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Interplant movement and spatial distribution of alate and apterous morphs of *Nasonovia ribisnigri* (Homoptera: Aphididae) on lettuce

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Abstract

Knowledge on colonization modes and interplant movement of *Nasonovia ribisnigri* can contribute to the development of optimal control of this pest. The aim of this study was to determine the spatio-temporal distribution and the mode of spread between adult morphs of *Nasonovia ribisnigri*, comparing spring and autumn lettuce protected crops. The spatial and temporal pattern was analyzed using the spatial analysis by distance indices (SADIE) methodology and other related displacement indices.

The population size of *N. ribisnigri* was greater in the autumn than in the spring growing seasons due to milder temperatures. The percentage of plants colonized by aphids was higher in spring than in autumn, showing the great dispersal potential of this aphid species independent of their population size. Differential propensity for initial displacement from the central plant was observed between adult morphs in spring, resulting in a greater ability of apterous than alate aphids to spread far away from the source plant. In autumn, both adult morphs showed an initial reduced displacement; however, the number of plants infested ($\approx 20\%$) with at least one aphid at this initial time (seven days) was similar for both adult morphs and both growing seasons. Analysis of the spatial pattern of both adult morphs revealed a predominantly random distribution for both spring and autumn trials. This pattern was achieved by a prevalent random movement over the area ($\gamma \approx 0.5$). These results highlight the ability of the apterous *N. ribisnigri* to spread within greenhouse lettuce crops early in the spring, suggesting that detection of the pest by deep visual inspection is required after lettuce emergence.

Keywords: lettuce aphid, interplant movement, spatial distribution, population ecology, SADIE analysis

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Introduction

Distribution patterns and dispositions of insects in space are of considerable ecological significance. Changes in dispersion patterns should be considered alongside changes in size when interpreting population dynamics (Southwood & Henderson, 2000).

Aphids have developed effective modes of dispersal that allow them to rapidly and efficiently colonize new habitats by active and passive movement (Robert, 1987). Distinct life cycles, life stages, adult morphs and direct/indirect damage must be taken into account when considering aphid movement because these factors determine colonization modes and

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interplant movement (Boiteau, 1997; Irwin *et al*. 2007). Aphid distribution has important economic consequences in agriculture when considered as a vector for plant viruses, as their movement patterns influence the timing and pattern of virus epidemics at field scale (Irwin *et al*. 2007; Moreno *et al*. 2007). Also, distribution patterns of aphids and their natural enemies are mutually conditioned by the simultaneous presence of both phytophagous insects and herbivores, with implications in the efficacy of biological control strategies in agroecosystems (Feng & Nowierski, 1992; Griffiths *et al*. 2008; Scorsetti *et al*. 2010; Lopes *et al*. 2010).

Colonization and distribution patterns of aphids are crucial in annual cropping systems such as lettuce, which is colonized by different aphid species from overwintering habitats early in the growing season. Among lettuce-colonizing aphids, the 'lettuce aphid', *Nasonovia ribisnigri* (Mosley) is a specialist aphid pest that produces significant economic losses for worldwide lettuce production. *N. ribisnigri* arrives early in the lettuce growing season, and the infestation commonly begins with invasion by alate adults migrating from primary or secondary hosts (Blackman & Eastop, 2000; Nebreda *et al*. 2004). *N. ribisnigri* colonizes the innermost leaves of developing lettuce heads, which is a habitat distinct from those of other aphid species that infest lettuce (Mackenzie & Vernon, 1988; Liu, 2004). Temperature and density are the main abiotic factors that influence the proportion of alate to apterous individuals of this aphid species, which affects biological and population parameters and has direct consequences for seasonal movement and dispersal of the population (Liu, 2004; Diaz & Fereres, 2005). Apterous aphids are the predominant morph at temperatures below 16°C, but the proportion of alate individuals rises to 60% at a temperature of 20°C, with a clear impact on the colonization mode over the different lettuce growing seasons (Diaz & Fereres, 2005). In general, the apterous morph colonizes new habitats by interplant walking as its single active mode of displacement, whereas alates displace by walking or flying. However, previous studies have revealed that *N. ribisnigri* alates have limited flight ability and, in consequence, their capture rate on intersection traps is low before they colonize lettuce plants (Liu, 2004; Nebreda *et al*. 2004).

Previous studies of the spatial distribution of this aphid species at field scale demonstrated that plants infested with *N. ribisnigri*, though scattered, were most often located near the margins of the crop (Mackenzie & Vernon, 1988), a spatial pattern differing from that observed for other aphid species colonizing outdoor lettuce crops (Palumbo, 2000). The aim of this study is to determine interplant movement of the different adult morphs of *N. ribisnigri* on lettuce grown in spring and autumn cycles under greenhouse conditions. Considering that *N. ribisnigri* is an aphid species of high economic interest and threatens lettuce production worldwide, our results contribute to the ecological baseline of knowledge to improve the management of this aphid species and for the development of further studies.

