

Interplant Movement of Potato Aphid (Homoptera: Aphididae) in Response to Environmental Stimuli

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ABSTRACT Potato aphid, *Macrosiphum euphorbiae* (Thomas), is a highly mobile aphid species that dominates aphid communities in Maine potato fields and may contribute to virus transmission between potato plants. We studied effects of simulated rain, wind, mechanical raking, fungicide application, reflective mulch, and predator [lady beetle, *Harmonia axyridis* (Pallast)] on the interplant movement of wingless adult potato aphids in greenhouse experimental arenas that imitated small segments of a potato field. The number of aphids dispersing from the central plant in the arena after a tested perturbation was recorded. Experiments were repeated with 3- to 4-wk-old plants with nonoverlapping canopies and with 4- to 5-wk old plants with canopies overlapping within rows. Aphids moved between potato plants even when canopies did not overlap and without any environmental perturbations. However, more aphids moved between larger plants with overlapping canopies. Rain significantly encouraged aphid movement between plants with nonoverlapping canopies. Wind, rain, and mechanical raking significantly encouraged aphid movement between plants with overlapping canopies. Regardless of canopy overlap, most aphids moved within the rows of potato plants. However, there was also considerable movement between the rows, even though the aphids had to walk over bare soil.

KEY WORDS *Macrosiphum euphorbiae*, canopy, environmental stimuli, dispersal

Aphids (Homoptera: Aphididae) constitute an important group of phytophagous insects that cause significant damage to potato crops all over the world. While direct feeding damage is usually insignificant from an economic standpoint, the transmission of potato viruses can cause substantial crop losses (Radcliffe et al. 1993). Potato aphid, *Macrosiphum euphorbiae* (Thomas), green peach aphid, *Myzus persicae* (Sulzer), and buckthorn aphid, *Aphis nasturtii* Kalt-enbach, are the three aphid species that commonly colonize potato (*Solanum tuberosum* L.) plants in northeastern United States and Canada (Radcliffe et al. 1993), with potato aphid being the dominant species in Maine (A.V.A., unpublished data). Although not a very efficient virus vector compared with the green peach aphid, it is still capable of transmitting Potato virus Y and, to a lesser degree, Potato leafroll virus (Radcliffe et al. 1993).

Short distance movement of colonizing viruliferous aphids may be responsible both for enlarging existing disease foci, as well as for creating new foci within the same field (Irwin and Thresh 1990). Because of their high mobility, winged aphids are generally considered to be more important in spreading viruses between plants than wingless aphids (Broadbent and Tinsley 1951, Wright et al. 1970, Boiteau and Parry 1985).

However, there is evidence that dispersal of wingless aphids can also result in infection of a substantial number of plants (Ribbands 1963, Hanafi et al. 1989, Flanders et al. 1991, Hodgson 1991). Boiteau (1997) and Alyokhin and Sewell (2003) showed that wingless potato aphid was the most mobile of the three potato-colonizing species. When forcibly removed from the host plant and released on the soil surface, a significant proportion of potato aphids was capable of colonizing potato plants located as far as 180 cm away from the release point (Alyokhin and Sewell 2003). Adult aphids were significantly more mobile compared with nymphs (Boiteau 1997).

Despite the intrinsic ability to move between potato plants over bare ground, aphids tested by Alyokhin and Sewell (2003) did not voluntarily leave potato plants. However, plants in that study were isolated by areas of bare ground, and their canopies did not touch each other. We hypothesized that interplant movement may be more significant when canopies of adjacent plants overlap, so that aphids can walk between plants without going to the soil surface. Also, a number of environmental perturbations, absent in the study by Alyokhin and Sewell (2003), may promote aphid movement. In a study conducted by Bailey et al. (1995), a central square region of an experimental arena was planted with oats infected with barley yellow dwarf virus and colonized with wingless bird cher-

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ry-oat aphids, *Rhopalosiphum padi* L. When that infection focus was subjected to external environmental stimuli such as rain, wind, pesticide applications, and natural enemies, the degree, rate, intensity, and timing of wingless aphid dispersal were influenced by the perturbations. This, in turn, influenced disease spread intensity and crop losses (Bailey et al. 1995). Similarly, rain and wind were of considerable importance in promoting dispersal of the English grain aphid, *Sitobion avenae* (F.) (Mann et al. 1995).

