Spatiotemporal distributions of wheat stem sawfly eggs and larvae in dryland wheat fields

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Abstract—The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), is the most serious insect pest of dryland wheat (*Triticum aestivum* L.; Poaceae) in the southern Canadian Prairies and the northern Great Plains of the United States. We characterized the spatial distribution pattern of *C. cinctus* eggs and larvae throughout the adult flight period in three dryland winter wheat fields in Montana. *Cephus cinctus* females laid eggs in wheat stems until a few weeks before wheat maturity, and most wheat stems received only one egg. Wheat stem samples collected along the field edges represented 12%–16% of the samples but 40%–95% of the infested stems. The highest numbers of *C. cinctus* eggs and larvae found in a single wheat stem were 16 and 4, respectively. On a field scale, both *C. cinctus* eggs and larvae were significantly aggregated along field edges in most of the sampling events. A comparison of indices of aggregation revealed that *C. cinctus* larvae were significantly more spatially aggregated than *C. cinctus* eggs. Based on our spatiotemporal analysis, we speculate that the majority of the eggs are initially laid along field edges, and ovipositing *C. cinctus* females do not distinguish between previously infested and uninfested wheat stems. Gradually, these eggs hatch and the larvae begin feeding; at the same time, the later emerging *C. cinctus* females oviposit farther into the wheat fields. One explanation is that ovipositing *C. cinctus* females avoid stems containing feeding larvae. The analysis of the temporal changes in the spatial distribution patterns of *C. cinctus* eggs and larvae is discussed in the context of possible integrated pest management strategies.

Résumé—Le cèphe du blé, *Cephus cinctus* Norton (Hymenoptera : Cephidae), est le ravageur le plus important du blé (*Triticum aestivum* L.; Poaceae) de zone aride dans le sud des Prairies canadiennes et le nord des Grandes plaines des États-Unis. Nous avons déterminé les patterns de répartition spatiale des oeufs et des larves de *C. cinctus* durant toute la période de vol des adultes dans trois plantations de blé de zone aride au Montana. Les femelles de *C. cinctus* pondent leurs oeufs dans les tiges de blé jusqu'à quelques semaines avant la maturité du blé et la plupart des tiges ne reçoivent qu'un seul oeuf. Les échantillons de tiges de blé récoltés sur le pourtour des champs représentent 12 % – 16 % des échantillons, mais ils contiennent 40 % – 95 % des tiges infestées. Les nombres maximaux d'oeufs et de larves de *C. cinctus* observés dans une même tige de blé sont respectivement 16 et de 4. À l'échelle du champ, tant les oeufs que les larves de *C. cinctus* ont une répartition contagieuse significative près des lisières dans la plupart des échantillonnages. Une comparaison des indices de contagion montre que les larves de *C. cinctus* ont une répartition spatiale significativement plus contagieuse que les oeufs. D'après notre analyse spatio-temporelle, nous posons en hypothèse que la majorité des oeufs sont pondus au départ le long des lisières des champs et que les femelles pondeuses de *C. cinctus* ne font pas de distinction entre les tiges de blé déjà infestées et les tiges non infestées. Les oeufs éclosent graduellement et les larves commencent à se nourrir, alors qu'au même moment, les femelles de *C. cinctus* à émergence plus tardive pondent plus vers l'intérieur des champs de blé. Une explication du phénomène serait que les femelles pondeuses de *C. cinctus* évitent les tiges qui contiennent déjà une larve en train de se nourrir. Nous discutons de l'analyse des changements temporels des patterns de répartition des oeufs et des larves de *C. cinctus* dans le contexte de stratégies possibles de lutte intégrée.

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Introduction

The infestation of field crops by many insect pest species is primarily driven by immigration, and characterizing the patterns of immigration

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provides basic knowledge that can be used in development of sampling plans and integrated management programs. In dryland wheat (*Triticum aestivum* L.; Poaceae) production in Montana, most growers practice yearly alternations between a planted crop and fallow residue, so the agricultural landscape is characterized by large, alternating patches of fallow wheat and growing wheat (Morrill *et al.* 2000). The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), is the most serious insect pest of dryland wheat in the southern Canadian Prairies and the northern Great Plains of the United States (Morrill 1997). From mid-May to late July, *C. cinctus* adults emerge in fallow wheat fields or grass habitats and immigrate into fields with growing crop (Morrill and Kushnak 1999). The adult life span of *C. cinctus* is about 1 week, comprising immigration, mating, and oviposition. Wheat stems become susceptible to *C. cinctus* after stem elongation, and eggs are laid in wheat stems between nodes. *Cephus cinctus* larvae feed on parenchyma cells in the interior of wheat stems (Ainslie 1920) of growing wheat plants. Ovipositing *C. cinctus* females tend to show a preference for the main stem of each wheat plant within the first weeks after stem elongation (T.B. Macedo, unpublished data), while later in the season eggs are laid indiscriminately in both tillers and main stems of wheat plants. Because developing *C. cinctus* larvae feed only on parenchyma cells, a high frequency of multiple *C. cinctus* larvae in individual wheat stems appears to impose considerable intraspecific competition. Thus, being able to assess whether a wheat stem has been oviposited in or not may be an advantageous trait for ovipositing *C. cinctus* females. At the onset of wheat maturity, late-instar *C. cinctus* move downwards and cut the interior perimeter of stems, which frequently results in stem lodging. The larvae overwinter inside the basal cut stem, typically below ground level (Runyon *et al.* 2002), and not only are multiple developing larvae in a single wheat stem competing for food, but only one of them can overwinter in each stem. Cannibalism and (or) intraspecific competition are therefore likely important factors in the overall population dynamics of *C. cinctus* (Ainslie 1920).

