On-Soil Movement and Plant Colonization by Walking Wingless Morphs of Three Aphid Species (Homoptera: Aphididae) in Greenhouse Arenas

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ABSTRACT Potato aphid, *Macrosiphum euphorbiae* (Thomas); green peach aphid, *Myzus persicae* (Sulzer); and buckthorn aphid, *Aphis nasturtii* Kaltenbach are polyphagous herbivores that commonly colonize potato plants, *Solanum tuberosum* L., in the northeastern United States and Canada. Their movement influences spatial and temporal patterns of viral spread within potato fields. We investigated aphid movement between potato plants early in the season, with a particular focus on their ability to walk over bare soil. On average, aphids survived 1.16 ± 0.04 d (mean ± SE) on the surface of bare soil; all of them dying within 3 d. Wingless aphids did not leave potato plants that were adequate as a food supply. When forcibly removed from the host plant and released on the soil surface, all three species colonized the nearest plant within 1 h. However, when given no other choice, a significant proportion of aphids was fully capable of colonizing potato plants as far as 180 cm away from the point of release. Potato aphid, which is the largest, was the most mobile of the three species. The green peach aphid was intermediately mobile, and the buckthorn aphid was the least mobile species.

KEY WORDS potato, aphids, virus transmission, movement

POTATO APHID, *Macrosiphum euphorbiae* (Thomas); green peach aphid, *Myzus persicae* (Sulzer); and buckthorn aphid, *Aphis nasturtii* Kaltenbach are polyphagous herbivores that commonly colonize potato plants, *Solanum tuberosum* L., in the northeastern United States and Canada. Populations of potato-colonizing aphids seldom reach densities sufficient for causing noticeable crop injury by sap feeding. However, their ability to transmit persistent potato viruses is an ominous threat to commercial potato production (Radcliffe et al. 1993, Radcliffe and Ragsdale 2002). These three species are also capable of transmitting nonpersistent viruses. However, most nonpersistent transmission is usually done by other aphid species that probe potato plants but do not colonize them (Boiteau et al. 1988, Radcliffe and Ragsdale 2002).

Vector movement has a great influence on spatial and temporal patterns of viral infections (Peters 1987, Irwin and Thresh 1990). Once initial inoculum is established, whether by immigrating viruliferous aphids or infected seed, further virus transmission throughout a potato field will probably depend on local within-field aphid movement from infected to uninfected plants. Short-distance movement of infective 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). Garrett and McLean (1983) reviewed the evidence associated with virus spread by aphids in several crops and concluded that the local vector activity accounted for the majority of virus spread in those crops. Using the continuous-time, deterministic, and compartmental mathematical model, Jeger et al. (1998) and Madden et al. (2000) also showed that local aphid dispersal was a potentially crucial component of the plant—aphid–virus system.

Currently, most management decisions are made based on the aphid abundance and/or on the proportion of aphid-infested plants. However, if aphids feed on the same plant for their entire life, even relatively high populations will not result in significant virus transmission. Alternatively, even a small population of highly 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 toward disrupting aphid movement, not just toward reducing aphid numbers. For example, proper timing of insecticide applications to eliminate aphids that are about to engage in interplant movement (rather than all aphids) may significantly reduce the amount of chemicals necessary for successful crop protection.

Overall, surprisingly little is known about local dispersal of potato-colonizing aphid species (Radcliffe and Ragsdale 2002). All three species have both winged and wingless parthenogenic summer forms. The production of winged summer migrants is encouraged by overcrowding and poor quality of host plants (Sutherland and Mittler 1971, Hodjat and Bishop 1978, Radcliffe et al. 1993, Muller et al. 2001). Because of their high mobility, winged aphids are

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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 mounting 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) compared propensity for dispersal of winged and wingless morphs of potato, buckthorn, and green peach aphids. Both winged and wingless individuals of all three species were fairly mobile; up to 47% of monitored individuals moved over a 24-h period from an excised potato leaflet to another leaflet 17.5 cm away. However, the experimental protocol used by Boiteau (1997) measured leaflet-to-leaflet movement and did not allow distinguishing between intra- and interplant movement. Hodgson (1978) described frequent intraplant movement of *M. persicae*, presumably in an attempt to maintain suitable feeding sites on rapidly growing plants. Therefore, it is possible that a significant amount of movement observed by Boiteau (1997) reflected aphid tendency to relocate within an already colonized plant rather than to move onto a new plant.

