**Movement of winged aphids is poorly understood despite its importance in disease vectoring in Washington potatoes**

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This essay explores the possibility that movements by winged aphid are largely local. If so, weedy plants and volunteers near potato fields are likely to be the major source of PLRV and PVY infections in Washington potatoes. General patterns in aphid flight behavior and flight capacity suggest that while long distance dispersal is common, local movements are much more common and should account for most disease movement into fields. This suggests that control of aphids in habitats surrounding potato fields and on field edges before they transmit the viruses they carry could be much more successful in reducing disease incidence than the existing "No Gap" pesticide use pattern practiced in much of Washington. In-field insecticides can only kill incoming aphids after they have had time to infect at least one plant. Experimental studies to test both the premises described here and alternative controls are suggested.

**Biology of Aphid flight**

For most aphids, including the green peach aphid, *Myzus persicae* (GPA), flight occurs to find mates or in response to environmental conditions. In northern latitudes, various aphid species fly to primary, overwintering host plants in the fall where they connect with sexual partners and lay eggs which overwinter. GPA uses peaches and potato aphid, *Macrosiphum euphorbiae* (PA) uses roses as their primary hosts. This is the only sexual cycle of the year and it is followed by many generations of mother aphids producing daughters parthenogenetically. In the spring or early summer, usually after one or more generations on the primary host, aphids again develop wings and fly to secondary host plants which are more than 200 species in both GPA and PA. In warmer climates or where there is a significant absence of overwintering hosts, both GPA and PA lose the sexual cycle and in some areas, such as central Washington, both forms of GPA (and perhaps PA) exist. These asexual or anholocyclic forms use secondary hosts year-round and pass the winter in warmer, sheltered microclimates. Currently we do not know what proportion of GPA or PA in Washington potato fields are of the sexual versus the asexual type, but the tools to determine this are available. More than a dozen genetically variable DNA markers (micro-satellite loci) have been used to characterize a few dominant, highly successful asexual clones in potatoes in England, where anholocyclic reproduction in GPA is the norm. Indeed, if clones in Washington potatoes were of just a few types year after year it would tell us that the asexual life cycle predominates and may help us discover overwintering hosts. This in turn could allow us to predict flight timing and perhaps the potential for disease status in early flying GPA and PA.

In addition to wing production for the sexual cycle, aphids produce winged forms in response to crowding or declining plant quality or senescence. Changing leaf quality drives departure from the primary host and drying of secondary hosts during warming weather drives aphids to hop-scotch their way between various weedy hosts and perhaps to potato fields or irrigated weeds near to fields. Movement occurs by individual alatae (winged females) during their lifetime and also as the sequential movements of multiple generations

of their offspring throughout the season. When an alate stops at a host plant she may lay a few young and move on or may stop permanently, losing the muscles that power her wings, and depositing young for the rest of her life.

Descriptive studies suggest that the winged forms take to flight a few hours to a couple of days after their molt to the adult stage, after their wings have hardened. They may not even feed before they walk up the plant and take flight. They fly during daylight and tend to fly during light winds, staying put during very high winds. Aphids typically fly up first, attaining a height of a few to several hundred meters, with some reaching a couple of thousand m above ground (Johnson 1956). Studies using tethered weather balloons with suspended aphid suction traps have shown that aphids become abundant at heights up to 100 m with logarithmically declining densities up to 2000 m (that is, most are in the bottom 100-200m). The most widely accepted explanation for this distribution in the air column is that during the daylight hours aphids are taking off throughout the day and returning to the ground after a few minutes to a few hours. In lab studies aphids are stimulated to fly up by the ultraviolet light or to the UV-containing light from the day time sky. They apparently stop flying upward due to a declining attractiveness to the UV and increasing attractiveness to the wavelengths they see reflected from the plants below. The attraction to foliage may develop in aphids after just a few minutes of flight suggesting the movement up and down in the air column is very dynamic throughout the day. It is easy to imagine how quick trips of an hour or less up 100-200 m and back down again are likely to displace aphids significantly from the plant they left below, and offering a way for aphids to reliably leave poor conditions and spread the risk for their offspring. Tangentially, aphids are not only stimulated to alight on plants reflecting the appropriate yellow-green wavelengths (and to our yellow pan traps), they are even more strongly attracted to plants and traps when they are surrounded or bordered by bare dirt or dead foliage, perhaps due to enhanced contrast with the surrounding habitats. Such behavior may also explain patterns of virus infections in potato fields, where infections are greatest on field margins (Figure 1).

