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Status of Sitodiplosis mosellana (Diptera: Cecidomyiidae) and its parasitoid, Macroglenes penetrans (Hymenoptera: Pteromalidae), in Montana

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Abstract

The orange wheat blossom midge, S. mosellana (Gehin) (Diptera: Cecidomyiidae), a global pest of wheat (Tritium aestivum L.), has recently invaded Montana's Golden Triangle, an important wheat producing region. Unchecked, S. mosellana populations can quickly grow to damaging levels. In this study, we document the prevalence of S. mosellana and its main natural enemy, Macroglenes penetrans (Hyme-noptera: Pteromalidae), in this newly invaded area of Montana, and compared the effects of irrigated versus dryland cropping systems on S. mosellana and its parasitoid. Different approaches to monitoring S. mosellana populations were examined, including pheromone traps for adults, collection of larvae from wheat heads, and overwinter sampling of soil to measure the levels of larvae and cocoons. Adults of the M. penetrans were surveyed through daily sweep net sampling. This study demonstrated that the emergence of M. penetrans was usually well synchronized with emergence of S. mosellana as the emergence of parasitoids occurred shortly after the pest with the highest peak (90%) at 26 June and 14 July, 2015, respectively. Irrespective of sampling techniques; pheromone traps or soil sampling, no sig-nificant difference was observed in population of S. mosellana between irrigated and dryland cropping systems. In contrary, cropping systems played a significant role in the abundance of parasitoids since the irrigated fields had significantly higher population of parasitoids (five times on an average) compared to dryland cropping system. The possible implications of these findings in monitoring of S. mosellane and the establishment of M. penetrans are discussed.

Keywords: Orange wheat blossom midge; Wheat; Biocontrol; Monitoring; Establishment

1. Introduction

The orange wheat blossom midge, Sitodiplosis mosellana (Gehin) (Diptera: Cecidomyiidae), is a widespread pest of wheat (Triticum aestivum L.) of Palearctic origin that was introduced into North America in the early 1800s. The distribution of this pest has since expanded to Alberta, Saskatchewan, Manitoba, British Columbia, Minnesota, North Dakota, and Montana (Felt, 1912; Knodel and Ganehiarachchi, 2008; Olfert et al., 2009). S. mosellana was first detected in northern and central Montana in 2000 (Shanower, 2005), near North Dakota where the midge had been detected earlier. Damage to the wheat crop in this region initially remained low, with only periodic minor outbreaks. Subsequently, in 2006, an outbreak occurred in north western Montana on spring wheat in the Flathead County (Stougaard et al., 2014). Initial estimates of wheat losses were over $1.5 million in Flathead County alone. Typically, S. mosellana can reduce yield 30e40%, with an average of 2e10%. However, when populations of S. mosellana are very high, crop losses can reach 100% (Blodgett, 2007). In North Dakota during 1990s, wheat growers lost an estimated $30 million in gross reve-nue due to S. mosellana attack (Knodel and Ganehiarachchi, 2008). According to Lamb (1998) and Lamb et al. (1999), losses in Canada exceeded US $38.65 million in Manitoba and US $77.30 million in Saskatchewan in 1995.

In Montana, adults of S. mosellana emerge from the soil between June and July (Shanower, 2005). Midges have just one generation per year and overwinter as mature larvae in the soil (Doane et al., 1987, 2002). Under moist field conditions, larvae leave their co-coons in late May or early June and spend several days on the soil surface before pupating (Doane et al., 1987). Adults emerge over a five-week period beginning in late June or early July (Lamb et al., 1999). Females lay their eggs on wheat heads during heading and anthesis (Doane et al., 1987). Larvae hatch after 4–7 days and feed on the developing kernels for 2–3 weeks, causing them to shrivel, crack, or become distorted (Dexter et al., 1987). Under favorable conditions such as rain or simply enough moisture in the soil, larvae drop from the wheat heads, burrow into the soil and spin a cocoon before overwintering (Olfert et al., 1985). Yield loss and broken kernels resulting from *S. mosellana* feeding reduce the grade of the harvested grain, lowering its value (Olfert et al., 1985).

Regarding control strategies, insecticides are usually applied during the adult flight period. However, because of strong winds in Montana, conditions may be unsuitable for insecticide application during this necessary window for treatment. Conventional pesticide management of *S. mosellana* recommends treatment if there is one adult midge per 4–5 wheat heads during heading (Elliott et al., 2007). Several insecticides have been found to be effective and can be applied to wheat at heading for *S. mosellana* control (Blodgett, 2007; El-Wakeil et al., 2013). Currently, the most common method of control is an application of chlorpyrifos (Lorsban™) or lambda-cyhalothrin (Warrior®), timed at peak adult emergence. Because peak emergence last only a few days and adults have short lives (Stougaard et al., 2014), timing of insecticide application is very important and pheromone traps, in this context, have potential as a tool to detect the start and the peaks of midge flights.