In the current study, we focused on aphid movement between potato plants early in the season, with a particular reference to their ability to walk on top of bare soil. As plants grow bigger, plant canopy in potato fields tends to close. Therefore, there is essentially little difference between intra- and interplant aphid movement late in the season. Conversely, potato plants early in the season are well separated from each other. Bare soil presents a potentially formidable barrier for wingless aphids. Furthermore, winged aphids autolyze their flight muscles soon after completing their maiden flight and settling on a host plant (Johnson 1957, 1959). Therefore, significant virus transmission within potato fields seems to be relatively improbable early in the season (Radcliffe and Ragsdale 2002), when spring migrants are still in the process of colonizing potato fields, and their progeny have not built up in high enough numbers to produce a significant number of alates. However, review of extensive evidence collected over a variety of geographic locations revealed substantial spread of persistently transmitted potato leafroll virus early in the season (Radcliffe and Ragsdale 2002).

Several factors (or their interaction) might be responsible for this seeming discrepancy. First, migrant aphids could bring the virus with them from infected fields elsewhere. Second, it is possible that spring migrants retain their flight muscles longer than summer migrants and visit more than one potato plant over their life span (Woodford 1968, Radcliffe and Ragsdale 2002). Third, virus transmission early in the season is probably facilitated by higher susceptibility of young potato plants to viral infections compared with mature potato plants (Sigvald 1985, Beemster 1987, DiFonzo et al. 1995). Finally, we might be underestimating the extent of interplant movement of wingless aphids. Working with cereal aphids, Griffiths et al. (1985), Sunderland et al. (1986), and Sopp et al. (1987) discovered that between 4 and 71% of the aphid population were found on the soil surface at any time. Also, Ferrar (1969) reported that wingless *M. persicae* were capable of moving on the soil surface, finding and colonizing host plants, and showed some tendency of leaving apparently suitable host plants, although little quantitative data were provided in that article. Obtaining more information on the amount of interplant movement of wingless potato-colonizing aphids was the major objective of the current study.

Materials and Methods

Aphids. Aphids were taken from the colonies currently maintained in our laboratory and originally collected from potato fields at Aroostook Experiment Farm in Presque Isle, ME. Potato aphids, green peach aphids, and buckthorn aphids were maintained separately on potted potato plants. All three colonies were started simultaneously. Our study was conducted over ≈1 yr, starting at the time when the colonies were 6 mo old. Field-collected individuals were annually infused into each colony in an attempt to keep its genetic composition close to that of the local field populations. Only wingless adults were used in the current study because previous studies have determined their higher mobility compared with nymphs (Boiteau 1997). Test animals were selected and assigned to treatments at random regardless of their age or clone, allowing us to control for possible confounding developmental and genetic effects (Ferrar 1969).

Experimental Arenas. Except for the experiment on aphid survival (see below), all the studies were conducted in three experimental arenas, each consisting of a wooden box (240 by 107 by 30 cm) filled with field-collected soil. The arenas were maintained in the greenhouse on a photoperiod of 18:6 (L:D) h (natural light supplemented by fluorescent growing lamps), 23 ± 2°C (mean ± SE), and 61 ± 2% RH. They were enclosed in a Saran screen cage with a transparent plastic roof. Potted potato plants used in the experiments were ≈3 wk old and 15 cm in height. The pots were sunk to the brim into the soil inside the arenas. Canopies of potato plants did not touch each other in any of the experiments.