If the aphids feed on the same plant for their whole life, even moderately high populations will not result in significant virus and disease spread. However, even a small population of extremely mobile aphids can infect a large number of potato plants. Obtaining more information on within-field aphid dispersal will allow fine-tuning control techniques, so that they are directed more toward disrupting aphid movement, not just toward reducing aphid numbers. For example, proper timing of insecticide applications may eliminate colonizing aphids that are about to engage in interplant movement (rather than all aphids), significantly reducing the amount of chemicals necessary for successful crop protection. Also, determination of environmental factors that are responsible for aphid dispersal may help in better forecasting the spread of plant viral diseases and provide clues for more efficient management practices. The objective of this study was to investigate the parameters that could potentially cause significant interplant movement of wingless potato aphids in a potato crop.

Materials and Methods

Insects and Foliage

Potato aphids were obtained from the laboratory colonies that were reared in an environmental chamber (model I-33VL; Percival Scientific, Boone, IA) at 20°C and 18 L:6 D photoperiod. The colonies were established by collecting aphids from potato fields on Aroostook Research Farm in the summer of 2004 and 2005. Two collections were made to minimize possible genetic drift related to prolonged rearing in captivity. Aphids were reared on potato plants (cultivar Kennebec) grown in 8-in diameter pots with Fafard (Fafard, Agawam, MA) planting mixture. Test plants (cultivar Kennebec) were grown in 6-in pots with Fafard planting mixture and were maintained in the University of Maine greenhouse at 20–25°C and natural daylength. Only wingless adult aphids were used for the study.

Experimental Arena

The experimental arena consisted of a rectangular wooden framed box (245 by 110 by 76 cm) with a styrofoam platform attached at 10 cm height from its base (Alyokhin and Sewell 2003). The styrofoam platform had nine holes (10 cm diameter) that accommodated potted 'Kennebec' potato plants. A single potted plant was sunk to the brim of each hole. The top

surface of the platform and pots were covered with a 2- to 3-cm layer of loamy soil collected from a potato field at the Aroostook Research Farm (Presque Isle, ME), creating a continuous soil surface for aphid movement. During each trial, soil was moistened after changing the plants in the cage. All nine plants were arranged in three rows of three plants each. Plants within the rows were spaced 20 cm apart, and the distance between the rows was 90 cm (this arrangement reflected approximate plant and row spacing in commercial potato fields in Maine). The arena was enclosed in a cage with saran screen sides and transparent plastic roof. The arenas were maintained in the greenhouse at 18 L:6 D photoperiod and 20–25°C.

Experiment 1

In this experiment, we attempted to quantify interplant movement of wingless potato aphids on 3- to 4-wk-old potato plants with nonoverlapping canopies in response to a number of abiotic stimuli. Thirty wingless potato aphids were released on the central plant in the experimental arena. The central plant was covered with a smaller metal frame saran screen cage (40 cm diameter, 52 cm high), allowing the aphids to settle. After 24 h, the cage was removed, and the experimental arena was exposed to one of the following perturbations.

Mechanical Raking. The primary objective of selecting this perturbation was to simulate the routine mechanical disturbances caused during various field management operations by the tractor or by farm personnel walking across the field. Mechanical disturbance was created by raking the plants with a four-pronged hand cultivator (prongs 6 cm in length and 1.5 cm apart) in a zigzag manner immediately after the aphid cages were removed.

Wind. A box fan (49.5 by 49.5 cm) was used to create wind disturbance. Immediately after the removal of aphid cage, the fan was directed toward the central plant at a speed of 4.5–5 m/s for 10 min. The wind speed was measured using a pocket anemometer, Kestrel (Nielsen Kellerman, Chester, PA). When in the air current, the plant stem bent at an angle of 15–20° from the central axis.

