The effect of seeding date on the development of Hessian fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), on spring wheat (Poaceae) in southern Manitoba[1]

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ABSTRACT

The Hessian fly *Mayetiola destructor* (Say) has both univoltine and bivoltine generations on spring wheat in Manitoba. The first generation attacks seedlings of spring wheat in June and mostly completes its development at the crown of plants in July. Adults of the second generation emerge in mid–July to early August and oviposit primarily on late-seeded plants. The second generation larvae form puparia in late July and August and remain dormant over the winter in the straw under stem sheaths. The seeding date of spring wheat affects whether first or second generation larvae develop on the crop, and the severity of stem breakage by the Hessian fly. Wheat sown in mid- to late May is attacked mostly by the first generation, and only suffers minor damage. Crop damage is highest when spring wheat is sown in the first two weeks of June and is caused by the feeding of second generation larvae. In most years, about 70% of the Hessian flies in southern Manitoba are bivoltine. The puparia of univoltine flies remain quiescent for the remainder of the summer and overwinter at the base or crown of wheat plants. In the four year field study survival of first generation puparia was >65%, compared to <10% for second generation puparia.

INTRODUCTION

The Hessian fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), is a serious pest of wheat *Triticum aestivum* L. in most major wheat growing areas (Barnes 1956; Berzonsky *et al*. 2003). The pest was introduced into North America in the 18th century (Osborn 1898), and is now throughout the United States and Canada (Buntin and Chapin 1990; Ratcliffe *et al*. 2000; Whistlecraft and Deakin 1992). In the many areas of the United

States, resistant winter wheat cultivars have provided the most reliable and economical control of the Hessian fly (Ratcliffe and Hatchett 1997), but no spring wheat cultivars grown in western Canada are known to be resistant, although one cultivar, 'Superb', is less susceptible to damage (Wise *et al*. 2006).

In western Canada, outbreaks of the Hessian fly are infrequent (McCullough 1987; Harris 1991) and the extent of its damage to spring wheat is not well documented. Turnock and Timlick (1990) found 5% of stems of 'Biggar' spring wheat from 11 fields in Manitoba were infested by Hessian fly.

In the northern winter wheat areas of the United States and in eastern Canada, the Hessian fly is bivoltine (Ratcliffe and Hatchett 1997), and in the southern United States it may produce three to six generations per year (Hoelscher and Turney 1985; Buntin and Chapin 1990). The Hessian fly in western Canada, where most wheat is sown in spring, has been observed to complete one full and a partial second generation per year (Criddle 1915).

The Hessian fly mainly damages spring wheat in western Canada by attacking stems during stem elongation which weakens the stem at the feeding site of the larvae. Yield losses occur when infested stems break (Criddle 1915; Mitchener 1923) or from reductions in seed number and size in spikes on infested unbroken stems (Wise *et al.* 2006). Damage to seedlings in western Canada has not been documented to cause yield losses as opposed to winter wheat in the United States where attack by multiple broods can cause additional yield losses in the autumn by killing seedlings or vegetative tillers (Hill and Smith 1925; Byers and Gallun 1972; Buntin 1999).

A delay in the seeding of winter wheat to escape fall infestation can prevent or reduce Hessian fly damage in many winter wheat areas of North America (Flint and Larrimer, 1928; Buntin *et al*. 1990). It is known that seeding date of spring wheat in western Canada may affect damage by the Hessian fly (Wise *et al*. 2006), but the differences in yield loss have not been documented. The effects of seeding date on the development of the Hessian fly on spring wheat in western Canada and on associated crop losses by this insect pest were the objectives of this study.