Natural enemies, where they are established, can be important regulators of *S. mosellana* populations. Many hymenopteran natural enemies attack *S. mosellana* in either its native or introduced range (Barnes, 1956). The main egg-larval parasitoids of this pest are: *Macroglenes penetrans* (Kirby) (Hymenoptera: Pteromalidae), *Platygaster* sp., (Hymenoptera: Platygastridae), and *E. error* (Fitch) (Hymenoptera: Platygastridae) (Affolter, 1987). Beirne (1971) was first to report *M. penetrans* parasitizing *S. mosellana* in Manitoba in 1954–1959, and it is assumed that this parasitoid likely arrived in North America together with the pest. However, *E. error* and *Platygaster* sp. were intentionally introduced to North America from Europe in 1934 to control *S. mosellana* (Olfert et al., 2003). An earlier accidental introduction of *E. error* into New England in the early 1800s failed to become established (Affolter, 1990). Recently, the first record of *E. error* in the Pacific Northwest was reported by Echegaray et al. (2016). These parasitoids are potentially a valuable tool in maintaining midge population levels below the economic threshold (Doane and Masner, 1991; Olfert et al., 2003). In addition, other North American natural enemies, such as soil dwelling native ground beetles (Coleoptera: Carabidae), are also known to feed on *S. mosellana* larvae in the soil between the time larvae entering winter diapause in the fall and when they pupate in the spring (Floate et al., 1990; Holland and Thomas, 2000; King et al., 2011). While these natural enemies have potential to reduce *S. mosellana* populations, their efficacy can vary substantially with local environmental factors, including the establishment of introduced natural enemies (Grevstad, 1999).

M. penetrans is the most important natural enemy of *S. mosellana* (Affolter, 1990). This parasitoid is widely distributed in Europe but its full distribution in Canada and United States is unknown (Doane et al., 1989). In Canada, *M. penetrans* plays an important role in controlling *S. mosellana* populations, parasitizing up to 80% of the midge larvae yearly (Elliott et al., 2011). In 2005, Shanower (2005) reported up to 52% of *S. mosellana* larvae to be parasitized by *M. penetrans* in Montana. Efforts to expand the influence of *M. penetrans* parasitism in Montana began in 2008 using *M. penetrans* introduced from North Dakota to areas where the parasitoid had not yet reached, particularly Kalispell, around Flathead, Montana (B. Stougaard, Personal communication). From 2008 to 2014, no evidence of establishment of the parasitoid in Kalispell was found and a second attempt to introduce the parasitoid was made, using a second population from Alberta. Approximately 700 *M. penetrans* were released in both Pondera and Flathead Counties (Kalispell) in July of 2014.

Larvae of *S. mosellana* feed on the developing wheat seed in a protected environment under the glume of the wheat seed. This concealed feeding niche protects the midge larvae from both parasitoids and pesticides, making timing of spraying critical for success (targeting adult midges) (El-Wakeil et al., 2013). The ability of parasitoids to actively target their host, to synchronize their emergence with that of *S. mosellana* larvae and to respond to changes in host populations makes them an attractive alternative to chemical control. The parasitoid *M. penetrans* is well synchronized with *S. mosellana* larvae and is able to reach them at their feeding sites.

The efficacy of such an introduced parasitoid, however, can be lessened if it fails to establish in a given area or if a highly mobile pest manages to disperse into regions not yet reached by the parasitoid. Travis et al. (2013) made predictions on how the dispersal of natural enemies (for example, specialist predators) should be governed by the spatio-temporal dynamics of its key prey species, proposing that greater predator emigration rates and progressively selective settlement behavior might result in predators dispersing over longer distances. In addition, host parasitization is dictated by the ability of the parasitoid to find its host at both long and short distances (Cronin and Reeve, 2014).

