

Within-field spatial distribution of *Cephus cinctus* (Hymenoptera: Cephidae) larvae in Montana wheat fields

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Abstract—The wheat stem sawfly, *Cephus cinctus* Norton, is a major insect pest in dryland wheat (*Triticum* L. spp.; Poaceae) fields in the northern Great Plains of the United States and in southern regions of the prairie provinces of Canada. Field infestations by this pest commonly show a distinct “edge effect”, with infestation levels highest at the field edge and declining inwards. In this study, we characterized the edge effect of *C. cinctus* infested wheat fields in Montana at four locations in two separate years. “Infestation level” refers to the average proportion of wheat stems infested with *C. cinctus* in samples collected in a given wheat field. The gradual decrease in *C. cinctus* infestation towards the centre of wheat fields is referred to as the “infestation slope”, and it was presented as a proportion of infestation level at field edges. We showed that (i) for most of the fields bordering grassland or fallow wheat, a simple exponential decline curve provided a significant fit to the infestation slope; (ii) the infestation slopes in different fields and in different directions within fields were similar and appeared to be independent of the overall infestation level; and (iii) the relationship between infestation level and the proportion of samples infested followed an asymptotic curve, which indicates a high level of dispersal of ovipositing *C. cinctus* females. The general perception has been that the edge effect of *C. cinctus* infestation is a result of ovipositing *C. cinctus* females being both weak flyers and short-lived, but our results do not fully corroborate this perception. Currently, the only reliable way to detect *C. cinctus* infestations is to dissect individual stems and look for developing instars. However, this type of sampling is extremely time consuming and labor intensive and therefore impractical for wheat growers. Increasing the understanding of the spatial patterns in *C. cinctus* infestations is a first step towards development of an optimal sampling plan for this important field pest. Thus, the results presented are relevant for researchers involved in sampling designs and integrated pest management procedures for field pests. We discuss behavioral and evolutionary factors that may contribute to the edge effect of *C. cinctus* infestations.

Résumé—Le cèphe du blé, *Cephus cinctus* Norton, est un insecte ravageur important du blé (*Triticum* L. spp., Poaceae) dans les champs arides des Grandes plaines du nord des États-Unis et des régions du sud des provinces canadiennes des prairies. Les infestations des champs par ce ravageur montrent souvent un « effet de lisière », les infestations étant plus fortes en bordure des champs et moindres vers le centre. Notre étude caractérise cet effet de lisière dans des champs de blé infestés par *C. cinctus* à quatre sites du Montana sur deux années différentes. Le « niveau d’infestation » représente la proportion moyenne des tiges de blé infestées par *C. cinctus* dans les échantillons prélevés dans un champ de blé donné. Le déclin graduel de l’infestation par *C. cinctus* vers le centre du champ est la « pente de l’infestation » et est représenté par le pourcentage du niveau de l’infestation par comparaison à celui en bordure du champ. Nous montrons que (i) dans la plupart des champs adjacents à des prairies ou des champs de blé en jachère, une simple courbe exponentielle décroissante s’ajuste de façon significative à la pente de l’infestation, (ii) les pentes d’infestation dans les différents champs et dans les différentes directions dans un même champ sont semblables et semblent être indépendantes du niveau global d’infestation et (iii) la relation entre le niveau d’infestation et le pourcentage d’échantillons infestés suit une courbe asymptotique, ce qui indique un fort niveau de dispersion des femelles de *C. cinctus* lors de la ponte. On explique généralement l’effet de lisière dans les infestations de *C. cinctus* par le

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fait que les femelles pondueuses ont un vol faible et qu'elles ne vivent pas longtemps, mais nos résultats n'appuient pas complètement ces explications. Actuellement, la seule méthode fiable pour détecter les infestations de *C. cinctus* est la dissection de tiges individuelles à la recherche de larves de divers stades en développement. Ce type d'échantillonnage exige beaucoup de temps et coûte très cher; il est donc peu pratique pour les cultivateurs de blé. La compréhension accrue de la structure spatiale des infestations de *C. cinctus* est une première étape dans la mise au point d'un plan d'échantillonnage optimal pour cet important ravageur des champs. Nos résultats sont donc d'intérêt pour les chercheurs impliqués dans la planification d'échantillonnage et les méthodologies de lutte intégrée contre les ravageurs des champs. Les facteurs comportementaux et évolutifs qui peuvent contribuer à l'effet de lisière des infestations de *C. cinctus* font l'objet d'une discussion.

[Traduit par la Rédaction]

Introduction

Taylor (1984) argued that a species' spatial distribution pattern is one of its most important ecological characteristics, both because it tends to be more stable than the population density between generations and (or) seasons and because it reflects how a species responds to spatial heterogeneity within a given sampled environment or habitat. In natural environments, insects often follow aggregated distribution patterns and are spatially associated with food sources, but what happens to insect distribution patterns in extensive crop monocultures or in food storage systems where food availability is virtually unlimited? Interestingly, several studies have documented the tendency of insects to aggregate spatially in both field crops (Feng and Nowierski 1992; Holland *et al.* 1999; Schotzko and Quisenberry 1999; Winder *et al.* 1999; Korie *et al.* 2000) and food storage systems (Nansen *et al.* 2004a, 2004b). Thus, food availability alone is unlikely to be the sole explanation for an observed spatial distribution pattern. A better understanding of how insect pests respond to environmental heterogeneity is of paramount importance for the development of relevant sampling plans and for implementation of precision-targeted management strategies.

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), is a major insect pest in dryland wheat (*Triticum* L. spp.; Poaceae) fields in the northern Great Plains of the United States and the Canadian prairie provinces. In Montana alone it is estimated to cause annual losses of at least US\$25 million (Montana State University Extension Service 1996). *Cephus cinctus* oviposits in wheat stems after the initiation of stem elongation (Ainslie 1920), and developing larvae feed on the parenchyma throughout the interior of the stems.