MATERIALS AND METHODS

The spring wheat cv. 'AC Barrie' was seeded in 2003 to 2005 and in 2007 at a rate of 80 - 100 kg/ha by hand or with a double disc press drill at the Agriculture and Agri-Food Canada Research Farm, Glenlea, Manitoba, Canada (49º38′N, 97º09′W). Seeding was done by hand when excess surface moisture prevented mechanized seeding. 'AC Barrie' was selected because it is susceptible to the Hessian fly (Wise *et al*. 2006) and was the most commonly grown cultivar in western Canada during the study (Canadian Wheat Board 2003, 2004, 2005). The plots were located in the fallow portion of a field with a wheat:fallow annual crop rotation. Plots were 10 m^2 to 16 m^2 and were sown on four dates at similar intervals each year between 16 May and 19 June (Tables 2, 3). The seeding dates were replicated four times and plots were arranged in a randomized complete block design. The fallowed areas around the plots were sown to 'Roblin' spring wheat on the last day of seeding, except in 2005 because of wet conditions.

Adult emergence next to the plots was monitored with galvanized metal cone traps. Five traps on 4 June 2004 and eight on 31 May 2005 were pushed 2-3 cm into the soil over wheat stubble infested with Hessian fly. The traps enclosed an area of 0.10 m^2. Two screened holes on the side provided ventilation and a plastic vial over an opening at the top collected adults.

Sampling consisted of 15 to 25 plants (Foster and Taylor 1974) randomly selected in each plot weekly from early June to August in 2003 to 2005 (growth stages 11 to 80, Tottman and Makepeace 1979). Plants were unearthed by a hand trowel and soil was removed from the roots. Samples were placed into a separate plastic bag for each plot and stored within a few hours. Eggs or larvae on young plants were assessed within four days after storage at 5°C, but older plants (growth stages 70 to 80) collected in August were stored at 10°C for up to three weeks.

The number of eggs on leaves, and larvae and puparia at nodes or at the base of plants (growth stages 11 to 29) were counted, using a dissecting microscope, and plants were assessed for feeding damage by larvae. Plants with elongated stems (growth stages 30 and above) were cut immediately above the first node without adventitious roots. A 'base' count of larvae and puparia was taken at and below this node, and a 'stem' count of eggs, larvae and puparia was taken from above the node. Larvae and puparia were exposed by pulling back the leaf or stem sheathes at the base or nodes. The puparia with broken exuviae or exit holes were examined for the presence of parasitoid remains (Hill and Pinckney 1940). Exuviae without any remains were recorded as being exited by an adult Hessian fly.

The mean numbers of larvae and puparia at the base or on the stems were calculated from collections (80-100 plants per plot) taken from mid-July to August. The number of first generation adults was estimated by counting puparia with adult fly emergence holes from samples collected in August (50-70 plants per plot). In 2007 puparia and adult fly emergence were estimated from a single collection (20-25 plants per plot) in early October. Plants with puparia were assessed for plant or tiller death. Assessments to determine the proportion of plants infested at the base or on the stems were taken from the mid-July to August or October collections.

At plant maturity in September or October, stem breakage by Hessian fly was estimated by counting the numbers of broken and unbroken stems in each plot from two 0.25-m^2 areas that were representative of the entire plot. In 2007, the stems of all plants in plots of the two last sowings that had been damaged by rains just after seeding, were examined for stem breakage. Yield losses were calculated from the percentage of stems that had broken and fallen to the ground.

Puparial survival. Plants were collected in September or October in all years to determine the emergence of adults (%) and mortality of puparia. The plants were cut, as for earlier collections, and all samples were stored at 2.0°±1°C, 0:24 L:D within 24 h in sealed plastic containers for at least 13 weeks (Harris and Rose 1989). Immediately after storage, five puparia from the base or stems were placed on a 5-7 mm layer of moistened sand in separate 10-ml glass vials. The vials were kept at room temperature, and adult Hessian flies and parasitoids were counted and removed from vials as they emerged. Puparia that did not eclose after five weeks were examined for immature or dead Hessian flies.