Material and methods

Experimental design

Experiments were carried out in a glasshouse located at the Instituto de Ciencias Agrarias (ICA-CSIC) (Madrid, Spain) (Lat. 40°43′97″N, Long. 3°68′69″W, Alt. 710 m). The glasshouse has a north-south orientation, with the door at the south side, measuring 6.14 m long × 6.43 m width and 4.26 m height at the gutters. The lettuce experimental microplots were placed in the glasshouse on tables measuring 5 m long × 0.81 m width and 0.85 m high. Each lettuce plot (1 × 1 m) was covered by an insect cage made of a metallic frame (1 × 1 × 1 m), with the walls and roof covered by a polyester anti-insect screen with a hole size of 100 µm (SefarMaissa S.A., Barcelona, Spain). The cage rested on a 1 × 1 m metallic tray, 5 cm high. The cage could be lifted from the floor, but the two parts provided a hermetic insect-proof cage when placed together and served to isolate aphids within the plot.

Lettuce experimental plots

Seeds of Romaine lettuce were sown in plastic pots (10 cm diameter) containing a mixture of soil and vermiculite (50:50). Two different lettuce cultivars were used for the experiments, 'Cazorla' for autumn and 'Aitana' for the spring growing season. Phenology data for the crop was recorded weekly according to the Biologische Bundesanstalt, Bundessortenamt and Chemical industry, hereafter referred to as BBCH-scale (Feller *et al*. 1995). The seedbeds were maintained in a growth chamber at a temperature of 26:20 (day:night) and a photoperiod of 14:10 h (L:D) until they were transplanted to greenhouse conditions when they reached stage 12 (BBCH-scale). Plastic multi-pots were placed on the tray covering all surfaces of the cage (1 m^2), which constituted the experimental plots comprising 13 columns and 13 rows. Lettuce seedlings were transplanted into the experimental plots described above following a herringbone/zigzag pattern. Plants were spaced 15 cm between columns and 10 cm within rows (fig. 1). Three times per week, lettuce seedlings were irrigated with nutritive solution 20:20:20 (N:P:K; Nutrichem 60, Miller Chemical and Fertilizer, Hanover, PA, USA).

Aphid colony

Nasonovia ribisnigri adults were obtained from a laboratory culture initiated from the progeny of one virginoparous apterous female collected in a lettuce field at Villa del Prado (Madrid, Spain) in 1999 and maintained on lettuce cultivar 'Cazorla' inside insect-proof cages in a growth chamber at a temperature of 23:18°C (day:night) and a photoperiod of 16:8 (L:D). Aphids of equal age and weight were selected for release onto lettuce plants. For this purpose, ten alate adult aphids from the colony were placed for 24 h in a plastic cage (9 cm diameter and 3 cm high) containing two filter paper disks and a lettuce leaf. After 24 h, adults were removed, and newly born nymphs were collected and reared on lettuce leaves in the plastic cages described above until they reached adulthood. Lettuce leaves were replaced every 2–3 days during this period. Aphids were removed just after they reached the adult stage and were transferred to the experimental plots.

Insect release and sampling methods

Two experiments were carried out in each growing season, autumn and spring. In each growing season, the population of *N. ribisnigri* was initiated with the release of either five apterous or five winged adults. In both experiments, aphids were released with the help of a camel's hair brush on the central plant (coordinates, x = 48 cm, y = 48 cm) (fig. 1) of the experimental plot. Each experiment was started with

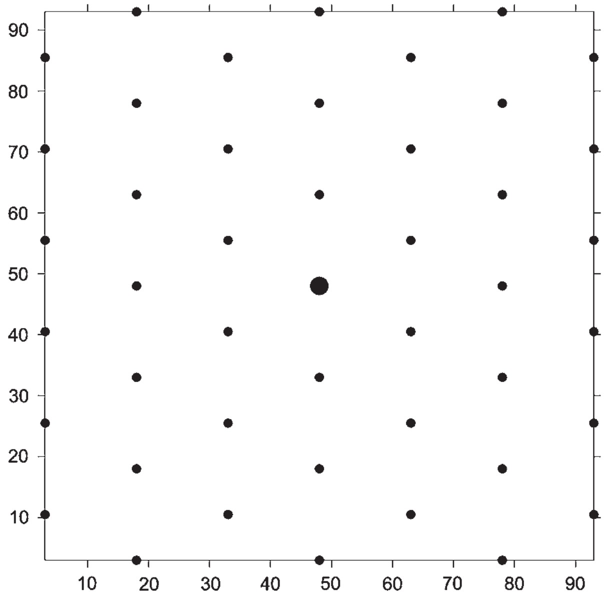

Fig. 1. Design of the experimental lettuce plot. Small bold circles (●) indicate the position of each lettuce plant within the plot (sampling units) and the large central bold circle (●) represents the position of the plant where aphids were released (x = 48, y = 48). Axes show distances in cm.