Late instars bore through stem nodes and damage vascular tissues. At the onset of plant senescence, mature *C. cinctus* larvae move downwards and cut the interior perimeter of stems, which frequently results in stem lodging. Overwintering inside the basal cut stem typically occurs below ground level, and stems are often cut below the soil surface (Runyon *et al.* 2002). *Cephus cinctus* individuals overwinter in the prepupal stage within a hypernaculum inside the stub, and a diapause of >90 days at 10 °C or lower is required before pupation can occur (Holmes 1982). In Montana, *C. cinctus* adults emerge from fallow wheat fields, grasses in road ditches, and grassland between late May and mid-July (Morrill and Kushnak 1999) and immigrate into growing wheat crops. The adult life-span is typically 1 week, which comprises the time windows for egg maturation, mating, and oviposition. Although some infested wheat plants show brown discoloration below nodes (Morrill *et al.* 1992), there are no consistent external visual cues to indicate whether a growing wheat stem is infested or not, and currently the only reliable way to detect *C. cinctus* infestations is to dissect individual stems and look for developing instars. However, this type of sampling is extremely time consuming and labor intensive and thus impractical for wheat growers. Increasing the understanding of the spatial patterns in *C. cinctus* infestations is a first step towards development of an optimal sampling plan that maximizes the benefits obtained from costly sampling efforts.

Surveys of wheat fields to determine the spatial distribution of *C. cinctus* infestation have shown that infestations have a marked "edge effect", with the greatest proportion of the infested wheat stems occurring along field edges and a gradual decrease in the proportion of infested stems towards the centre (Pesho *et al.*

1971; Holmes 1982; Morrill *et al.* 2001; Runyon 2001; Sing 2002). This observed edge effect has conventionally been explained by the short life-span of *C. cinctus* adults in combination with informal observations concluding that *C. cinctus* adults are weak flyers (Ainslie 1920), but there has been no detailed study of this hypothesis. Throughout this article, the term “infestation level” refers to the average proportion of wheat stems infested with *C. cinctus* in samples collected in a given wheat field. The gradual decrease in *C. cinctus* infestation towards the centre of wheat fields is referred to as the “infestation slope”, and it is presented as a proportion of infestation level at field edges. If the combination of a short adult life-span and weak flight ability is the sole explanation for the edge effect in *C. cinctus* infestation, one would expect (i) the infestation level to be highest at field edges bordering fallow wheat fields, grassland, and road ditch grasses, as these adjacent habitats provide a source for *C. cinctus* infestations; (ii) the infestation level to be comparatively lower at field edges bordering other types of vegetation; (iii) the width of the infested zone near field edges to be narrower in fields with a low infestation level compared with fields with higher infestation levels, because in wheat fields with low infestation levels there would be lower intraspecific competition and therefore less reason for ovipositing *C. cinctus* females to move very far into the wheat fields; and (iv) the relationship between average infestation level and the proportion of samples infested to be exponential, because of aggregation of infestation along field edges.

In this study, we examined data sets collected in 1998 and 1999 from four field sites in Montana and characterized the *C. cinctus* infested zone in each wheat field. The infestation level along field edges was evaluated, and the steepness of the infestation slope was determined for all fields. The relationship between average infestation level and the proportion of samples infested was determined. The combination of short adult life-span and poor flight ability of ovipositing *C. cinctus* females has been considered the explanation for the observed edge effect, but here we discuss behavioral and evolutionary factors that may contribute to the observed edge effect of *C. cinctus* infestations.

Materials and methods

Wheat stem samples

An entire field or a section of a field was divided into a regular grid with 50 m between grid points and a reference point (0, 0) in either the southeastern corner or the southwestern corner of each sampled area. Wheat stem samples were collected immediately before harvest in August 1998 and 1999. A sample represented all wheat stems within a 0.10-m² area at each grid point, and we did not discriminate between primary stems and tillers. Wheat stem samples were brought to the laboratory, and stems were dissected lengthwise with an X-ACTO[®] knife (Hunt Corp., Statesville, North Carolina) to determine the presence or absence of *C. cinctus* larvae. Owing to cannibalism (Ainslie 1920), more than one *C. cinctus* larva is rarely found in infested stems at the time of wheat maturity, so wheat stems were considered either infested or uninfested.

Field sites

We sampled wheat fields that varied in terms of size, external dimensions, planting time (spring wheat or winter wheat), stems (hollow or solid), wheat variety, and mean wheat stem density (Table 1). All sampled fields were located within 150 km of each other in the predominantly dryland production area between Havre, Cut Bank, and Great Falls in north-central Montana, referred to as the “Golden Triangle”. In Chester, we collected samples only in 1998; at the other three field sites (Ledger, Loma, and Pendroy), one of two adjacent fields was sampled at each site in both 1998 and 1999. For most dryland wheat production in Montana, planted areas alternate yearly between crop and fallow rotations, so infestations of *C. cinctus* are often caused by insects immigrating into wheat fields from neighboring fallow fields or grass vegetation.

Loma is located about 800 m above sea level. Two large, elongate fields were planted with a hollow-stemmed spring wheat variety in both years. A portion representing 19% of the west field was sampled in 1998 and a portion representing 12% of the east field was sampled in 1999 (Fig. 1). Bordering the sampled areas of the Loma wheat fields were fallow wheat, crop wheat, and grassland for each year. In both years, wheat stem samples were collected along most of the entire north–south dimension of the

