The spatial distribution of canopy-resident and ground-resident cereal aphids (Sitobion avenae *and* Metopolophium dirhodum) *in winter wheat*

Linton Winder, Colin J. Alexander, Chris Woolley, Joe N. Perry & John M. Holland

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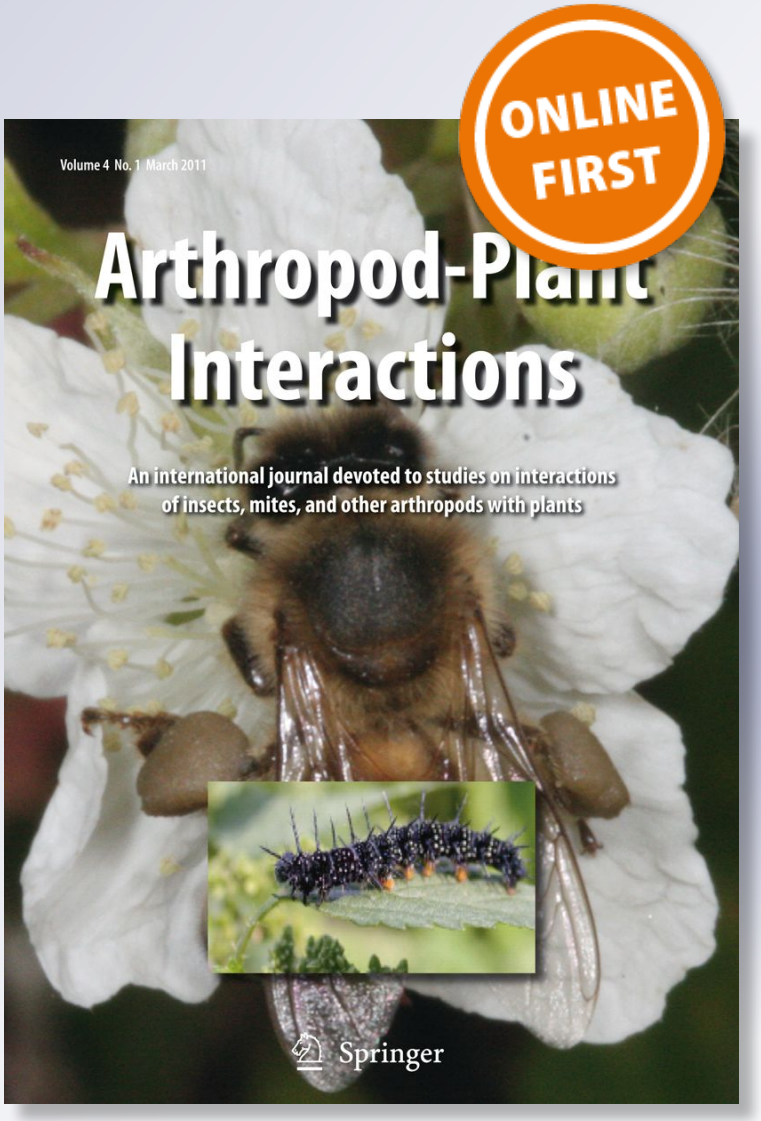

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ORIGINAL PAPER

The spatial distribution of canopy-resident and ground-resident cereal aphids (*Sitobion avenae* and *Metopolophium dirhodum*) in winter wheat

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Abstract We investigated, within two cereal fields in Southern England, the within-canopy spatial distribution of the aphids *Sitobion avenae* and *Metopolophium dirhodum* in relation to crop yield and plant nitrogen. We extended the study to investigate the spatial distribution of aphids that fell to, or returned from, the ground in order to estimate availability of the within-canopy aphid population to ground-active predators. We revealed that crop canopy aphid spatial pattern was associated with nitrogen or yield. Differences were evident between species: *S. avenae* was generally negatively associated with yield or plant nitrogen, whilst *M. dirhodum* exhibited positive association. For both aphid species, we observed strong spatial pattern for aphids falling to the ground and conclude that this could, in part, mediate the effectiveness of ground-active predators as pest control agents.

Keywords *Sitobion avenae* · *Metopolophium dirhodum* · Fall-off · Integrated pest management · Cereal · Aphid

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L. Winder (✉)
Department of Natural Sciences, Faculty of Social and Health Sciences, Unitec Institute of Technology, Auckland, New Zealand
e-mail: lwinder@unitec.ac.nz

C. J. Alexander
Biomathematics and Statistics Scotland, BioSS Office, The James Hutton Institute, Invergowrie, Dundee, Scotland, UK

C. Woolley
41 Green End, Fen Ditton, Cambridge, Cambridgeshire CB5 8SX, UK

J. N. Perry
Plant and Insect Ecology Division, Rothamsted Research, Rothamsted, Harpenden, Herts, UK

J. M. Holland
Farmland Ecology Unit, Game and Wildlife Conservation Trust, Fordingbridge, Hants SP6 1EF, UK

Introduction

Aphids are common pests of cereal crops and are known to have patchy within-field distributions (Alexander et al. 2005; Winder et al. 2001; Winder et al. 1999). Such patchy distributions are important because spatial pattern is likely to mediate the amount of damage caused by aphids through direct yield loss (Möwes et al. 1997), reduction in quality (Basky and Fónagy 2007) or virus transmission (Chapin et al. 2001). Spatial pattern will also influence the interaction between aphids and the natural enemies that contribute to their suppression or control (Harwood et al. 2001; Winder et al. 2005). Two aphid species are most commonly found in U.K. cereals: the English grain aphid *Sitobion avenae* (Fabricius, 1775) and the rose grain aphid *Metopolophium dirhodum* (Walker, 1849). *S. avenae* is predominantly an ear-feeding species (thus affecting yield or crop quality directly), whilst *M. dirhodum* feeds on leaves and is considered to be a less important pest because it has a lower impact on yield (Dixon 1987; van Emden and Harrington 2007).

Crop husbandry is known to influence the population development of aphids within cereal crops, and increased nitrogen content can enhance aphid population development (Aqueel and Leather 2011;Chaul et al. 2005; Honêk and Martinková 2002; Rowntree et al. 2010), which are also increased by the application of nitrogen fertiliser (Duffield et al. 1997; Ehsan-Ul-Haq and van Emden 2002;

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Khan and Port 2008), although the effects are often variable. Therefore, if crop nitrogen influences aphid population growth, its within-field variability (Delin 2004) may contribute to aphid spatial distributions. The first part of this study investigated the spatial distribution of cereal aphids infesting the crop and used yield and crop nitrogen measurements as simple indicators of crop quality. We hypothesised that aphid spatial pattern would be associated with these host plant characteristics and also measured soil moisture as it is known to influence aphid development (Ehsan-Ul-Haq and Van Emden 2003) and epigeal natural enemy spatial pattern (Holland et al. 2007).

