

The spatio-temporal distribution of adult *Ceutorhynchus assimilis* in a crop of winter oilseed rape in relation to the distribution of their larvae and that of the parasitoid *Trichomalus perfectus*

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Abstract

The spatio-temporal distribution of *Ceutorhynchus assimilis* Payk. (Coleoptera: Curculionidae) adults caught in a rectangular grid of flight traps in a crop of winter oilseed rape (*Brassica napus* L.) was mapped and was analysed using Spatial Analysis by Distance Indices (SADIE). Their distribution was compared to that of their larvae and that of their parasitoid *Trichomalus perfectus* (Walker) (Hymenoptera: Pteromalidae) in pods. The distribution of immigrating *C. assimilis* adults was consistent with their arrival at the crop boundaries and movement within the

crop towards its centre. Adult *C. assimilis* were aggregated at all times, invasion being on two fronts, leading to the formation of two major clusters within the crop. Large areas of the crop remained relatively unpopulated. During the emigration phase, numbers declined simultaneously in all parts of the crop. The distributions of adult and larval *C. assimilis* and of larval *T. perfectus* were spatially associated. The distribution of the parasitoid did not show a density dependent relationship with that of its host. We discuss the movements of insects which underlie their population distributions, the value of integrating spatial information into improved management strategies for *C. assimilis* and the potential for the spatial targeting of insecticides to reduce the amount applied and to conserve *T. perfectus*.

Introduction

Parasitoids can provide an effective and environmentally benign means of biological control of some insect pests. Their effectiveness is dependent on good coincidence in time and space between adult parasitoids and the host stage attacked. The larvae of the cabbage seed weevil, *Ceutorhynchus assimilis* Paykull (synonym *Ceutorhynchus obstrictus* [Marsham]) infest immature pods of oilseed rape. Throughout Europe (von Rosen, 1964; Lerin, 1987), the pteromalid wasp *Trichomalus perfectus* (Walker) is a widely distributed and important larval ectoparasitoid of *C. assimilis*, often killing in excess of 70% of larvae in crops (Murchie & Williams, 1998). More information about the within-field temporal and spatial distributions of this parasitoid in relation to that of its host could lead to ways of enhancing its effectiveness as a biological control agent in an IPM strategy. Care must be taken that other components of the strategy, particularly insecticides, do not jeopardise the conservation of parasitoids. The application of insecticides can have a serious impact on parasitoid survival, either directly

through contact with or ingestion of insecticide, or indirectly through reduction in host numbers (Prueffer-Klein, 1977; Axelsen, 1994; Pałosz et al., 1994).

A recently proposed strategy for the management of *C. assimilis* on winter oilseed rape (Alford et al., 1996; Murchie et al., 1997b) aims to conserve populations of *T. perfectus* by the temporal targeting of insecticide treatments to avoid the main immigration period of the parasitoid into crops. *Trichomalus perfectus* immigrates after flowering, three to four weeks later than its host (Laborius, 1972; Dmoch, 1975) and the recent decline in the use of insecticide post-flowering in the UK appears to have resulted in substantially increased rates of parasitism (Alford et al., 1996).

Targeting insecticide treatments to crop areas with greatest pest densities could offer even greater potential for the conservation of parasitoids and for the reduction of pesticide use. Understanding the movement of pests and parasitoids into and within the crop is a prerequisite for such a strategy. Both *C. assimilis* and *T. perfectus* are univoltine. They overwinter as adults in perennial vegetation or litter in woodland and field boundaries and fly to oilseed rape crops in spring (Dmoch, 1965; Dmoch & Klimek, 1975). Crops of oilseed rape are annual and do not follow each other in rotation; therefore they provide ephemeral patches of hosts which both the pests and their parasitoids must locate. The changing spatial patterns of each insect species within the crop are likely to reflect behavioural responses to cues from their hosts (plants or herbivorous insects), subject to the influence of environmental factors such as wind direction and the location of overwintering sites. Any differences between the spatial distributions of a pest and its parasitoid(s) could offer opportunities for spatial targeting of insecticide treatments to kill the pest but conserve the parasitoids.

The spatial and temporal distributions of various insect pests in oilseed rape have been the subject of several publications in recent decades but in most studies, the spatial information collected was limited, statistical analysis was minimal or absent, and parasitoids were not included. Effective spatial targeting of pesticides within crops will depend upon the collection and modelling of fully spatially referenced data (Debouzie et al., 1987; Weisz et al., 1995; Evans et al., 1998). Few studies in oilseed rape have used two-dimensional arrays of sampling points and none have been able to fully exploit the spatial information collected (Thioulouse et al., 1984; Thioulouse, 1987; Lerin, 1995; Murchie et al., 1999).