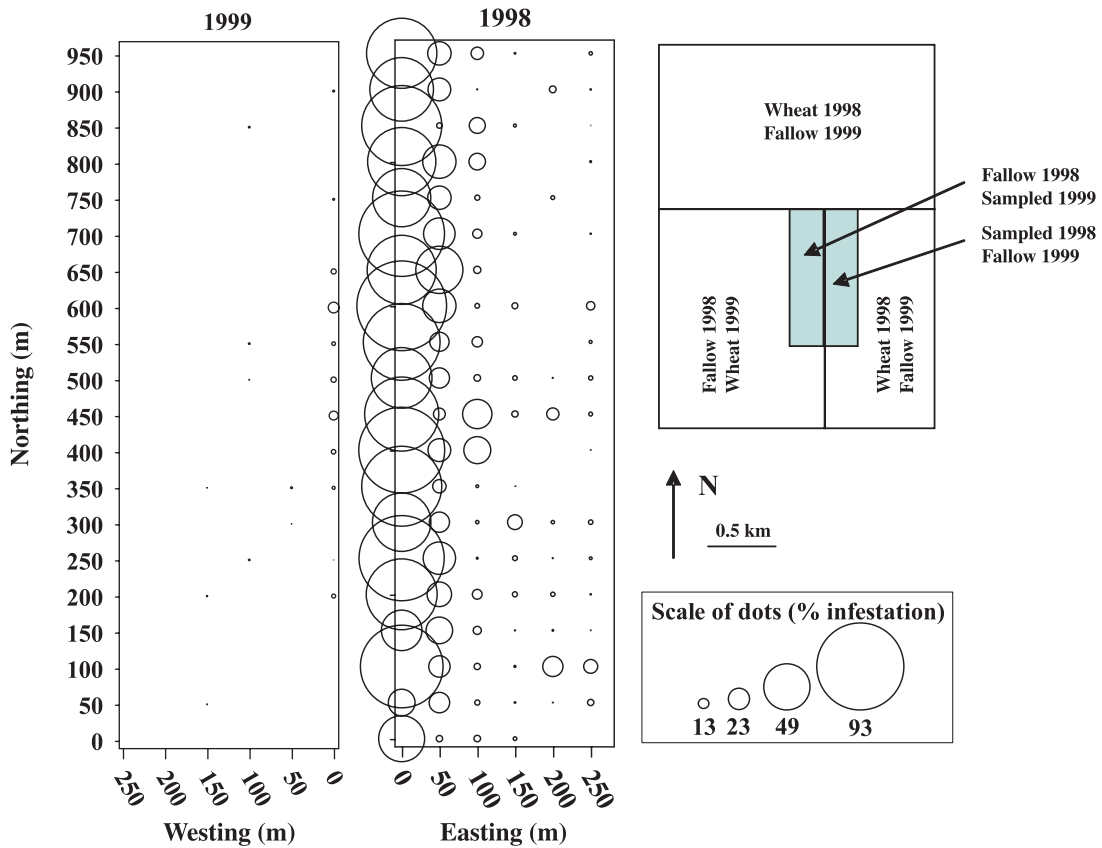
Table 1. Summary of wheat stem samples collected from six fields in north-central Montana in 1998 and 1999.

Field site	Year	Wheat stem	Wheat variety	Planting time	Sampled area (km ²)	No. of wheat stem samples	No. of wheat stems	Average (SE) stem density (no. of stems/sample) [†]	Total no. of <i>C. cinctus</i> larvae	Infestation level
Loma	1998	Hollow	Rocky	Winter	0.24	120	5414	45.1 (1.6)**	1248	0.202 (0.024)
Ledger	1998	Solid	Lew	Spring	0.23	112	4516	40.3 (1.2)ns	285	0.067 (0.008)
Pendroy	1998	Hollow	Rocky	Winter	0.16	79	6909	87.5 (3.4)*	218	0.035 (0.004)
Chester	1998	Solid	Ernest	Spring	0.24	120	4019	33.5 (0.9)ms	1332	0.333 (0.025)
Loma	1999	Hollow	Rocky	Winter	0.24	120	9014	75.1 (1.9)***	74	0.010 (0.002)
Ledger	1999	Solid	Rambo	Spring	0.23	107	5190	48.5 (1.2)ms	18	0.004 (0.001)
Pendroy	1999	Solid	Rambo	Spring	0.19	96	3861	40.2 (1.4)ms	15	0.005 (0.003)

Note: Stem samples consisted of stems collected from a 0.1-m² area at points of a 50 m × 50 m grid. Infestation level is the average (SE) proportion of wheat stems infested by *Cephus cinctus*.

[†]Linear regression analyses were conducted with stem density as the descriptive variable for the *C. cinctus* infestation level; ns, nonsignificant; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

Fig. 1. Spatial distribution of *Cephus cinctus* infestations in two wheat fields at Loma, Montana. The sampled area is measured in metres from a reference point (0, 0) at the southern junction of the two fields.



wheat field, but samples were collected only within 250 m of the field edge in the east–west direction (Fig. 1). A total of 120 wheat stem samples were collected in each year.

Ledger is located about 1100 m above sea level. Two large fields were planted with a solid-stemmed spring wheat variety in both years. A portion representing 43% of the east field was sampled in 1998 and a portion representing 43% of the west field was sampled in 1999 (Fig. 2). Bordering the sampled Ledger wheat fields were fallow wheat and crop wheat for each year. A total of 112 wheat stem samples were collected in 1998, and 107 were collected in 1999.

Pendroy is located about 1300 m above sea level. The two adjacent fields were planted with a hollow-stemmed winter wheat variety in 1998 and a solid-stemmed spring wheat variety in 1999. The entire north field was sampled in 1998, and a portion representing 55% of the south field was sampled in 1999 (Fig. 3). Bordering the sampled Pendroy wheat fields were a

grazed horse pasture, barley, and fallow and crop wheat. The sizes of the two Pendroy fields differed, and 79 and 96 wheat stem samples were collected in 1998 and 1999, respectively.

Chester is located about 1000 m above sea level. One elongate field was planted with a solid-stemmed spring wheat variety in 1998, and the entire field was sampled (Fig. 4). Bordering the sampled area were fallow wheat and grassland. A total of 120 wheat stem samples were collected.