Although multiple *C. cinctus* eggs and larvae in single wheat stems have been reported previously (Holmes *et al.* 1963; Holmes 1982), the frequency and the spatial distribution of such events are not well studied. At the population level, one possible advantage of multiple *C. cinctus* larvae in individual wheat stems is that it reduces the level of "expressed parasitism" (Weaver *et al.* 2005), as parasitized *C. cinctus* larvae are more vulnerable to cannibalism than unparasitized conspecifics. Cannibalism of parasitized *C. cinctus* larvae means that parasitoid larvae are eliminated, and the expressed parasitism is therefore zero. Thus, a high frequency of multiple *C. cinctus* larvae in individual wheat stems may reduce the efficacy of biocontrol agents.

In this study, we characterize the temporal changes in the spatial distribution patterns of *C. cinctus* eggs and larvae throughout the adult flight period in three dryland winter wheat fields in Montana. This study is part of an ongoing research effort to improve our understanding of *C. cinctus* mortality factors during the wheat growing period and to implement spatially targeted strategies for management of *C. cinctus* along field edges.

Materials and methods

Variation in *C. cinctus* emergence

We evaluated the variation in *C. cinctus* development at the onset of the adult flight period. On 10 and 13 June 2004, we sampled residual wheat stubs (stubs remaining after harvest) from two fallow wheat fields (Fields 1 and 2) near Choteau in north-central Montana (UTM (Universal Transverse Mercator) Zone 12, 5315800 N, 418900 W). A sample of residual wheat stubs represented 10 cm of row, which was equivalent to approximately 40 stubs, some of which were cut by overwintering sawfly larvae (Table 1). Residual wheat stub samples were collected in a 10 point by 10 point grid with 5 m between grid points (N = 100 per field). The total number of stubs was determined for each sample, and we split all sawfly-cut stems with an X-ACTO knife (Hunt Corp., Statesville, North Carolina) to count (*i*) the number of stubs with clear indication of *C. cinctus* cutting the previous year and (*ii*) the number of stubs with an overwintering larva, pupa, or adult (male or female). If a stub showed clear indication of cutting but no *C. cinctus* individual was found inside, the immature *C. cinctus* individual was classified as having died during the overwintering period. If a stub had clear marks of *C. cinctus* cutting and

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the frass plug at the cut end of the stub was either breached or missing, a *C. cinctus* adult was considered to have emerged. A characteristic circular emergence hole was often seen in the frass plug. The hole was usually not much smaller than the frass plug.

Sampling of wheat stems

We characterized the temporal and spatial trends in the occurrence of *C. cinctus* eggs and larvae throughout the adult flight period. We sampled three dryland wheat fields at two locations: two fields (Fields 3 and 4) near Choteau in north-central Montana (UTM Zone 12, 5315800 N, 418900 W) and one field (Field 5) near Churchill in southwestern Montana (UTM Zone 12, 5066150 N, 467900 W). Fields 3 and 4 were planted with the winter wheat variety *T. aestivum* 'Neeley', while Field 5 was planted with the spring wheat variety *T. aestivum* 'McNeal'. On 12 June 2004, 132 sampling points were established in Field 3, and 187 points in Field 4, while on 19 June 2004, 140 sampling points were established in Field 5. In Fields 3 and 4, a row consisted of 11 sampling points 10 m apart in a south–north direction, and consecutive rows were 20 m apart from one side of the field to the other. In Field 5, we initially established the same grid of sampling points as in Fields 3 and 4, but rows ran east to west. For the last seven sampling events in Field 5, we included three additional rows of grid points (5 and 10 m from the southern field edge and 5 m from the northern field edge). These additional rows of sampling points were included in Field 5 because we observed a very strong decline in the occurrence of *C. cinctus* along both field edges. The *C. cinctus* adult flight period in Montana normally starts around mid-May and lasts into July (Morrill and Kushnak 1999), but cool weather conditions in May 2004 delayed the onset of the *C. cinctus* adult flight period. Thus, sampling of wheat stems in each field was not initiated until mid-June, and it continued until the end of the flight period in late July.