The spatial arrangement of sampled counts of any species may be regular, random or clustered, regardless of the properties of the frequency distribution of the counts. For two species, whatever the spatial pattern of the counts of the individual species, the two populations may display positive spatial association, as for diseased plants and their pathogen, dissociation (negative spatial association), as for an insect host in refuge from its parasitoid attacker (e.g., Reeve & Murdoch, 1986), or randomness with respect to one another. Traditionally, patterns for a single species have been measured using the relationship between variance and mean (e.g., Taylor, 1984; Clark & Perry, 1994), and association between two species has been measured by the correlation coefficient (Murchie et al., 1999), but in both of these approaches the information concerning the locations of the counts is discarded. A new methodology termed SADIE (Spatial Analysis by Distance IndicEs; Perry, 1995, 1998a, b) enables the spatial information in a two-dimensional array of sample counts to be used as part of the analysis.

In this study SADIE techniques are used to characterise the spatio-temporal distribution of adult *C. assimilis* in a crop of winter oilseed rape and to compare this distribution with that of its larvae and that of the larvae of its parasitoid *T. perfectus*. These distributions are discussed

in relation to the movement of the pest and the parasitoid and the potential for the spatial targeting of insecticide treatments to kill *C. assimilis* but to conserve *T. perfectus*.

Materials and methods

Crop site. Samples were taken from a commercially grown crop of winter oilseed rape (cv. Apex) in an approximately rectangular field (6.6 ha) at Husborne Crawley, Bedfordshire, UK, in 1995 (Fig. 1). The field was bordered to the south-west by a small area of deciduous woodland and, on the other boundaries, by hedges with herbaceous undergrowth and mature deciduous trees. In 1994, the nearest crop of winter oilseed rape (69 ha) had been situated 20 m away (at its closest point), to the north and west of the experimental field; this was a potential source of overwintering insects.

Sample locations. Thirty-six sample locations were defined, positioned in an approximately rectangular array within the field (Fig. 1); four (19, 22, 28 and 34) were displaced slightly to avoid field edges or a footpath. The standard spacing between rows and columns was 43.5 m and the minimum distance between sample locations and the crop boundary was 8 m (locations 1-7, 15, 22, 28 and 34).

Crop growth stage. The growth stage (G.S.) of the crop was recorded weekly at eight sample locations (1,5,15,17,19,21,30,32) using the main racemes of five randomly chosen plants per location and using the key by Sylvester-Bradley (1985).

Insect sampling. Adult *C. assimilis* were sampled from 20 April (10% flowers open, G.S. 4.1)

to 11 July 1995 (G.S. 6.5 - 6.7) using insect flight traps at each sample location. Traps were positioned at the height of the crop canopy and were raised weekly as necessary to keep pace with crop growth. The traps consisted of four yellow-painted PVC vanes each 90×500 mm high, the long edges of which were mounted radially (90° apart) on a 20 mm o.d. PVC pipe, supported on a metal pole. A large colourless polypropylene funnel (200 mm i.d. at its widest point) was inverted and fixed above the vanes (Murchie, 1996). Insects alighting on the vanes moved upward by phototaxis or negative geotaxis into the funnel, through a perspex (plexiglass) tube (50 mm long × 34 mm i.d.) and into a collecting jar containing 70% ethanol mounted above.

Insect pests of oilseed rape are attracted to the crop by volatiles which the plants release (Bartlet, 1996). To assist them in competing with the host plants that surrounded them, each flight trap was baited with two volatiles, 2-propenyl isothiocyanate (2-P NCS) and 2-phenylethyl isothiocyanate (2-PE NCS), which are released by Brassicaceae and are attractive to a range of insects associated with oilseed rape (Bartlet, 1996; Smart & Blight, 1997; Murchie et al., 1997a). These host-plant volatiles were formulated for slow-release by their incorporation into polythene vials (2-P NCS) and into sponges enclosed in polythene bags (2-PE NCS) to provide a release rate for each of *c.* 6-7 mg per day. The baits were fixed within the perspex tubes of the traps and were replaced every five weeks. Insects were collected from each trap on 25 April and, thereafter, at weekly intervals until 11 July and were stored in 70% ethanol for subsequent examination and counting.

Numbers of *C. assimilis* larvae and their parasitism by *T. perfectus* were assessed in a random sample of 20 mature plants taken on 3 July (G.S. 6.3 - 6.5), 5 m to the north of each of 19 sample locations (encircled in Fig. 1). Ten intact pods were taken at regular spacings from the main raceme and ten were taken from the third lateral raceme of each plant. Each pod was

examined for the presence of a live or dead *C. assimilis* larva, an ectoparasitoid larva, a pupa or pupal exuvia, or an exit hole in the pod wall made by an emerging *C. assimilis* larva or ectoparasitoid adult (the latter was distinguishable by the presence of an ectoparasitoid pupal exuvia). All larval ectoparasitoids were assumed to be *T. perfectus* as this species comprised >99% of ectoparasitoids reared from parasitised *C. assimilis* collected from Husborne Crawley and from Rothamsted (28 km distant) during 1992-1994 (Murchie, 1996).

Meteorological data. Maximum and minimum temperature, rainfall and wind direction (at 09.00 h) were recorded daily at a site 250 m to the south-east of the experimental crop.

Analysis of insect distributions. The spatial distributions of sampled insects were represented as contour maps of density, interpolated by minimum curvature using Unimap 2000 software (Uniras Ltd., Slough, UK).