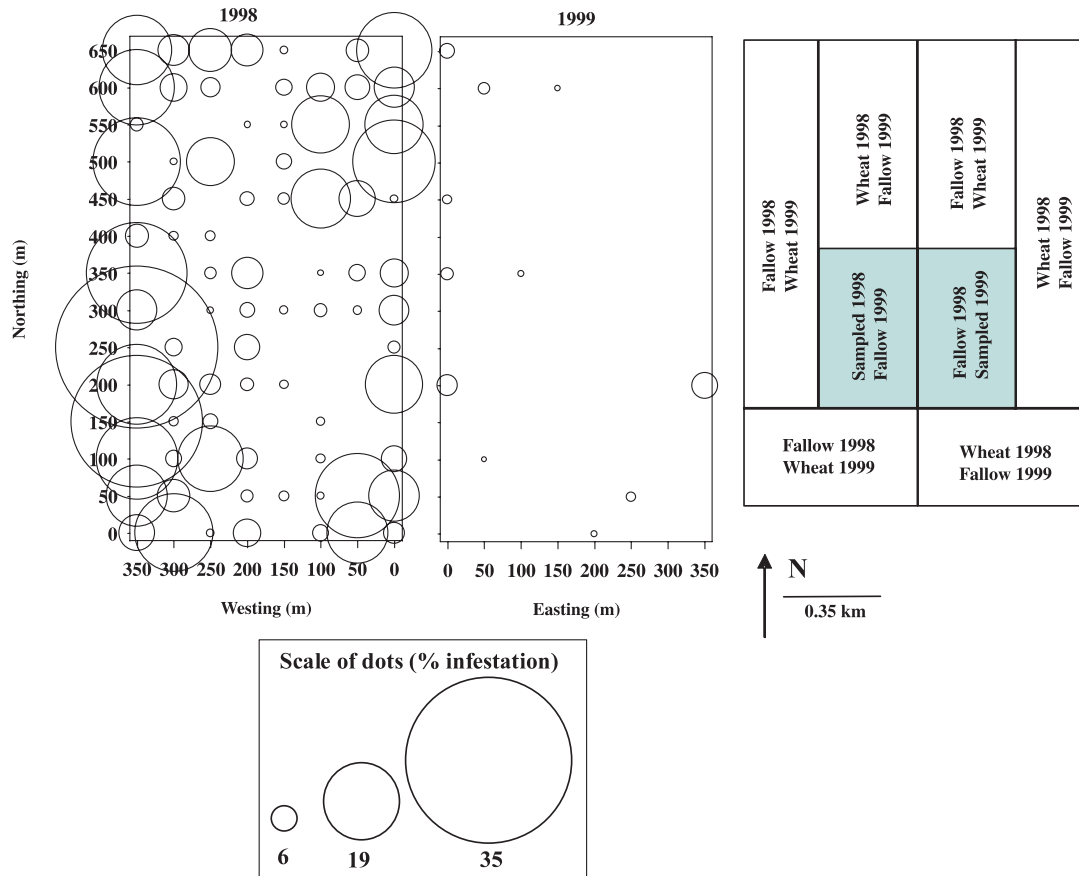
Edge effect analysis

Because of considerable annual and between-field variation in levels of *C. cinctus* infestation, we decided to standardize the infestation slopes to the average infestation level at the field edge. An asymptotic curve (Eq. 1) was used to describe the infestation slope:

$$I(x) = a + b \times e^{-cx} \tag{1}$$

where *I* is the infestation level at distance *x* from the field edge, and *a*, *b*, and *c* are fitted

Fig. 2. Spatial distribution of *Cephus cinctus* infestations in two wheat fields at Ledger, Montana. The sampled area is measured in metres from a reference point (0, 0) at the southern junction of the two fields.



coefficients. Equation 1 was fitted to all field edges bordering either fallow wheat or grassland (potential sources of ovipositing *C. cinctus* females immigrating into the wheat fields).

Results

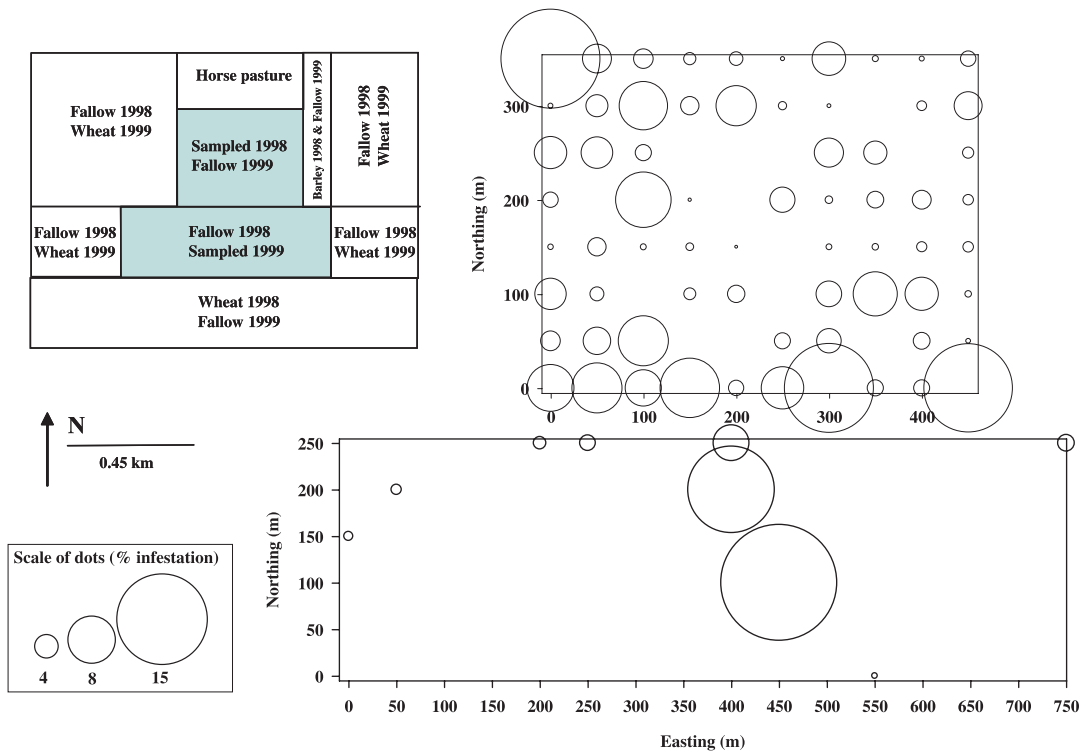
Overall *C. cinctus* infestation level

Attributes of sampled wheat fields varied considerably with regard to wheat varieties and field size, and average wheat stem density varied as much as twofold between fields (Table 1). Thus, with considerable between-field variation, these seven fields were considered suitable data sets for a comprehensive study of the edge effect of *C. cinctus* infestations in dryland wheat fields in Montana. A total of 754 samples were collected, and 3190 *C. cinctus* larvae were found in close to 39 000 individual wheat stems. The average proportion of wheat stems infested with *C. cinctus* (i.e., the