Documentation of the occurrence of *C. cinctus* individuals in wheat stems requires splitting of stems, so it becomes highly labor-intensive to sample large fields if samples are collected frequently. To overcome this challenge, we decided to collect only a single wheat stem at each sampling point for each sampling event. Thus, in this study a wheat stem sample was equal to one wheat stem. For each sampling event, 132–187 samples were collected from each field. Especially within the first few weeks after stem elongation, *C. cinctus* tends to infest primarily the main stems of wheat plants (T.B. Macedo, unpublished data), so these stems were considered the most reliable indicators of whether the given wheat plant was infested or not. Flag leaves of main stems are typically longer than those of tillers, so individual wheat stems were sampled by grabbing a handful of wheat leaves at the canopy level within 1 m of the marked grid point and splitting (using an X-ACTO knife) the wheat stem with the longest flag leaf. When encountering multiple eggs within a wheat stem, important questions are whether they were laid by the same female and whether they were laid during the same oviposition event. DNA testing would be required to determine how many *C. cinctus* females laid the eggs; since that was beyond the scope of this study, we decided that two eggs in the same stem would be considered the result of separate oviposition events if they were placed at least 1 cm apart. Thus, the number of eggs per oviposition event is here defined as the number of eggs within a 1-cm piece of stem.

Spatial distribution of *C. cinctus* eggs and larvae

The statistical analyses of numbers of *C. cinctus* eggs and larvae were based upon the total numbers per stem without taking the number of oviposition events into account. We evaluated whether the spatial distribution patterns of *C. cinctus* eggs and larvae deviated significantly from a random distribution for each sampling event in each wheat field. We used the software package SADIE (spatial distance index) for MS-DOS to analyze the spatial distributions of *C. cinctus* eggs and larvae in each wheat field for each sampling event. SADIE is used to quantify the total effort required to move data counts (in this case, number of *C. cinctus* eggs or larvae per stem) to a completely regular spatial distribution. This effort is expressed in an index of aggregation, I_a, and the observed effort is compared with that of a random distribution. We used default settings with a seed value of 13 and 5000 randomizations. SADIE has been used widely in spatial studies of arthropods in field crops (Perry 1995; Perry *et al.* 1996; Holland *et al.* 1999; Korie *et al.* 1999). For a list of publications, consult the SADIE Web site (http://www.rothamsted.bbsrc.

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ac.uk/pie/sadie/SADIE_home_page_1.htm). An initial analysis with PROC UNIVARIATE in SAS® 9.0 (SAS Institute Inc. 2002) was conducted to confirm that the aggregation indices of *C. cinctus* eggs and larvae could be considered normally distributed. Subsequently, we used PROC MIXED in SAS 9.0 to conduct a one-way ANOVA of these indices of aggregation. In addition to the characterization of spatial distribution patterns, SADIE was used to generate cluster indices for each sampling point. In the calculation of cluster indices, actual counts of eggs and larvae are weighed according to counts obtained in the vicinity of each sampling point. For instance, a large number of eggs or larvae in a stem receives a large positive cluster index (*i.e.*, >1.5) and is denoted a patch cluster if stems at adjacent sampling points also contain large numbers of eggs or larvae. A sample with a large number of eggs or larvae receives a low positive cluster index (0–1.5) if the adjacent samples have low numbers of eggs or larvae. Similarly, a wheat-stem sample with a low number of eggs or larvae receives a more negative cluster index (*i.e.*, < –1.5), denoted a gap cluster, if the adjacent samples also have low numbers, while a sample with a low number of eggs or larvae receives a weaker negative cluster index (–1.5 to 0) if the adjacent samples have high numbers of eggs or larvae. To assess the temporal change in spatial distribution patterns of *C. cinctus* eggs and larvae, we calculated mean cluster indices for each row number in each of the sampling events and used TableCurve 3D® version 4 for Windows (Systat Software Inc. 2002) to develop surfaces of the relationship between date, row number, and cluster indices. We investigated which polynomial curve fit consistently gave the highest F value when applied to cluster indices of *C. cinctus* eggs and larvae and selected the following curve fit:

$$C(x,y) = a + bx + cx^2 + dy \qquad [1]$$

where x is row number, y is day after June 11, and a, b, c, and d are fitted coefficients. All six curve fits were highly significant ($P < 0.01$).

Results

Cephus cinctus emergence

In wheat-stubble samples collected during the first days of the *C. cinctus* adult flight, we found considerable variation in development among the *C. cinctus* individuals (Table 1). This variation in developmental phenology helps explain the length of the flight period, with adults gradually emerging between mid-May and early July. On average, a sample contained 40 stubs, of which about 12% had been cut by *C. cinctus*. The mortality (difference between cut stems and cut stems without *C. cinctus* individuals) was about twice as large for Field 1 compared with Field 2. The average number of *C. cinctus* larvae per sample was about fivefold higher in Field 1 than in Field 2, while more *C. cinctus* adults had emerged from Field 2 than from Field 1, which suggests a slight difference in overall development of *C. cinctus* populations between the two wheat fields (Table 1).