S. mosellana adults are weak flyers, primarily locating susceptible wheat at short range by means of plant volatiles (Birkett et al., 2004). The movement and establishment of *S. mosellana* into new areas is therefore driven by the movement of air masses during brief weather events (Drake and Farrow, 1988; Miao et al., 2013). Recently, densities of *S. mosellana* have increased in the wheat growing regions of western and central Montana since the pest's first detection there in 2006 and 2012, respectively. This eruption of the pest in newly invaded wheat-growing regions has led many to speculate that the pest has left behind natural control factors, including *M. penetrans*. However, additional abiotic factors could also affect *S. mosellana* population dynamics (Doane et al., 2000). Precipitation, either through rainfall or irrigation, plays an important role in midge adult emergence from the soil, as does temperature (Elliot et al., 2009). Differences in emergence and the timing of emergence under irrigated versus dry conditions have not yet been evaluated. Moisture does, however, interact with insect emergence from the soil and from wheat heads. Larval emergence from wheat heads usually coincides with a summer rainfall, presumably because it loosens the soil, facilitating larval entry into the soil (Pivnick and Labbé, 1993).

The incorporation of parasitism by *M. penetrans* into an integrated pest management program may allow for more stable control while lowering pesticide use. Reduced pesticide use will in turn promote the conservation of non-target beneficial insects in the crop like the wheat stem sawfly *Cephas cinctus* (Nort) parasitoids *Bracon cephi* (Gahan) and *Bracon lissogaster* (Mues.) (Hymenoptera: Braconidae), which share the same flight season as *S. mosellana* (Runyon et al., 2002). Carabid ground beetle predators of *S. mosellana* are another important group of *S. mosellana* natural enemies in Montana wheat fields that may be harmed by pesticide applications (Floate et al., 1990). Late insecticide applications can actually prove detrimental to pest control by reducing certain populations of these parasitoids (Elliott et al., 2011).

The present study was undertaken to determine the prevalence and dispersal rate of *S. mosellana* and its dominant parasitoid *M. penetrans* in central Montana. The main objectives of this study were 1) to compare the abundance of *S. mosellana* in dryland and irrigated wheat fields, 2) to monitor the population of *S. mosellana* parasitoids in dryland and irrigated wheat fields, and 3) to observe the effect of different sampling methods on predictions of

S. mosellana abundance.

2. Materials and methods

2.1. Study area

Surveys for this study were carried out in 2014 and 2015 in central Montana near Valier (N 48° 18′37.4148′, W 112°2519.0956′), a wheat producing region known as the Golden Triangle. *S. mosellana* was first documented in this region in 2012, and since then wheat fields in the area have had persistent populations of *S. mosellana*. Wheat in this area is produced in both dryland and irrigated fields, in rotation with canola (*Brassica napus* L.), pea (*Pisum sativum* L.), or barley (*Hordeum vulgare* L.). The dominant crops in the region are spring and winter wheat. Surveys were conducted from 10 May to 31 July, 2015 in spring wheat to span the flight season of *S. mosellana* and *M. penetrans*. A total of 34 sites were selected (Table 1). At each study site, *S. mosellana* abundance was estimated in four different ways: 1) pheromone traps for adult midges (2015 only), 2) counts in wheat seed heads for midge larvae (2015 only), 3) counts in soil cores of midge larvae or cocoons and associated parasitoids (2014 and 2015), and 4) sweep net sampling for adult parasitoids (2015 only). Both dryland and irrigated spring wheat fields were sampled in roughly equal numbers.

2.2. Pheromone trapping of adult midges

Midge populations were surveyed in 2015 using delta traps baited with pheromone lures ((2S,7S)-nonadiyl dibutyrate) (Great Lakes IPM, Inc., Vestaburg, MI), with sticky card inserts, (Scentry®) at all of the 34 study sites (Table 1). Delta traps were painted green to reduce non-target catch and positioned at the height of the wheat canopy. At each site, a single trap was placed 20 m in from the field edge, and trap height was adjusted weekly to match the height of the wheat canopy. The *S. mosellana* pheromone used in the traps attracts only male *S. mosellana* (Gries et al., 2000). Therefore, total midge population was calculated using documented sex ratios and average flight potential for male midges (Hao et al., 2013). Because sex ratios for *S. mosellana* typically range from 1:1 (Smith et al., 2004a) to 1.15:1.00 (Elliot et al., 2009) across most populations, and because both male and female *S. mosellana* typically fly less than 500 m, we estimated local minimum female numbers near each trap from male trap catch by assuming t the sex ratio of 1:1 and a flight distance of 400 m.

Table 1
Density of *Sitodiplosis mosellana* larvae + cocoons (L + P) in soil/m^2 in winter of 2014–2015 and pheromone catch of male *S. mosellana* adults in each field in 2015.