12 lettuce experimental plots, which were randomly distributed on three tables inside the glasshouse. Sampling was done at seven, ten, 14 and 21 days after aphid release. Three replicates (cages) were made for each sampling date. The number and morph of aphids present on each of the plants (45) within the experimental plot were determined by removing plants and counting the number of aphids per plant in the laboratory (destructive sampling). Lettuce plants were cut off at ground level with scissors and were placed in plastic bags labelled with the exact position of the plant within the plot (x and y coordinates in cm). Sampling was done at seven, ten, 14 and 21 days after aphid release. Lettuce plots were replicated three times for each sampling date. Aphid population density on each plant and the percentage of lettuce plants infested by more than one aphid at each sampling date (N) were recorded. Temperature inside the glasshouse where the experiment was conducted was recorded daily.

Statistical analysis

Spatial patterns of *N. ribisnigri* within lettuce plots were described by the aggregation (Ia) and clustering indices (vi and vj) provided by the SADIE (spatial analysis by distance indices) method (Perry, 1995, 1998). This method can identify areas in which observed counts are arranged at random or form clusters of units in two forms: patches when there is a high density of counts near each other or gaps composed of areas with relatively few or zero counts in nearby sampling points (Perry *et al.* 1999). Units with counts greater than the overall mean are assigned a patch cluster index (vi), which by convention is positive; meanwhile, units with counts less than the mean are assigned a negative gap cluster index (vj). Also, centroids (C) (the average position of adult aphids in the experimental plot) were used to calculate δ. The statistic, δ, provided by SADIE, was defined as the displacement of the entire aphid population and was calculated as the distance between the centroid (C) of aphid positions and the place where aphids were initially released, which was the lettuce plant located in the middle of the plot (x = 48, y = 48). Other statistics suggested by Korie *et al.* (1998) were summarized to describe aphid movement as follows: Φ, the average of the squared distances of the position of each aphid to the centroid; Δ, average distance of aphid positions from the central release focus; and γ, relative degree of movement between and within rows of the lettuce plants. When aphid movements were entirely along a row, the value of γ would be 1; if their movements were entirely perpendicular to the rows, then γ would be 0; and, if there were completely random movement, then the γ value would be 0.5. All statistics were subjected to a two-way analysis of variance (ANOVA), using the general linear model (GLM) procedure of the SPSS statistical package (SPSS, 2003).

Results

Population growth of Nasonovia ribisnigri *apterous and alate morphs*

The population growth rate of *N. ribisnigri* was higher in autumn than in spring, independent of the adult morph released at the beginning of the experiment (fig. 2); however, significant differences were detected only for alates individuals at the first sampling date (seven days after aphid release) (F = 30.25; df = 1; $P = 0.005$). When alate morphs were released in the experimental plot, the population reached a mean maximum of 293 individuals per plot 21 days later in autumn (lettuce stage, 16) and 250 individuals per plot in spring (lettuce stage, 17). However, when the population was started with the release of apterous instead of alate aphids, much larger differences were observed in the total population growth between the autumn (770 aphids per plot) and the spring (618 aphids per plot) growth cycle 21 days after aphid release (fig. 2c, d).

When we considered whole population growth, we observed a similar initial dispersion of aphids (seven days) for both adult morphs and both lettuce growing seasons, reaching 20% of infested lettuce plants (fig. 2). However, from ten to 21 days after aphid release, dispersion of aphids within the plot was higher in spring (reaching 95–100% of plants infested) than in autumn (72–88% of plants infested). Nevertheless, fewer lettuce plants were colonized by aphids when the population started with the release of alates (fig. 2a, b) than with apterous individuals (fig. 2c, d). This trend was observed in both spring and autumn lettuce growing seasons.

The mean maximum and minimum temperatures registered in the glasshouse during the experiments performed in spring were 25 ± 0.4°C and 19.5 ± 0.32°C, whereas in autumn the mean maximum and minimum temperatures were 20 ± 0.5°C and 14.3 ± 0.6°C, respectively.