In 2004, puparia at the base of plants in the two earliest sowings were collected on 21 and 28 July and were tested as above, except puparia were kept at room temperature and were not moved to cold storage until after eclosion had ceased for five weeks.

Plants also were collected at crop maturity from late maturing commercial fields at La-Salle (49°38´N, 97°12´W), Rosenhoff (49°25´N, 97°25´W), and Otterburne (49°30´N, 97°03´W) in the Red River Valley of Manitoba on 9 September 2005. The fields were about 15 to 35 km from the Glenlea site. Broken stems were severed at the crown and overwintered, as for the plot studies. After overwintering, puparia were placed onto moist sand in separate glass vials and exuviae from empty puparia were counted. Hessian fly and adult parasitoids were counted as they emerged in the vials. Puparia that did not eclose were dissected to determine if they had been parasitized.

The proportion of plants infested by first and second generation Hessian flies and stem breakage for the four seeding dates each year were analyzed by ANOVA and Tukey's Multiple Range test (P>0.05) to determine differences among seeding dates.

RESULTS

Weather data and crop growth. Mean temperatures at Glenlea from May to August in 2003, 2005, and 2007 were about 1°C above 30 year means of 16.8°C (Environment Canada 2008). In 2004, mean temperatures were 1°C to 5°C below normal for all four months. Moisture levels during these months were within 10% of 30 year means (293.2 mm) in 2003 and 2007, 38% above in 2004, and more than 50% above in 2005. May and August of 2004 and June and July of 2005 had about double the normal rainfall levels.

Plants in most plots each year produced 3-5 tillers per plant. The low temperatures in 2004 delayed germination and crop growth by a week to 10 days. Heavy rainfall killed many newly emerging plants in the second seeding of 2004, and in the last seeding of 2005 and 2007. Plants which survived in the damaged plots in 2004 were of normal height and many produced more than twice as many tillers as plants in other plots. In the damaged plots only five tillers per plant, which equaled the mean found in the other plots, were assessed. Plants damaged in 2005 and 2007 were very short and had only one to three tillers per plant.

Number of generations. All immature stages and eclosed puparia of Hessian flies were collected on spring wheat. Two peaks of egg and larval development were identified, corresponding to two generations (Fig. 1).

First generation. Adult Hessian flies were captured in cone traps and eggs were found on seedlings in the first week of June. Egg densities on seedlings in all years were highest in the second week of June, ranging from 0.6 to 3.0 eggs per plant each year. Oviposition lasted for about three weeks in 2003 and 2005 and for about four weeks in 2004 (Fig. 1).

Larvae were first collected on 9-10 June (Fig. 1). In 2003 and 2004, about 5% were already third instars, indicating some oviposition had occurred more than one week earlier. Larvae were most abundant from late June (2003) to the second week of July (2004). The first puparia were found during the period of peak larval abundance, and empty exuviae began to appear about two weeks later. By early August, adult Hessian flies had exited from nearly 60% of the puparia in 2003 and 50% in 2005, but less than 20% in 2004 (Fig. 2). At crop maturity, adults had emerged from 40% to 64% of first brood puparia in 2003 to 2005 (Table 1).

After an overwintering period, adults emerged from 12% to 30% of the puparia for a total emergence of 67% to 77% from puparia in the late collections (Table 1). The post-overwintering emergence represented 17% to 42% of all first generation adult emergence. Hymenopterous parasitoids killed 18% to 28% of the puparia, and 4% to 8% died from unknown causes.

Second generation. A second population of eggs was laid during the second or third week of July (Fig. 1) on leaves of plants in the later seeded plots. Larvae were found at the stem nodes soon thereafter, and densities were highest during the last week of July or the first week of August (Fig. 1). Puparia began to form by the end of July in 2003 and 2005 but not until 11 August in 2004 (Fig. 2). A few empty puparia were found each year. All these puparia contained the remains of a parasitoid.

