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What is the source of potato psyllids colonizing Washington, Oregon, and Idaho potato fields?

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In the early- to mid-1900's potato psyllid was a sporadic but highly damaging pest in potato and tomato crops, largely along a north-south corridor on either side of the Rocky Mountains. Damage was caused by outbreaks of a plant disorder ("psyllid yellows") due to feeding activities of the psyllid. In the late 1900's and early 2000's, potato and tomato growers in the southern U.S. and northern Mexico began to experience outbreaks of a new type of damage, initially of unknown cause but eventually found to be associated with potato psyllid and a bacterium vectored by the psyllid (reviewed in Munyaneza 2012). The disease in potatoes leads to streaking of tubers ("zebra chip") and substantial losses in yields. Zebra chip was first observed in northern Mexico in 1994, and has expanded its range steadily northwards since that initial appearance to reach the major potato growing regions of Washington, Oregon, and Idaho in 2011 (Fig. 1).

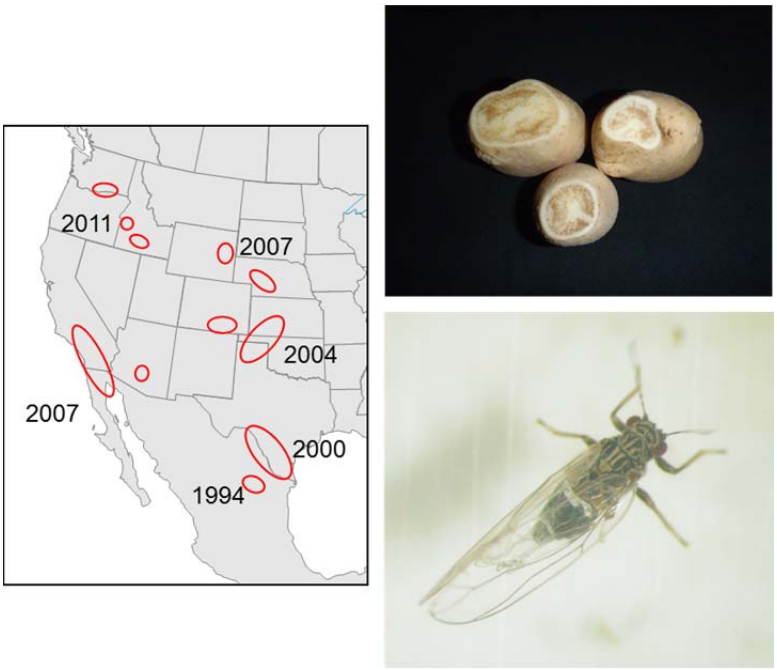

Figure 1. First detection of zebra chip disease (data from multiple sources).

Efforts to manage zebra chip disease in Washington, Oregon, and Idaho (hereafter, "PNW") are complicated by an inability to answer a simple question: What is the source of psyllids colonizing potatoes in these states? In the absence of this information, growers are faced with difficulties in predicting when and in what numbers psyllids will arrive in a field, combined with uncertainties in predicting where hotspots are likely to develop. While it might seem a simple matter to determine the source of psyllids arriving in fields, the answer is actually fairly complex, for two reasons. First, there has been historical acceptance that psyllids in northern growing regions are migrants that recolonize the region each year from breeding areas in the southern U.S. and northern Mexico. This historical interpretation has tended to color our views in understanding epidemiology of zebra chip, and we are only now beginning to reevaluate this thesis. A second issue is the failure until quite recently to appreciate that potato psyllid actually comprises a mixture of genetically differentiated populations ("haplotypes"), each with an incompletely described biology. Here, we summarize the timeline of discoveries that have led to our current understanding of psyllid presence in the PNW growing region.

Overwintering, dispersal, and the haplotype issue

A common theme in the early- to mid-1900's was that the northern geographic limits of potato psyllid were governed by the psyllid's capacity to survive freezing temperatures, combined with an absence of host plants suitable for psyllid survival in late winter and early spring preceding the potato crop. Thus, there were two perceived seasonal bottlenecks that affected how far north the psyllid could overwinter (Fig. 2). First, overwintering in the PNW would require the psyllid to have a level of winter cold-hardiness that allows it to survive freezing temperatures. Many species of psyllids have this winter capability, so cold-hardiness in potato psyllid should not be unexpected. In fact, many species of psyllids overwinter off of their host plants (often on perennial "shelter" plants, such as conifers), thus winter survival occurs even in the absence the host plant. The second bottleneck is perhaps more important. This limiting factor is the apparent lack of plants that the psyllid can survive upon between the end of overwintering and the appearance of the potato crop (Fig. 2: "host plant bridge"). Once temperatures begin to warm in late winter, the psyllid requires a plant host suitable for feeding and survival. Economic entomologists struggled with this question throughout the mid-1900's in trying to explain the psyllid's summer presence in northern states, but with no clear resolution of the problem.