Experiment 1. The main objective of the first experiment was to determine how long aphids survive on the surface of bare soil away from their host plants. Aphid survivorship was tested in small arenas inside an environmental chamber (Percival Scientific, Boone, IA) maintained in the greenhouse on a photoperiod of 18:6 (L:D) h, 20 ± 1°C (mean ± SE), and 46 ± 2% RH. Each arena consisted of a clear plastic petri dish lid (9.5 cm in diameter), half filled with field-collected soil. The soil was moistened daily. To prevent aphid escape, the dish was covered by a clear ventilated plastic container (9.5 cm in height by 9 cm in diameter). The container was turned upside-down and fitted inside the dish. In experimental arena, 10 adult aphids were placed on the top of the soil by using a camel's-hair brush. In control arena, 10 adult aphids were placed on an excised potato leaflet inserted in a small plastic vial filled with tap water. Aphids were checked for signs of life every 24 h by visual observations and gentle probing with a soft camel's-hair brush. Aphids that did not move in response to probing were considered to be dead. The number of live aphids was recorded daily in the experimental and control arenas until all aphids in the experimental arenas were dead. Leaflets in the control arenas were replaced as needed.

The experiment was repeated 10 times for each aphid species. Homogeneity of survival functions for the three aphid species and the effect of host plant presence on aphid survival were tested by the generalized Wilcoxon tests (PROC LIFETEST, SAS Institute 1999). As described above, the experiment was terminated after all the aphids in the experimental arena were dead, but a significant number of aphids in the control arena were still alive. Therefore, survival times of aphids in the control arena that were still alive at the end of the experiment were included in the analysis as censored observations (Lee 1992).

Experiment 2. This experiment tested aphid ability to move on the surface of bare soil between rows of potato plants. Three potted potato plants spaced 20 cm apart were placed in a single row on one side of each arena. Twenty potato aphids, 20 buckthorn aphids, and 20 green peach aphids were released in each arena by individually placing them on top of the soil with a soft camel's-hair brush. During the first replication, aphids in one arena were placed 90 cm (one row) away from the row of plants, whereas aphids in the other two arenas were placed 180 cm (two rows) away from the row of plants. During the second replication, aphids in one arena were placed 180 cm away from the row of plants, whereas aphids in the other arena were placed 90 cm away from the row of plants. During the third replication, aphids in two arenas were placed 90 cm away from the row of plants, whereas aphids in the third arena were placed 180 cm away from the row of plants. This way, at the end of the experiment we had a total of 80 aphids of each species released 90 cm away from the plants, and a total of 80 aphids of each species released 180 cm away from the plants. Potato plants were checked 48 h after the release, and the numbers of aphids colonizing each plant were recorded separately for each species.

Effects of aphid species and distance between the release point and potato plants on the proportion of aphids colonizing potato plants were analyzed using logistic regression (PROC LOGISTIC, SAS Institute 1999). Because of its nominal nature, the species variable was replaced by design dummy variables created using effect coding (Polit 1996).

Experiment 3. The third experiment was carried out to check if wingless aphids finding themselves on the ground within a potato row colonize the nearest plant within the same row, or if some of them move between the rows. Eight potted potato plants were arranged in three rows (two rows of three plants on the sides and one row of two plants in the middle) inside the arena. The pots were sunk to the brim into the soil. Plants within the side rows were spaced 20 cm apart. Distance between the rows was 90 cm. Such an arrangement reflected approximate plant and row spacing in commercial potato fields in Maine. The plants within the middle row were spaced 50 cm apart (i.e., a three-plant row with the middle plant missing). Two laboratory-reared potato aphids, green peach aphids, or buckthorn aphids were released in the center of the arena (on the place of a missing central plant). Each species was released into its own arena separately from other species. Released aphids were observed for 1 h, or until they colonized one of the plants in the arena, or until they climbed up the arena wall. The amount of time between aphid release and plant colonization was recorded.

This experiment was repeated 12 times; a total of 24 aphids of each species was tested. The proportion of aphids displaying a certain movement pattern (colonizing a plant, climbing up arena wall, not moving during the entire duration of the experiment, and moving on the soil surfaces but not colonizing a plant) was compared among the species using chi-square test (PROC FREQ, SAS Institute 1999). Elapsed time between aphid release and plant colonization was compared among the species using one-way analysis of variance (ANOVA) (PROC GLM, SAS Institute 1999). Aphids not colonizing a plant were excluded from the ANOVA.