Seasonal infestation trends

A summary of the infestation level in wheat stem samples from the three dryland wheat fields is presented in Table 2. In Field 3, we sampled a total of 924 stems, of which 259 (28%) were infested with a total of 334 *C. cinctus* eggs and (or) larvae, and in 8 stems both eggs and larvae were found within a single stem. In Field 4, we sampled a total of 1496 stems, of which 355 (24%) were infested with a total of 437 *C. cinctus* eggs and (or) larvae, and in 18 stems both eggs and larvae were found within a single stem. In Field 5, we sampled a total of 1750 stems, of which 261 (15%) were infested with a total of 332 *C. cinctus* eggs and (or) larvae, and in 11 stems both eggs and larvae were found within a single stem. In Field 3, the total number of *C. cinctus* eggs (218) was about twice the total number of encountered *C. cinctus* larvae (116), which suggested considerable mortality during the weeks of sampling, but this was not consistent with the data from Fields 4 (233 eggs and 204 larvae) and 5 (165 eggs and 167 larvae). In Fields 3 and 4, there was a gradual increase in the proportion of wheat stems infested throughout the sampling period (Fig. 1). In Field 5, the seasonal pattern of infestation was slightly different from that in the other two fields, but in all three fields the proportion of infested stems was 30%–35% of the sampled stems at the end of the sampling period.

Frequency distribution of eggs in all field samples

Tables 3–5 present the frequency distributions of *C. cinctus* eggs and larvae for each

Table 1. Results of dissection of cut stems in fallow wheat fields at the onset of the *Cephus cinctus* adult flight period.

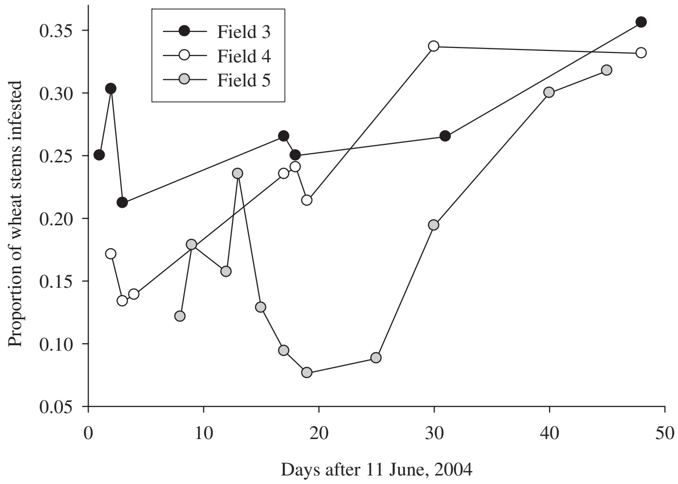
Field	Mean (SE) no. of stubs/sample	Mean (SE) no. of cut stems[†]					Mortality (%)[§]
		Total	With larvae	With pupae	With adults	With emerged *C. cinctus*[‡]	
1	40.89 (1.25)	6.4 (0.38)	0.73 (0.09)	3.37 (0.30)	0.94 (0.13)	0.36 (0.06)	19.89 (2.47)
2	40.24 (0.95)	3.95 (0.30)	0.14 (0.04)	1.61 (0.17)	0.83 (0.11)	1.05 (0.15)	7.91 (1.65)

[†]Stubs with clear indication of *C. cinctus* cutting.
[‡]Stems with clear indication of *C. cinctus* cutting and the frass plug at the cut end of the stem either penetrated or missing.
[§]Percentage of stubs with clear indication of *C. cinctus* cutting but no *C. cinctus* individual found inside.

Table 2. Wheat stem samples and abundance of *Cephus cinctus* eggs and larvae.

Field	No. of stems collected	No. of sampling events	Eggs			Larvae		
			No. of stems infested	Total no. of eggs	Mean (SE) no. of eggs/stem	No. of stems infested	Total no. of larvae	Mean (SE) no. of larvae/stem
3	924	7	156	218	1.40 (0.09)	103	116	1.13 (0.03)
4	1496	8	176	233	1.32 (0.11)	179	204	1.14 (0.03)
5	1750	10	112	165	1.47 (0.09)	149	167	1.12 (0.03)

Fig. 1. Temporal *Cephus cinctus* infestation trends in three dryland wheat fields (Fields 3–5). Wheat stems were considered infested if either eggs or larvae were found.