The second part of this study investigated the spatially explicit distribution of aphids that are falling to, or returning from, the ground, hypothesising that these distributions would be closely linked. Aphids are know to have a defence mechanism whereby they fall to the ground in response to their natural enemies or alarm pheromones (Irwin et al. 2007), and they are also probably dislodged by mechanical means through movement of the crop. The dislodged aphids rarely return to the same host plant. The rate at which aphids fall to the ground has been well studied, and in wheat it is known that this process affects a significant proportion of the canopy-resident aphid population, with reported fall-off rates ranging from 20 % to 95 % day^{-1} and typically in the range of 20–35 % day^{-1} (Kerzicnik et al. 2010; Sopp et al. 1987; Sunderland et al. 1986; Winder 1990; Winder et al. 1994). Thus, the number of dislodged aphids often exceeds the number that are directly predated or parasitised (Minoretti and Weisser 2000).

Due to this turnover, the aphid population is divided into canopy-resident and ground-resident subpopulations. Spatial separation of these subpopulations provides a mechanism for niche partitioning (Finke and Snyder 2008), whereby multiple predator species act on a single target prey. Some natural enemies such as syrphids (Diptera: Syrphidae) and coccinellids (Coleoptera: Coccinellidae) attack aphids directly on their host plant within the crop canopy, whilst a multitude of ground-active predators such as carabids (Coleoptera: Carabidae) and some linyphiids (Araneae: Linyphiidae) actively consume aphids whilst they are on the soil surface (Sunderland et al. 1986; Symondson et al. 2002). Ground-resident aphids may die before they reach a new host and are exposed to considerable predation pressure that can subsequently affect aphid spatial distribution and the spread of aphid-borne viruses (Annan et al. 1999). Virtually nothing is known about aphid fall-off in spatially explicit terms, yet it is known that predatory success of ground-active species such as *Pterostichus cupreus* (Coleoptera: Carabidae) is dependent on the spatial distribution of their prey (Bommarco et al. 2007).

Methods

Field methods

We monitored the distribution of cereal aphids in two conventionally managed winter wheat fields (Horseparks, 8.1 ha, and Oakmead, 5.4 ha sown in mid-October 2001 with the variety 'Claire') located within 500 m of each other at Seale-Hayne Agricultural College, Devon, Southern England. No insecticides were applied to the fields during the study. A sampling grid was established within each field. In both fields, a grid of 82 sampling locations in an offset pattern was set up within an area of 120 m by 168 m (Fig. 1). An accurate location (<1 m) for each sampling point was established by a handheld GPS unit (Trimble Geoexplorer 3, Trimble Navigation Ltd, Sunnyvale, California, USA), and each location was designated with a flexicane extending beyond crop height with a waterproof card bearing its location number. In order to prevent lodging of the crop by trampling, a narrow path was cut with a 'strimmer' from tractor wheel tracks to each sampling location. Twenty-five tillers were individually marked (using small waterproof cards tied to each tiller) at each location within a 0.5-m^2 area. Aphid counts, recording species and number by direct observation, were taken on the 25 marked tillers on five occasions in Horseparks and six occasions in Oakmead. Crop growth stage following the method of Zadoks et al. (1974) was also recorded. Sample dates were planned at weekly intervals, but the actual day on which counts were made were weather dependent and were only conducted on fine days. Aphid counts for each location were calculated by averaging the 25 individual counts, and aphid densities (number m^{-2}) were generated by combining the count data with crop density measurements. Additionally, aphid loading during the growing season was calculated by calculating 'aphid days' for each sampling location following the method of Ruppel (1983).

When the crop had matured and was ready for harvest, plants were collected at each sampling location from an area of 0.1 m^2 and crop density (ears m^{-2}), yield (g m^{-2}), % grain N and % leaf N determined. Nitrogen levels were determined using a Leco Nitrogen Analyser; three ears and three leaves were sampled, dried to a constant weight and ground prior to analysis. Additionally, soil moisture was recorded on one occasion (26 July); for each sampling location, three soil moisture recordings were made to a depth of 5 cm using a hand-held probe (ThetaProbe Soil Moisture Sensor, Delta-T, Cambridge, UK) and then averaged to provide a single value.

Aphid fall-off was also measured. Five 245 mm × 95 mm sticky traps (cut from PestWest electrocutor sheeting supplied by Agrisense) were placed horizontally at each location and sampling occasion for 24 h. Following

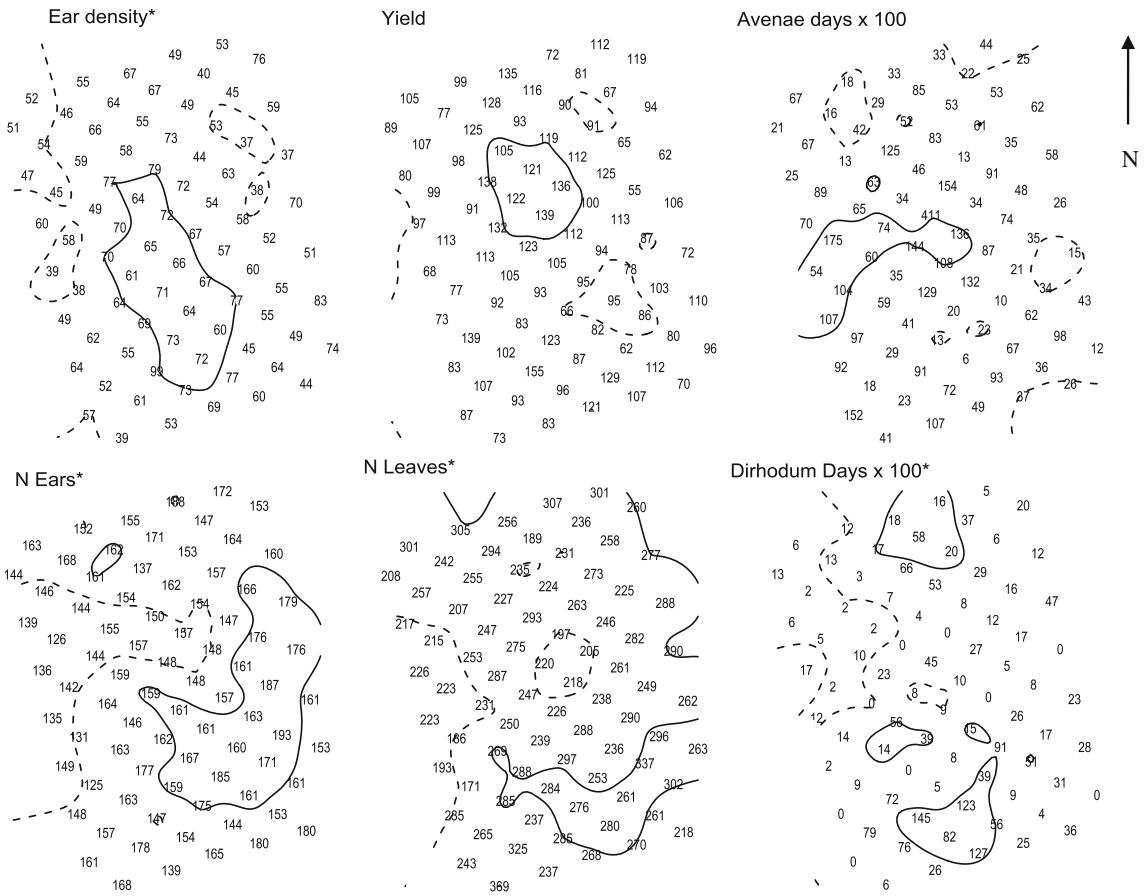

Fig. 1 Spatial pattern of ear density (number m^{-2}), yield (g m^{-2}), %N in ears, %N in leaves, *S. avenae* aphid days and *M. dirhodum* aphid days for the field Horseparks. The *map* contours indicate clusters of relatively large counts (areas bounded by *solid line*) or 'patches', for which $v_i > 1.5$, and small counts (areas bounded by *hatched line*), for which $v_j < -1.5$. *Denotes where measurable spatial pattern could be detected