Spatial distributions of *C. assimilis* were analysed and compared over time, between sexes, between adults and larvae, and with the distribution of *T. perfectus* larvae using SADIE (Perry, 1998a, b). By permuting the observed insect counts amongst the sample units, SADIE enables the spatial characteristics of the observed arrangements to be assessed by randomisation procedures, using indices and tests of randomness.

To describe the spatial pattern in single sets of 36 counts of adult *C. assimilis* from flight traps, three indices were used, the main SADIE index I_a and two subsidiary indices, J_a and K_a (Perry, 1998a). The values of I_a and K_a are around unity for random arrangements of the observed counts and exceed unity for arrangements where the counts are aggregated. The index J_a discriminates between patterns where there is one major cluster, for which its value is greater

than unity, and two or more clusters, for which its value is equal to or less than unity. The centre of gravity of the sample units was denoted as O . For a nearly rectangular array of traps, O is close to the centre of the array (Fig. 1). The centre of gravity of the spatially referenced counts is denoted as H . When counts occur predominantly towards one edge of a sampled area, the position of H is relatively far from O and the value of I_a is large, indicating an aggregated pattern. The displacement of H from O , termed δ (Perry & Klukowski, 1997), provides a simple descriptive summary of spatial pattern. Whereas the index I_a measures pattern over the entire sample area, the index K_a provides an approximate measurement of smaller scale pattern within a restricted area around H where the bulk of the observed counts occurred (Perry & Klukowski, 1997).

For comparisons between two sets of counts, the SADIE index I_m was used (Perry 1998b). I_m is greater than zero for associated populations, around zero for populations positioned at random with respect to one another, and less than zero for dissociated populations. These techniques were applied to sets of counts from 19 or 36 sample locations. The index was used to measure the spatial association of the same species measured in the same traps on pairs of occasions; here, greater association indicates a greater degree of stability of spatial distribution. It was also used to quantify the spatial association between males and females, between adults and larvae and between pests and parasitoids measured simultaneously in the same sample units. Associated with each SADIE index is a formal exact significance probability, derived from the randomisations described above.

Results

Spatio-temporal distribution of C. assimilis. A total of 553 *C. assimilis* were caught in the 36 flight traps from 20 April (G.S. 4.1) to 20 June (G.S. 6.3) and few were caught thereafter. Flight traps did not catch *T. perfectus* in sufficient numbers for analysis. The spatial distributions of weekly catches of *C. assimilis* from 20 April to 13 June are displayed as a time-series of eight contour maps (Fig. 2). Visual examination of the mapped counts suggested two main phases of crop colonization, representing crop invasion and subsequent population decline. Invasion began from the south-east and south-west field boundaries and appeared to spread from these areas to other parts of the crop. The two foci almost merged to give a single cluster covering most of the south and, less densely, parts of the north of the crop at the peak of the colonisation period (16 - 23 May), which occurred after completion of flowering on the main raceme (G.S. 5.8 - 5.9). From 23 May - 13 June, abundance declined in all parts of the crop previously colonised, with those parts most heavily infested being the last to maintain a population. SADIE analyses of these distributions are presented in Table 1. Notably, the value of δ was large early in the season, and became progressively smaller until 6 June. This reinforced the suggestion that the distribution patterns during the phase when insect numbers declined did not merely repeat in reverse those of the invasive phase. The preponderance of *C. assimilis* in the south, and their relative scarcity in large areas of the crop, ensured that the spatial distribution was aggregated on all dates, I_a always significantly exceeding unity (Table 1). The invasion on two fronts was confirmed by the index J_a , which was not significantly more than unity except near the peak of *C. assimilis* abundance (9-16 May) and at the end of colonisation (13-20 June; Table 1). At a smaller scale than the whole crop, there was also noticeable pattern in *C. assimilis* distribution in the south of the field where almost all of these insects occurred. This was confirmed by values of index K_a which were substantially larger than unity especially from 2 May to 30 May, and with relatively small probability (P) values on several occasions.

The distributions of *C. assimilis* adults in successive weeks showed marked similarities from 20 April to 6 June (Fig. 2) as shown by all statistics. The correlation coefficients for comparisons of successive weeks were consistently large, as were the values of I_m which were almost always significant (Table 2). This result is expected, given the monotonic decline in δ and the consistent changes in the two colonisation phases outlined above. With increasing time-lags between the weeks compared, the degree of association between distributions of *C. assimilis* adults decreased (Table 3), the mean values of I_m showing a monotonic decline from 2.98 to 1.48, suggesting an evolving pattern of pest distribution.

Spatial distributions of male and female adult C. assimilis. Overall, more male than female *C. assimilis* were caught (69% male, Table 4), the proportion of males exceeding 80% in April and declining to *c.* 50% in June. SADIE analysis of the total catch (all dates) of male and female *C. assimilis* (Table 4) indicated a similar spatial pattern to that found for most of the weekly catches, with strong aggregation ($I_a > 1$), evidence for more than one cluster ($J_a \approx 1$) and the existence of small-scale pattern ($K_a > 1$). There was no evidence for differential distributions of males and females within the field. Their spatial patterns had similar characteristics (Table 4) and were strongly associated ($I_m = 2.93$, $P < 0.05$). The distribution of females is displayed (Fig. 3a). Separate analysis of each week's catch showed that the male and female distributions were most strongly associated when they were most abundant (9 May to 6 June).