sampling event. In Field 3, as many as 10 eggs were found in a single stem (29 June), and these eggs represented 23% of all the eggs for that sampling event (Table 3). For all sampling events, at least 69% of the eggs were found in separate stems, while 10%–20% of the infested wheat stems contained 2 eggs or more. No eggs were found in the last sampling event (29 July). Also in Field 3, *C. cinctus* larvae were found only in the last four sampling events, and only one or two larvae per stem were found. The frequency distribution of larvae was similar to that of eggs: 70%–80% of the larvae were found in separate stems. However, in the last sampling event, 94% of the larvae occurred in separate stems, which suggests that intraspecific competition, cannibalism, or parasitism had influenced the population dynamics. In Field 4, 16 eggs were found in a wheat stem collected on 28 June at the field edge (Table 4), and these were probably oviposited in three separate events (1, 7, and 8 eggs). More than two thirds of eggs were found in wheat stems containing only one egg, while 10%–15% of the eggs were found in stems with 2 or more eggs. No eggs were found in the last sampling event (29 July). In Field 4, as many as 4 *C. cinctus* larvae were found in a single stem (12 July), but about 80% of the larvae were found in wheat stems containing only one larva (Table 4). In Field 5, 11 eggs were found in a single stem (24 June), but at least 63% of the eggs were found in wheat stems that contained only one egg (Table 5). No eggs were found in the last two sampling events. As many as 4 *C. cinctus* larvae were found in a single wheat stem (21 July), but all other larvae-infested stems in Field 5 contained either 1 or 2 larvae. Of the 4170 wheat samples, 838 were infested; of these, 37 (4.4%) contained both *C. cinctus* eggs and larvae, 4 had five oviposition events, and 13 had four oviposition events. Thus, although multiple *C. cinctus* instars were found in individual stems, 706 stems (84%) contained only one egg or larva.

Oviposition along edges

Wheat-stem samples from the rows along field edges corresponded to 12%–16% of all samples per field, and for most of the sampling events these samples corresponded to more than 40% of the total number of infested stems. For the first six sampling events in Field 5, between 80% and 95% of the infested stems were collected along field edges, but the predominance of infestation along the field edges gradually declined during the last five sampling events. This seasonal trend suggests that the *C. cinctus* adults immigrated progressively farther into the wheat field during the later part of the sampling period. In Field 4, the occurrence of infested wheat stems along the field edges increased for the first three sampling events and then subsequently decreased, as observed for Field 3. In Field 3, we observed only a slight seasonal variation in the relative level of *C. cinctus* infestation along the field edges.

Table 3. Frequency distribution of *Cephus cinctus* eggs and larvae in wheat stem samples from Field 3.

	No. of eggs/stem								No. of larvae/stem		
Date	1	2	3	4	5	6	10	Total no. of eggs	1	2	Total no. of larvae
12 June	0.79	0.15	0.03	0.00	0.00	0.03	0.00	33	0.00	0.00	0
13 June	0.85	0.12	0.02	0.00	0.00	0.00	0.00	80	0.00	0.00	0
14 June	0.82	0.18	0.00	0.00	0.00	0.00	0.00	84	0.00	0.00	0
28 June	0.80	0.07	0.00	0.04	0.10	0.00	0.00	120	0.82	0.18	13
29 June	0.69	0.13	0.00	0.13	0.00	0.00	0.04	115	0.73	0.27	14
12 July	1.00	0.00	0.00	0.00	0.00	0.00	0.00	12	0.85	0.15	39
29 July	1.00	0.00	0.00	0.00	0.00	0.00	0.00	33	0.94	0.06	50

Note: Values are proportions of stems found with the given number of eggs or larvae.

Table 4. Frequency distribution of *C. cinctus* eggs and larvae in wheat stem samples from Field 4.

	No. of eggs/stem							No. of larvae/stem				
Date	1	2	3	5	11	16	Total no. of eggs	1	2	3	4	Total no. of larvae
13 June	0.94	0.06	0.00	0.00	0.00	0.00	34	0.00	0.00	0.00	0.00	0
14 June	0.80	0.20	0.00	0.00	0.00	0.00	30	0.00	0.00	0.00	0.00	0
15 June	0.69	0.31	0.00	0.00	0.00	0.00	34	1.00	0.00	0.00	0.00	1
28 June	0.76	0.03	0.09	0.06	0.03	0.03	74	0.95	0.05	0.00	0.00	20
29 June	1.00	0.00	0.00	0.00	0.00	0.00	31	0.79	0.21	0.00	0.00	23
30 June	0.95	0.05	0.00	0.00	0.00	0.00	23	0.75	0.25	0.00	0.00	25
11 July	0.83	0.17	0.00	0.00	0.00	0.00	7	0.84	0.09	0.05	0.02	72
29 July	0.00	0.00	0.00	0.00	0.00	0.00	0	0.98	0.02	0.00	0.00	63

Note: Values are proportions of stems found with the given number of eggs or larvae.

Table 5. Frequency distribution of *Cephus cinctus* eggs and larvae in wheat stem samples from Field 5.