removal, the numbers of aphids were recorded (discounting aphids found on the extreme edge of the sticky material in case they had climbed directly onto the sheeting), and the number caught (number m^{-2} day^{-1}) was calculated by pooling data from the five traps for each location and then correcting to m^{-2}. Means for each sample date were calculated by averaging values from the 82 sampling locations. Regression was done to determine the relationship between mean aphid density within the crop canopy and the mean rate of aphid fall-off (number falling m^{-2} day^{-1}), pooling the data from the two fields.

In addition, the re-climbing of plants by aphids was recorded on one occasion (5th July) in the field Horseparks. Twenty climbing traps were positioned at each sampling location, the design of the traps following that of Winder (1990). Each trap was constructed from a 200 mm length of dowelling with an inverted plastic bottle (18 mm wide, 48 mm long) placed over the stick at one end to prevent it from getting wet. High-tack adhesive tape (25 mm wide, manufactured by 3 M, product code 927) was wrapped around the stick and served to trap the aphids as they attempted to climb and re-enter the crop canopy.

Spatial analysis

Spatially explicit representations of these data were constructed using Spatial Analysis by Distance Indices (SADIE) utilising 'red–blue' plot methodology (Perry and Dixon 2002; Winder et al. 2001; Perry et al. 1999). Red–blue plots provided a means of visualising neighbourhoods of consistently high counts (patches) or consistently low counts (gaps) within the area being studied. When using this method, patches are usually shown in red and represent neighbourhoods of counts higher than the sample mean, m. Gaps are usually shown in blue and represent neighbourhoods of counts lower than the sample mean m. In this analysis, 'red' patches or 'blue' gaps were represented by areas bounded by solid or hatched lines, respectively, to provide monochrome representation.

At a given location, each sampling unit had an x, y field coordinate and a corresponding count c, which represented the value of the variable being analysed. Using these data, we generated SADIE red–blue plots for the aphid data, soil moisture, yield and nitrogen measurements. Data were integerised if required as values must be used in this format and the nonparametric option was used for aphid counts as the variance greatly exceeded the mean. Each sampling unit was ascribed an index of clustering: either a positive v_i index for patch units with $c_i > m$ or a negative v_j index for gap units with $c_j < m$. The cluster values were then used to generate contour maps that show patch and/or gap neighbourhoods. We used SadieShell version 2.0 (available for download at http://home.cogeco.ca/~sadiespatial/index.html) for all analyses and maps were generated in Surfer 10 (Golden Software).

Pairwise comparison of red–blue plots allowed spatial similarity between variables to be determined, described in terms of local 'association' or 'dissociation'. The method effectively overlays the two red–blue plots and determines whether there is correspondence at the local (sampling unit) scale, after allowing for spatial autocorrelation (Dutilleul 1993). Local association indicated correspondence between cluster types (i.e. there was measurable patch–patch and/or gap–gap cluster index coincidence), whilst local dissociation indicated that the opposite was the case (i.e. there was measurable patch-gap or gap-patch coincidence).

Tests for local spatial association were conducted by paired (bivariate) comparisons using N_AShell (version 1, also downloadable). Local spatial association was measured using the index χ_k, the statistic being based on the similarity between the clustering indices drawn from the two data sets. χ_k was positive if local association was evidently present due to similarity of cluster indices (v_k/v_k or $-v_k/-v_k$) and negative if local dissociation was present ($v_k/-v_k$ or $-v_k/v_k$). An overall spatial association statistic X was calculated from the mean of these local values, equivalent to a simple correlation coefficient, and was positive when association was evident and negative for dissociation (Winder et al. 2001). The method provided a formal test of significance; $P < 0.025$ for association, whilst $P > 0.975$ for dissociation.

Results

Crop characteristics

For the field Horseparks, mean crop density (±1 s.e.) was 593.5 ± 13.3 ears m^{-2}. Strong spatial pattern was evident; density was measurably higher within the centre of the field (Fig. 1; Table 1). Mean yield was 993.1 ± 23.6 g m^{-2}, and no measurable spatial pattern could be detected, although there was some indication that high yields occurred centrally. Mean ear and leaf nitrogen was 1.58 % ± 0.02 and 2.57 % ± 0.04, respectively. Nitrogen in ears and leaves were locally associated ($\chi = 0.44$, $P < 0.01$), and both exhibited very strong spatial pattern, with gap areas on the western side of the field and patches towards the east. Strong local association was evident between yield and ear nitrogen levels ($\chi = 0.71$, $P < 0.01$). Mean soil moisture was 10.43 % ± 0.01 and exhibited strong spatial pattern (Table 1), although it was not locally associated with any other measured variable.

For the field Oakmead, mean crop density was 539.4 ± 12.3 ears m^{-2} with a measurable patch along the western edge of the field (Fig. 2; Table 1). Mean yield was 958.6 ± 19.6 g m^{-2}, although no measurable spatial pattern was evident. Mean ear and leaf nitrogen was 1.8 % ± 0.1 and 2.9 % ± 0.1, respectively. Nitrogen in ears and leaves was locally associated ($\chi = 0.77$, $P < 0.01$) and exhibited strong spatial pattern, with a gap area on the western edge of the field and patch areas centrally. Strong local association between yield and ear nitrogen was evident ($\chi = 0.68$, $P < 0.01$). Mean soil moisture was 8.69 % ± 0.01 and exhibited strong spatial pattern (Table 1), although it was not locally associated with any other measured variable.