Survival of second generation puparia never exceeded 12.5% in any collection (Table 1). At all sites and years, puparia were killed mainly by chalcidoid parasitoids (Wise 2007), and an average of 17% died from unknown causes. In the latter cases, the dead larvae were either desiccated and covered with mycelia or liquefied by a bacterial infection.

Seeding dates. Crops were attacked by overwintering adults as the first or second leaf unfolded (growth stage 11 and 12). In all years, Hessian fly infestations by first brood populations were lowest in plots sown on or after 9 June (Table 2). In two of the four years, June sowings had fewer ($P<0.05$) infested plants than those sown 2-3 weeks earlier (Table 2).

No plants collected in 2003 and 2004 were killed by the feeding of first generation larvae, and <10% of infested plants had one or two dead tillers. In 2005, no dead plants were found, but 72% (n=54) of infested plants in the first seeding, 67% (n=30) in the second, and 80% (n=25) in the third had at least one tiller that was killed by first generation larvae.

A higher percentage of adults emerged without an overwintering period in the earliest sowings in 2003 ($F_{3,9}=5.0$, $P=0.026$, n=1098) and in 2005 ($F_{3,9}=9.72$, $P=0.035$, n=218) than in the last sowings. In both years, 64-65% of adults in the first seeding emerged without diapause versus 38-39% in the last seeding. Adult emergence without diapause in the first seeding (33%) was also higher than the last seeding (17%) in 2004 (33%), but results were not significant ($P>0.05$).

Although densities varied greatly among years, second generation populations increased the later the crops were sown (Table 3). Crops sown in the first or second week of June had higher second generation infestations than crops sown three to four weeks earlier ($P<0.05$), except in 2007 when populations were higher for sowings in the first week but not in the third week of June ($P>0.05$) (Table 3).

Stem breakage largely reflected infestation levels of the second generation. Breakage was higher ($P<0.05$) for the last versus the earliest seeding date (Table 4) except for the last seeding date in 2007. Many infested plants in the earliest sowings had few broken stems. These plants were mostly infested by first brood larvae which concentrated their feeding at the base of the plants.

DISCUSSION

While the Hessian fly is widespread throughout southern Manitoba, it is not known to cause serious yield losses in the province. In this study, seeding dates used by most growers contributed to the low incidence of damage. Growers are recommended to seed wheat early in the growing season, *i.e.*, before 1 June, to maximize yields (Wolfe *et al*. 1978; Manitoba Agriculture 1998). Crops sown by 22 May in this study had up to 7-fold less stem breakage than crops sown two to three weeks later.

Hessian flies use chemical and visual cues (Harris *et al*. 1993) and wheat plants of suitable size and maturity (Hill *et al*. 1943; Morrill 1982) to locate oviposition sites. Plants sown in this study by 22 May were mostly too mature to attract females or for second generation larvae to develop. Very few main shoots or early tillers on these plants were found to be infested. Since the main shoot and first two tillers of spring wheat in western Canada contribute two-thirds or more to the total yield (Hucl and Baker 1989a, b), second generation larvae mostly attack the least productive tillers in early seeded crops.

Crops are more susceptible to damage if sown in the first week to 10 days of June. In most years, these crops attract first brood females, and second generation larvae feed mostly at the upper nodes of the main shoot or first tillers of these crops. Feeding at these nodes maximizes the likelihood of stem breakage and the potential for further yield losses from seed shrinkage and fewer seeds forming in spikes of infested standing stems (Wise *et al*. 2006). These symptoms were characteristic of the damage to susceptible spring wheat cultivars by the Hessian fly in Oregon (Smiley *et al.* 2004).

Plants sown after 10 June, particularly sowings just before the 20 June cut-off date for crop insurance in western Canada, are readily attacked by second generation larvae but are less prone to stem breakage than plants sown in early June. The lower breakage in late sowings can be attributed to plants more likely being stunted and having smaller spikes which places less stress on damaged areas of the stems.