Date	No. of eggs per stem					Total no. of eggs	No. of larvae per stem			Total no. of larvae
	1	2	3	5	11		1	2	4	
19 June	0.74	0.15	0.00	0.12	0.00	22	0.00	0.00	0.00	0
20 June	0.63	0.19	0.13	0.05	0.00	26	0.00	0.00	0.00	0
23 June	0.64	0.18	0.18	0.00	0.00	26	0.00	0.00	0.00	0
24 June	0.71	0.05	0.14	0.08	0.02	39	1.00	0.00	0.00	1
26 June	0.74	0.21	0.00	0.05	0.00	21	1.00	0.00	0.00	5
28 June	0.82	0.18	0.00	0.00	0.00	13	1.00	0.00	0.00	2
30 June	1.00	0.00	0.00	0.00	0.00	6	1.00	0.00	0.00	8
6 July	1.00	0.00	0.00	0.00	0.00	2	1.00	0.00	0.00	13
11 July	1.00	0.00	0.00	0.00	0.00	4	0.88	0.12	0.00	28
21 July	0.00	0.00	0.00	0.00	0.00	0	0.75	0.21	0.04	44
26 July	0.00	0.00	0.00	0.00	0.00	0	0.88	0.12	0.00	47

Note: Values are proportions of stems found with the given number of eggs or larvae.

Spatial distribution of *C. cinctus* eggs and larvae

In Fields 3 and 4, most indices of aggregation suggested that both *C. cinctus* eggs and larvae were spatially aggregated ($P < 0.05$) (Table 6). On 15 June, only a single larva was found in Field 4, so the SADIE analysis was not conducted for larvae for this sampling event. In three sampling events in Field 5 (28 June, 6 and 11 July), the index of aggregation of *C. cinctus* eggs was not significantly different from that of a random spatial distribution, while the distribution pattern of eggs was found to be significantly aggregated in the remaining sampling events. *Cephus cinctus* larvae in Field 5 were found to be significantly aggregated in all sampling events except for 24 June (only one larva found; Table 4) and 11 July. Comparison of the indices of aggregation of *C. cinctus* eggs and larvae revealed that larvae were significantly more aggregated than eggs ($F_{[1,38]} = 4.72$, $P = 0.036$).

Although there were indications of patch clusters (positive cluster indices) of *C. cinctus* eggs along both field edges, the indices only rarely exceeded 1, which suggested only weak clustering of eggs. In addition, strong gap clusters (negative cluster indices < –1.5) were rarely seen and occurred almost exclusively in the final sampling events with observed oviposition. In comparison, both patch clusters and gap clusters of *C. cinctus* larvae were observed in all three fields and occurred throughout the sampling period. During the course of sampling, cluster indices of eggs were either constant or decreasing (Figs. 2*a*, 2*c*, 2*e*), while those of *C. cinctus* larvae were either constant or increasing (Figs. 2*b*, 2*d*) (except for rows 1–3 in Field 5; Fig. 2*f*). A gradual decrease in cluster index values of *C. cinctus* eggs likely reflects a combination of a decrease in overall oviposition (Table 3) and an increase in the number of eggs hatched, which leads gradually to a more uniform distribution of the eggs remaining in the wheat field. The predominant increase in cluster indices of *C. cinctus* larvae demonstrated that *C. cinctus* larvae became more abundant as eggs continued to hatch, which resulted in an expected increase in cluster indices during the course of sampling.

Discussion

More insight into the spatiotemporal distribution of *C. cinctus* infestations in dryland wheat

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Table 6. Indices of aggregation (I_a) for *Cephus cinctus* eggs and larvae in three dryland wheat fields.

		Eggs		Larvae	
Field	Date	*n*	I_a	*n*	I_a
3	12 June	45	1.608**	0	
	13 June	47	1.339*	0	
	14 June	33	1.423**	0	
	28 June	47	1.84**	13	1.825**
	29 June	44	1.332*	14	1.689**
	12 July	2	1.439*	39	2.21**
	29 July	0		50	1.603**
4	13 June	34	1.593**	0	
	14 June	30	1.716**	0	
	15 June	34	1.907**	1	
	28 June	63	2.214**	20	2.632**
	29 June	42	1.424*	23	2.204**
	30 June	23	1.130	25	2.142**
	11 July	7	1.407*	72	2.402**
	29 July	0		63	1.645**
5	19 June	22	1.675**	0	
	20 June	26	1.837**	0	
	23 June	26	1.696**	0	
	24 June	41	1.532*	1	1.102
	26 June	21	1.432*	5	2.061**
	28 June	15	1.253*	3	1.564**
	30 June	6	1.438*	8	1.813**
	6 July	2	0.785	54	2.436**
	11 July	4	0.843	13	0.0976
	21 July	0		32	1.665**
	26 July	0		51	2.495**

Note: The software package SADIE was used to calculate indices of aggregation of eggs and larvae for each sampling event. *n*, total number of eggs or larvae for each sampling event. *, $P < 0.05$; **, $P < 0.01$.