Comparison of distributions of C. assimilis adults, their larvae and T. perfectus larvae. The mean cumulative catch of *C. assimilis* adults in 19 flight traps from 20 April to 20 June was 18.4 ± 4.3 weevils per trap. On 3 July there was evidence of *C. assimilis* larvae and *T. perfectus* larvae in 35.7 ± 2.9 and 20.3 ± 1.8 pods per trap location, respectively (400 pods examined per location). The distributions of *C. assimilis* adults and larvae showed some inconsistencies

especially in the northern quarter of the crop where traps caught few adults but plants contained relatively many larvae (Figs. 3a & b). Although the correlation coefficient between numbers of adult female and larval *C. assimilis* was only 0.30, SADIE indicated that they were spatially associated ($I_m = 3.48$, $P = 0.003$). The distributions of both *C. assimilis* larvae and *T. perfectus* larvae appeared to be aggregated into regions c. 0-80 m from crop edges and were strongly associated (Figs. 3b & c; $I_m = 4.82$, $P < 0.003$). The mean proportion ectoparasitism of *C. assimilis* larvae was 0.568 (S.E. 0.031) and this did not vary with host density. In the absence of density dependence, the slope of a linear regression of \log_{10} (parasitoid number) on \log_{10} (host number) is expected to be unity. Here, the slope was 1.09 (S.E. 0.19), indicating no evidence of density dependence at the range of host density sampled (21-65 larvae per 400 pods) and at the sampling scale used. The distributions of adult female *C. assimilis* and of *T. perfectus* larvae were also associated ($I_m = 2.54$, $P = 0.02$) but the index for association of adult male *C. assimilis* and *T. perfectus* larvae was not significant ($I_m = 1.40$, $P = 0.14$).

Meteorological data. Average air temperatures for April, May and June differed from the 30-year averages (9.1° C, 11.4° C and 13.9° C, respectively) by +1.5° C, +0.5° C and -0.1° C, respectively. Rainfall for each month (19 mm, 29 mm and 16 mm, respectively) was 63%, 46% and 71%, respectively, less than the 30-year average. During the 62 days from 20 April to 20 June for which flight trap catches were analysed, wind direction was variable, showing northerly, southerly, easterly and westerly vectors on 38, 24, 28, and 32 days, respectively. During *C. assimilis* immigration (20 April to 23 May) winds with a northerly vector were most common (23 days out of 34) but the maximum daily air temperature exceeded 15° C, the threshold for mass flight by *C. assimilis* (Bonnemaison, 1957; Dmoch, 1965; Free & Williams 1979b), on 14 days only. On these days, no wind direction prevailed, with northerly, southerly, easterly and westerly wind vectors predominating on 3, 5, 3 and 3 days, respectively.

Discussion

The sampling of adult *C. assimilis* from points arranged in a grid pattern across the entire crop, together with the mapping of their spatial distributions over time and analysis by SADIE, has produced a much more detailed and informative picture of the pattern of crop colonisation by this pest than has hitherto been achieved. Free & Williams (1979a) sampled from ten crops of winter rape along line transects and from discrete points and showed that, during immigration (April and May), *C. assimilis* adults infested crop edges more than crop centres, particularly on large crops, and that the proportion at the crop edge gradually diminished as adults spread further into the crop (June and July). Others have also reported the edges of crops to be more heavily infested by *C. assimilis* than their centres (Risbec, 1952; Thiem, 1970; Khüne, 1977). The present study has revealed the complexity of the pattern of crop colonisation by this pest, with invasion on multiple fronts, significant aggregation throughout colonisation and on different scales, and a simultaneous decline of infestation in all areas of the crop towards the end of flowering. This study provides no direct evidence concerning the movement of individual *C. assimilis*. However, the evolving pattern of their distribution and the decline in the value of δ during immigration is consistent with the arrival of *C. assimilis* close to the crop boundary followed by their movement towards the crop interior.

More male than female *C. assimilis* were caught throughout the trapping period. This could reflect either the relative flight activity of males and females or a male-biased sex ratio on the crop or both. The flight traps used for sampling were activity traps and would have caught more males than females, irrespective of their relative abundance on the crop, if males displayed

more flight activity as they searched for more ambulatory, ovipositing females with which to mate (Dmoch, 1965). Sex ratios on crops can be variable. Free & Williams (1979b) sampled the canopy of five crops of winter rape with sweep nets and found a male-biased sex ratio on two, an equal sex ratio on two and a female-biased sex ratio on the fifth. Earlier immigration to crops by males than females has been suggested by Risbec (1952) and Dmoch (1965) but disputed by Bonnemaïson (1957). Such a strategy might hold a reproductive advantage for males if they are the first to mate with newly-arrived virgin females. The two sexes were caught in the same areas of the crop and there was no evidence that females were distributed more at crop edges than males, as found by Murchie et al., (1999).