Plants infested as seedlings by first generation larvae did not show damage symptoms common to winter wheat seedlings (Anderson and Harris 2006). Dead or severely damaged shoots were found on some infested seedlings in 2003 and 2004, but these plants continued to produce new shoots and outgrew the damage. Young plants those years were frequently infested by another insect pest of wheat, the frit fly, *Oscinella frit* (L.). This insect is a serious pest of wheat in eastern Europe (Lauva and Shutele 1977), but it is not known to cause economic yield losses to spring wheat in North America. Frit fly larvae fed mostly on newly developing secondary shoots, masticating the tissue and killing the shoot. First generation Hessian fly larvae, conversely, fed mostly at the elongated internodes of large primary tillers at the crown of the plant.

In 2005 when growing conditions were less suitable than the previous two years, 67-80% of all infested plants had at least one dead tiller. Plants that year had few tillers, and first generation larvae were found more frequently on small secondary shoots than in previous years, causing their death. Plants in 2005 were less able to compensate for early tiller loss than in 2003 and 2004 because of poor growing conditions. Thus, damage to seedlings may contribute to lower yields in years of poor plant growth and, if some compensatory growth does occur, to a delay in wheat maturation.

Many first generation adults emerge after spring wheat fields are suitable for oviposition and for larvae to develop. Late-appearing females can produce a second generation in southern Manitoba if they find an alternate host since there are 4-6 weeks of temperatures suitable for larval development. Perennial grasses known to support Hessian fly reproduction, such as *Hordeum jubatum* L. and *Elytrigia repens* (Zeiss *et al*. 1993), are abundant in southern Manitoba, but it is not known if flies will seek these plants this late in the season.

Hessian flies are both univoltine and bivoltine on spring wheat in southern Manitoba each year. Adults emerge in late May to late June, depending on the weather, and females lay eggs on newly emerged wheat. The larvae feed at internodal areas of the plant crown for two to three weeks, and either first brood adults emerge about two weeks later or puparia aestivate during the summer and then overwinter. The presence of univoltinism and multivoltism in Hessian fly populations has also been found in Kansas, Germany and England (Barnes 1958), albeit at lower prevalence than in these studies.

No second generation adults were observed in any year of the study. Empty casings of second generation puparia were found, but all had been exited by a parasitoid. This bivoltine life cycle is similar to populations in the eastern and northern United States (Flint and Larrimer 1928, Ratcliffe and Hatchett 1997), except puparia of bivoltine flies in Manitoba do not have a summer dormancy.

In southern Manitoba, bivoltinism is the dominant condition, varying from 58% to 84% of the annual population in the studies. As seen in 2004, cool weather in the summer may reduce the frequency of bivoltinism. Puparia exposed to warmer conditions in July and August before overwintering that year had 14% higher adult emergence, or 18% higher incidence of bivoltinism, than puparia in the field (Table 1). Thus, emergence by first generation adult Hessian flies in southern Manitoba can be affected by climatic conditions, and, for many flies, univoltism is facultative.

Hessian fly populations can greatly increase in areas with multiple generations (Buntin and Chapin 1990). In southern Manitoba, population increases by bivoltine flies are reduced largely by seeding dates and puparial mortality. In the four years of the study, over 90% of all spring wheat fields in Manitoba were sown on dates in May that are unsuitable or less favourable for second generation development (Manitoba Agriculture and Food, 2002-2005). When second generation populations do develop, they are subject to >90% puparial mortality, primarily by parasitoids (Table 1).

In conclusion, the seeding of spring wheat before June in Manitoba can greatly reduce damage by the Hessian fly. The effect was four-fold; fewer stems are infested by second generation larvae, first generation larvae concentrate feeding at the crown of primary tillers where feeding is more tolerated, plants in good growing conditions can compensate for early season damage, and lower yielding late tillers are more likely to be attacked.