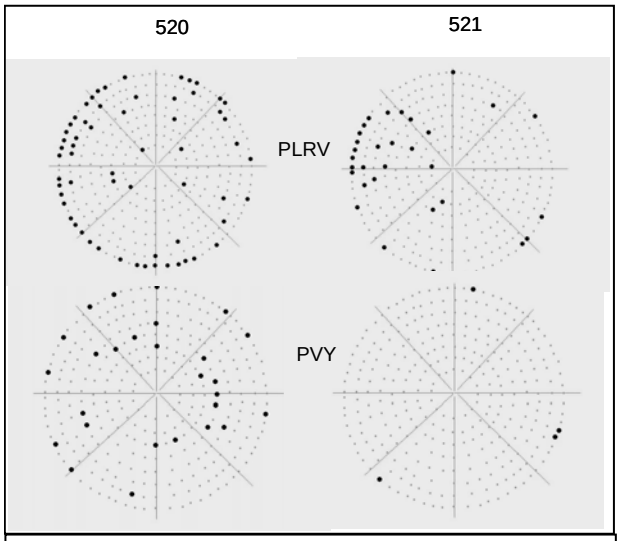



Figure 1. Pattern of infection of two potato circles (520 and 521) by PLRV (above) and PVY (below). Foliage was systematically sampled from 320 plants in each field and tested for PLRV and PVY (o-isotype) by ELISA. Dark spots identify positives.

**How far do aphids fly?**

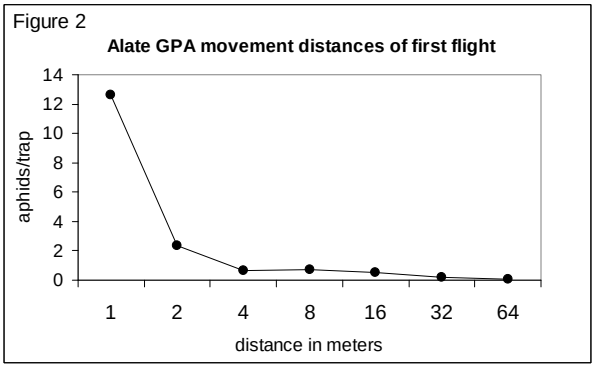
With a flight speed of only about 1-3 miles per hour, aphids are at the mercy of updrafts and the higher wind speeds often encountered above the boundary layer nearer the ground (above 100 m). Capture of aphids by wind currents best explains studies where aphids have been collected high on snow-covered mountains, in nets deployed from airplanes, and from a ship in the center of the Pacific Ocean. Entomologist from Hawaii's

Bishop museum collected GPA, PA, and several important PVY-vectoring grain aphids including bird cherry oat aphid, *Rhopalosiphum padi,* aboard ship several hundreds of miles from the nearest land. Prevailing wind patterns remains the favored explanation for the appearance in England of GPA with high levels of a form of insecticide resistance, which was known to be high in France. Similarly, low level jet streams have been implicated in the annual appearance of GPA in the Dakotas, carried north on currents from southern regions where they can overwinter. These long distance movements have often been interpreted as an adaptation of various aphids to "harness" the wind to move to greener pastures, an adaptation we call migration. However, for the well studied France to Britain movements and our south to north movements in the plains states, there have been no studies describing the return of aphids back to their sources. Without such a return, especially for the plains states, migration is a misnomer and potentially a dead end. After a few generations in the Dakotas, offspring of immigrants GPA will perish from cold even in the most sheltered spots and absence of peach host prevents overwintering as sexual forms.

Long distance movements are also explained by aphids being inadvertently caught up by upper atmosphere winds and moving in them. This idea is also consistent with the number of aphids in the air column: densities slowly increase from ground level up to about 100m-200m, then decrease rapidly up to 2000 m or more. It is aphids that are at the higher altitudes and at much lower densities that are likely to be caught by low level jet streams and storm fronts moving across continents. In other words, aphids which have traveled long distances are unlikely to be in the majority, and for any given point where aphids can develop nearby, immigration from those nearby sources seems more likely than from distant sources.

The examples of long distance, wind driven, movements provide a striking contrast with studies of short distance movements of aphids. Captures of radio-labeled alatae of GPA in interception traps was mostly within 4 meters from the source where they where they developed and acquired the radioactivity in spiked plants (Figure 2; modified from Harrewijn et al. 1981). The pattern seen in Figure 2 reflects a pattern that is nearly universal in insect dispersal and should not be ignored: there is a geometric decrease in the number of insects for a given sample area as distance from the source increases. These contrasting studies which show very short movements by alates versus the high altitude movements point to the need to test even more completely the hypothesis that most aphid movement is local. To do so we need better tools than used in the past.

Figure 2




The many dozens of studies of aphid movement in the field have been compromised by the absence of suitable tools to reliably mark them in situ and to capture significant numbers of flying aphids after marking. Even attractive yellow pan traps yield very small numbers of aphids. While suction traps are unbiased and sample large volumes of air, they represent large investments for each point in space they sample. Using radiolabels in nature has become nearly impossible to get approved and the overall conclusion from many studies using fluorescent powders is that they are much too expensive to mark adequate numbers of aphids on plants in nature, and are often too toxic as well. Over the last three years my lab has been developing and testing a sensitive, nontoxic and inexpensive method of marking

aphids in the field and a simple and inexpensive method of capturing them from large air volumes. Realistic field experiments will be underway by the time this is read.