Rain. A simulated rainfall of ≈ 2 cm/h was created with an adjustable eight-pattern shower wand, Gentle Rain (Melnor, Winchester, VA). The rain shower wand was fixed to the experimental arena using metal clamps. The showerhead was set exactly over the central plant in the experimental arena using the telescopic arrangement of metal pipes of the shower wand. The central plant colonized with wingless potato aphids was exposed to simulated rain for 10 min. A rain gauge was affixed to the bottom of the arena near the central plant and rainfall was measured each time that this treatment was applied.

Reflective Mulch. After carefully removing the aphid cage from the colonized central plant, a part of the experimental arena surface under the foliage of the central plant was covered with aluminum foil (38.1 by 38.1 cm; Reynolds Kitchens, Richmond, VA).

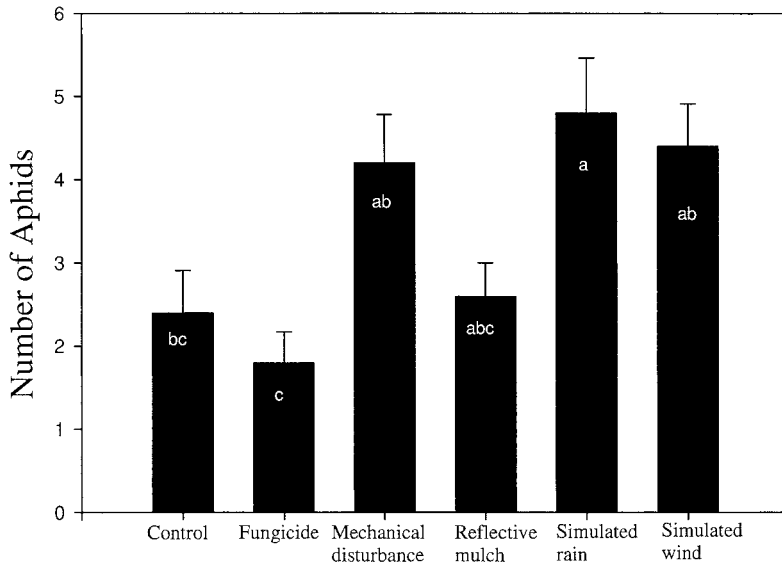


Fig. 1. Mean numbers of *M. euphorbiae* moving from the central release plant to the surrounding plants after several environmental perturbations. Plant canopies did not overlap.

A thin layer of soil covered the outer boundary (1 cm) of the aluminum foil, aligning it with the soil surface of the experimental arena.

Fungicide. One milliliter of flowable mancozeb [corresponding to the field application rate of 455.34 g (A.I.)/liter] was diluted in 300 ml of water and applied to the central plant on the experimental arena using a hand spray bottle. The bottle lever was squirted three times, thus delivering ≈ 2.25 ml of fungicide uniformly to the plant.

Undisturbed Control. Experimental set up was as described above but without any perturbations.

The numbers of living and dead adult aphids on the release plant, the surrounding plants, and the soil surface were recorded 2 h after perturbations. Nymphs that were occasionally produced by the released aphids were not counted. Each treatment was replicated five times with time and experimental arena, with a total of 150 individuals tested for each treatment.

Experiment 2

The impact of adult lady beetle, *Harmonia axyridis* (Pallast), was studied using a protocol similar to the one in the previous experiment. Immediately after removing a metal frame cage (see above), a single lady beetle was released on the central aphid-infested plant. The beetle was removed from the arena after 15 min. If the beetle left the central plant, it was removed from the arena and immediately replaced with another beetle.

Experiment 3

In this experiment, we studied whether aphid movement increases in response to simulated environmental perturbations on plants with overlapping canopies. The experimental protocol was similar to the previous

two experiments except that we used 4- to 5-wk-old plants with canopies touching each other within each row (but not between the rows). Because of the difficulty encountered in finding aphids on those larger plants, we trimmed their canopies, leaving 18–20 leaves per plant. The lady beetle disturbance was combined with the abiotic environmental stimuli (mechanical raking, simulated rain, simulated wind, fungicide, and reflective mulch) in a single experiment. The experiment was replicated five times as described above.