infestation level) was about 20-fold higher in 1998 than in 1999 at Loma and Ledger, while the average infestation level at Pendroy was about 6-fold higher in 1998 than in 1999. In 1998, at least 70% of all samples from each of the four fields contained wheat stems infested with *C. cinctus*, and infested stems were found in 96% of all samples from Chester. Chester also had the highest average level of infestation (33.3%). In 1998, the highest proportions of infested wheat stems in a sample were 44% and 16% at Ledger and Pendroy, respectively. In 1999, as many as 90% of the wheat stem samples were not infested (Ledger), and the highest proportion of infested wheat stems in a sample was obtained from Loma (13%). At Pendroy in 1999, only 9 of the 96 wheat stem samples were infested with *C. cinctus* larvae, and the percentage of stems infested did not exceed 15% in any of these samples.

Because of the considerable variation in wheat stem density among fields, we used

Fig. 3. Spatial distribution of *Cephus cinctus* infestations in two wheat fields at Pendroy, Montana. The sampled area is measured in metres from a reference point (0, 0) in the southwestern corner of each field.



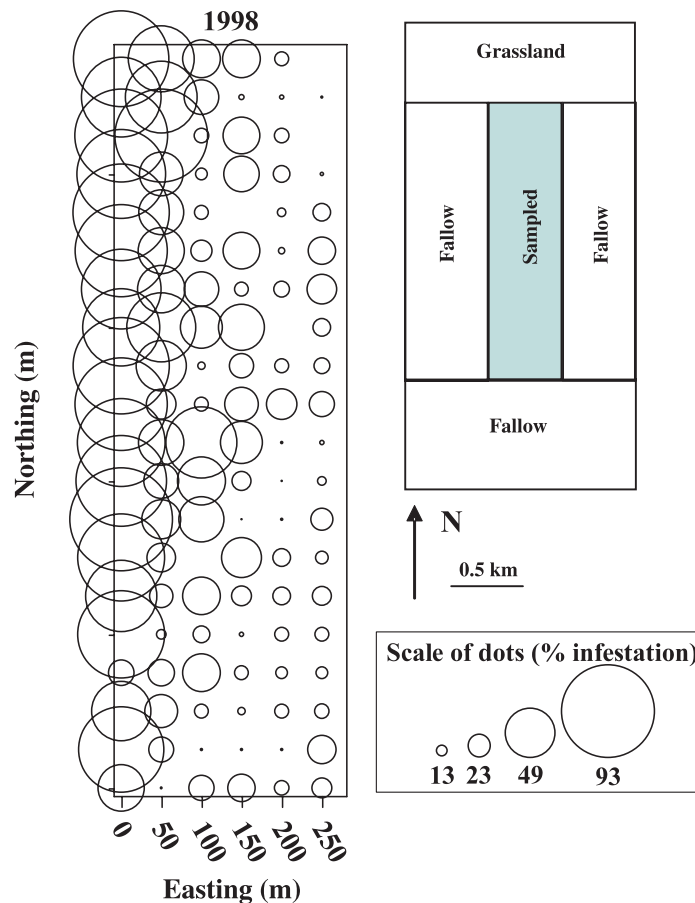
wheat stem density as a descriptive variable for the *C. cinctus* infestation level in each of the seven fields. In three of the seven fields (Loma 1998, Loma 1999, and Pendroy 1998), there was a significant linear relationship between wheat stem density and *C. cinctus* infestation level, while this relationship was nonsignificant in the remaining four wheat fields (Table 1). The coefficient of determination, adjusted R^2 , of the significant relationship for the three fields was quite low (0.06–0.10), which suggested that factors other than wheat stem density contributed more to the *C. cinctus* infestation level throughout wheat fields.

Infestation level at field edges

At Loma, the eastern edge in 1998 and the western edge in 1999 bordered a growing wheat crop, which is not a source of ovipositing *C. cinctus* females. As a result, the infestation in the Loma 1998 field was almost exclusively caused by insects moving eastwards into the field, while in 1999, movement was also almost unidirectional but was westward (Fig. 1). In both years at Loma and in 1998 at Chester, field edges bordering a potential source of insects

displayed a clear edge effect (Fig. 5a). At Ledger in 1998, there was adjacent fallow wheat on the western, southern, and eastern sides of the field, and road followed by wheat crop to the north of the field, so the ovipositing *C. cinctus* females likely immigrated into the field from multiple directions (Fig. 2). Similarly in 1999, there was adjacent fallow wheat on four sides of the field; however, *C. cinctus* infestation was detectable only along the western edge. The steepness of the infestation slope in 1999 was very similar to that observed in the same direction (west to east) in 1998. In both years, the western field edges at Ledger, which bordered a potential source of insects, displayed a clear edge effect (Fig. 5b). At Pendroy in 1998, where there was fallow wheat on the western and southern sides, while the vegetation on two other sides comprised habitats that are less susceptible to *C. cinctus*, the infestation level was clearly highest along the western and southern edges (Fig. 3) but did not decline towards the centre of the field (Fig. 5c). At Pendroy in 1999, the average *C. cinctus* infestation level along all field edges was <1% and therefore no edge effect analysis was conducted. We fitted

Fig. 4. Spatial distribution of *Cephus cinctus* infestations in a wheat field at Chester, Montana. The sampled area is measured in metres from a reference point (0, 0) in the southwestern corner of the field.