Table 1 Mean cluster index v_i for patches and v_j for gaps, with associated probability, P, for tiller density (number m^{-2}), yield (g m^{-2}), % nitrogen in ears and % nitrogen in leaves for the two fields Horseparks and Oakmead

Field	Cluster type	Crop density		Yield		N (ears)		N (leaves)		Soil moisture	
		Cluster index	*P*	Cluster index	*P*	Cluster index	*P*	Cluster index	*P*	Cluster index	*P*
Horseparks	Patch	1.42	0.02*	1.15	0.14	1.78	<0.01*	1.41	0.02*	2.42	<0.01*
	Gap	−1.24	0.07	−1.15	0.16	−1.65	<0.01*	−1.26	0.06	−2.34	<0.01*
Oakmead	Patch	1.49	<0.01*	1.29	0.06	1.48	0.01*	1.78	<0.01*	1.34	n.s.
	Gap	−1.59	<0.01*	−1.23	0.09	−1.58	<0.01*	−1.68	<0.01*	−1.19	0.04*

*Denotes where measurable spatial pattern could be detected

Table 2 Crop growth stage (GS, Zadoks scale), aphids tiller^{-1} (per tiller) and m^{-2} (density) within the crop canopy and number of aphids falling to the ground m^{-2} day^{-1} (fall-off) from the fields Horseparks and Oakmead

Date	GS	*S. avenae*			*M. dirhodum*		
		Per tiller	Density m^{-2}	Fall-off	Per tiller	Density	Fall-off
Horseparks							
9 June	59	1.40 ± 0.4	30.9 ± 7.7	9.8 ± 1.5	5.6 ± 0.8	131.0 ± 18.5	54.7 ± 10.8
13 June	60	3.2 ± 0.5	73.3 ± 12.4	23.5 ± 3.0	7.9 ± 1.1	189.5 ± 27.6	43.1 ± 4.5
28 June	71	13.5 ± 1.4	318.1 ± 37.4	117.3 ± 10.3	1.3 ± 0.3	34.0 ± 10.0	27.3 ± 2.9
5 July	75	11.6 ± 1.3	275.4 ± 32.5	136.7 ± 14.6	0.3 ± 0.1	6.6 ± 2.7	35.4 ± 9.0
10 July	77	7.7 ± 1.0	175.3 ± 23.1	20.9 ± 3.0	0.2 ± 0.1	4.2 ± 2.3	5.5 ± 1.1
Oakmead							
9 June	59	0.7 ± 0.2	16.5 ± 5.6	5.2 ± 1.2	4.5 ± 0.7	100.0 ± 15.4	20.0 ± 2.6
16 June	60	1.4 ± 0.2	30.5 ± 5.4	8.8 ± 1.6	6.5 ± 0.9	146.6 ± 20.1	25.1 ± 2.8
23 June	69	5.6 ± 0.6	119.2 ± 12.9	11.5 ± 1.4	1.5 ± 0.3	33.1 ± 6.5	29.9 ± 2.7
30 June	71	4.7 ± 0.5	99.4 ± 10.3	20.3 ± 2.3	0.8 ± 0.3	17.5 ± 6.6	11.5 ± 1.4
5 July	75	3.8 ± 0.4	76.8 ± 7.0	17.4 ± 2.0	0.48 ± 0.15	10.3 ± 3.4	22.5 ± 5.7
14 July	77	4.3 ± 0.5	84.8 ± 9.6	12.0 ± 1.8	0.2 ± 0.1	4.3 ± 2.6	6.2 ± 1.1

Aphid values expressed as arithmetic mean (±1 s.e.)

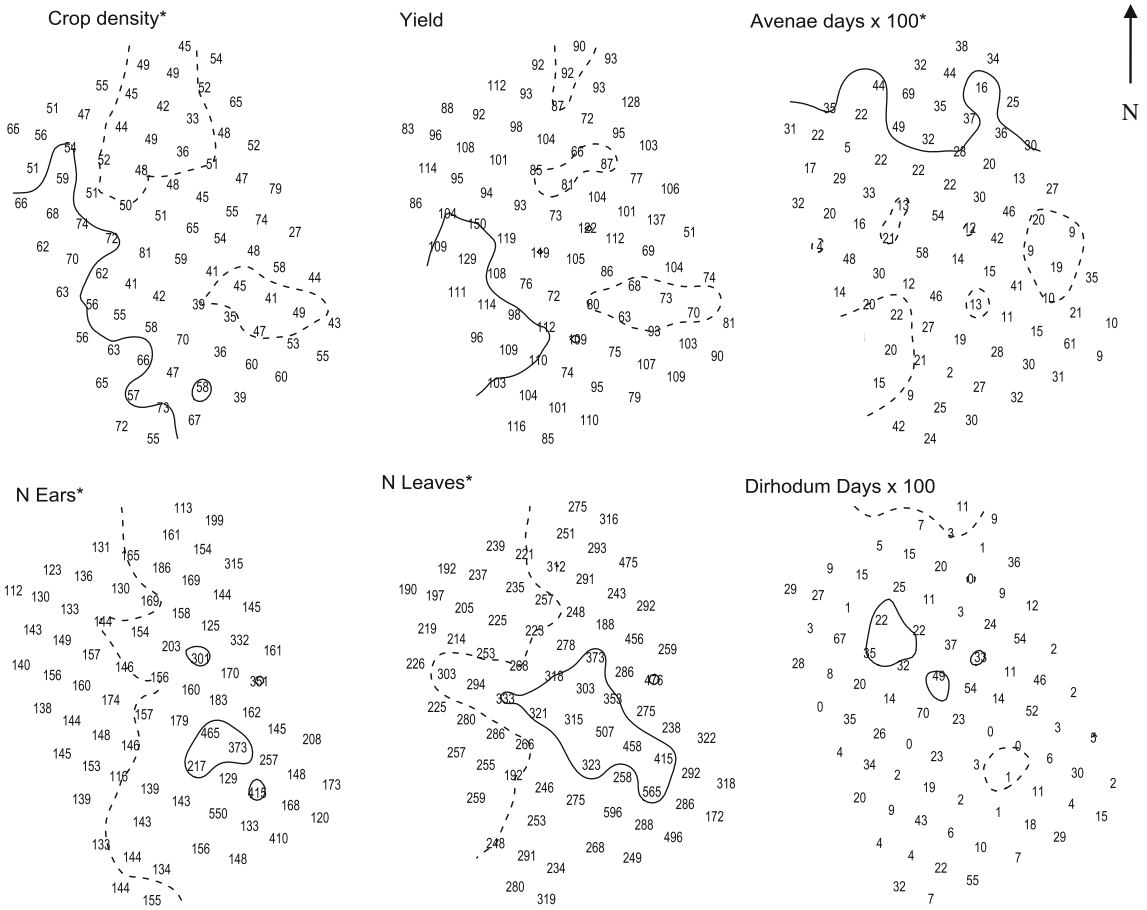

Fig. 2 Spatial pattern of ear density (number m^{-2}), yield (g m^{-2}), %N in ears, %N in leaves, *S. avenae* aphid days and *M. dirhodum* aphid days for the field Oakmead

Aphids within the crop canopy and falling to the ground

For Horseparks, *S. avenae* and *M. dirhodum* populations peaked on 28 June and 13 June, respectively (Table 2). The crop flowered in mid-June, and the *S. avenae* population was sufficiently high at this time to exceed the damage threshold of an increasing population of greater than five aphids tiller^{-1} (George and Gair 1979). For both species, spatial pattern within the crop was generally not evident. *S. avenae* fall-off exhibited significant spatial pattern on