Statistical Analyses

Data normality was determined using Wilk-Shapiro test (PROC UNIVARIATE; SAS Institute 2002) and found to be normal ($W = 0.9704$; $P = 0.5527$ for experiment 1; $W = 0.9065$; $P = 0.2582$ for experiment 2; and $W = 0.9517$; $P = 0.1283$ for experiment 3). The data were analyzed using one-way analysis of variance (ANOVA; PROC ANOVA; SAS Institute 2002). Proportions of aphids that moved between the rows and within the rows were compared using logistic regression (PROC LOGISTIC; SAS Institute 2002).

Results

Experiment 1

Relatively few aphids moved even in the presence of simulated environmental disturbances compared with experimental controls (Fig. 1). Aphid densities on plants surrounding disturbed release plants were significantly different from the plants surrounding undisturbed control plants ($F = 5.85$; $df = 5,29$; $P = 0.0011$). However, Tukey's test showed that only rain treatment was significantly different from the control (Fig. 1). On average, 4.56 ± 0.44 (SE) aphids were

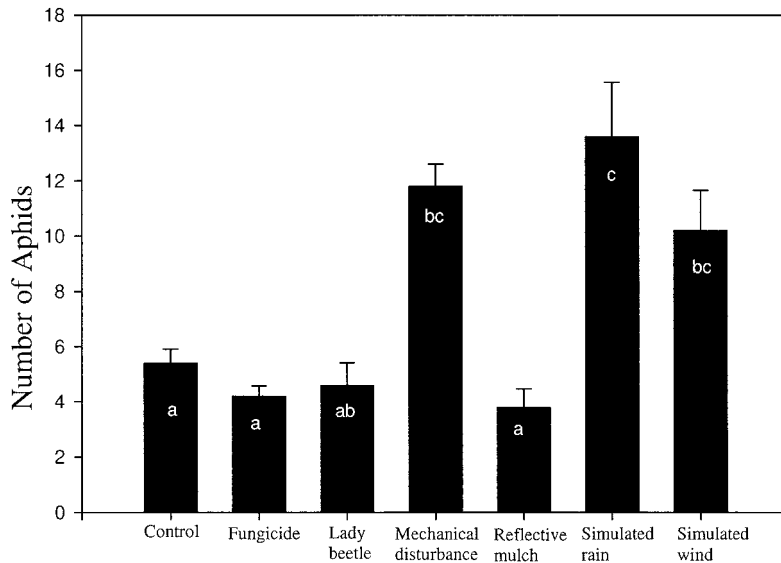


Fig. 2. Mean numbers of *M. euphorbiae* moving from the central release plant to the surrounding plants after several environmental perturbations. Plant canopies overlapped within rows. Bars followed by the same letter were not significantly different (Tukey test, $P > 0.05$).

missing or dead by the end of the experiment. There was no significant treatment effect on the number of missing or dead aphids ($F = 0.97$; $df = 5,29$; $P = 0.4551$). Of the aphids that moved, 64% traveled between plants within the same row of release, whereas the remaining 36% traveled between the rows. Environmental perturbations did not encourage aphid movement between the rows ($\chi^2 = 9.81$; $df = 5$; $P = 0.0808$).

Experiment 2

The mean aphid densities found on the plants surrounding the central release plant were 0.6 ± 0.40 and 1.4 ± 0.37 for the treatment and control arenas, respectively. On average, 1.6 ± 0.24 of released aphids were observed to be eaten by the predator, and only two aphids were missing in the entire experiment. Results were very similar to the previous study, with no discernible effect of lady beetle disturbance detected ($F = 0.08$; $df = 1,9$; $P = 0.7885$). Seventy-nine percent of released aphids moved within the rows, and 21% moved between the rows. Lady beetle perturbation did not affect proportion of aphids moving between the rows ($\chi^2 = 2.06$; $df = 2$; $P = 0.3564$).

