the timing of crop and pest phenologies (Elliott and Mann 1996; Elliott *et al.* 2009). The model examined the impact of seedling emergence dates and subsequent phenological development on *S. mosellana* oviposition and confirmed that earlier crop development resulted in the occurrence of the crop heading stage before appearance of peak adult *S. mosellana* populations. Further, the *M. penetrans* sub-model indicated that adult emergence of the parasitoid usually occurred after peak emergence of *S. mosellana* adults. Predictions of *M. penetrans* and *S. mosellana* phenologies may permit producers to time insecticide applications in order to reduce the impact on parasitoids and other beneficial insects (Chavalle *et al.* 2015). The model can also be used to understand potential impacts of climate change on this tri-trophic interaction and provide a foundation for future research to evaluate innovative management options for *S. mosellana*.

Finally, the tri-trophic model described here represents a novel approach to modelling pest interactions with its host plant and natural enemies, in an agro-ecosystem model framework. We have demonstrated that agro-ecosystem models can be initialised based on climate, weather, seeding date, physiological characteristics, or using survey data to integrate the life cycles of multiple species and create output (*e.g.*, phenology, interactions, emergence dates) that can be used to support decision making by growers. The model described here is spatial, in that it can be initialised across multiple locations and produce location-specific predictions based on local weather conditions and wheat midge populations. Thus, the agro-ecosystem models for wheat midge differ from existing wheat midge forecast tools due to its spatial nature (*i.e.*, model can be initialised with local survey data), ability to follow cohorts of individuals, and integrate multiple factors that affect wheat midge survival. The agro-ecosystem model can also be scaled up in terms of complexity to include other pests of wheat, and their natural enemies, to provide growers with a comprehensive outlook on potential pest issues in their wheat crops, which will be the focus of future model development.

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References

Affolter, F. 1990. Structure and dynamics of the parasitoid complex of the wheat midges *Sitodiplosis mosellana* (Géhin) and *Contarinia tritici* (Kirby). International Institute of Biological Control, European Station, Delemont, Switzerland.

Alberta Agriculture and Forestry. 2019. Ministry of Alberta Agriculture and Forestry [online]. Available from https://www.alberta.ca/agriculture-and-forestry.aspx [accessed on 20 February 2020].

Bahlai, C.A., Weiss, R.M., and Hallett, R.H. 2013. A mechanistic model for a tri-trophic interaction involving soybean aphid, its host plants, and multiple natural enemies. Ecological Modelling, **254**: 54–70.

Barnes, H.F. (editor). 1956. Gall midges of economic importance. Volume VII: gall midges of cereal crops. Crosby Lockwood & Son, London, United Kingdom.

Basedow, T. 1977. Der Einfluss von Temperatur und Niederschlägen auf Diapause und Phänologie der Weizengallmücken *Contarinia tritici* (Kirby) und *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae). Zoologische Jahrbücher Abteilung für Oecologie und Geographie der Tiere, **104**: 302–326.

Basedow, T. and Gillich, H. 1982. Untersuchungen zur Prognose des Auftretens der Weizengallmücken *Contarinia tritici* (Kirby) und *Sitodiplosis mosellana* (Géhin) (Diptera, Cecidomyiidae). II. Faktoren, die ein Schadauftreten der Mücken verhindern können. Anzeiger für Schädlingskunde, Pflanzenschutz, und Umweltschutz, **55**: 84–89.

Basedow, T. and Schütte, F. 1971. Untersuchungen zum Uberliegen der Weizengallmucken *Contarinia tritici* (Kirby) und *Sitodiplosis mosellana* (Géhin) in Nordeutschland in Sommer 1970. Nachrichtenblatt des Deutschen Pflanzenschutzdienstes, **23**: 4–8.

Basedow, T. and Schütte, F. 1973. Neue Untersuchungen über Eiablage, wirtschaftliche Schadensschwelle und Bekämpfung der Weizengallmücken (Diptera: Cecidomyidae). Zeitschrift für Angewandte Entomologie, **73**: 238–251.