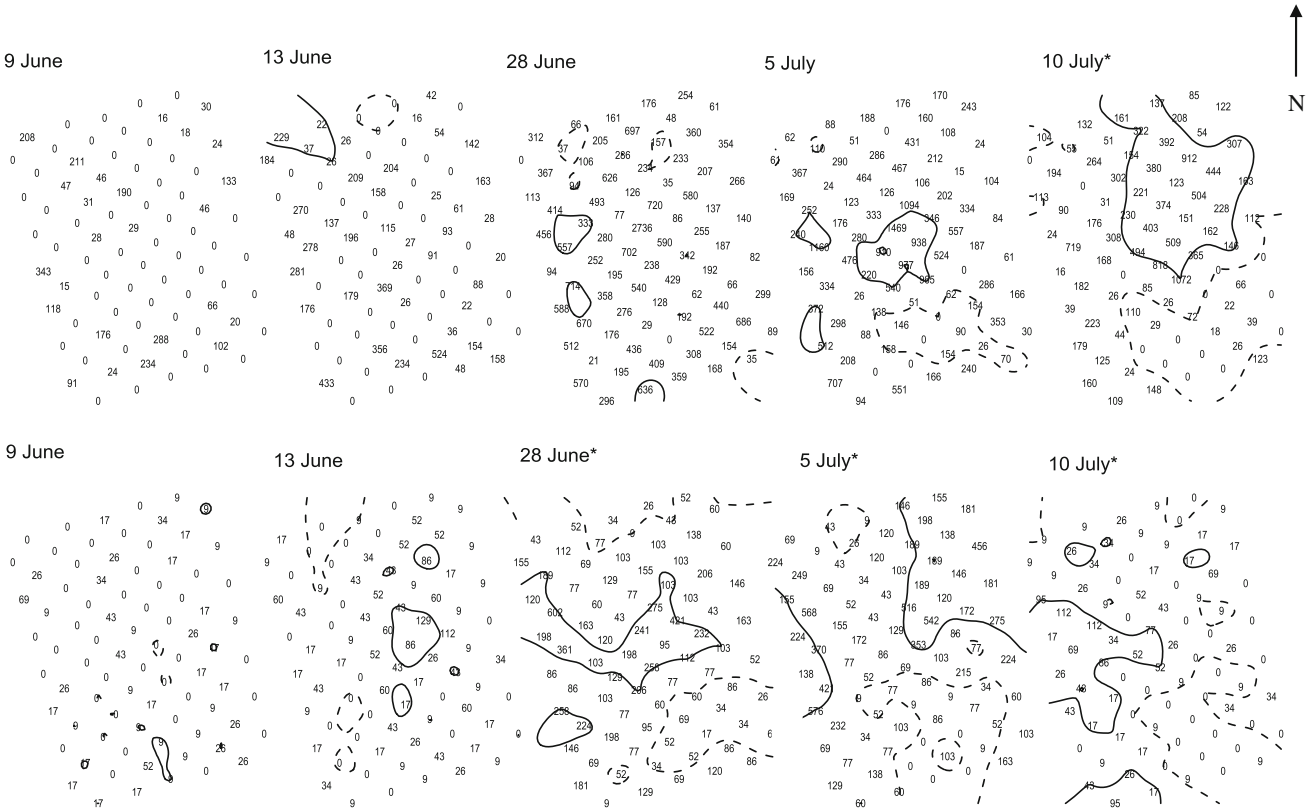

Fig. 3 Spatial pattern on each sampling date of *S. avenae* on the crop, number m^{-2} (*upper series*), and falling to the ground, number m^{-2} day^{-1} (*lower series*), for the field Horseparks

Table 3 Mean cluster index v_i for patches and v_j for gaps, with associated probability, *P*, for the aphids *S. avenae* and *M. dirhodum* found on the crop and on the ground within the field Horseparks

Date	Cluster type	*S. avenae*—crop		*S. avenae*—ground		*M. dirhodum*—crop		*M. dirhodum*—ground	
		Cluster index	*P*	Cluster index	*P*	Cluster index	*P*	Cluster index	*P*
9 June	Patch	0.88	0.79	1.08	0.24	1.00	0.42	0.98	0.50
	Gap	−0.88	0.81	−1.00	0.41	−1.06	0.28	−1.02	0.37
13 June	Patch	0.92	0.69	1.11	0.20	1.21	0.09	1.25	0.06
	Gap	−0.87	0.84	−1.11	0.20	−1.29	0.05*	−1.23	0.08
28 June	Patch	1.13	0.18	1.41	0.01*	1.04	0.33	1.25	0.07
	Gap	−1.12	0.17	−1.46	0.01*	−1.06	0.28	−1.27	0.06
5 July	Patch	1.24	0.07	1.70	<0.01*	1.07	0.26	1.01	0.38
	Gap	−1.24	0.14	−1.76	<0.01*	−1.07	0.27	−1.04	0.33
10 July	Patch	1.83	<0.01*	1.62	<0.01*	1.03	0.39	1.14	0.14
	Gap	−1.86	<0.01*	−1.61	<0.01*	−1.01	0.35	−1.14	0.15
Aphid days	Patch	1.19	0.12	–	–	1.39	0.01*	–	–
	Gap	−1.25	0.07	–	–	−1.45	0.02*	–	–