Field study sites	Type	L + P/m^2 mean ± SD	Adults/trap mean ± SD
Mageris	Dryland	0 ± 0	249 ± 7.6
Sunburst	Dryland	0 ± 0	–
MFE	Irrigated	39 ± 3.4	2524 ± 24.3
Sil Farm	Irrigated	78 ± 2.8	–
Akin	Irrigated	0 ± 0	244 ± 3.6
Birch	Irrigated	0 ± 0	289 ± 6.6
Wingina	Dryland	0 ± 0	519 ± 4.3
Fretheim	Irrigated	0 ± 0	267 ± 4.2
Banka W	Dryland	39 ± 2.6	15 ± 4.3
GC	Dryland	78 ± 6.2	101 ± 2.8
JVD chucks	Irrigated	195 ± 4.7	366 ± 7.3
Banka E	Dryland	39 ± 2.2	62 ± 2.6
Crawford	Irrigated	156 ± 6.3	1 ± 0.5
Banka #1	Dryland	0 ± 0	499 ± 8.6
Banka #2	Dryland	78 ± 4.1	40 ± 2.1
Banka #3	Dryland	78 ± 3.6	62 ± 6.6
Banka #4	Dryland	117 ± 2.8	15 ± 2.9
Hoss	Irrigated	0 ± 0	1 ± 0.3
Parm	Dryland	39 ± 6.3	5 ± 2.4
Wheeler	Dryland	0 ± 0	85 ± 8.7
Moon	Irrigated	0 ± 0	4 ± 2.1
Valley	Irrigated	0 ± 0	2 ± 1.7
Section	Dryland	0 ± 0	274 ± 6.6
Hunter	Irrigated	0 ± 0	9 ± 2.2
Dewey	Irrigated	39 ± 3.4	1 ± 0.4
Turk	Irrigated	39 ± 4.8	6 ± 1.8
Webster	Irrigated	156 ± 8.2	2 ± 0.7
KB Stark	Irrigated	742 ±8.6	28 ± 1.3
Dean #2	Dryland	0 ± 0	39 ± 4.1
Pondera5	Irrigated	117 ± 4.4	2644 ± 22.3
WTARC1	Irrigated	117 ± 6.3	750 ± 11.4
WTARC2	Dryland	0 ± 0	249 ± 6.5
KB #2	Irrigated	39 ± 4.1	244 ± 7.2
Casey	Dryland	39 ± 2.7	245 ± 9.2

2.3. Wheat head infestation rates

Wheat heads were sampled before *S. mosellana* larvae began dropping to the soil (31 July to 4 August 2015), and no rainfall occurred during the sampling period. Previous studies have suggested that rainfall can stimulate *S. mosellana* larvae to drop to the soil (Olfert et al., 1985). A total of 200 wheat heads were selected randomly from each site. These wheat heads were removed from the plants, placed in mesh linen bags, and were immediately transported to the laboratory and dried under low humidity at room temperature before individually threshing wheat heads by hand to extract larvae. The average number of wheat heads per square meter was measured in each study site by randomly placing a square meter quadrat in three haphazard locations in each field and counting the total number of wheat stems post-harvest. The percentage of wheat infested out of the 200 randomly sampled wheat heads was calculated and multiplied by our estimate of stems/m^2 to estimate larvae in wheat heads/m^2.

2.4. Densities of wheat head midge overwintering in soil

The densities of *S. mosellana* overwintering stages in soil were investigated in all 34 sites (Table 1). Overwintering *S. mosellana* populations in soil (larvae and cocoons) were sampled in the fall of 2014 (12 sites) and spring of 2015 (the remaining 22 sites) using a 5.7 cm dia bulb planter to extract a core to a depth of 7.6 cm. Soil samples were taken along transects starting 30 m from the edge of the field, with 10 samples per transect spaced 10–15 m apart. Each site was sampled only once, with only one transect. Soil samples were held at 6 °C until *S. mosellana* larvae and cocoons were separated from inorganic material using a soil washer (Flote-Tech Model A, R.J. Dausman Technical Services Inc., Rochester, Indiana, USA), where the organic material was gently broken apart from inorganic material with water movement and air bubbles. Organic debris, including *S. mosellana* stages, was routed to a fine collection screen where larvae and cocoons were collected with forceps and placed in alcohol for examination and counting.

2.5. Parasitoid sweep net survey

Adult *M. penetrans* parasitoid abundance was estimated concurrently with sampling of wheat heads for *S. mosellana* larvae by the use of sweep netting, done at eight field sites in Pondera County (fields were nearby Western Triangle Research Center, Montana). Each sample consisted of 20 sweeps (180°) along a haphazardly directed line across the sample field within 400 m of the *S. mosellana* pheromone traps. Sweep net samples were taken once a day, five days per week, from wheat heading through anthesis (1 June to 30 July, 2015). Sweeps were at the level of the wheat head ears and most of the sampling was done in the morning. Adult parasitoids similar in general appearance to *M. penetrans* were collected from field samples and later identified and counted in the laboratory using reference specimens. Sex ratios of *M. penetrans* populations were calculated based on morphological characters (Doane et al., 1989).