**Marking and trapping aphids**

Ideally, aphids should be marked in their natural habitat using a nontoxic material sprayed on the plant; the mark is acquired just by walking on the residue on the plant before taking flight (or by feeding on the plant in the case of an internal label). A recent study (Jones et al 2006) provided just such a marker which was being used to mark moths moving between tree fruit crops. The mark consists of a cheap, readily available protein, chicken egg albumen (egg white in a 10% solution in water). The mark can readily be rinsed from captured aphids and detected with great sensitivity using ELISA and commercially available antibodies against chicken albumen. The mark is complimented by a new aphid trapping method which overcomes the problem of wind resistance of other traps used since the 1930s, all requiring very strong supports and must be kept relatively small to prevent wind damage. These constraints have prevented sampling large cross-sectional areas which is needed to collect significant numbers of aphids. The trap we have designed consists of clear plastic mesh (gill net) with a 1 cm grid. While this wide grid allows some aphids to pass through, it catches more than half and requires very little restraint even in a high winds. Pictured at right is a 20 cm width of this net suspended between 3 pieces of 10' PVC (3/4" sch. 20) and secured with a 'bungee' cord to a pair of tent stakes in the ground. This trap stayed up through a summer with occasional wind gusts exceeding 30 MPH, is easy to assemble and move, and is inexpensive. We have also deployed the mesh by clamping it over yellow pan traps, providing the attractive properties and ease of the pan trap while keeping externally marked aphids dry and separated from one another. We have also suspended the mesh from a 7 m tower to test to our own satisfaction that aphids are indeed flying at significant heights.

Figure 3. A teepee trap consisting of 3 pieces of 10' PVC and the net staked to the ground (see text).

Capture and removal of aphids from the mesh is facilitated by the use of a new trap adhesive ("Sticky Stuff" provided by Tanglefoot Inc.) which is latex-based and remains sticky after drying. Hence, the aphids do not become covered with an oily adhesive allowing us to recover the protein mark for ELISA. Additional

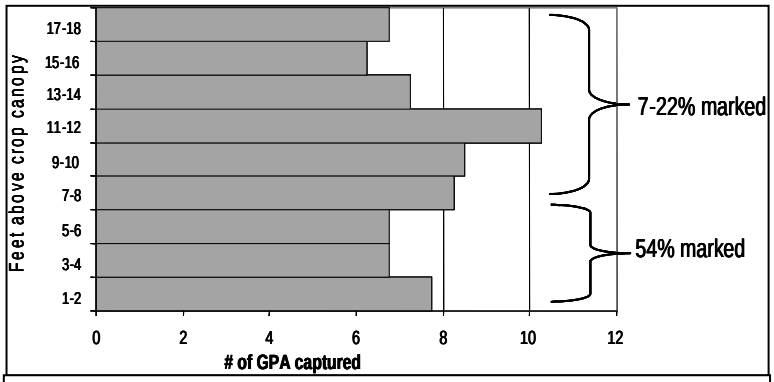



Figure 4. Marked GPA up to 18' above potatoes

advantages of the sticky netting are that larger insects are not retained and it is inexpensive ($0.04/ft$^2$). Our 2006 lab studies show that most aphids that walked over the egg residue become marked (85-100%). In field studies using a 16' by 16' plot of potatoes sprayed with egg albumen, 42% of aphids captured with the teepee trap were marked. With the 7 m tower, between 7 and 22% of aphids tested between 9 and 20 ft were marked, and more than 50% of those captured below 9 ft were marked (Figure 4). Finally, studies in the field using pan traps deployed at increasing distances form the central plot in a grid fashion provided captures up to 60 m from the source and marking rates between 0 and 50% (11% average; data not shown).

**2008 and Beyond**

Planned studies of movement by GPA and possibly other aphids will consist of marking sources of aphids near potato fields, followed by capture in mesh trap and testing for the mark. If captures of marked aphids confirm our hypothesis that aphids are arriving to new potato fields from selected weedy sources we will begin experiments to test alternative control approaches that will either control aphids before they reach potatoes or will reduce pesticide use in potato fields. Three specific approaches are being considered: control of aphids directly on the weedy source plants, such as patches of nightshade on field borders, where irrigation overspray supports plants and aphids; planting attractive trap crops on field borders combined with use of systemic insecticides in the trap crop; use of a quick knockdown insecticide (pyrethroid) or one that disables aphid vectoring (Fulfill) just on field margins reducing spread throughout the field by incoming viruliferous aphids. Finally, my lab will pursue improved trap designs better suited for fieldsmen use for aphid monitoring

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