Experiment 3

Mechanical raking, simulated rain, and simulated wind significantly encouraged aphid movement from the release plant to the surrounding plants ($F = 10.51$; $df = 6,34$; $P = 0.0001$) when leaves of adjacent plants were touching (Fig. 2). On average, 4.05 ± 0.39 (SE) aphids were missing or dead at the end of the experiment. None of the treatments had significant effect on the number of missing or dead aphids ($F = 1.09$; $df =$

$6,34$; $P = 0.3944$). The proportion of aphids that moved within and between the rows was 65% and 35%, respectively. Treatments had an overall significant effect on the proportion of aphids moving between the rows ($\chi^2 = 17.72$; $df = 6$; $P = 0.0070$; Fig. 3). Analysis of maximum likelihood estimates in logistic regression revealed that wind was the only factor promoting aphid movement between the rows ($\chi^2 = 15.38$; $P < 0.0001$).

Discussion

Results of this study confirm that potato aphid is fairly mobile between and among the plant rows. Wingless adults moved between potato plants even when canopies did not touch each other and when there were no environmental perturbations. This is different from the earlier results reported by Alyokhin and Sewell (2003), whose study apparently underestimated the ability of such aphids to move between plants. The observed differences between these studies might be explained by the difference in aphid colonies, plant cultivars, or some other yet unknown factors.

When plant canopies did not overlap, interplant movement of wingless adult potato aphids was influenced at a statistically detectable level only by rain disturbance. However, we did observe the higher numerical tendency of aphids to disperse from the release plant when it was exposed to simulated wind and mechanical disturbance treatments.

Aphid dispersal was further enhanced when plant canopies overlapped. The number of aphids found away from the release plant in experiment 3 more than doubled compared with experiments 1 and 2. Also, the influence of rain, wind, and mechanical per-

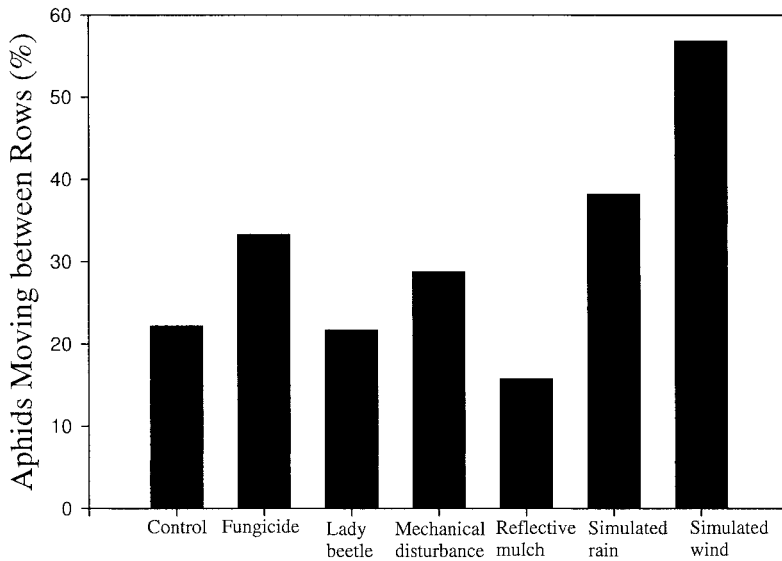


Fig. 3. Mean proportions of *M. euphorbiae* moving from the central release plant to the surrounding plants of different rows after several environmental perturbations. Plant canopies overlapped within rows.

turbations became more pronounced. As in experiment 1, those three perturbations were responsible for most movement. Maximum aphid density on the surrounding plants was found in the simulated rain treatment, followed by the mechanical raking and wind treatments. Our results were consistent with the studies conducted by Mann et al. (1995) and Zúñiga (1985), who reported that dispersal of apterous *R. padi* and *S. avenae* increased with increasing rain intensity and duration, as well as with wind speed. On the contrary, Bailey et al. (1995) found that, although wind significantly promoted dispersal of *R. padi* in oats, rain did not have such an effect. This difference in results may be explained by a number of factors such as aphid species and origin, plant architecture, plant growth stage, spacing between the plants, and variation in the wind speeds and rain intensities. For example, the rain intensity was considerably lower in the study by Bailey et al. (1995) compared with rain intensity used by Zúñiga (1985) (2 versus 3 cm/h, respectively).