2.6. Data analysis

Abundances of wheat head midges and their parasitoid *M. penetrans* were compared in irrigated vs. dryland cropping systems using t-tests. Phenology diagrams for male *S. mosellana* catch in pheromone traps and for both sexes of *M. penetrans* caught in sweep net samples were constructed from sample data and the 10, 50 and 90 percentile points for abundance were calculated in relation to a scale of cumulative degree days (DD) (above 5 °C) starting on 1 January of each year. Daily precipitation values were obtained for the study area using the USDA-NRCS weather station located at the Western Triangle Agricultural Research Center (N 48.307404, -W111.921977). Correlations between midge populations and pheromone traps at study sites were evaluated using linear models in the statistical package R. Data were log transformed where necessary to maintain model assumptions.

3. Results

3.1. Pheromone trap catch of adult midges, 2015

Summed overall 34 sites in the study area, the phenology of wheat head midge emergence (Fig. 1) showed that the first *S. mosellana* adults in 2015 were collected on 16 June. By 23 June, 10% of *S. mosellana* had emerged (8.50 ± 1.00 days after first midge emergence; mean ± SE) and 752 DD had accumulated at or above 5 °C. Fifty percent of *S. mosellana* had emerged by 26 June (11.70 ± 0.50 days after first midge emergence) at 1045 DD. On 30 June (1453 DD), 90% of *S. mosellana* had emerged (25 ± 2.50 days after first collection). A few additional *S. mosellana* adults continued to be caught throughout July, well after the majority of the crop had progressed past susceptibility (boot – early heading). The presence of *S. mosellana* followed a pattern of a large initial emergence peak followed by a long tail of declining trap captures throughout the season (Fig. 1A). In 2015, peak emergence occurred at all survey sites on 29 June (1149 DD). Late maturing wheat tillers were present throughout the flight season of *S. mosellana* in this study.

Pheromone traps caught a total of 10,918 male *S. mosellana* from all study sites. The populations of *S. mosellana* were not significantly ($P < 0.05$) different between irrigated and dryland cropping systems (1571.00 ± 517.49 and 1730 ± 1101.01 per trap, respectively; mean ± SE) ($t = -0.13$, $df = 2.91$, $P = 0.90$). Pheromone trapping area was estimated to be up to 1800 m^2 (0.18 ha) based on the flight potential of the male midge (Hao et al., 2013). The calculated midge population per hectare, assuming an even sex ratio, was therefore 18,123.07 ± 5286.61 midges; mean ± SE (of both sexes) per hectare. The estimated egg load for a population of this size, and thus the damage potential assuming a mean of 80 eggs/female (Pivnick and Labbé, 1993), was 724,922.83 ± 211,504.44 eggs/hectare; mean ± SE. This number represents the maximum number of wheat seeds that could be infested per hectare assuming each egg is laid on a separate seed.

3.2. Wheat-head infestation rates

Counts of *S. mosellana* larvae in wheat heads yielded 54.92 ± 26.07 midges/m^2, which adjusts to 549,214.29 ± 260, 677.46 larvae per hectare. The estimates of larval populations observed in wheat head and pheromone traps (assuming each egg hatches and develops successfully into a larva) were not significantly different, although they were nearly significant ($t = 2.20$, $df = 9.38$, $P = 0.05$). In addition, no correlation was observed between the number of *S. mosellana* larvae found in wheat heads per hectare and the number of *S. mosellana* adults caught in pheromone traps across all sampled fields ($F_{1,6} = 0.37$, $P = 0.56$, $R^2 = 0.05$) (Fig. 2A).

3.3. Densities of S. mosellana overwintering stages in soil

Despite a trend for higher numbers of *S. mosellana* in the soil of irrigated cropping systems, differences were not significantly different between irrigated and dryland systems ($t = -1.52$, $df = 18.85$, $P = 0.15$). The number of *S. mosellana* sampled from soil did not correlate with the number of adult *S. mosellana* in pheromone traps ($F_{1,6} = 0.18$, $P = 0.68$, $R^2 = 0.03$) (Fig. 2B) nor the number of larvae in wheat heads in this study($F_{1,6} = 0.14$, $P = 0.72$, $R^2 = 0.02$) (Fig. 2C). Soil sampling predicts 636,160.71 ± 219,623.83 midge/hectare (mean ± SE), in contrast to the 549,214 midge/hectare predicted by end of season larval counts and the 18,123 midge/hectare predicted by pheromone traps.