fields may be used to develop sampling plans that provide representative information about the insect density in both time and space. Early-planted trap vegetation between late-planted wheat fields has been proposed as a management strategy for *C. cinctus* infestations (Holmes 1982; Morrill and Kushnak 1999; Morrill *et al.* 2000), and knowledge of the spatiotemporal distribution of *C. cinctus* infestations may be used to determine the optimal width of such trap strips. Based on this study of *C. cinctus* infestations in three dryland wheat fields in Montana, we conclude that (*i*) there was considerable variation in the developmental stage of *C. cinctus* individuals found in stubs at the onset of the adult flight period; (*ii*) *C. cinctus* females laid eggs in wheat stems until a few weeks before wheat maturity; (*iii*) most wheat stems were oviposited in only once; (*iv*) we observed marked mortality during the wheat growing period in only one of three fields (Field 3); (*v*) the samples collected along the field edges, which represented 12%–16% of the samples, accounted for 40%–95% of the infested stems; (*vi*) both *C. cinctus* eggs and larvae were spatially aggregated in most of the sampling events; and (*vii*) *C. cinctus* larvae showed significantly higher levels of spatial aggregation than *C. cinctus* eggs. Several conditions varied among fields, including (*i*) wheat variety (one field (Field 5) was planted with spring wheat, while the other two fields were planted with winter wheat), (*ii*) geographical orientation of sampling grids, (*iii*) vegetation

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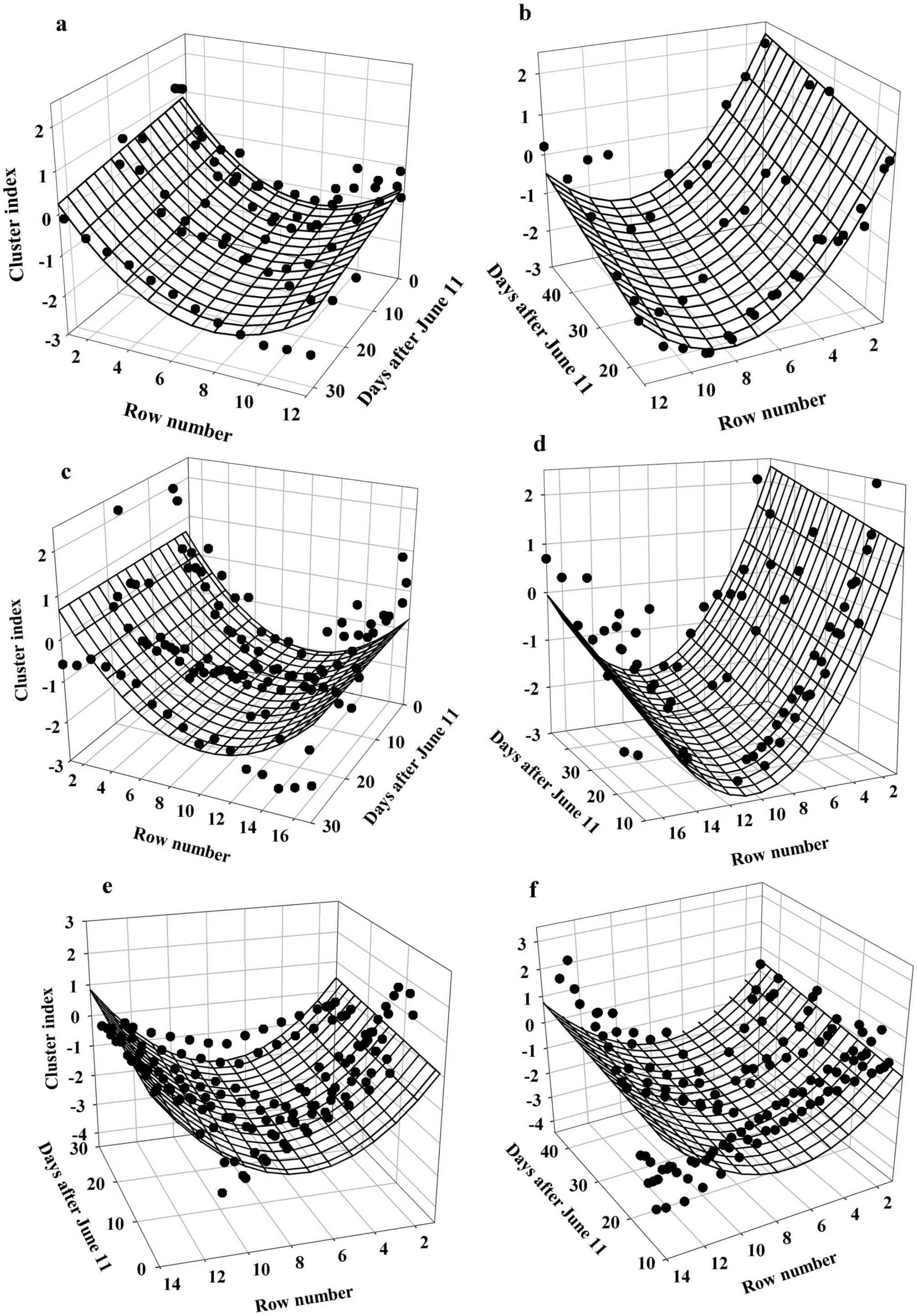
Fig. 2. Mean cluster indices of *Cephus cinctus* eggs and larvae per row number of samples collected across wheat fields, calculated with the software package SADIE for each sampling event. Field 3: *a*, eggs; *b*, larvae. Field 4: *c*, eggs; *d*, larvae. Field 5: *e*, eggs; *f*, larvae. Dots denote observed mean cluster indices. The mesh in each graph is a polynomial curve (eq. 1) that was fitted to observed mean cluster indices with row number and days after 11 June as independent variables.