Movement and spatial distribution of N. ribisnigri *alates in spring and autumn*

Some aphids were not recovered when sampling the experimental plots seven days after the initial release. Only 73.3% and 88.6% were recovered in the spring and autumn trials, respectively. In both growing seasons, 13.4% and 12.1%

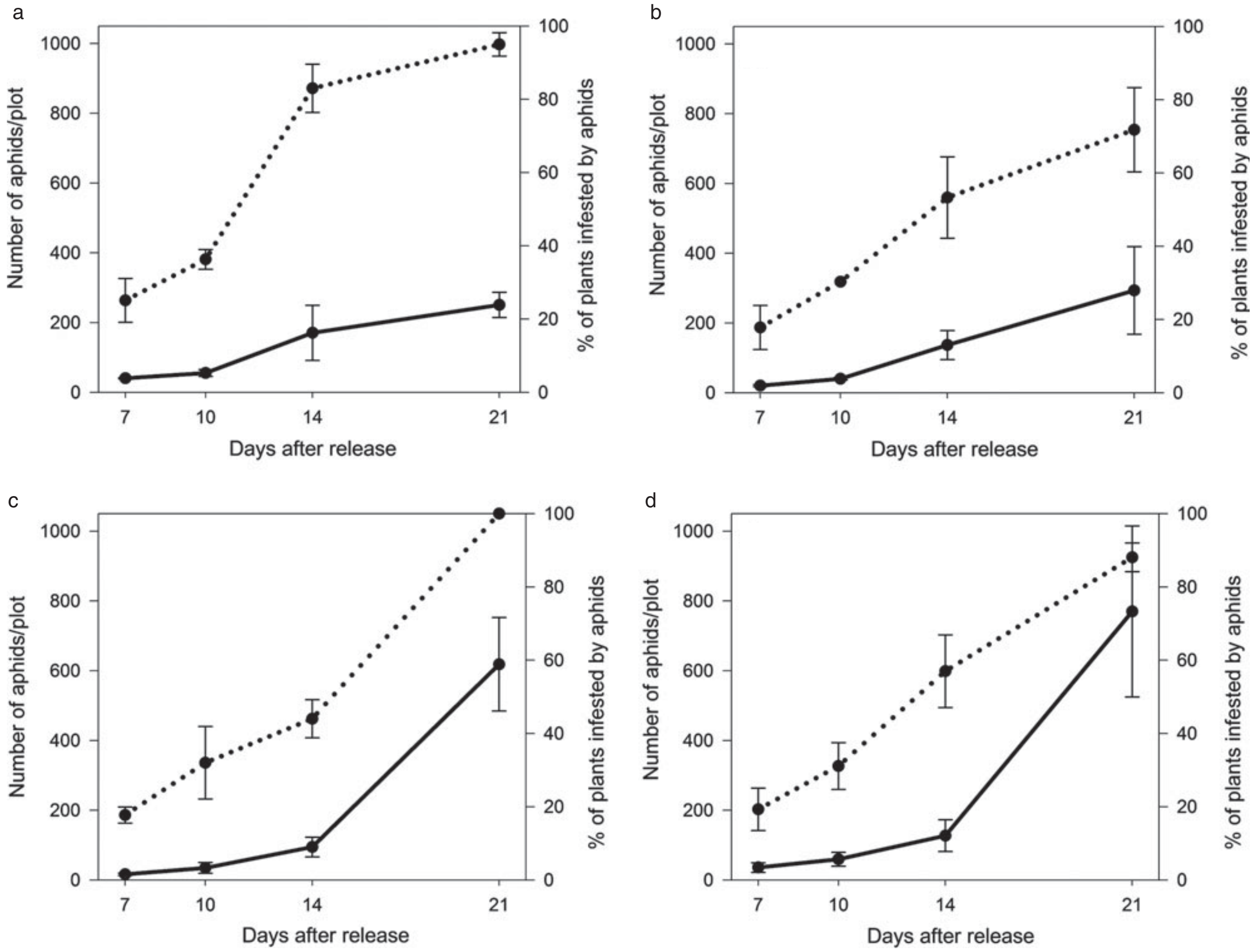

Fig. 2. Aphid density per plot and percentage of lettuce plants infested by *Nasonovia ribisnigri* when population started with (a, b) five alates or (c, d) five apterous aphids released on the central lettuce plant of each plot (x = 48, y = 48) in the (a, c) spring and (b, d) autumn; —●—, Total population; ••●••, % of plants occupied.

of the initial individuals remained on the source plant (x = 48 cm, y = 48 cm) or on nearby lettuce plants. The position of alate aphids within the plot exhibited an initial reduced displacement both in spring and autumn lettuce growing seasons, as revealed by the position of the centroid (C) in each replicate (fig. 3a, b).

In spring, the lowest values for the mean displacement distance (δ = 15.2 ± 4.9 cm) and the mean distance moved (Δ = 26.1 cm) were detected seven days after aphids release, when the population of *N. ribisnigri* was composed of only the initial alates and their offspring (table 1). However, the maximum δ (29.5 ± 8.0 cm) and Δ (41.9 cm) values were reached ten days after the beginning of the experiment, when the first generation of *N. ribisnigri* was completed (table 1). In autumn, the maximum value of δ (25.6 ± 7.2 cm) was also detected at ten days after aphid infestation, though the maximum Δ (40.5 cm) was recorded 21 days after aphid release.