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Table 1. Percentage of adults from first and second brood puparia of *Mayetiola destructor* that emerged without (ND) or after diapause (AD) in southern Manitoba 2003-05, and mortality of Hessian flies by hymenopterous parasitoids or by an unknown cause.

Sampling data				Adult emergence (%)			% Mortality[1]	
Year	Site	Date	n	ND	AD	Total	Parasitism	Unknown
First generation								
2003	Glenlea	9 Sep	900	63.9	12.6	76.5	19.9	3.6
2004	Glenlea	5 Oct	497	39.6	29.1	68.7	27.7	3.6
		21-28 Jul	703	53.5	16.8	70.3	23.0	6.7
2005	Glenlea	11 Aug-15 Sep	344	52.6	21.5	74.1	18.3	7.6
2007	Glenlea	2 Oct	80	44.8	22.5	67.3	26.3	7.5
Second generation								
2003	Glenlea	9 Sep	800	0	0.4	0.4	73.8	25.8
2004	Glenlea	5Oct	433	0	12.0	12.9	78.8	9.2
2005	Glenlea	15 Sep	48	0	10.4	10.4	72.9	16.7
	LaSalle	9 Sep	200	0	12.5	12.5	68.0	19.5
	Otterburne	9 Sep	62	0	3.2	3.2	85.5	11.3
	Rosenhoff	9 Sep	365	0	7.9	7.9	73.4	18.9
2007	Glenlea	2 Oct	79	0	6.3	6.3	75.9	17.7

[1]Mortality assessed at puparial stage of Hessian fly.

Table 2. The proportion of spring wheat plants infested by first generation *Mayetiola destructor* when sown on four seeding dates per year in southern Manitoba, 2003-2005 and 2007.

	Proportion of infested plants			
Seeding date	2003	2004	2005	2007
16-22 May	0.73±0.04a*	0.67±0.02a	0.28±0.02a	0.07±0.02a
28-31 May	0.47±0.05b	0.62±0.05a	0.14±0.01b	0.17±0.03a
03-05 June	0.35±0.02b	0.61±0.05a		0.18±0.08a
09-10 June	0.35±0.02b	0.55±0.02a	0.11±0.02bc	
17-19 June			0.03±0.02c	0.04±0.02a
$F_{3,9}$	30.52	1.50	26.18	2.66
P>F	<0.0001	0.28	<0.0001	0.11

*Means in each column followed by the same letter are not significantly different according to Tukey's Multiple Range test (*P*>0.05).

Table 3. The proportion of spring wheat plants infested by second generation *Mayetiola destructor* when sown on four seeding dates per year in southern Manitoba, 2003-2005 and 2007.

	Proportion of infested plants			
Seeding date	2003	2004	2005	2007
16-22 May	0.23±0.06c*	0.45±0.03b	0.04±0.01b	0.17±0.03a
28-31 May	0.68±0.06b	0.64±0.08a	0.03±0.01b	0.16±0.06a
3-5 June	0.87±0.03a	0.80±0.04a		0.25±0.03a
9-10 June	0.96±0.02a	0.79±0.02a	0.09±0.01b	
17-19 June			0.27±0.05a	0.13±0.01a
$F_{3,9}$	121.1	17.4	32.4	3.31
P>F	<0.0001	0.0004	<0.0001	0.071

*Means in each row followed by the same letter are not significantly different according to Tukey's Multiple Range test (*P*>0.05).

Table 4. Stem breakage (%) by *Mayetiola destuctor* to spring wheat sown on four seeding dates per year in southern Manitoba, 2003-2005 and 2007.