3.4. Macroglenes penetrans adult survey

M. penetrans sweep net catch peaked shortly after peak capture of wheat head midges in pheromone traps (Fig. 1B). In 2015, peak parasitoid emergence occurred on 2 July (1235 DD). Meanwhile, *M. penetrans* flight period lasted from 23 June to 31 July. Ten, 50, and 90% population emergence occurred 3.40 ± 1.30, 17.50 ± 0.60 and 31.30 ± 11.90 SE days after the first parasitoid was captured in a given field (26 June, 1 July, and 14 July, 2015, respectively). We found no correlation between the number of *S. mosellana* adults captured in pheromone traps and the number of *M. penetrans* adults captured in sweep nets ($F_{1,6} = 0.15$, $P = 0.72$, $R^2 = 0.14$).

Irrigation significantly increased the abundance of *M. penetrans* in wheat fields compared to dryland cropping systems ($t = 2.89$, $df = 4.07$, $P = 0.04$). Irrigated fields had on average five times as many *M. penetrans* as dryland cropping systems (Fig. 3). Meanwhile, the sex ratio of *M. penetrans* varied between sampling sites. Despite an apparent bias toward females among parasitoids (2:1 F:M overall), differences were not statistically significant in this study ($t = 1.49$, $df = 13.25$, $P = 0.16$), and at individual study sites the ratio of male to female *M. penetrans* varied greatly.

4. Discussion

The enemy release hypothesis posits that species escape natural population controls when they invade a new geographic area lacking key specialized natural enemies (Keane and Crawley, 2002). Enemy release hypothesis maintains that species introduced into a new region experience a competitive advantage over native species due to a relative reduction in regulation by natural enemies (Louda and Potvin, 1995; Eschtruth and Battles, 2009). In most cases, the newly invaded area was previously inaccessible to the pest insect or its natural enemy due to physical barriers like oceans, mountains, deserts or even rivers (Wittenberg and Cock, 2001).

Phenology plays an important role in the prediction and management of pest insects. The flight phenology of *S. mosellana* was consistent with degree-day models developed by Elliot et al. (2009) and Jacquemin et al. (2014). In this study, we observed that the initial peak emergence of midge corresponded with degree day estimates with insects to maturity, especially in dryland cropping systems. The studies by Gaafar et al. (2011) and El-Wakeil et al. (2013) indicated that the flight range of *S. mosellana* likewise correlated with rainfall events. Peak adult emergence comprises