The mean spread (ln Ø) of aphid populations was similar within and between spring and autumn growing seasons (table 1). In autumn, the mean relative between- to within-row movement (γ) indicates that alates showed completely random movement with respect to rows (γ = 0.5). However, in spring, the movement occurred along the central row as well (γ = 0.6) at the first (seven days) and the last (21 days) sampling dates (table 1). According to the SADIE indices, the distribution of alate aphids on lettuce plants appeared to be regular seven days after release as shown by the mean value of $Ia \leq 1$. However, a moderate aggregation was observed between ten and 21 days after aphid release. According to the *Ia* index values, clustering indices (*vi* and *vj*) were not significant over the sampling period ($vi < 1.5$ and $vj > -1.5$) (table 1).

Movement and spatial distribution of N. ribisnigri *apterae in spring and autumn*

When populations of *N. ribisnigri* were started with the release of five apterous aphids, the percentage of individuals recovered seven days after release ranged from 73.3% to 100% in spring and autumn, respectively.

No apterous individuals were found in spring on the initial central source plant; however, in the autumn trial, 20% of the apterous remained on the central source plant after one week of observation. Differences in displacement were observed for

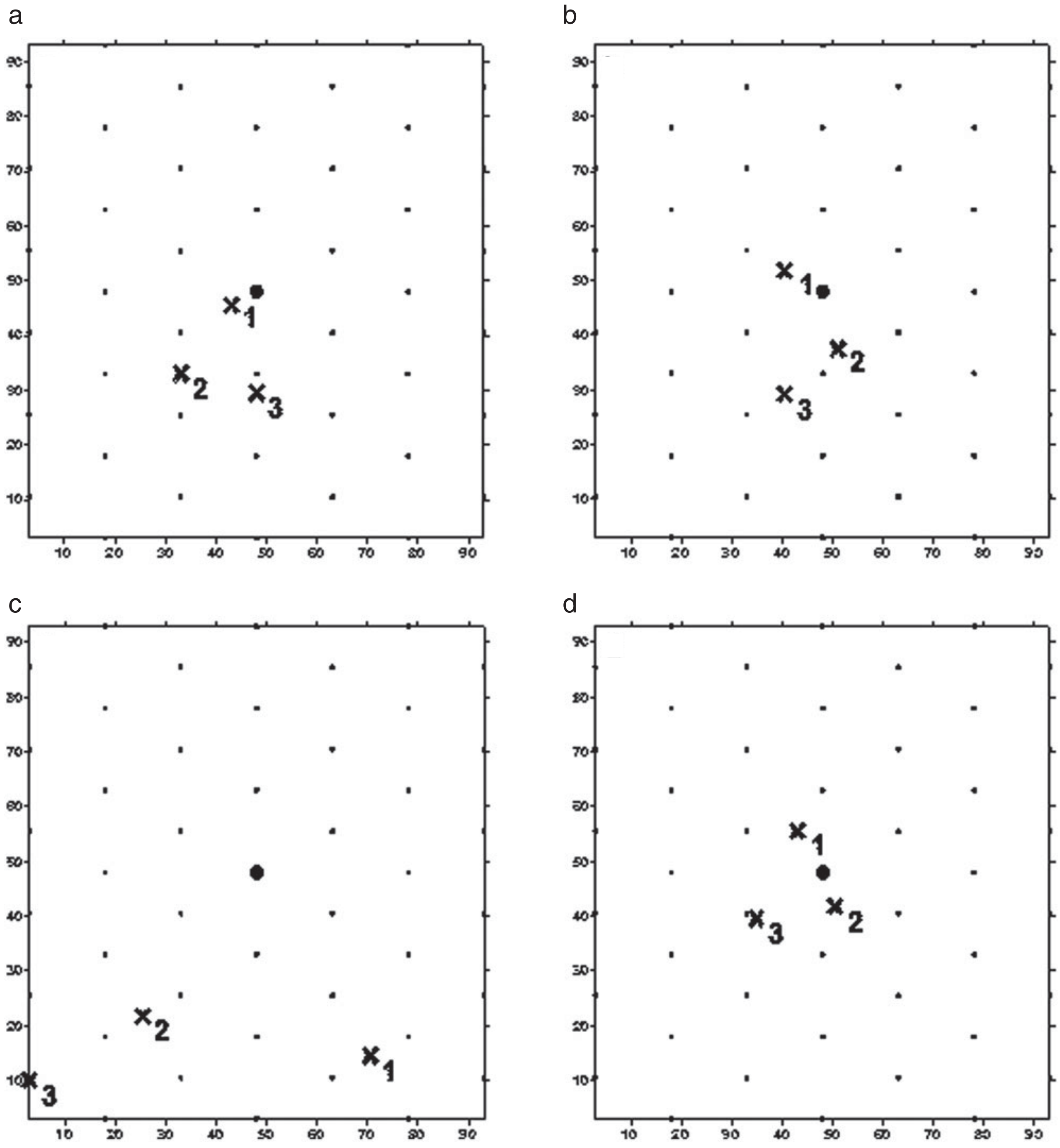

Fig. 3. Position of the centroids (C) seven days after the release of (a, b) five alates or (c, d) five apterous *Nasonovia ribisnigri* on the central lettuce plant of each plot (x = 48, y = 48) in (a, c) spring and (b, d) autumn trials, respectively. X_1, X_2, X_3 indicates the position of C in each replicate. Axes show distances in cm.