Equation 1 to the average infestation slopes outlined in Figure 5 and found that there was a significant exponential decline in *C. cinctus* infestation level from field edges inwards in 6 of the 10 fields (Table 2).

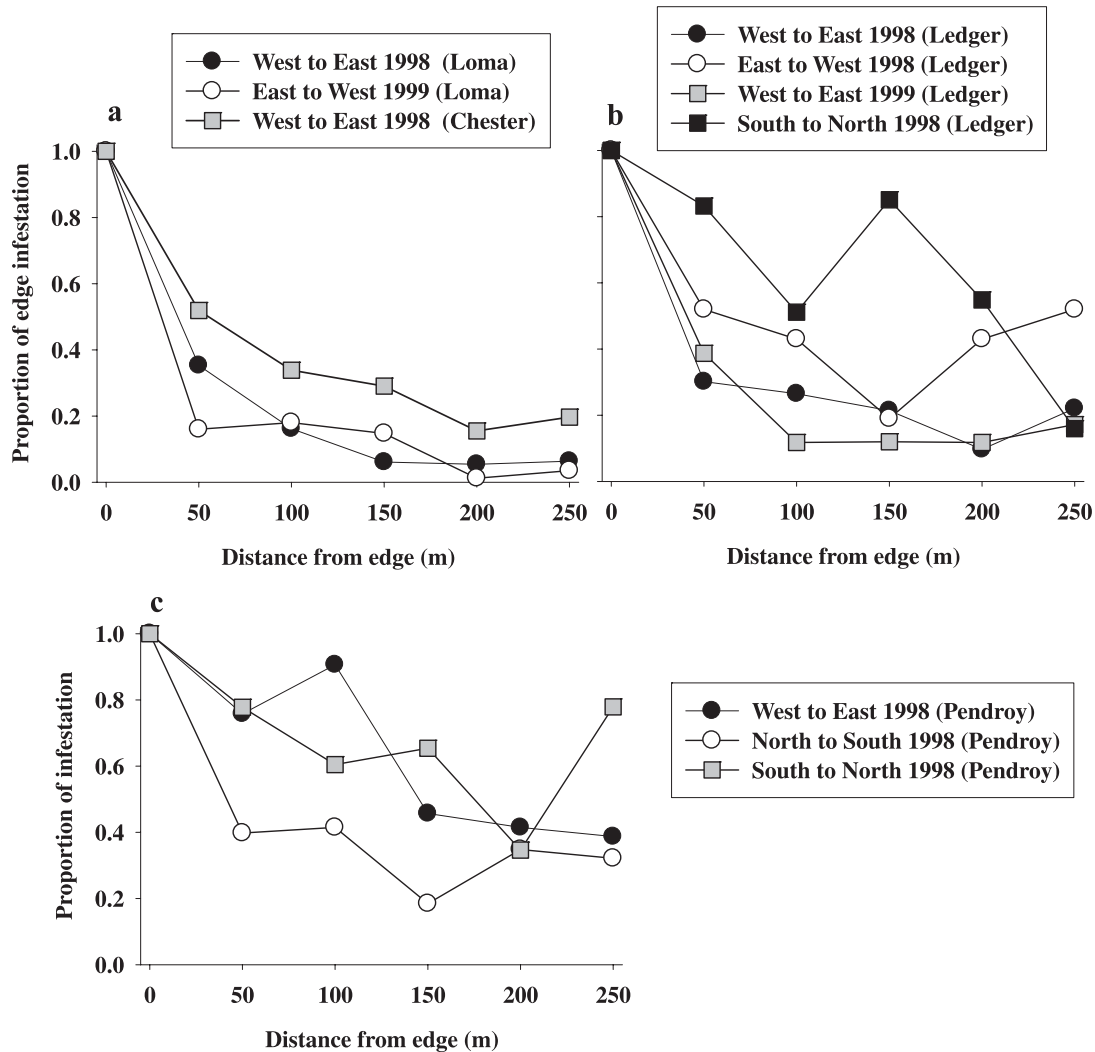
An overall assessment of the analysis indicated that even though the overall infestation level varied approximately 80-fold among fields, field edges bordered different habitats, and infestation slopes projected in different directions into wheat fields, the coefficients from the curve fits suggested considerable similarity among the fields included in this study.

Relationship between infestation level and number of infested samples

With only one sampling event from each field, we can only speculate about the way *C. cinctus* infestations gradually progressed within each field during the wheat growing season. However, the data sets from different fields

with varying levels of infestation may be used to analyze the relationship between distribution of *C. cinctus* infestations (*e.g.*, the number of samples with infested wheat stems) and the overall infestation level. In general, one of three theoretical relationships may be expected. (1) A straight line (solid line in Fig. 6), *i.e.*, a constant relationship, would suggest that the likelihood of finding an infested stem in a sample is independent of whether the other stems in the same sample are infested. Such a constant relationship would be expected for populations with no intraspecific competition. (2) If the average infestation level increases proportionally more than the number of infested samples (area below solid line in Fig. 6), then an “aggregation relationship” is occurring. An aggregation relationship would be expected for poorly mobile insects or insect populations that benefit from living in clusters. (3) If the number of infested samples increases proportionally more than the

Fig. 5. Edge effect of *Cephus cinctus* infestations. The infestation slope was determined in different directions into wheat fields from edges bordering either fallow wheat fields or native grassland (see Fig. 1) at Loma (a), Ledger (b), and Pendroy (c), Montana. Equation 1 was fitted to each infestation slope (Table 2).



average infestation level (area above solid line in Fig. 6), then a “dispersion relationship” is occurring. A dispersion relationship would be expected for mobile insects or insect populations with high levels of intraspecific competition. Data sets from all seven wheat fields were located above the line in Figure 6, which suggests that there is a dispersion relationship between the average infestation level and the number of infested samples.