*Denotes where measurable spatial pattern could be detected

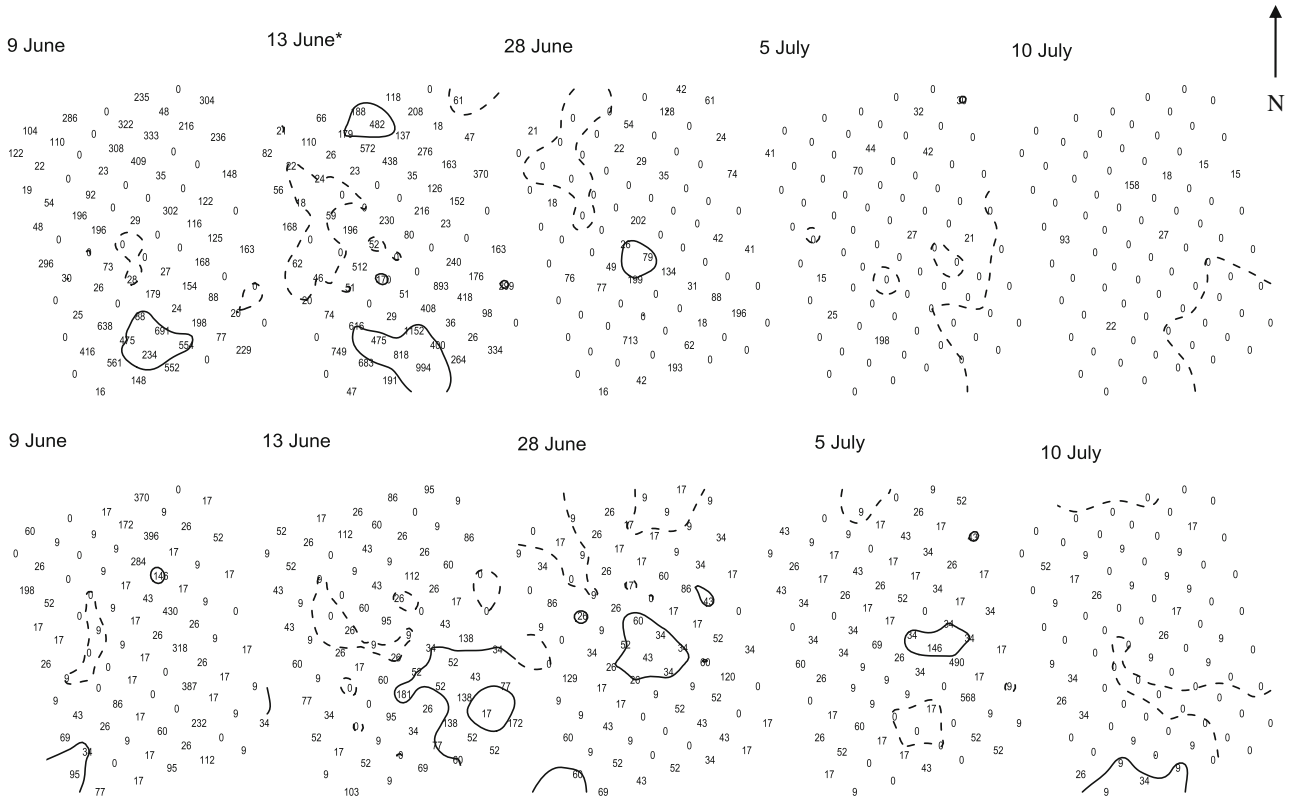

Fig. 4 Spatial pattern on each sampling date of *M. dirhodum* on the crop, number m^{-2} (*upper series*), and the ground, number m^{-2} day^{-1} (*lower series*), for the field Horseparks

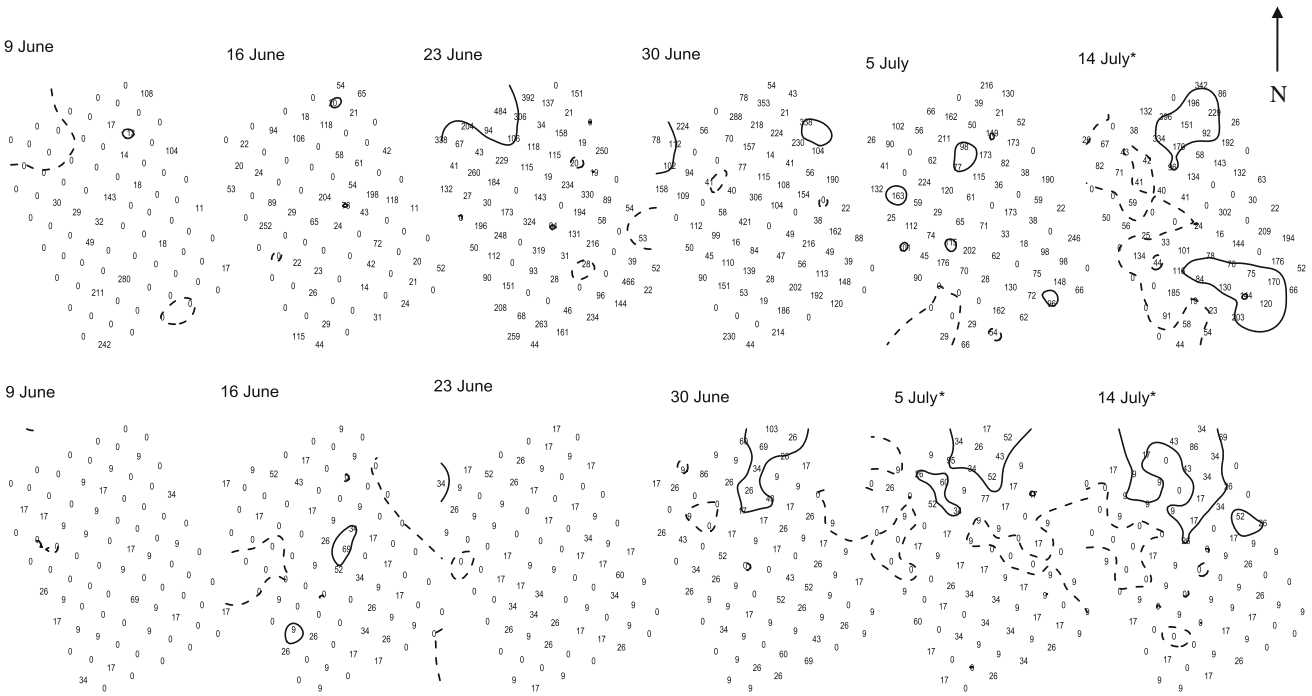

Fig. 5 Spatial pattern on each sampling date of *S. avenae* on the crop, number m^{-2} (*upper series*), and falling to the ground, number m^{-2} day^{-1} (*lower series*), for the field Oakmead

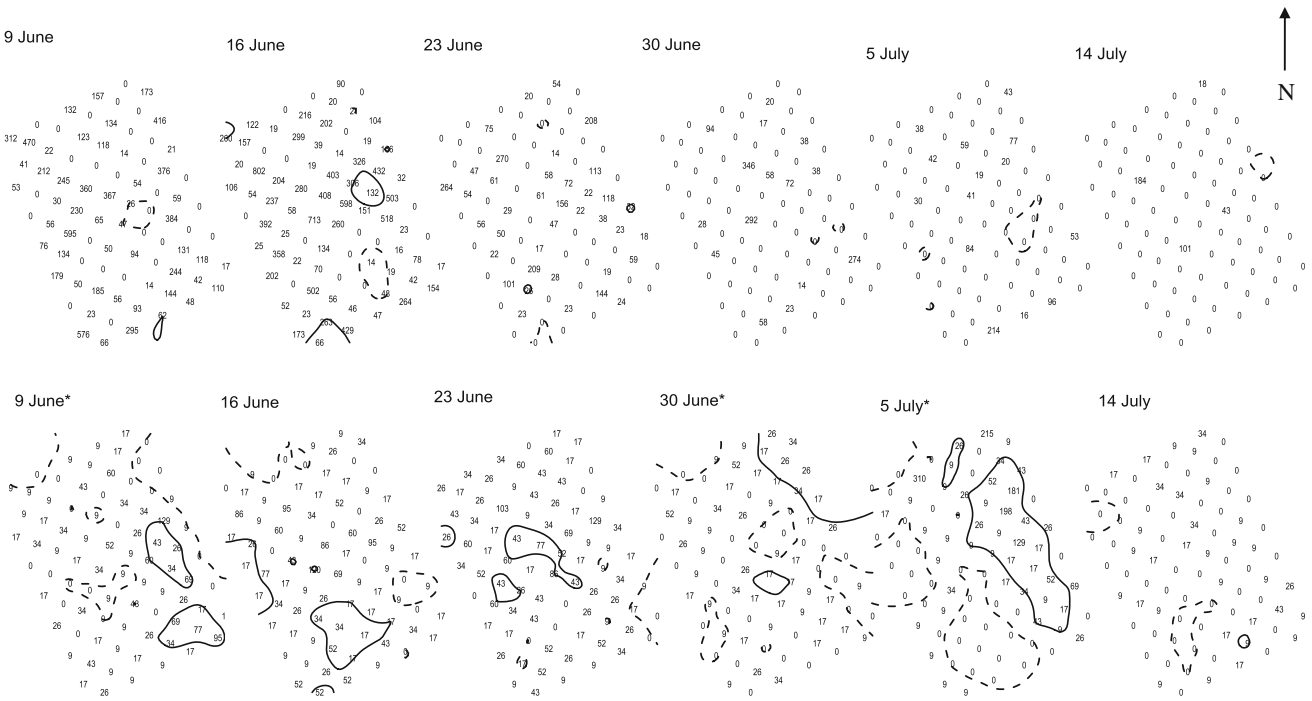

Fig. 6 Spatial pattern on each sampling date of *M. dirhodum* on the crop, number m^{-2} (*upper series*), and the ground, number m^{-2} day^{-1} (*lower series*), for the field Oakmead