N. ribisnigri apterous adults between spring and autumn lettuce growing seasons (table 2) by the centroid position (*C*) at the first sampling date (seven days) (fig. 3). The position of *C* for apterous aphids was located further away from the central release plant in spring compared to the position of *C* in the autumn trial (fig. 3c, d). As a consequence, the values of δ and Δ were higher in spring (δ = 41.2 ± 4.0 cm; Δ = 47.7 cm) than in the autumn trials (δ = 10.5 ± 2.6 cm; Δ = 25.7 cm) at the first sampling date (seven days) (table 2).

As observed for the alate morph, the mean spread (ln Ø) for apterous individuals was similar within and between lettuce growing seasons, and the γ values ranged in spring from 0.3 to 0.7

Table 1. Summary data of movement indices of *Nasonovia ribisnigri* alate adult morph during spring and autumn trials.

Variable	Spring				Autumn			
	Days after aphid release				Days after aphid release			
	7	10	14	21	7	10	14	21
δ^a	15.2 ± 4.9	29.5 ± 8.0	22.7 ± 5.5	22.3 ± 6.8	13.2 ± 3.6	25.6 ± 7.2	13.3 ± 4.0	18.8 ± 5.2
Δ^b	26.1	41.9	34.8	39.5	35.3	31.6	33.0	40.5
$\ln(\Phi)^c$	5.8	7.1	6.4	7.2	7.2	6.8	7.0	7.0
γ^d	0.6	0.5	0.5	0.6	0.5	0.5	0.5	0.4
Ia^e	0.843 ± 0.100	1.116 ± 0.124	1.322 ± 0.121	1.158 ± 0.120	0.973 ± 0.037	1.240 ± 0.149	0.965 ± 0.131	1.189 ± 0.249
$\overline{vi}^f$	1.000 ± 0.079	1.043 ± 0.898	1.317 ± 0.138	1.130 ± 0.077	0.960 ± 0.052	1.195 ± 0.125	0.967 ± 0.078	1.242 ± 0.173
$\overline{vj}^g$	−0.879 ± 0.046	−1.122 ± 0.123	−1.315 ± 0.120	−1.160 ± 0.124	−0.970 ± 0.033	−1.234 ± 0.151	−0.958 ± 0.136	−1.185 ± 0.2555

[a] mean displacement of alate aphids ± SE, in cm; [b] mean distance moved, in cm; [c] mean aphid spread, in cm²; [d] mean relative movement between- to within-row movement;
[e] mean aggregation index calculated by SADIE method ± SE; [f, g] $\overline{vi}$ and $\overline{vj}$ are mean cluster indices calculated by SADIE methodology and refers to patch and gaps, respectively ± SE.

at 14 days, indicating that movement occurred mainly along the central row. However, in autumn, the γ values were approximately 0.5, which indicates that the movement of apterous appeared to be almost at random (table 2).

Aggregation and clustering indices indicate a random distribution within the plot for the spring trial; however, in autumn, aggregation was only observed at the last sampling date (21 days). Seven days after aphid release, there were interactions between adult morph and lettuce growing season for the mean displacement of aphids (δ) (F = 13.8, df = 1, *P* = 0.006) and for the aggregation index (*Ia*) (table 3). The same trend was observed for the gap clustering index ($\overline{vj}$) (F = 11.6, df = 1, *P* = 0.009) (table 3). However, no effects were detected between adult morph and lettuce growing season for the mean distance moved by adults (Δ) (*F* = 5.4, df = 1, *P* = 0.049) or for the patch clustering index ($\overline{vi}$) (F = 11.6, df = 1, *P* = 0.009) (table 3).

Discussion

Integrated pest management (IPM) decisions are based on routine monitoring of pest populations, for which knowledge of their distribution over the crop growing season is essential. This distribution is related to factors other than population size (Southwood & Henderson, 2000). The results of this study under glasshouse conditions showed that population growth of *N. ribisnigri* for both alate and apterous morphs seems to be higher in autumn than in spring; however, no significant differences were detected, with the expection of alates individuals in the spring trial at the first sampling date.