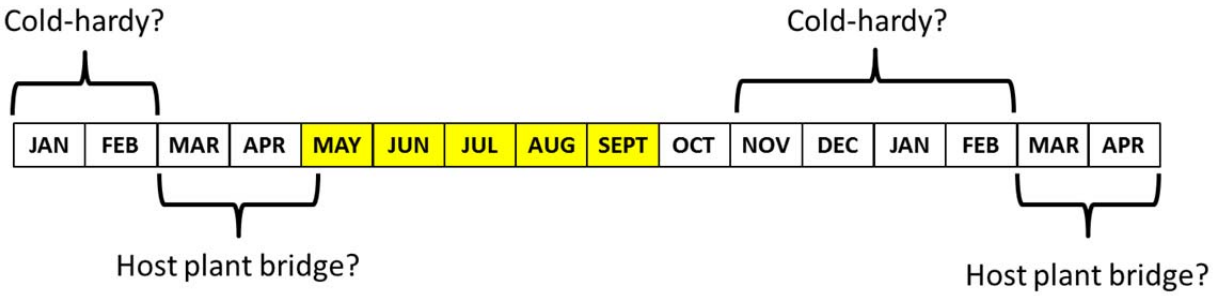

Figure 2. Hypothesized bottlenecks limiting northern residency of potato psyllid. Yellow: potato crop.

Given these perceived limiting factors, summer presence of the psyllid in outbreak regions along the Rocky Mountain corridor was assumed to be due to psyllid dispersal from winter breeding grounds in southern Texas and neighboring areas (Fig. 3A). Winter populations of the psyllid are readily visible on non-cultivated plant hosts in south Texas and northern Mexico, extending westward to Baja California and southern California. The psyllid then often disappears completely in summer from the warmer of these overwintering regions, apparently in response to summer heat, about at the time that it begins to show up in regions north of the overwintering area. The absence of obvious overwintering populations in those northern states, combined with an apparent lack of suitable hosts in early spring, led to the 1900's consensus that summer populations of psyllids in northern potato crops arrive there as migrants

from southern overwintering grounds (Fig. 3A) rather than as locally overwintered residents. That view is only now being reevaluated, prompted by a mix of molecular and biological study.

A molecular analysis led to the discovery in the mid-2000's (Liu et al. 2006) that psyllids from California and Baja California differed genetically from psyllids of north-central Mexico and the central U.S. (Fig. 3B: blue vs green circles), leading to their labeling as distinct genetic types, or haplotypes: Western haplotype (green circles) and Central haplotype (blue circles). Additional molecular analysis in 2011 confirmed that psyllids from potato crops in the central U.S. comprised largely or exclusively psyllids of the Central haplotype, and that populations of the psyllid westward of these sampling locations became increasingly or solely of the Western haplotype (Fig. 3C; Swisher et al. 2012).