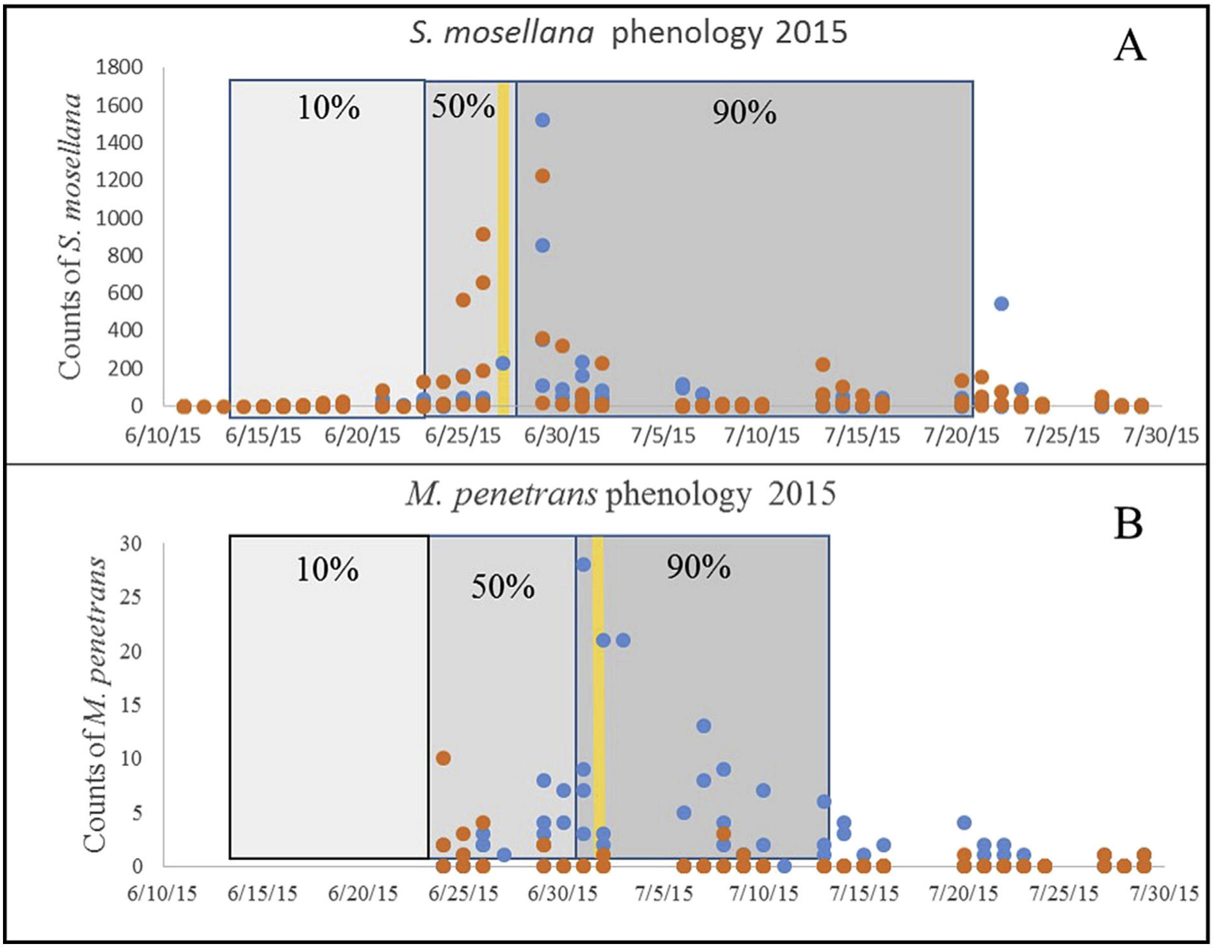

Fig. 1. Flight phenology of *Sitodiplosis mosellana* (A) (male only) and *Macroglenes penetrans* (B) (both sexes) in Pondera County in 2015 in irrigated (blue) and dryland (orange) cropping systems. Gray areas denote the percentage of population emerged and the yellow bar denoted the peak emergence date.(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the majority of the midge population and is the target for pesticide application. The long tail of presence of males spanned most of the growing season and occurred after the majority of the crop was no longer susceptible to *S. mosellana* attack and is therefore not a target for control. Presumably, these late-emerging midges were finding susceptible wheat heads in the late maturing wheat tillers (Kobata et al., 1992), but the importance of this food source to *S. mosellana* population dynamics has not yet been investigated.

Late tillers are presumably important for the parasitoid *M. penetrans* as well, as a source of hosts. Peak *M. penetrans* emergence closely followed that of *S. mosellana* and similarly extended throughout the summer. *M. penetrans* lays its eggs inside the eggs and early instar larvae of *S. mosellana* (Doane et al., 1989). *S. mosellana* carries 4—105 eggs (mean of 80) per female (Doane et al., 2013; Smith and Lamb, 2004), while *M. penetrans* carries an average of 205 ± 20 eggs per female (Affolter, 1990). Higher egg loads lead to potentially faster population growth, which in turn leads to effective population regulation of the host insect by the natural enemy. By our calculations, *M. penetrans* in this study area produced as much as 2 × as many eggs as *S. mosellana* in the same area. Our study did not measure the correlation between rainfall and irrigation events and parasitoid emergence, but Chavalle et al. (2015) hypothesized that parasitoid emergence is triggered by the same rainfall that induces host emergence. Given the low population level of midges and *M. penetrans* in the study area, correlations may become more apparent as populations continue to build.

The *S. mosellana* population in the vicinity of Valier, Montana, appears to be low, with fewer adult males caught per pheromone trap than in heavily infested areas of north western Montana, North Dakota, and western Canada (Knodel and Ganehiarachchi, 2008; Lamb et al., 1999; Olfert et al., 2009). Soil samples of larvae indicated highly variable populations depending on sampling location. Soil samples gave estimates of midge numbers that were many times greater than either pheromone traps or larval counts, but soil sampling is known to be inaccurate at low levels of infestation (Elliot et al. 2009). It is known that some midges overwinter for more than one season, but it is not likely that the number would be so many times greater than the emerged population, as was found with this study. Most likely, the overestimation in soil samples rests with estimating the sample area, as relatively few midge larvae and cocoons were found in any particular soil sample. Clearly, more work needs to be done on this method of predicting midge populations.