three of the five sampling dates (28 June, 5 July and 10 July), whilst none could be detected for *M. dirhodum* (Figs. 3, 4; Table 3). Local association between aphid density and fall-off was detectable for *S. avenae* on the 9 June ($\chi = 0.22$, $P = 0.022$) and 10 July ($\chi = 0.32$, $P < 0.01$) and for *M. dirhodum* on the 10 July ($\chi = 0.29$, $P < 0.01$).

For Oakmead, *S. avenae* and *M. dirhodum* populations peaked on 23 June and 16 June, respectively (Table 2). *S. avenae* slightly exceeded the damage threshold at flowering. Aphid spatial pattern within the fields was generally not evident (Figs. 5, 6; Table 4). *S. avenae* fall-off exhibited spatial pattern towards the end of the season (5 and 14 July; Fig. 5; Table 4), whilst spatial pattern was also evident for *M. dirhodum* on three sampling dates (9 June, 30 June and 5 July; Fig. 6; Table 4). Local association between aphid density and fall-off was not detectable for either species, apart for *M. dirhodum* on the 9 June ($\chi = 0.239$, $P = 0.02$).

There was a significant positive relationship between aphid density on the ears and the rate of fall-off for both *S. avenae* and *M. dirhodum* (Fig. 7). At a density of 50 aphids m^{-2}, 29 and 46 % of individuals fell to the ground day^{-1}, and at a density of 500 m^{-2}, 18 and 9 % of individuals fell to the ground for *S. avenae* and *M. dirhodum*, respectively.

Aphids returning to the crop (Horseparks, 5 July)

For *S. avenae*, there was strong spatial pattern (Fig. 8), with a patch along the western field margin and two gap areas ($v_i = 1.51$, $P < 0.01$, $v_j = -1.559$, $P < 0.01$). Local association between aphid fall-off and return was also evident ($\chi = 0.26$, $P = 0.02$), indicating that aphid return was predominantly occurring where aphid fall-off was high. Very few *M. dirhodum* were caught (20 individuals) on the climbing traps, so no analyses were possible. It was not known whether this was due to *M. dirhodum* being unable to re-climb or whether the traps were ineffective for this species.

Aphid days and crop characteristics

For Horseparks, local dissociation was evident between *S. avenae* aphid days and leaf nitrogen ($\chi = -0.28$, $P > 0.99$). Dissociation was also evident to some extent for ear nitrogen, although the test statistic was marginally nonsignificant ($\chi = -0.21$, $P = 0.953$). Positive local association was evident between *M. dirhodum* and leaf nitrogen ($\chi = 0.31$, $P < 0.01$; $\chi = 0.32$, $P < 0.01$). Hence, there was some indication that for *S. avenae*, patches of high aphid day loading were dissociated with crop nitrogen, whilst the opposite was the case for *M. dirhodum*. No measurable local association between crop yield and aphid days could be detected.

For Oakmead, *S. avenae* and *M. dirhodum* aphid days were not measurably associated or dissociated with ear or leaf nitrogen. *S. avenae* was locally dissociated with yield ($\chi = -0.22$, $P = 0.98$), whilst *M. dirhodum* was locally associated with yield ($\chi = 0.25$, $P = 0.02$).

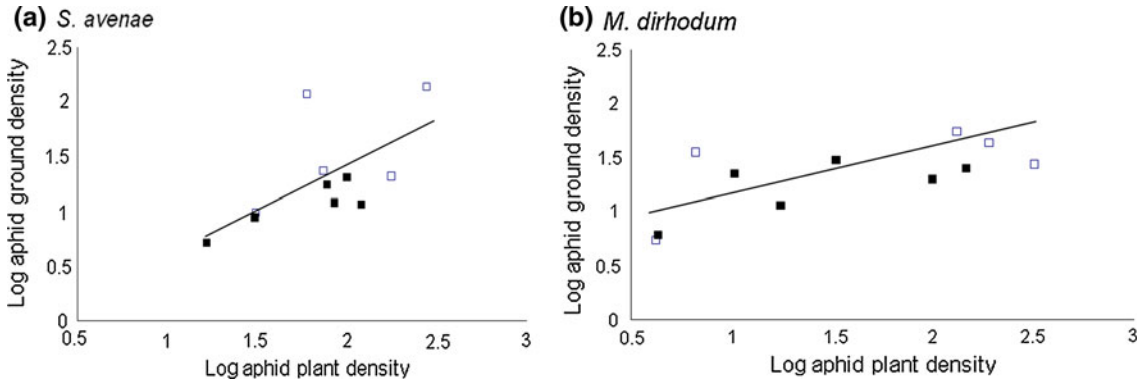

Fig. 7 Relationship between aphid density (D, number m^{-2}) and fall-off (F, number m^{-2} day^{-1}) for **a** *S. avenae* and **b** *M. dirhodum* for the fields Horseparks (*open square*) and Oakmead (*filled square*). Overall regression relationships: *S. avenae*—$\log_{10}F = 0.78\log_{10}D\text{-}0.16$, $r = 0.63$, $P = 0.04$; *M. dirhodum*—$\log_{10}F = 0.3\log_{10}D + 0.84$, $r = 0.67$, $P = 0.02$

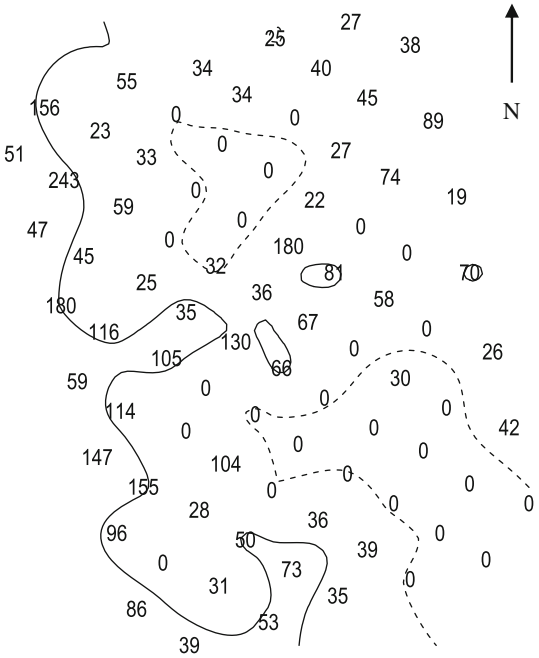

Fig. 8 Spatial pattern of *S. avenae* climb-back (total caught), recorded in an experiment conducted on the 5th July in Horseparks

Discussion

This intensive field study described aphid spatial pattern within two conventionally managed cereal fields. Within both fields, there was measurable pattern with regards to crop density, ear and leaf nitrogen, and soil moisture, yet we were unable to detect any spatial pattern with regard to yield in either field. The application of fertiliser may have overcome any natural variation in soil fertility, whilst variation in soil moisture may not have been sufficient to impact on yield. Aphid populations within the crop canopy at the field scale were largely spatially unstructured within both fields and for both species. However, at the local scale, aphid populations were associated or dissociated with the measured crop parameters, indicating possible linkage.