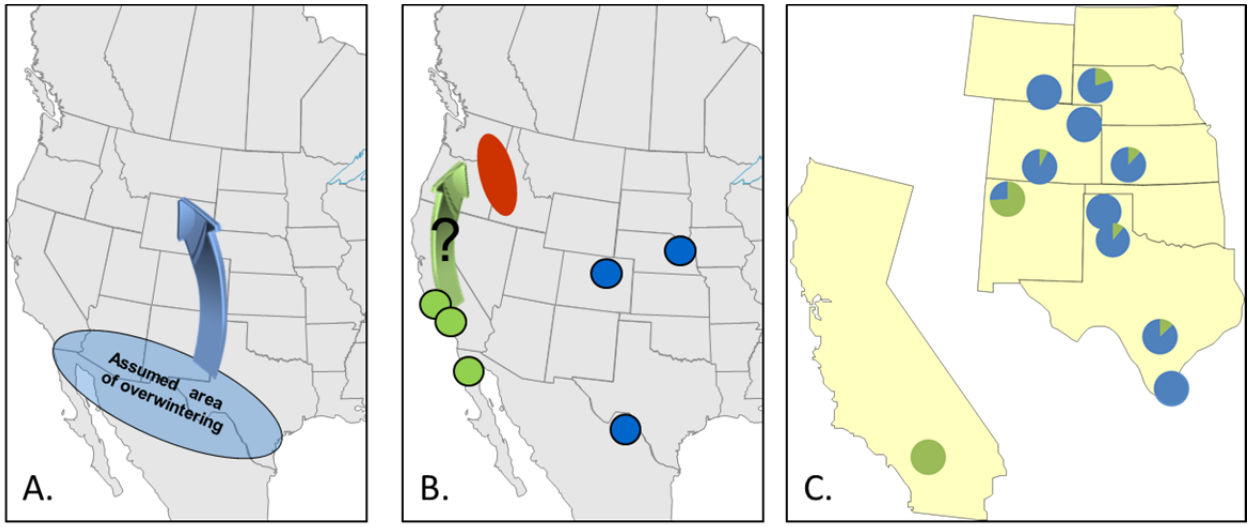

Figure 3. (A) Historical interpretation of psyllid outbreaks along Rocky Mountain corridor. (B) Discovery of Western (green), Central (blue), and Northwestern (red) haplotypes (2006-2012), and original hypothesis for source of psyllids responsible for the 2011 zebra chip outbreak (green arrow). (C) Haplotype frequencies in potato/tomato fields of the central U.S. and southern California (modified from Swisher et al. 2012); Western (green), Central (blue).

The discovery that potato psyllid comprises a mixture of genetic types was accompanied in 2011 by an outbreak of zebra chip in Washington, Oregon, and Idaho. The Western haplotype was abundant in heavily damaged potato fields in these locations (Swisher et al. 2012), and the assumption was that infective psyllids of this haplotype had dispersed northwards from southern coastal regions (Fig. 3B: green arrow). This led to the idea that there might actually be two routes of dispersal northwards, one along the Rocky Mountain corridor (Central haplotype), and a second along the coastal states (Western haplotype). As a final complicating factor, a third haplotype (Northwestern) was discovered in 2012 at locations in Washington, Oregon, and Idaho (Fig. 3B: red oval; Swisher et al. 2012). This haplotype has yet to be found outside of these 3 states, suggesting that it overwinters in these states rather than arriving there as a migrant from southern regions.

Bittersweet nightshade and potato psyllid: an essential PNW association?

With the idea that at least one haplotype of potato psyllid is resident in the northwestern U.S., a search was initiated to discover overwintering and early spring (pre-potato) hosts of the psyllid. A perennial nightshade, bittersweet nightshade (*Solanum dulcamara*), was found to support winter populations of potato psyllid in Oregon, Washington, and Idaho (Jensen et al. 2012, Murphy et al. 2013). This plant is an introduction from Europe, and is the only common perennial *Solanum* in the Pacific Northwest. Herbarium records indicate that bittersweet nightshade has been in the PNW since at least the 1890's. The plant grows in large stands often near water and fence lines, and overwinters as a mat of dormant, above-ground stem material (Fig. 4). Adult and immature potato psyllids are found on dormant stems

throughout winter. Because of its perennial life history, bittersweet nightshade allows egglaying by the psyllid very early in the new season. Adult psyllids containing mature eggs can be collected from nightshade all winter (Fig. 5). Females exhibit a burst of egg maturation in late March with the first appearance of new foliage (Fig. 5: red oval), accompanied by egglaying on the weed. The psyllid appears to complete a post-winter generation on nightshade in the Pacific Northwest, before emergence of the potato crop (Jensen et al. 2012, Murphy et al. 2013).

Figure 4. Large stands of *Solanum dulcamara* in spring and in winter.