Although the distributions of adult female (cumulative total) and of larval *C. assimilis* were spatially associated, they were not coincident in all parts of the crop. Free & Williams (1979a) reported similarly that numbers of adult *C. assimilis*, caught by sweep net along line transects, did not closely reflect the spatial distribution of larvae. These inconsistencies may result from a number of causes. Again, flight traps may reflect the flight activity of females rather than the abundance of ovipositing females in the crop canopy. Cumulative totals of females may not reflect total oviposition activity because females may not oviposit at a constant rate throughout their colonisation of the crop. Ovipositing females may move and redistribute themselves within the crop canopy in such a way that they are not caught in flight traps. Distributions derived from flight trap catches are also likely to be inaccurate should the catchment areas of neighbouring traps overlap, i.e., if the distance over which insects are attracted to traps is large in relation to the distance between traps. When presented at a location well removed from an oilseed rape crop, extracts of oilseed rape attracted weevils to traps over 20 m (Evans & Allen-Williams, 1993). The catchment area of our plant-volatile baited traps was unknown, but, competing against the background of volatiles released from the surrounding

plants in the crop, it seems likely that the radius of attraction to the traps was considerably reduced. Differences have been demonstrated in the attraction of seed weevils to traps situated adjacent to a rape crop and baited with various isothiocyanates (released at 6-30 mg per day) using a trap spacing of only 10 m (Smart et al., 1997). It seems likely, therefore, that the trap spacing of 43.5 m was sufficient to reflect differences in flight activity in this crop.

The close spatial association between densities of *T. perfectus* larvae and *C. assimilis* larvae indicates that the presence of its host was the main determinant of the distribution of *T. perfectus*. This conclusion is perhaps not surprising but, given that >40% of hosts in the crop remained unparasitised, parasitoid distribution could potentially have been more restricted than that of its host. For example, increased host-finding efficiency or search persistence could result in higher parasitism rates at sites in the crop first invaded by parasitoids than elsewhere, in the same way as some pests tend to be more abundant at crop edges (Free & Williams, 1979a). Host-density dependent parasitoid behaviour can also lead to differences in host and parasitoid distributions (Norowi et al., 2000). However, it is clear that no such factors supervened to limit *T. perfectus* distribution. The uniform and large proportion of larvae parasitised over the crop area occupied by the host concurs with the results of Ulber & Vidal (1998) and shows that this parasitoid dispersed throughout its host range and that its host-finding efficiency did not vary within that range. Little is known about how *T. perfectus* locates the rape crop; it has not been caught in traps baited with rape plant volatiles, such as isothiocyanates, as have some other parasitoids of rape pests (Murchie et al., 1997a), but it has been reported to use the frass produced by the last larval instar to locate its host within the crop (Dmoch & Rutkowska - Ostrowska, 1978). The lack of apparent spatial density dependence with respect to its host is in agreement with the study of Ulber & Vidal (1998) but the spatial scale of sampling can affect the detection of such a relationship (Walde & Murdoch, 1988; Norowi et al., 2000). It is important

to note that density dependence is not a prerequisite for the persistence of a host-parasitoid association (Pacala et al., 1990) nor, probably, for the effectiveness of a parasitoid in depressing a pest population (Ulber & Vidal, 1998). The close coincidence of host and parasitoid spatial distributions indicates that even a spatially targeted post-flowering application of insecticide would have been as likely to kill *T. perfectus* as *C. assimilis*. Therefore, at present, temporal targeting rather than spatio-temporal targeting of insecticide treatments must remain the prime strategy for protecting this parasitoid (Alford et al., 1996).

The aggregated nature of the distribution of *C. assimilis* adults in the crop, if confirmed by further studies to be a general phenomenon for this pest, has implications for the design of accurate sampling procedures to support decisions on the need for insecticide application. In the UK, the recommended procedure for advisory purposes is to assess *C. assimilis* on three occasions during flowering and to use the largest mean number per plant from the three assessments to determine whether the economic threshold has been exceeded (Lane & Walters, 1993; Walters & Lane, 1994). On each occasion, the assessment is made by counting the *C. assimilis* caught when the tops of each of 20 plants are beaten over a white tray; the plants are randomly selected along a line transect into the crop. Where populations are as aggregated as in the crop studied, sampling along transects into crops would provide inaccurate estimates of abundance and contribute to the reported unreliability of the method (Walters & Lane, 1994). There is an acknowledged need for the improvement of population assessment methods for this pest and our study suggests that these should be based on more research into and information on its spatial distribution.