Density of aphids per plant followed a similar trend, because fewer plants were infested with aphids in autumn than in spring ten to 21 days after the initial artificial infestation. This pattern of colonization was independent of population size and increased the risk of crop losses in spring due to potential cosmetic damage and consequent rejection by markets. These results obtained in glasshouses are opposite from those obtained by Nebreda *et al.* (2004) in outdoor lettuce crops in central Spain, where they found a larger population density of *N. ribisnigri* per plant in spring than in autumn crops. Differences in population growth found between outdoor and protected lettuce may be related to temperature fluctuations because *N. ribisnigri* showed a strong preference to develop and reproduce in temperatures close or below the optimal developmental values needed for lettuce growth (Diaz & Fereres, 2005). Therefore, *N. ribisnigri* was probably very sensitive to the high maximum temperatures that were reached in spring under glasshouse experimental conditions. Also, fluctuations in the activity and population density of natural enemies between the autumn and spring could explain why the population density of *N. ribisnigri* was larger in spring than in autumn in outdoor crops grown in central Spain.

When populations began with alates, a lower population growth rate was observed in both lettuce growing seasons, which could be due to the longer developmental time and lower fecundity usually attributed to alates, when compared to apterous aphids (Dixon, 1987).

In our experiments, we used alates to represent a fast early primary infestation by *N. ribisnigri.* At the initial phase of colonization (seven days), we concluded that immigrant alates landing on protected lettuce had an initial limited displacement rate from the source plant, the fact that they were able to colonize a high number of neighbouring plants (20%)

Table 2. Summary data of movement indices of *Nasonovia ribisnigri* apterae adult morph during spring and autumn trials.

Variable	Spring				Autumn			
	Days after aphid release				Days after aphid release			
	7	10	14	21	7	10	14	21
δ^a	41.2 ± 4.0	22.1 ± 9.1	18.0 ± 4.1	12.5 ± 1.9	10.5 ± 2.6	17.7 ± 8.3	36.4 ± 11.3	14.4 ± 5.1
Δ^b	47.7	35.0	39.2	42.9	25.7	24.9	44.6	39.2
$\ln(\Phi)^c$	6.0	6.5	7.2	7.6	6.9	6.2	6.4	7.4
γ^d	0.5	0.3	0.7	0.5	0.5	0.4	0.4	0.5
Ia^e	1.168 ± 0.055	0.993 ± 0.532	1.170 ± 0.145	1.157 ± 0.616	0.927 ± 0.058	0.927 ± 0.572	1.094 ± 0.114	1.441 ± 0.294
$\overline{vi}^f$	1.039 ± 0.020	1.015 ± 0.059	1.187 ± 0.127	1.054 ± 0.094	0.968 ± 0.072	0.977 ± 0.024	1.064 ± 0.061	1.293 ± 0.238
$\overline{vj}^g$	− 1.175 ± 0.057	− 0.990 ± 0.051	− 1.172 ± 0.150	− 1.144 ± 0.608	− 0.920 ± 0.060	− 0.915 ± 0.068	− 1.099 ± 0.122	− 1.406 ± 0.260

[a] mean displacement of apterae aphids ± SE, in cm; [b]mean distance moved, in cm; [c]mean aphid spread, in cm^2; [d]mean relative movement between- to within-row movement; [e]mean aggregation index calculated by SADIE method ± SE; [f, g]$\overline{vi}$ and $\overline{vj}$ are mean cluster indices calculated by SADIE methodology and refers to patch and gap, respectively ± SE.

Table 3. Results of the two-way ANOVA for the effect of the adult morph and lettuce growing season on the movement and distribution of *N. ribisnigri* seven days after aphid release.

Source of variation	MS	F	df	*P*
Mean displacement (δ)				
Corrected model	612.1	13.6	3	0.002
Adult morph	408.4	9.0	1	0.017
Lettuce growing season	807.1	17.9	1	0.003
Adult morph × lettuce growing season	620.8	13.8	1	0.006
Error	44.9		8	
Mean distance moved (Δ)				
Corrected model	284.9	2.7	3	0.110
Adult morph	189.1	1.8	1	0.211
Lettuce growing season	112.2	1.1	1	0.326
Adult morph × lettuce growing season	553.4	5.4	1	0.049
Error	102.4		8	
Aggregation index (*Ia*)				
Corrected model	0.057	10.1	3	0.004
Adult morph	0.058	10.4	1	0.012
Lettuce growing season	0.009	1.6	1	0.238
Adult morph × lettuce growing season	0.103	18.4	1	0.003
Error	0.006		8	
Patch clustering index ($\overline{vi}$)				
Corrected model	0.004	0.354	3	0.788
Adult morph	0.001	0.136	1	0.722
Lettuce growing season	0.010	0.866	1	0.379
Adult morph × lettuce growing season	0.001	0.059	1	0.815
Error	0.011		8	
Gap clustering index ($\overline{vj}$)				
Corrected model	0.052	6.7	3	0.014
Adult morph	0.045	5.8	1	0.042
Lettuce growing season	0.020	2.6	1	0.145
Adult morph × lettuce growing season	0.090	11.6	1	0.009
Error	0.008		8	

compared with the whole population notwithstanding. This pattern of settling and dispersal is in agreement with that described by Irwin *et al.* (2007) for a colonizing non-aphid vector species, which consists of forming a small colony after alighting on plants and then flying to neighbouring plants around the initial source, dispersing their offspring more widely and probing more host plants. Also, our finding agrees with observations made by Liu (2004), who detected limited flight ability for *N. ribisnigri* alates.