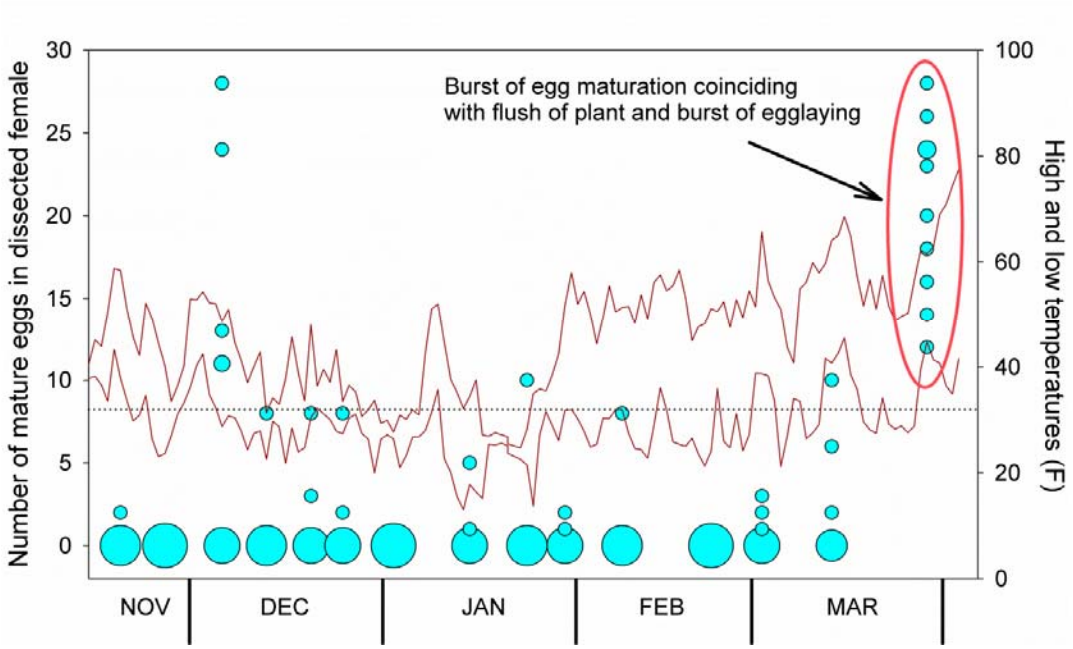

Figure 5. Number of mature eggs (left axis) in dissected females collected from bittersweet nightshade throughout winter. Size of blue circle is proportional to frequency of females in that egg maturity class. Light brownish lines show high and low temperatures at collection site (right axis).

Evidence is also beginning to suggest that bittersweet nightshade may be an overwintering host primarily for a single haplotype, the Northwestern haplotype (Fig. 6). Psyllids collected from potato fields in Idaho, Oregon, and Washington may comprise a mixture of haplotypes at the end of the growing season, with a suggestion that the local resident (Northwestern haplotype) increases in relative abundance as we move northwards. However, this mixing of haplotypes seems to disappear in winter for psyllid populations collected from bittersweet nightshade (Fig. 6; Swisher et al. 2013). Despite the

presence of the Western and (in limited numbers) Central haplotypes in potatoes during the growing season, apparently neither haplotype is present in high numbers in winter on nightshade. Either these two haplotypes overwinter other than in association with bittersweet nightshade, or they fail to overwinter in the PNW in appreciable numbers.

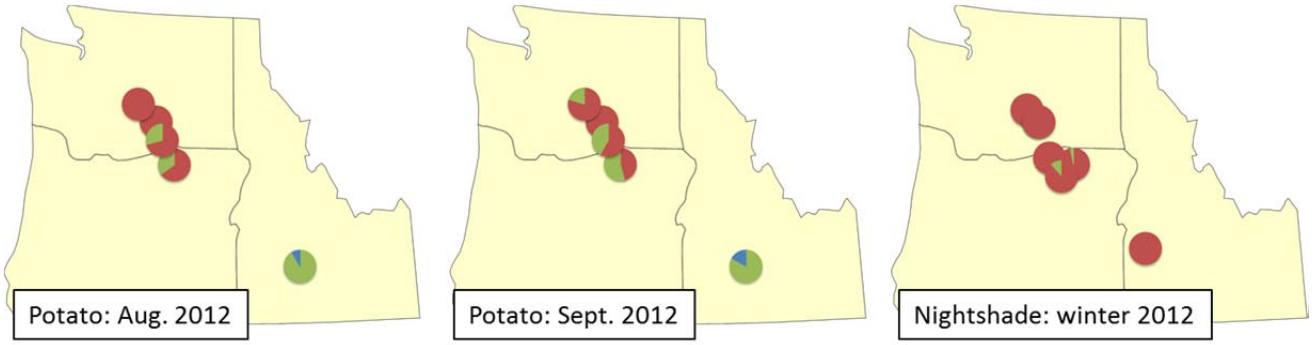

Figure 6. Haplotypes in potato fields (late summer 2012) and overwintering on bittersweet nightshade at multiple locations in the PNW. Modified from Swisher et al. (2013). Haplotypes: Northwestern (red), Western (green), and Central (blue).