Discussion

This analysis of *C. cinctus* infestations in Montana dryland wheat fields confirms earlier

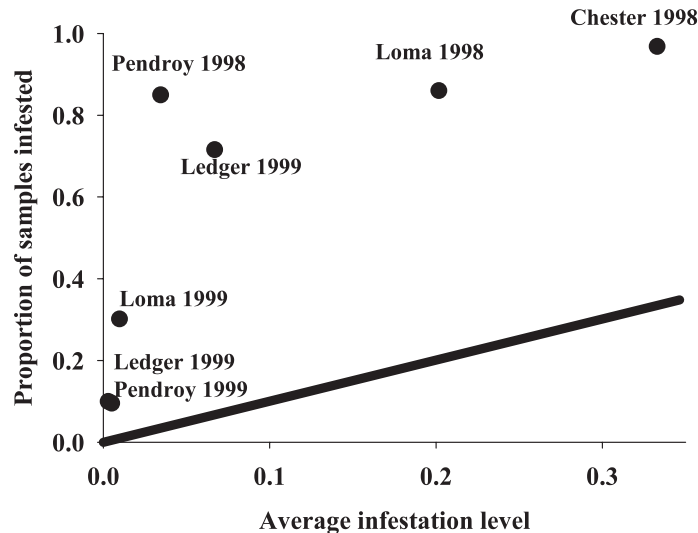
observations that an edge effect is typically observed at field edges bordering fallow wheat crop or grassland. This pattern of declining *C. cinctus* infestations towards the centre of wheat fields was observed in fields with both high and low infestation levels. Numerous studies have characterized the within-field spatial distribution pattern of carabid beetles (Bryan and Wratten 1984; Wallin 1985; French and Elliott 1999; Holland *et al.* 1999; Korie *et al.* 2000), other insect predators (Bryan and Wratten 1984; Holland *et al.* 1999), parasitoids (Longley *et al.* 1997), and aphids (Dean 1973; Elliott and Kieckhefer 1986, 1987; Feng and Nowierski 1992; Longley *et al.* 1997; Winder

Table 2. Curve-fit analyses of *Cephus cinctus* infestation slopes 50–250 m from wheat field edges.

Field	Year	Direction of migration	Edge infestation	Adjusted R^2	F value	a	b	c
Chester	1998	W to E	0.8	0.983	143.59**	0.173	0.823	0.016
Loma	1998	W to E	0.716	0.998	1366***	0.048	0.952	0.023
Loma	1999	E to W	0.04	0.953	52.11**	0.043	0.912	0.046
Ledger	1998	W to E	0.187	0.958	57.91**	0.037	0.81	0.036
Ledger	1998	E to W	0.096	0.716	7.62			
Ledger	1998	S to N	0.011	0.464	3.17			
Ledger	1999	W to E	0.012	0.978	111.98**	0.032	0.886	0.027
Pendroy	1998	W to E	0.054	0.696	6.73			
Pendroy	1998	N to S	0.077	0.892	1.99	0.052	0.691	0.037
Pendroy	1998	S to N	0.041	0.283	21.67*			
Average						0.064	0.846	0.031

Note: Edge infestation is the average *C. cinctus* infestation level along field edges. Adjusted R^2 is the coefficient of determination. Equation 1 was fitted to the infestation slopes in Figure 5, and the coefficients a , b , and c were determined for the significant curve fit; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

Fig. 6. Relationship between average *Cephus cinctus* infestation level (proportion of wheat stems infested) and number of infested samples in seven wheat fields in Montana. The solid line indicates a 1:1 relationship, which would be expected if the relationship was constant; the area below the line indicates an “aggregation” relationship; and the area above the line indicates a “dispersion” relationship.



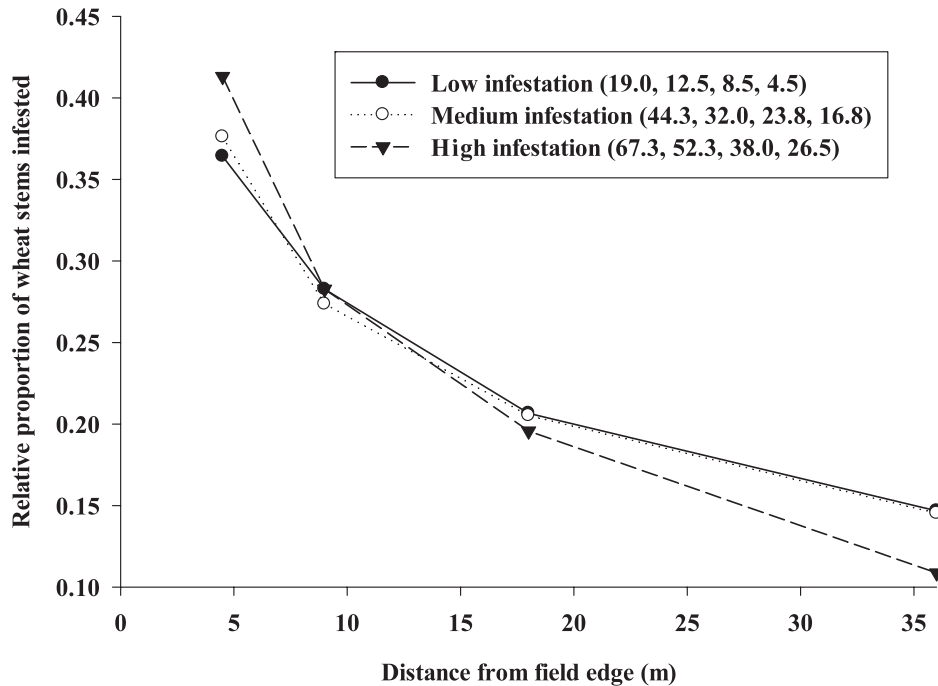
et al. 1999) in cereal fields, and these studies have outlined important temporal changes in insect spatial distribution patterns (Dean 1973; Wallin 1985; Holland *et al.* 1999; Winder *et al.* 1999; Korie *et al.* 2000) and have provided the baseline for sampling plans. Also, several studies have demonstrated an “edge effect” similar to that of *C. cinctus* infestations (Lewis 1969; Holland *et al.* 1999; Winder *et al.* 1999), but we know of no studies in which the

characteristics of an edge effect have been compared among fields with different infestation levels.