Wheat head larval sampling indicated that the expected damage to the 2015 spring wheat crop in the study area, with an estimated 549,214 *S. mosellana* larvae/hectare, will mean a loss of at most 0.79 bushels/hectare or 0.021 tons/hectare. This equates to approximately 2.15% damage to the 2015 wheat crop in the study region. Spray treatment may be necessary if ~6% of the crop is expected to be damaged, as this is the level where detection of damage is likely

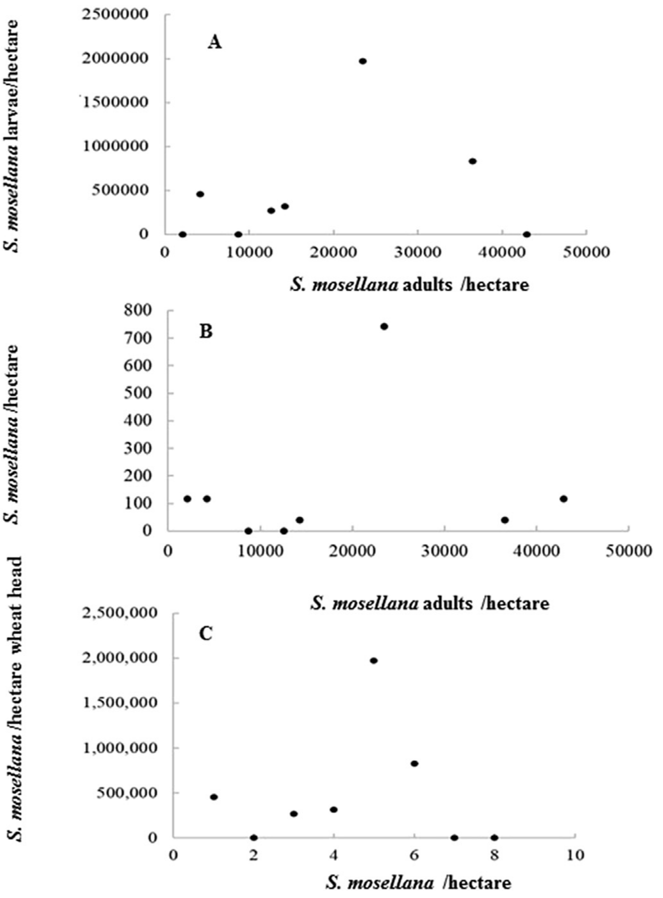

Fig. 2. (A)The number of *Sitodiplosis mosellana* larvae found in wheat heads per hectare compared with the abundance of adults caught in pheromone traps in the same field in 2015. (B) The number of *S. mosellana* per hectare in the pheromone traps compared with the number of midges in the soil in the same field. (C) The number of *S. mosellana* estimated per hectare compared with the number of larvae removed from wheat heads in the same fields.

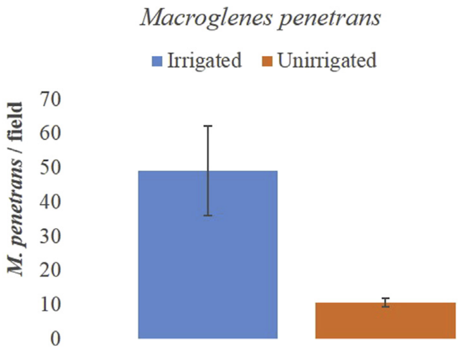

Fig. 3. *Macroglenes penetrans* abundance in irrigated (blue) fields and dryland (orange) cropping systems (t = 2.8891, df = 4.065, $P = 0.04375$). * indicates $p < 0.05$ significance level.(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

at the grain elevator and a downgrading of the crop may occur (Smith et al., 2004b).

Two tangible findings from this study are the underestimation of the trapping distance of the pheromone traps and the high density of *M. penetrans* natural enemies in the area. Pheromone traps caught 30% more adult midges than was expected from an area within 400 m of traps. However, this increase is small enough that error due to the flight capability of the male midge could explain this difference. Meanwhile, the abundance of *M. penetrans* in the study area is promising for midge control. In other parts of Montana, *M. penetrans* has readily established where it was introduced for biological control. In Canada, where *S. mosellana* control has been measured using the percentage of larvae in wheat heads that are parasitized, *M. penetrans* is capable of 40–80% control of *S. mosellana* (Olfert et al., 2003). The data generated in this study indicate that this level of control is possibly already occurring in this area of Montana. Further studies are required to determine the parasitism rate of *S. mosellana* by *M. penetrans* in Montana, but early estimates look promising. The information generated by this study is an important first step in developing an integrated pest management program for this pest in Montana. Effective pesticide application should take into account when the pest is most vulnerable and when natural enemies are present. Further efforts are underway to import two additional egg-larval parasitoids, *Platygaster tuberosula* Kieffer and *E error* from Saskatchewan (Canada) to Montana to further control midge populations.

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