Finally, we are now beginning to surmise that bittersweet nightshade – in addition to acting as a "bridge" host – is also a critical part of the psyllid's winter physiology. Late summer psyllids of the Northwestern haplotype that are collected from potato and then allowed access to bittersweet nightshade will rapidly develop an ability to survive temperatures at least as low as 10 ^{o}F (Fig. 7). Psyllids that were denied access to nightshade had substantially lower survival. Interestingly, this response may not be universal across haplotypes. Psyllids of the Central haplotype showed a similar induced response to nightshade, although with lower survival on either host than psyllids of the Northwestern haplotype, whereas no psyllids of the Western haplotype survived the 10 ^{o}F exposure (Fig. 7). These preliminary data suggest that psyllids of the Western haplotype – the presumed source of the 2011 ZC outbreak in the PNW – are not able to survive temperatures that the other two haplotypes are able to tolerate.

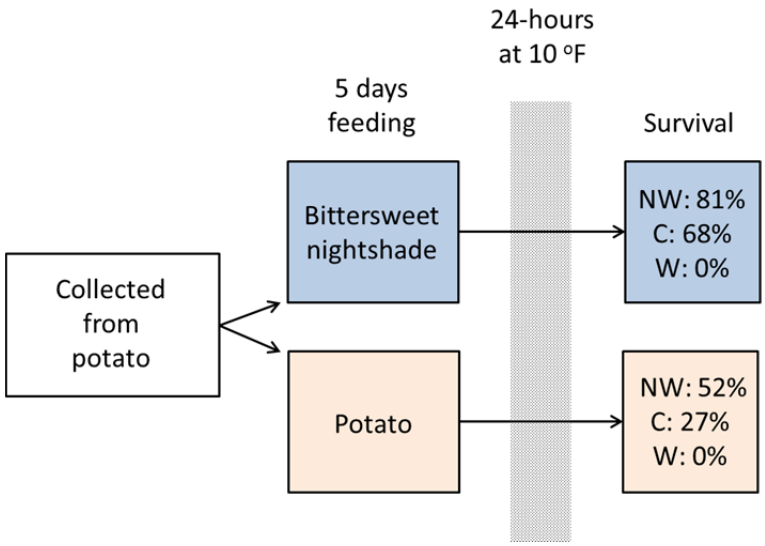

Figure 7. Induced cold-hardiness of Northwestern and Central haplotypes prompted by feeding on bittersweet nightshade. NW: Northwestern haplotype; C: Central haplotype; W: Western haplotype.

Conclusions and Questions

Outbreaks of potato psyllid along the Rocky Mountains have confounded entomologists since the early 1900's, due to uncertainties about the geographic source of psyllids in these regions. That shortcoming in knowledge complicates our efforts to manage potato psyllid and zebra chip in Washington, Oregon, and Idaho. The issue is now more complex than it was last century given our recent realization that potato psyllid actually comprises a mixture of genetic types that appear to differ in geographic distribution, cold-hardiness, and dispersal tendencies. Entomologists of the mid-1900's realized that an understanding of psyllid outbreaks in northern growing regions requires answers to two questions: (1) Is the psyllid cold-hardy enough to overwinter in those northern regions? (2) If so, what plant species are available in early spring to act as a "bridge" between the overwintering state and colonization of the germinated potato plant in late spring? We have made progress over the last several years in addressing these two questions, particularly with the realization that an introduced perennial weed, bittersweet nightshade, is likely to be an important part of the psyllid's overwintering and post-winter life history. However, many questions remain unanswered and merit our attention. Of these, we consider the following to be the most important:

- Are other perennial relatives of potato and bittersweet nightshade "bridge" hosts for the psyllid?
- Does the zebra chip pathogen overwinter in the PNW?
- Do non-host "shelter plants" such as conifers contribute to psyllid overwintering, much as they do for many other psyllid species?
- Do haplotypes other than the Northwestern haplotype overwinter in the PNW?
- How much movement is there by psyllids between nightshade and potato, and what factors (host or environment) govern this movement?
- Do volunteer potatoes or cull piles have a role in the post-wintering biology of the psyllid?

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