The aphid dispersal to the surrounding plants could have been partially caused by increased emigration from the central plant after perturbation and partially by the dislodgement of aphids from the central plant followed by arrival to nearby plants. Studies conducted by Zúñiga (1985) revealed that 76.8% of *R. padi* and 68.7% of *S. avenae* were dislodged from wheat seedlings when rainfall was simulated (at a rate of 3 cm/h for 30 min) as opposed to 11% and 18.4% dislodgement from controls not subjected to rain treatment. We also commonly observed aphid dislodgement in our experiments, but did not quantify its occurrence.

We did not find significant movement of aphids from the central plant equipped with reflective mulch. A number of studies state that reflective mulch re-

duces aphid landing, overall densities, virus incidence, and spread in different crops (Toscano et al. 1979, Basky 1984, Heimbach et al. 2001, Greer and Dole 2003). However, it apparently did not elicit escape response in potato aphids tested in our study.

There was no significant movement of aphids from the central plant perturbed with the release of the ladybeetle. The interactions between potato aphid and *H. axyridis*, such as prey finding, feeding behavior, spatial distribution of prey-predator on plants, or escape from predator, are not yet clearly understood. It is possible that adult *H. axyridis* is not an important mortality source for potato aphid, and trade-offs between sustaining some mortality from predation and uncertainties of movement are resolved in favor of the former. Moreover, prey-predator interactions are dependent on their density ratio (Van Driesche and Bellows 1996). In our treatment, we maintained prey-predator ratio of 30:1 for 10 min, with prey being distributed over a fairly large plant with relatively complex architecture. Therefore, it is possible that the disturbance was not strong enough to have a noticeable effect on aphid movement.

A considerable proportion of aphids ($\approx 35\%$) moved between the rows of potato plants. That proportion was similar for both nonoverlapping and overlapping canopies. However, the total number of aphids that moved (within and between rows) in overlapping canopies was more than twice as large as the total number of aphids moving in nonoverlapping canopies. Originally, we hypothesized that canopy closure within the rows would facilitate aphid movement between the plants because aphids could move between the plants without having to cross areas of bare ground. However, results of this study suggest that larger plant size also promoted aphid movement between the rows. Indeed, as plant size increased, the

distance between plants decreased even when their canopies did not touch each other. Therefore, it was easier for migrating aphids to cross between the rows. Aphids are capable of finding their host plants using both olfactory and visual cues (Ferrar 1969, Pelletier 1990, Isaacs et al. 1993, Eckel and Lampert 1996, Hori 1999, Eigenbrode et al. 2002, Alvarez and Srinivasan 2005, but also see Fereres et al. 1999), both of which are likely to be more obvious at a closer distance. Furthermore, some of the dislodged aphids could have actually found themselves closer to the plant in a different row, leading to its preferential colonization (Alyokhin and Sewell 2003).

Our results confirm that aphid dispersal is influenced by the interaction of plant characteristics and various environmental factors. Rain, wind, and mechanical perturbations have a significant potential to cause interplant movement of wingless potato aphids, especially later in the season, when potato plants have dense foliage and overlapping canopies. The dispersal is not limited to movement within the rows even when canopies between the rows do not touch each other. This is likely to have implications for modeling virus spread in potato crops, and may provide certain insights for other plant-vector-virus systems. Also, environmental disturbances should be taken into account when making pest management decisions. For example, suppressing aphid populations may be more important before periods of rainy or windy weather, while planting wind-breaking hedgerows may help reducing virus transmission in potato crops. However, a better understanding of a given pathosystem is required before making more specific management recommendations.

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