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along field edges, (*iv*) geographical location, and (*v*) weather conditions. Most of these variables were unaccounted for, so we did not include any statistical between-field comparisons but rather focused on the spatiotemporal dynamics within each field.

"Edge effect" of *C. cinctus* infestations

Insects are spatially distributed in uniform, random, or aggregated patterns (Southwood 1987), primarily in response to the environment in which they live. Taylor (1984) considered the spatial distribution pattern of an organism to be one of its most important ecological characteristics, because it tends to be more stable than the population density among generations and (or) seasons. Studies based on sampling of wheat stems at wheat maturity have demonstrated that *C. cinctus* infestations in dryland winter wheat fields typically show a distinct "edge effect", with the highest level of infestation along field edges and a gradual decline inwards (Pesho *et al.* 1971; Holmes 1982; Morrill *et al.* 2000; Runyon 2001; Sing 2002). In a study of wheat-stem samples collected at wheat maturity in six dryland wheat fields, Nansen *et al.* (2005) described the gradual decline in *C. cinctus* infestation level from field edges and less than 200 m inwards into wheat fields. The authors documented a significant exponential decline of *C. cinctus* infestation at six of nine field edges bordering either fallow wheat crop or grass habitats. In addition, the analysis by Nansen *et al.* (2005) suggested that, proportionally, the spatial distribution pattern of *C. cinctus* infestations 0–200 m from field edges is independent of the overall infestation level. While this edge effect of *C. cinctus* infestations is well described, the current study provides the first analysis of how this edge effect evolves during the course of *C. cinctus* oviposition.

Temporal dynamics of *C. cinctus* infestations

We found that cluster indices and indices of aggregation of *C. cinctus* eggs were highest early in the sampling period and that the distribution of eggs became less aggregated over time. This trend may be explained, at least partially, by a gradual decrease in total numbers of eggs found in samples, but it also suggests that proportionally more eggs were laid farther into wheat fields late in the sampling period. The spatial distribution analysis of *C. cinctus* larvae revealed that the level of patch clustering increased over time (temporal increase in cluster index values) and that this trend was more pronounced along field edges than in the center of wheat fields. Thus, while *C. cinctus* eggs became more uniformly distributed as the season progressed, the distribution of *C. cinctus* larvae became more aggregated along field edges over time. A probable interpretation of the temporal changes in spatial distribution patterns is described in five sequential steps: (1) *C. cinctus* adults emerge from grasslands and fallow wheat fields and immigrate into growing wheat crops; (2) initially, the majority of eggs are laid along field edges; (3) ovipositing *C. cinctus* females do not distinguish between previously infested and uninfested wheat stems; (4) *C. cinctus* eggs hatch and the larvae start to feed, causing physiological changes in the wheat plants; and (5) later immigrating females may respond to signaling compounds emitted by the wheat plants (which is consistent with laboratory studies; G.E. Peck, unpublished data) and move farther into wheat fields to avoid ovipositing in stems containing larvae. Such a sequence of events would explain why the distribution pattern of *C. cinctus* eggs became increasingly more uniform over time. It is uncertain whether eggs laid late in the wheat growing period will have enough time before wheat maturity to hatch and complete immature life stages, so late-developing *C. cinctus* immatures may represent a lower risk of wheat yield loss than early-developing immatures. Thus, if most early *C. cinctus* infestations occur along the field edges, then control strategies for this pest should focus on spatially targeted approaches along the edges of dryland wheat fields.

Perspectives

In addition to basic knowledge of the field biology of *C. cinctus*, insight into the temporal variation in the spatial distribution patterns of *C. cinctus* eggs and larvae during the wheat growing period is important for future research on management strategies. For instance, the current finding that single eggs are laid in most wheat stems is encouraging for ongoing research on release programs of natural enemies (Morrill *et al.* 1998; Runyon *et al.* 2002) because a high frequency of multiple *C. cinctus* larvae in individual wheat stems may reduce the level of "expressed parasitism" (Weaver *et al.* 2005): if multiple *C. cinctus* larvae are present in a single wheat stem and not all are

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parasitized, then the parasitized larvae are highly vulnerable to cannibalism from unparasitized conspecifics. Cannibalism of parasitized *C. cinctus* larvae eliminates parasitoid larvae, and the expressed parasitism is therefore zero. Also, oviposition by *C. cinctus* was recorded for an extended part of the wheat growing period, which means that natural enemies can potentially find suitable late-instar hosts over an extended period. Finally, the potential of using early-planted trap strips around later planted wheat crops as a protective strategy against *C. cinctus* (Holmes 1982; Morrill *et al.* 2000) is encouraged by the results of this study, since *C. cinctus* infestations were significantly aggregated along edges throughout the wheat growing period.

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