Seeding date	2003	2004	2005	2007
16-22 May	11.1±2.7c	4.1±0.8b	0b	1.9±0.3ab
28-31 May	18.3±2.9c	16.2±4.6ab	0.6±0.6b	3.5±0.7ab
3-5 June	38.7±5.7b	14.0±4.6ab		4.7±1.3a
9-10 June	86.5±3.2a	25.8±5.2a	0.6±0.6b	
17-19 June			3.7±1.5a	0.7±0.4b
$F_{3,9}$	177.6	4.85	6.13	5.41
P>F	<0.0001	0.028	0.015	0.021

Fig. 1. The timing of egg deposition and larval development of *Mayetiola destructor* on spring wheat at Gleanlea, Manitoba, 2003-2005.

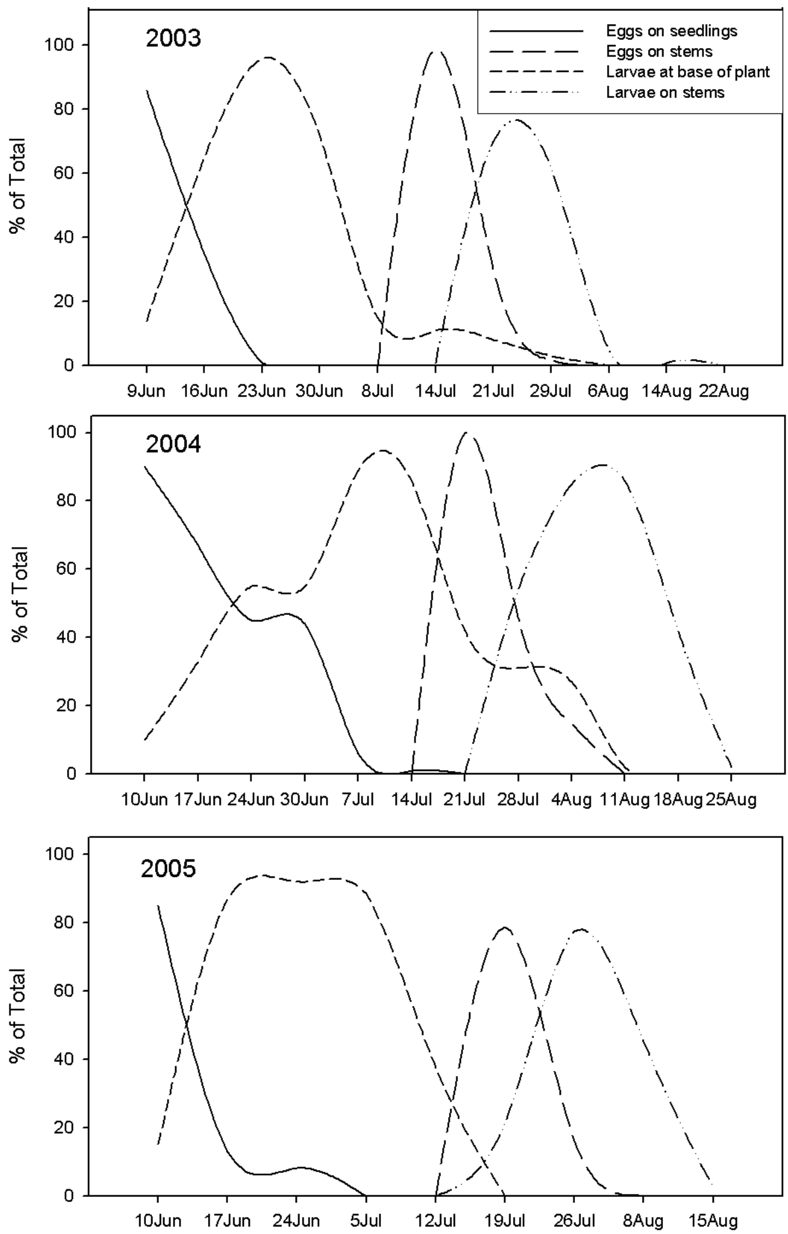

Fig. 2. The timing of puparial development and emergence of first generation adults of *Mayetiola destructor* on spring wheat at Glenlea, Manitoba, 2003-2005.