In Horseparks, *S. avenae* and *M. dirhodum* were locally dissociated and associated with crop nitrogen, and in Oakmead, the species were locally dissociated and associated with yield, respectively. *M. dirhodum* populations resided in the most productive parts of the field (Möwes et al. 1997; Honek 1991) and presumably had little effect on crop quality, whilst the more economically important *S. avenae* probably negatively influenced crop quality at the local scale, evidence by the dissociations we detected. This study was only based on two fields, so conclusions that could be drawn were limited. Further studies using more sophisticated measures of nitrogen, yield and soil moisture would further enhance our understanding of these processes. Although the fields were on the same farm, there were differences evident in aphid population growth, spatial structure and associations with crop parameters. The reason for these differences are unknown, but they probably relate to the initial conditions of the establishing aphid population (i.e. localised immigration of winged immigrants and the resident overwintering population), microclimatic and topographical differences, differences in soil fertility influencing crop growth and differences in the impact of natural enemies (Irwin et al. 2007; Evans 2008).

For *S. avenae*, spatial pattern within the crop was detected only late in the season, whilst we were able to detect emergence of strong spatial pattern for falling *S. avenae* much earlier in the season. We demonstrated limited local association between crop canopy aphid density and fall-off, although our expectation was that they would be closely linked. There are two likely explanations: either fall-off is not as strongly linked to the within-canopy population as we expected and might be influenced by other factors such as microclimate or the presence of

Table 4 Mean cluster index v_i for patches and v_j for gaps, with associated probability, *P*, for the aphids *S. avenae* and *M. dirhodum* found on the crop and on the ground within the field Oakmead

Date	Cluster type	*S. avenae*—crop		*S. avenae*—ground		*M. dirhodum*—crop		*M. dirhodum*—ground	
		Cluster index	*P*	Cluster index	*P*	Cluster index	*P*	Cluster index	*P*
9 June	Patch	0.93	0.57	0.87	0.82	−0.95	0.57	1.32	0.04*
	Gap	−0.95	0.60	−0.88	0.79	0.90	0.67	−1.33	0.04*
16 June	Patch	0.88	0.73	1.04	0.30	1.01	0.34	1.20	0.09
	Gap	−0.90	0.72	−1.06	0.27	−0.97	0.52	−1.22	0.09
23 June	Patch	1.03	0.31	0.83	0.70	0.94	0.59	1.17	0.13
	Gap	−1.03	0.35	−0.90	0.92	−0.94	0.60	−1.17	0.13
30 June	Patch	1.01	0.40	1.10	0.20	0.83	0.92	1.33	0.04*
	Gap	−0.94	0.61	−1.12	0.18	−0.80	0.96	−1.32	0.04*
5 July	Patch	1.04	0.26	1.34	0.04*	0.90	0.70	1.74	<0.01*
	Gap	−1.03	0.35	−1.36	0.03*	−0.90	0.68	−1.83	<0.01*
14 July	Patch	1.39	0.02*	1.37	0.03*	0.84	0.87	1.00	0.41
	Gap	−1.52	<0.01*	−1.66	<0.01*	−0.81	0.90	−1.01	0.38
Aphid days	Patch	1.42	0.01*	–	–	0.96	0.47	–	–
	Gap	−1.51	<0.01*	–	–	−1.00	0.43	–	–

*Denotes where measurable spatial pattern could be detected

natural enemies. Alternatively, the field counts may have failed to characterise the within-canopy population effectively (Trumble et al. 1982) although previous studies using the same sampling intensity were able to detect pattern for *S. avenae* and *M. dirhodum* (Winder et al. 2001, 2005). For *M. dirhodum*, we found little evidence of spatial structure within either field, whilst aphid fall-off did exhibit spatial pattern, detected in both early and late season. We also demonstrated, albeit on only one sampling occasion and for one species (*S. avenae*), that there was correspondence between aphid fall-off and their subsequent return to the crop canopy by climbing. This correspondence was probably due to aphids travelling only short distances before returning to the crop (Alyokhin and Sewell 2003).

Aphid spatial structure may also be created by differential predation levels within the field. Predation must be mediated to some extent by aphid fall-off as this is vital for ground-active predators that rely on this process to access aphid prey. Considerable variation in the activity of ground-active predators occurs during the growing season both within and between fields (Holland et al. 2009). Whether the spatial structure evident for aphid fall-off could mediate an aggregative numerical response for ground-active predators (Monsrud and Toft 1999; Harwood et al. 2001) warrants further study. There is some evidence that predators respond to aggregations of prey: for example, linyphiid spiders have been shown to construct webs where prey were relatively more abundant (Harwood et al. 2003; Harwood et al. 2004; Romero and Harwood 2010), whilst carabid predators such as *Agonum dorsale* Pont. may aggregate into areas of high aphid density (Bryan and Wratten 1984; Winder et al. 2001). It is also known that ground-active predators can reduce return rates of aphids to the crop canopy (Winder 1990; Duffield et al. 1996). Recent evidence indicates that ground-active predators respond relatively slowly to aphid infestations and are less effective at providing control than aerial natural enemies, for example, parasitoids and syrphids (Schmidt et al. 2003; Schmidt et al. 2004; Holland et al. 2008, 2012). However, the contribution of different predatory guilds varied between these studies—being dependent on the local abundance of natural enemies varying across a range of scales from within-field to landscape (Tscharntke et al. 2007; Holland et al. 2009).

Further investigation into these effects would enhance our understanding of processes that regulate the biological control potential of natural enemies found within agro-ecosystems. Although a number of studies have been conducted that describe aphid fall-off, relatively little is known with regard to the mechanisms that cause it or indeed the proportion that are actually dead that might be scavenged rather than predated. It may be useful to focus further studies on the interaction between the aphid sub-population resident on the ground rather than within the crop canopy itself, thereby revealing ground predator/prey interactions more effectively. Availability of aphids to ground-active predators is mediated by the rate at which aphids are dislodged and fall to the ground, and predator–predator interactions that enhance predation rates are known to exist (Losey and Denno 1998; Griffiths et al. 2008). A better understanding of how pest control is delivered by a community of natural enemies would aid the

development of integrated pest management, a practice that will become mandatory for all EU farmers from 2014 (Directive 209/128/EC).

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