Basedow, T. and Schütte, F. 1982. Die Populationsdynamic die Weizengallmücken *Contarinia tritici* (Kirby) und *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyidae) in zwei Norddeutschen Weizenanbaugebeiten von 1969 bis 1976. Zoologische Jahrbücher Abteilung für Ökologie und Geographie der Tiere, **109**: 33–82.

Chavalle, S., Buhl, P.N., Censier, F., and De Proft, M. 2015. Comparative emergence phenology of the orange wheat blossom midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae) and its parasitoids (Hymenoptera: Pteromalidae and Platygastridae) under controlled conditions. Crop Protection, **76**: 114–120.

Cheng, W., Long, Z., Zhang, Y., Liang, T., and Zhu-Salzman, K. 2017. Effects of temperature, soil moisture and photoperiod on diapause termination and post-diapause development of the wheat blossom midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae). Journal of Insect Physiology, **103**: 78–85.

Ding, H. and Lamb, R.J. 1999. Oviposition and larval establishment of *Sitodiplosis mosellana* (Diptera: Cecidomyiidae) on wheat (Gramineae) at different growth stages. The Canadian Entomologist, **131**: 475–481.

Doane, J.F. 1988. Biology and biological control potential of a wheat midge parasite, *Pirene penetrans* in Saskatchewan. Final Report to Agriculture Development Fund. Agriculture and Agri-Food Canada, Saskatoon, Saskatchewan, Canada.

Doane, J.F., Mukerji, M.K., and Olfert, O. 2000. Sampling distribution and sequential sampling for subterranean stages of orange wheat blossom midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae) in spring wheat. Crop Protection, **19**: 427–434.

Doane, J.F. and Olfert, O. 2008. Seasonal development of wheat midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae), in Saskatchewan, Canada. Crop Protection, **27**: 951–958.

Doane, J.F., Olfert, O., and Mukerji, M.K. 1987. Extraction precision of sieving and brine flotation for removal of wheat midge, *Sitodiplosis mosellana* (Diptera: Cecidomyiidae), cocoons and larvae from soil. Journal of Economic Entomology, **80**: 268–271.

Elliott, R.H. and Mann, L.W. 1996. Susceptibility of red spring wheat, *Triticum aestivum* L. cv. Katepwa, during heading and anthesis to damage by wheat midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cedidomyiidae). The Canadian Entomologist, **128**: 367–375.

Elliott, R.H., Mann, L., and Olfert, O. 2009. Calendar and degree-day requirements for emergence of adult wheat midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae) in Saskatchewan, Canada. Crop Protection, **28**: 588–594.

Elliott, R.H., Mann, L., and Olfert, O. 2011. Calendar and degree-day requirements for emergence of adult *Macroglenes penetrans* (Kirby), an egg-larval parasitoid of wheat midge, *Sitodiplosis mosellana* (Géhin). Crop Protection, **30**: 405–411.

Environment and Climate Change Canada. 2019. Historical data [online]. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html [accessed 20 February 2020].

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

Gagné, R.J. and Doane, J.F. 1999. The larval instars of the wheat midge, *Sitodiplosis mosellana* (Gehin) (Diptera: Cecidomyiidae). Proceedings of the Entomological Society of Washington, **101**: 57–63.

Hallett, R.H., Goodfellow, S.A., Weiss, R.M., and Olfert, O. 2009. MidgEmerge, a new predictive tool, indicates the presence of multiple emergence phenotypes of the overwintered generation of swede midge. Entomologia Experimentalis et Applicata, **130**: 81–97.

Hinks, C.F. and Doane, J.F. 1988. Observations on rearing and diapause termination of *Sitodiplosis mosellana* (Diptera: Cecidomyiidae) in the laboratory. Journal of Economic Entomology, **81**: 1816–1818.