The aggregated distribution of *C. assimilis* adults in this crop also suggests a potential for spatial targeting of insecticide treatments to areas where pests are most abundant (Weisz et al.,

1995), thereby maximising control of the pest while minimising pesticide use. The recommended time for the application of pyrethroid to kill adult *C. assimilis* on winter rape is during flowering, between 20 pods set on the main raceme (G.S. 4.7) and 80% petal fall (G.S. 5.8; Whitehead, 1998); this timing avoids the main immigration flights of *T. perfectus* (Alford et al., 1996). In this study, the crop was between these stages during 2-16 May. During this period, *C. assimilis* adults infested only about 40-50% of the crop and pest densities varied considerably within the infested areas. If insecticide had been applied to the whole crop during this time, much would have been applied to uninfested areas. It is not a feasible proposition for the grower or advisor to measure patterns of *C. assimilis* abundance within individual crops. However, in the future, advances in our knowledge of the environmental factors and behavioural responses determining the spatio-temporal distributions of this pest and its parasitoid, may lead to the development of integrated pest management strategies for oilseed rape which incorporate spatially targeted treatments, e.g., push-pull or stimulo-deterrent diversion strategies (Miller & Cowles, 1990).

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Table 1. Analyses of the spatial distributions of adult *C. assimilis* caught in 36 flight traps weekly from 20 April to 20 June 1995

Sample period	No. of <i>C. assimilis</i>		δ (m)	SADIE Index and associated P value					
	Mean per trap	(SE)		I_a ¹	P	J_a ²	P	K_a ³	P
20-25 April	0.44	(0.22)	110.7	1.62	<0.005	1.22	0.28	0.99	0.62
25 April - 2 May	0.88	(0.30)	69.6	1.49	0.014	0.91	0.76	1.03	0.15
2-9 May	1.06	(0.23)	58.6	1.94	<0.005	1.08	0.16	1.08	<0.005
9-16 May	3.50	(0.68)	49.1	1.71	<0.005	1.14	0.04	1.03	0.10
16-23 May	4.92	(0.96)	46.2	1.63	<0.005	1.09	0.16	1.05	0.08
23-30 May	2.92	(0.63)	44.1	1.57	0.010	1.02	0.41	1.09	0.01
30 May - 6 June	1.31	(0.29)	43.0	1.40	0.022	1.06	0.25	1.01	0.33
6-13 June	0.19	(0.11)	106.5	1.52	0.015	1.47	0.16	1.03	0.10
13-20 June	0.14	(0.10)	141.7	1.51	0.010	3.05	0.005	1.00	0.78

¹ Values of $I_a > 1$ indicate aggregation within the sample area.

² Values of $J_a \leq 1$ indicate the presence of multiple clusters when $I_a > 1$.

³ Values of $K_a > 1$ indicate aggregation at a small scale.

Table 2. Comparison of distributions of adult *C. assimilis* caught in flight traps in successive weeks

Periods compared		Sample correlation	SADIE index I_m ¹	P value
20 – 25 April	v. 25 April – 2 May	0.64	3.80	0.003
25 April – 2 May	v. 2 – 9 May	0.55	2.48	0.025
2 – 9 May	v. 9 – 16 May	0.60	2.37	0.013
9 – 16 May	v. 16 – 23 May	0.86	3.27	0.003
16 – 23 May	v. 23 – 30 May	0.78	3.61	0.001
23 – 30 May	v. 30 May – 6 June	0.71	3.17	0.100

¹ Values of $I_m > 0$ indicate that the distributions are associated.

Table 3. Values of the I_m index for comparisons of adult *C. assimilis* distributions between weeks separated by increasing lags