Experiment 4. The fourth experiment investigated the propensity of wingless aphids to emigrate from potato plants. Nine potted potato plants were arranged in three rows of three plants each inside the arena and sunk to the brim into the soil. As in the previous experiment, plants within the rows were spaced 20 cm apart, and the distance between the rows was 90 cm.

Laboratory-reared adult wingless aphids were released on the central plant inside of the arena (all three aphid species on a single plant). For all trials, density of released aphids was based on the 20-yr means recorded at the unsprayed potato plots used as a control for insecticide trials at Aroostook Experiment Farm (unpublished data). Those depended on the plant size (i.e., number of leaves per plant) and were equal to ≈1.2 potato aphids, 0.7 green peach aphids, and 1.5 buckthorn aphids per one leaf of a potato plant. Number of released aphids of each species was recorded during each trial. Immediately after aphid release, the central plant was covered with a wooden frame Saran screen cage for 24 h, allowing aphids to settle down. After the 24-h settling down period, the cage was carefully removed. Aphid number on the previously uninfested eight plants within each arena was counted 48 h after the cage removal.

The experiment was replicated six times (three arenas × two replications in time). Because no aphids colonized any of the uninfested plants (see below), no statistical analysis was conducted.

Results

Experiment 1. On average, aphids survived 1.16 ± 0.04 d (mean ± SE) on the surface of bare soil; all of

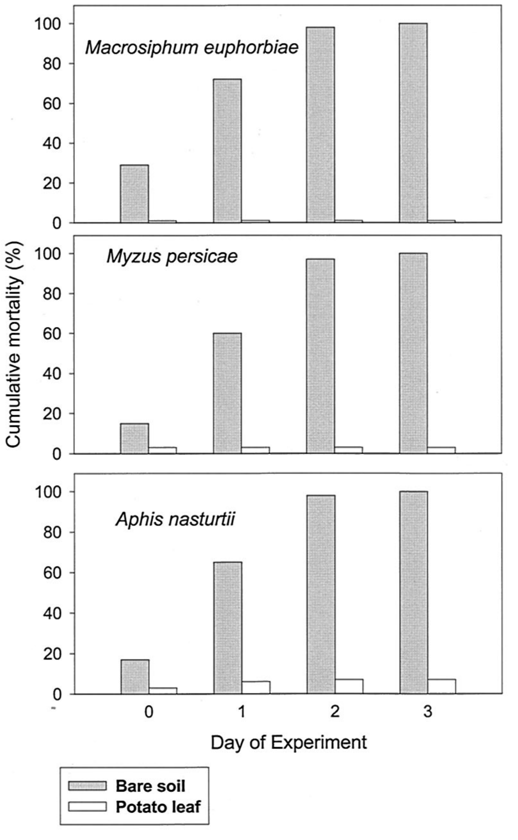

Fig. 1. Cumulative mortality of aphids maintained on bare soil (experimental treatment) and on a potato leaf (control treatment). The experiment was discontinued after the death of all aphids maintained on bare soil.

them died within 3 d (Fig. 1). The majority of control aphids was still alive at the end of the experiment (Fig. 1). There was no difference in survival of the three tested species ($\chi^2 = 0.6044$, df = 2, $P = 0.7392$), but the absence of potato leaves significantly shortened the life span of tested individuals ($\chi^2 = 517.1$, df = 1, $P < 0.0001$).

Experiment 2. Only a single buckthorn aphid was encountered on a potato plant (180 cm from the place of its release) over the entire duration of this experiment. Therefore, statistical analysis was limited to potato aphids and green peach aphids. When released 90 cm away from potato plants, 50.0 ± 15.3% of potato aphids and 31.7 ± 15.9% of green peach aphids colonized potato plants. When released 180 cm away from potato plants, 41.7 ± 22.1% of potato aphids and 11.7 ± 9.3% of green peach aphids colonized potato plants. Logistic regression provided a good description of the collected data (Score test; $\chi^2 = 21.06$, df = 2, $P < 0.0001$). Both aphid species ($\chi^2 = 15.43$, df = 1, $P < 0.0001$) and distance of release ($\chi^2 = 5.68$, df = 1, $P = 0.0171$) had a significant effect on plant colonization.