In our study, the initial spatial pattern of dispersal changed over time when the first generation of immigrant alates was completed and followed by one to several generations of highly fecund but apterous individuals, which have long been considered to be sedentary. However, a striking result concerning displacement obtained in our study was the greater ability of apterous aphids to spread far away from the source plant compared to alates during the first seven days after aphid infestation. The differential propensity for movement between adult morphs in spring was not observed in autumn, when aphids tend to disperse less, reducing the risk to plants of becoming infested by aphids at harvest time. The ability of apterous aphids to colonize new habitats is common among different aphid species and may be a strategy for this pest to ensure full utilization of their immediate environment (Hodgson, 1991). Our results also indicate the capacity of the *N. ribisnigri* apterous morph to colonize new plants by walking on bare soil, because during these experiments lettuce plants were not able to form leaf bridges. A previous report showed a similar behaviour for *Macrosiphum euphorbiae* (Thomas), *Myzus persicae* (Sulzer) and *Aphis nasturtii* Kaltenbach, all of which were able to colonize potato plants far away from the release point by walking on the soil and to survive in such conditions for more than one day (Alyokhin & Sewell, 2003). On the other hand, we must consider that the number of plants used in our small-scale study (45 plants m^{-2}) was very high compared with those used at field scale (3–4 plants m^{-2}), which reduced the risk of failing to find a new lettuce plant, as would occur under field conditions. However, the high density of lettuce m^{-2} used in this study should be compared to those used in beds for lettuce seedling production, on which early detection and control of aphids is crucial.

For both adult morphs and growing seasons, aggregation indices revealed a predominantly random distribution of adults within the plot, with an incipient spatial structure ($Ia > 1$) revealed by patches ($\overline{vi}$) that did not increase with time. This behaviour constitutes an essential strategy for *N. ribisnigri* adults to reduce interspecific competition and optimize resource availability and quality to maintain fitness. Lombaert *et al*. (2006) concluded that the effect of dispersal parameters on aphid fitness depends strongly on plant characteristics and aphid-plant specialization, as occurs with *N. ribisnigri*, which has a close relationship with lettuce and occupies a restricted niche within the lettuce plant.

The random spatial pattern obtained in our study was reached by a prevalence random movement over the experimental area ($\gamma \approx 0.5$), which indicates that secondary infestation of *N. ribisnigri* within a greenhouse may occur both between plants within the same row and between different rows. The same trend was observed in outdoor lettuce, where no significant differences were found in the number of aphids or infested plants between outer lettuce columns and rows (Mackenzie & Vernon, 1988). However, an opposite behaviour has been observed for potato-colonizing aphids, which were not able to move between the rows of young potato plants (Alyokhin & Sewell, 2003).

Considering the whole population in a field and using Taylor's Power Law as an index of aggregation, *N. ribisnigri* showed an intermediate level of aggregation, while *Macrosiphum euphorbiae* and *Myzus persicae* displayed a much less aggregated spatial pattern on an outdoor lettuce crop (Palumbo, 2000). Also, the spatial heterogeneity at the local scale revealed in our study should be taken into account when implementing an augmentation biological control strategy to control *N. ribisnigri* on lettuce, because the release sites of the biological control agents need to be consistent with the distribution of the pest. Smyrnioudis *et al*. (2001) observed that the search pattern of the parasitoid *Aphidius ropalosiphi* to locate *Rhopalosiphum padi* individuals appeared to be random. However, information on the spatial pattern of parasitoids or predators controlling *N. ribisnigri* under greenhouse lettuce crops is lacking.

Previous studies on the spatial distribution of indigenous natural enemies such as the entomopathogenic fungi *P. neoaphidis* showed no significant differences in the density of *N. ribisnigri* infected by the fungus between the edge and the centre of lettuce greenhouses (Scorsetti *et al*. 2010).

Our study may contribute to the management of *N. ribisnigri* in commercial lettuce bed production and to optimize early detection to reduce aphid outbreaks under high plant density conditions. However, further experiments are necessary to determine distribution of this aphid species under greenhouse or open field lettuce production to develop an effective monitoring program.

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