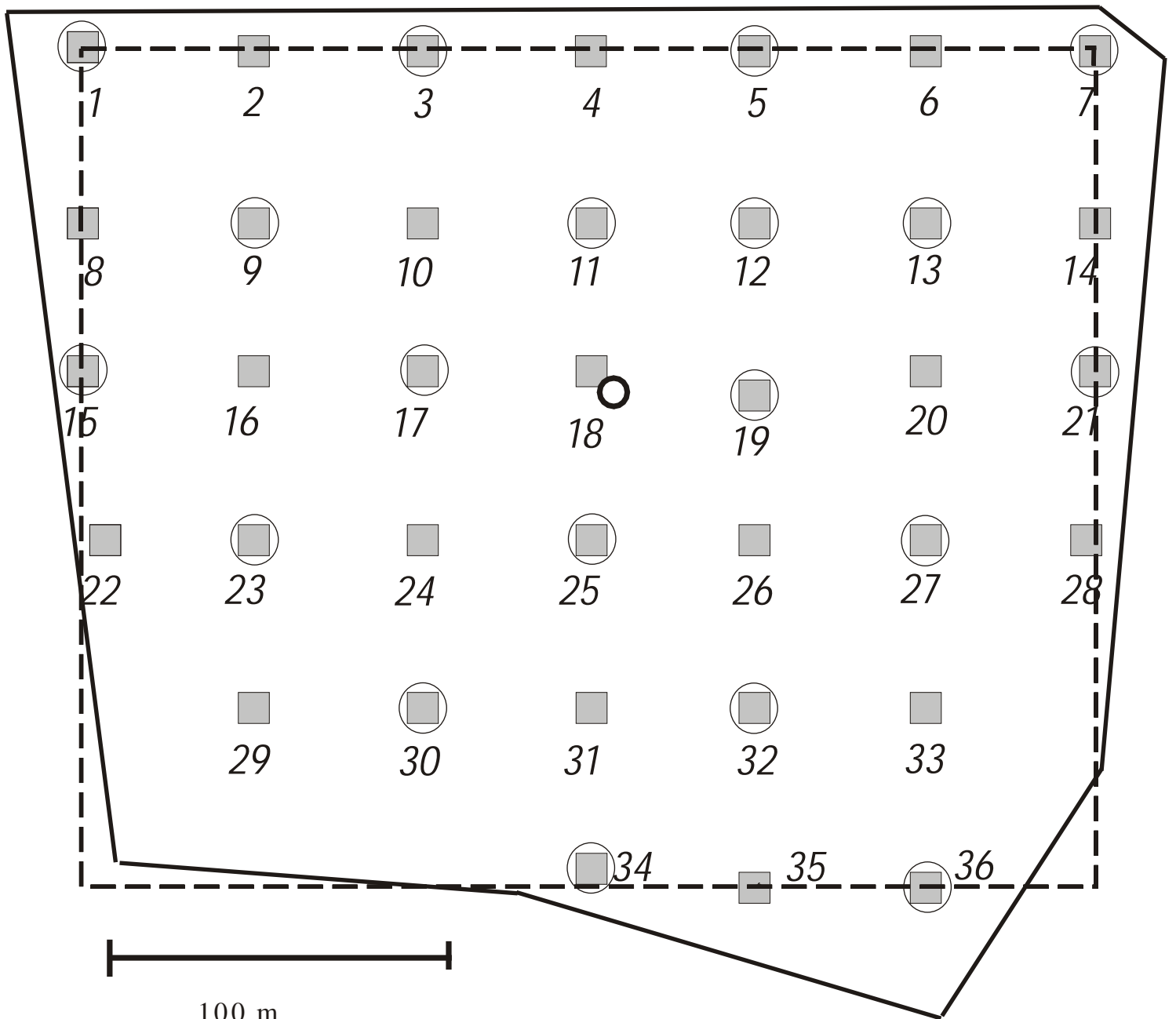
Lag (weeks)	First week compared				
	25 April - 2 May	2 -9 May	9 -16 May	16 - 23 May	23 - 30 May
1	2.48	2.37	3.27	3.61	3.17
2	2.55	2.59	2.84	3.77	
3	1.95	3.14	2.46		
4	1.43	2.30			
5	1.48				

Table 4. Analyses of the distributions of the total numbers of adult *C. assimilis* caught during 20 April to 20 June 1995

Species	Sex	Mean no. per trap	SE	δ (m)	SADIE index and associated P value					
					I_a ¹	P	J_a ²	P	K_a ³	P
<i>C. assimilis</i>	♀♀ + ♂♂	15.3	2.8	49.8	1.90	<0.005	1.06	0.20	1.05	0.020
<i>C. assimilis</i>	♀♀	4.8	0.9	45.8	1.73	<0.002	1.05	0.25	1.05	0.086
<i>C. assimilis</i>	♂♂	10.6	2.0	51.6	1.89	<0.002	1.06	0.21	1.08	0.012

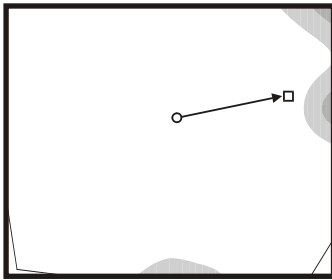
^{1,2,3} See footnotes to Table 1.

- Figure 1. Plan of experimental field with locations of samples and mapped area.
- Figure 2. Time series of adult *C. assimilis* densities interpolated from 36 flight trap samples. Five density classes are shown with contours equally spaced on a logarithmic scale ($\log_{10} n + 1$), the maximum class (darkest shade) representing ≥ 15 weevils per trap, the minimum class < 1 per trap. $\bigcirc = O$, the centre of gravity of the sample locations; $\square = H$, the centre of gravity of the mapped counts; \rightarrow indicates distance from O to H , i.e. δ ; G.S. = main raceme growth stage.
- Figure 3. Distributions of insects interpolated from samples taken at 19 locations in seven density classes with contours equally spaced on a logarithmic scale ($\log_{10} n + 1$). Classes with larger values are represented by darker shades. Maximum and minimum classes, respectively, represent: (a) ≥ 15 and < 0.6 adult female *C. assimilis* per trap (total for 20 April to 20 June); (b) ≥ 70 and ≤ 21 *C. assimilis* larvae per 400 pods; (c) > 27 and < 8 *T. perfectus* larvae per 400 pods.