Jacquemin, G., Chavalle, S., and De Proft, M. 2014. Forecasting the emergence of the adult orange wheat blossom midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae) in Belgium. Crop Protection, **58**: 6–13.

Lamb, R.J., Wise, I.L., Olfert, O., Gavloski, J.E., and Barker, P.S. 1999. Distribution and seasonal abundance of *Sitodiplosis mosellana* (Diptera: Cecidomyiidae) in spring wheat. The Canadian Entomologist, **131**: 387–397.

Li, Z., Zalucki, M.P., Yonow, T., Kriticos, D.J., Bao, H., Chen, H., *et al.* 2016. Population dynamics and management of diamondback moth (*Plutella xylostella*) in China: the relative contributions of climate, natural enemies and cropping patterns. Bulletin of Entomological Research, **106**: 197–214.

Maywald, G.F., Kriticos, D.J, Sutherst, D.W., and Bottomley, W. 2007. DYMEX model builder, user guide. Hearne Scientific Software. Melbourne, Australia.

Miller, P., Lanier, W., and Brandt, S. 2001. Using growing degree days to predict plant stages. Montguide MT200103 AG 7/2001. Cooperative Extension Service, Montana State University, Bozeman, Montana, United States of America.

Mukerji, M.K., Olfert, O., and Doane, J.F. 1988. Development of sampling designs for egg and larval populations of the wheat midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae), in wheat. The Canadian Entomologist, **120**: 497–505.

North Dakota Agricultural Weather Network. 2019. Wheat growing degree days/growth stages and midge degree days [online]. Available from https://ndawn.ndsu.nodak.edu/wheat-growing-degree-days.html [accessed 25 November 2019].

Oakley, J.N., Cumbleton, P.C., Corbett, S.J., Saunderst, P., Green, D.I., Youngs, J.E.B., and Rodgers, R. 1998. Prediction of orange wheat blossom midge activity and risk of damage. Crop Protection, **17**: 145–149.

Olfert, O., Elliott, R.H., and Hartley, S. 2009. Non-native insects in agriculture: strategies to manage the economic and environmental impact of wheat midge, *Sitodiplosis mosellana,* in Saskatchewan. Biological Invasions, **11**: 127–133.

Olfert, O., Weiss, R.M., and Elliott, R.H. 2016. Bioclimatic approach to assessing the potential impact of climate change on wheat midge (Diptera: Cecidomyiidae) in North America. The Canadian Entomologist, **148**: 52–67.

Pivnick, K.A. and Labbé, E. 1993. Daily patterns of activity of females of the orange wheat blossom midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae). The Canadian Entomologist, **125**: 725–736.

Reeher, M.M. 1945. The wheat midge in the Pacific Northwest. Circular 732. United States Department of Agriculture, United States Government Printing Office, Washington, District of Columbia, United States of America.

Shahbandeh, M. 2019. Wheat - production volume worldwide 2011/2012–2019/20 [online]. Available from www.statista.com/statistics/267268/production-of-wheat-worldwide-since-1990 [accessed 5 May 2019].

Smith, M.A.H. and Lamb, R.J. 2004. Causes of variation in body size and consequences for the life history of *Sitodiplosis mosellana*. The Canadian Entomologist, **136**: 839–850.

Yonow, T. and Sutherst, R.W. 1998. The geographical distribution of the Queensland fruit fly, *Bactrocera* (*Dacus*) *tryoni*, in relation to climate. Australian Journal of Agricultural Research, **49**: 935–953.

Yonow, T., Zalucki, M.P., Sutherst, R.W., Dominiak, B.C., Maywald, G.F., Maelzer, D.A., and Kriticos, D.J. 2004. Modelling the population dynamics of the Queensland fruit fly, *Bactrocera* (*Dacus*) *tryoni*: a cohort-based approach incorporating the effects of weather. Ecological Modelling, **173**: 9–30.

Zadoks, J.C., Chang, T.T., and Konzak, C.F. 1974. A decimal code for the growth stages of cereals. Weed Research, **14**: 415–421.

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