Experiment 3. All potato aphids moved during 1-h observation period, but 12.5% of green peach aphids and 16.7% of buckthorn aphids did not leave their release point. Eighty-three percent of potato aphids, 66.7% of green peach aphids, and 58.3% of buckthorn aphids colonized potato plants located within the same row where they were released. No aphids moved between the rows. The remaining aphids either stayed on the soil surface until the end of our observations (4.2% of potato aphids, 20.8% of green peach aphids, and 20.8% of buckthorn aphids) or climbed the wall of the observational arena (12.5% of potato aphids, 4.2% of buckthorn aphids, but no green peach aphids). The proportion of aphids displaying a particular movement pattern was significantly different among the species ($\chi^2 = 45.02$, df = 2, $P < 0.0001$). On average, it took potato aphids 738.9 ± 146.6 s (mean ± SE) to find and colonize a potato plant. Green peach aphids and buckthorn aphids were substantially slower, with 1471.9 ± 170.2 and 2155.4 ± 193.5 s, respectively, passing between aphid release and plant colonization. The difference among the species was statistically significant ($F = 17.71$; df = 2, 46; $P < 0.0001$).

Experiment 4. No aphids were encountered on any of the eight potato plants surrounding the release plant.

Discussion

Migration occurs at a cost, both in uncertainty and energy expense (Rankin et al. 1986, Loxdale et al. 1993, Ward et al. 1998). Therefore, it is not surprising that wingless aphids did not leave potato plants offering an adequate food supply. When removed from the host plant and released on the soil surface, all three species tested in our experiment were able to find the nearest plant and colonize it within a relatively short time. These findings are consistent with those of Ferrar (1969). Both olfactory and visual cues may play a role in host-plant finding by a number of aphid species (Ferrar 1969, Pelletier 1990, Isaacs et al. 1993, Eckel and Lampert 1996, Hori 1999, Eigenbrode et al. 2002), although their relative contribution is still unclear and is likely to vary among species and between morphotypes within a species. We do not know how aphids found potato plants in our study. However, their alighting on the nearest plant as opposed to randomly colonizing plants within the arenas implies the presence of some kind of an orientation mechanism. This outcome also means that the movement of wingless forms between the rows of young potato plants is very unlikely.

Despite not willingly moving over long distances, all three species were capable of surviving off host plants for 24–48 h and walking on the soil surface between potato plants. Potato aphid, the largest aphid, was also the most mobile of the three species. The green peach aphid was less mobile, and the buckthorn aphid displayed the least amount of locomotory activity. When given no other choice, a significant proportion of potato aphids and green peach aphids were fully capable of colonizing potato plants located as far as 180 cm (approximately two rows) away. Finding a single buckthorn aphid on a potato plant 180 cm from the release point indicates that this species may also cover substantial distances walking on the soil surface, but its success rate is much lower than that of the other two species.

Our study has been conducted in the controlled laboratory and greenhouse setting. Therefore, our results indicate intrinsic propensity and ability of potato-colonizing species to move between young potato plants, but do not quantify the amount of such movement under field conditions. In the field, interplant movement is likely to be affected by a number of biotic and abiotic factors. However, aphids walking on the soil surface will be vulnerable to predation by a variety of arthropods (Griffiths et al. 1985, Sunderland et al. 1986). Therefore, at least some of them will be intercepted before arriving on a new host plant, probably resulting in lower colonization rates than the ones observed in the current study. However, a number of environmental perturbations might also encourage aphid movement. For example, Bailey et al. (1995) showed that wind, herbicide applications, coccinellid predators, crowding, mechanical disturbance, drought, and virus infection affect movement of wingless bird cherry-oat aphids, *Rhopalosiphum padi* (L.), and spread of barley yellow dwarf virus in oats. A similar situation might exist in potato–aphid–virus system, but no information is yet available on this subject. Although our study provides initial insight into the issue, further investigations are required to find out the true extent of aphid movement between potato plants in the field.

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