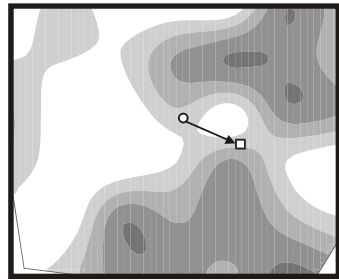


- boundary of crop
- - - boundary of mapped area
- ⊠ sample location (flight traps and plant samples; not to scale)
- sample location (flight traps only; not to scale)
- centre of gravity of sample locations () ○

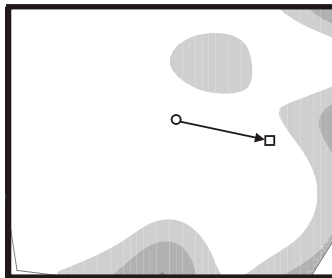
Figure 2



20-25 April, G.S. 4.1

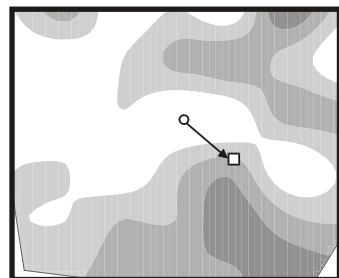


16-23 May, G.S. 5.8-5.9

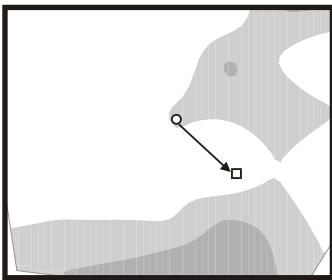


25 April - 2 May, G.S. 4.1-4.8

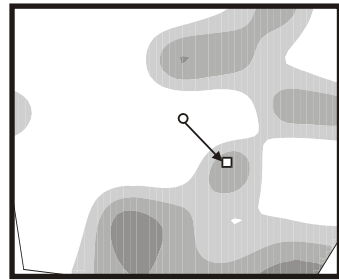
100m



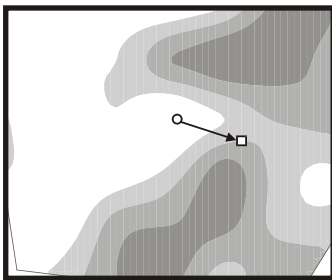
23-30 May, G.S. 5.8-6.3



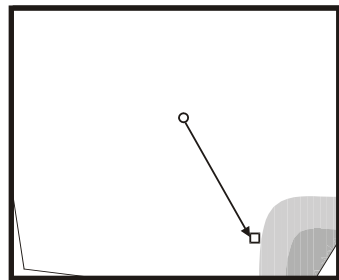
2-9 May, G.S. 4.2-5.7



30 May - 6 June, G.S. 6.2-6.3

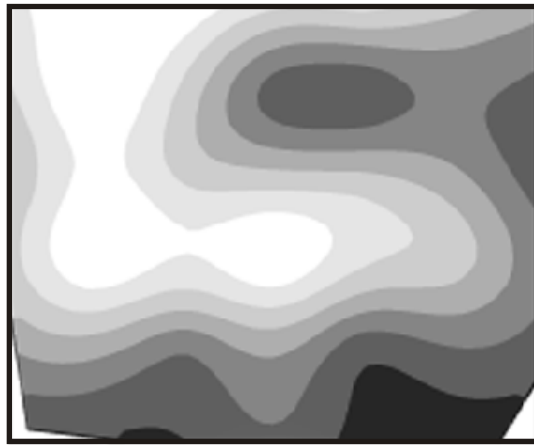
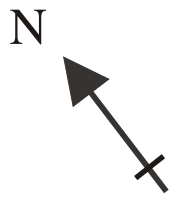


9-16 May, G.S. 4.8-5.9

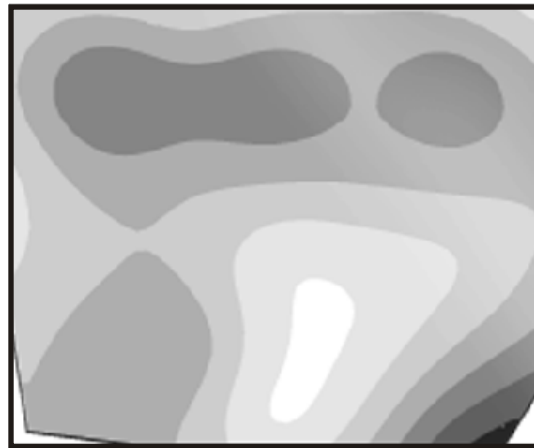


6-13 June, G.S. 6.2-6.3

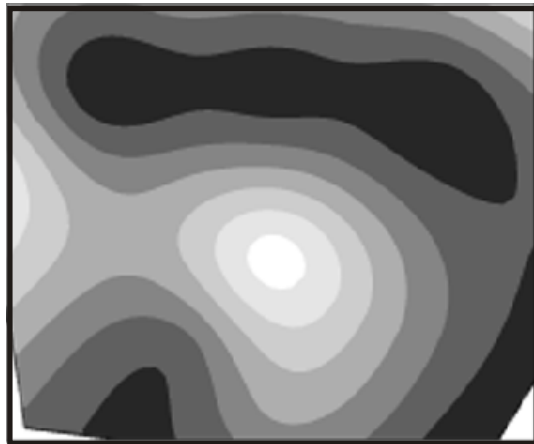




a. ~~Clus~~ *Clus* similis



b. ~~Crvas~~ *Crvas* similis



c. ~~Trypa~~ *Trypa* defectus