Infestation slope and infestation level

The general explanation of the edge effect is that *C. cinctus* adults are poor flyers and are short lived, so they tend to infest wheat stems near field edges, which they encounter first when they move into the wheat fields from

Fig. 7. Proportion of wheat stems infested with *Cephus cinctus* versus distance from the field edge, for three wheat fields with different levels of infestation (low, medium, and high). Data from Holmes (1982) were standardized by dividing by the average infestation level at the field edge and then plotted against distance from the field edge. The actual data from Holmes (1982) are presented in parentheses after each infestation level.



adjacent fallow fields or grass habitats. But if this is really “the whole story”, then one would expect very few infested stems towards the centres of fields when the overall level of infestation is low, because at low infestation levels there would be no reason for *C. cinctus* females to move very far into wheat fields. We have shown, contrary to this hypothesis, that the proportion of infested stems 50–250 m into wheat fields was a fairly constant proportion of the infestation level at field edges. Holmes (1982) divided 10 wheat fields into three groups according to their overall infestation level (high, medium, and low). We have transformed the *C. cinctus* distribution data from Holmes (1982) at each distance from the edge into a proportion of the total, and the curves for the three infestation levels are almost identical (Fig. 7). Thus, the transformed data from Holmes (1982) are consistent with our results showing that the steepness of the infestation slope appears to be independent of the overall infestation level. There was a noteworthy difference between the spatial distribution pattern observed at Pendroy and those observed at

Loma, Ledger, and Chester. Between-field variation in the spatial distribution pattern of *C. cinctus* infestations is consistent with the results of Runyon (2001) and Sing (2002), and it underscores the importance of conducting more research into the factors that determine the spatiotemporal variation in *C. cinctus* infestations. We have no clear explanation for the evidently less infested field border at Pendroy, but the spatial distribution of *C. cinctus* infestations in wheat fields is believed to be affected by the developmental stage of host plants. Sing’s (2002) results suggested that the edge effect of *C. cinctus* infestations is more distinct in winter wheat than in spring wheat fields, and the most likely explanation is that stem elongation has typically begun in the wheat plants by the time the *C. cinctus* adults initiate their flight period, so the host plants are susceptible to infestation. However, if spring wheat is planted late or its development is delayed by unfavorable weather conditions, then wheat stem elongation occurs after the beginning of the *C. cinctus* flight period, and this delay in host plant development is believed to cause a more even distribution of

C. cinctus infestations throughout wheat fields (Sing 2002).

Alternative interpretation of the edge effect

In addition to confirming that the *C. cinctus* infestation level is highest along edges, we also demonstrated that *C. cinctus* infestations were considerably dispersed within each field. These results may appear to be contradictory, but we argue that this distribution may be the result of a well-adapted foraging strategy for original grassland hosts. Originally proposed by Criddle (1917) and later discussed by Sing (2002), a possible explanation for the apparent density-independent steepness of the infestation slope in Chester, Loma, and Ledger might be that ovipositing females are evolutionarily adapted to small clusters of bunchgrass on the grass prairie and that they oviposit only a few eggs in each of the clusters, so movement between scattered oviposition sites is possibly part of their oviposition behavior. In open grassland, prevailing wind direction and wind speed may play an important role in the movement of ovipositing *C. cinctus* females among bunchgrass patches and may reduce the likelihood of females re-infesting the same grasses. However, wind speed and direction are probably less important within wheat fields (dense vegetation) because the ovipositing *C. cinctus* females predominantly relocate within the crop canopy and only occasionally fly above this canopy (D. Weaver, personal observations). Thus, unidirectional movement into the wheat field by ovipositing *C. cinctus* females would be an ovipositional strategy that resembles that occurring or hypothesized to occur in grassland, and it would explain why the infestation slope appears to be independent of density. Ovipositing *C. cinctus* females therefore lay most of their eggs along field edges, which they encounter first, but even in fields with low infestation levels they continue to move inwards to disperse their offspring, which explains why >65% of the wheat stem samples contained infested stems when the overall infestation level exceeded 5% (Fig. 6). An important component of this oviposition strategy is that although multiple eggs may be laid within wheat stems, only one larva emerges from each stem (Holmes 1982). Thus, cannibalism is an important factor in these population dynamics (Ainslie 1920), and it is not known whether ovipositing *C. cinctus* females are able to determine whether a wheat stem is already infested or not. Further research

is required to determine whether the larval distribution pattern is different from that of eggs, and factors such as cannibalism and potential responses of *C. cinctus* females to odors from infested wheat plants probably have to be taken into account when explaining the observed spatial distribution pattern of immature *C. cinctus* in wheat fields.

With the considerable acreage of most dryland wheat fields in the northern Great Plains of the United States and in southern regions of the prairie provinces of Canada, it is a serious challenge to develop reliable sampling plans and monitoring programs for *C. cinctus*. One of the key elements in successful management of insect pest populations in field crops is in-depth knowledge of how the within-field spatial distribution of the pest is affected by environmental conditions and infestation level. Such knowledge provides the baseline for development of reliable sampling plans and for assessments of efficacy of implemented management strategies. The analysis presented here suggests that the edge effect of *C. cinctus* infestations can be modeled mathematically and that it is fairly consistent among wheat fields. Based on our analysis, we hypothesize that ovipositing *C. cinctus* females probably lay most of their eggs along field edges and subsequently migrate inwards, following a predominantly unidirectional path. Thus, the results presented here justify further research into spatially targeted monitoring programs, sampling plans, and pest control strategies along wheat field edges.

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