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Matrimony vine and potato psyllid in the Pacific Northwest: a worrisome marriage?

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Until the 2011 growing season, potato psyllid was considered to be primarily or strictly a problem in regions outside of Washington, Idaho, and Oregon. This bit of complacency is fairly understandable. Despite a history of psyllid outbreaks in North America known from at least the late 1800s, no wide-scale damage had been seen in regions of the Pacific Northwest, outside of some hotspots in southeast Idaho (Fig. 1). Indeed, the accepted wisdom in the 1900s was that potato psyllid was unable to overwinter in northern latitudes, and that outbreaks extending into Montana and similar latitudes were due to dispersal by psyllids northwards from winter and spring habitats in the southern U.S. and northern Mexico (Fig. 1).

The perception that potato psyllid was not a concern in the Pacific Northwest was shattered in 2011, when an outbreak of zebra chip disease caused substantial economic damage in all three states. Five years later, we still do not know what conditions led to that outbreak. The most important question was and continues to be: what are the sources of potato psyllids that colonize potato fields in late May and early June? Not knowing the source of psyllids makes it difficult to predict when potato psyllids will arrive, and impossible to predict in what fields the psyllids

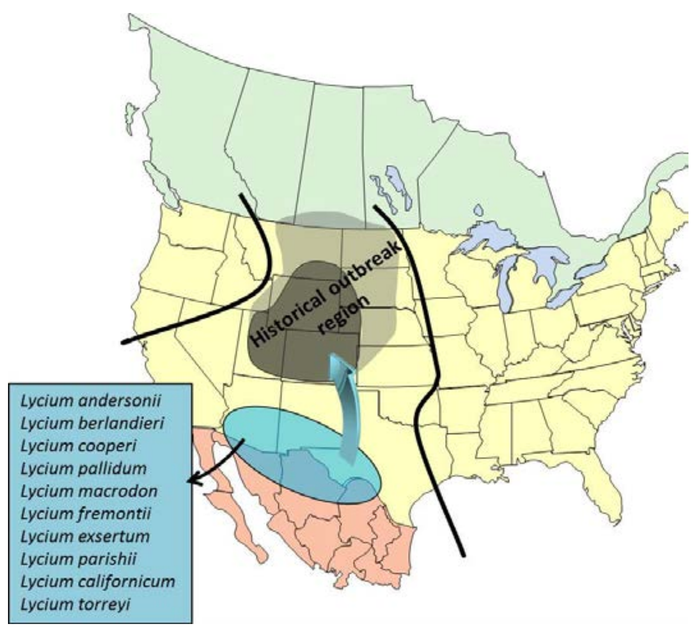

Figure 1. Known or potential winter/spring *Lycium* host plants of potato psyllid in the southern U.S., and hypothesized route of dispersal from this region. Developed from information in Romney 1935, 1939; and Wallis 1955.

will arrive. We are becoming more convinced that psyllids in potato fields of the Pacific Northwest are year-round residents, not migrants from more southern regions, and that they show up in crop fields as local migrants from non-crop hosts. The difficulty is in testing this hypothesis.

With the aid of a $2.7 M grant from the USDA's Specialty Crop Research Institute, we are beginning to address this question (WSU News; https://news.wsu.edu/2015/10/05/wsu-receives-2-7-million-to-research-costly-potato-threat). These funds, awarded to Washington State University, are allowing scientists in Washington, Oregon, and Idaho to examine what non-crop species contribute to psyllid colonization of potato. We are taking a three-pronged approach in addressing this question: examination of genetic similarity of psyllid populations on crop and non-crop plants; landscape-wide modeling of host plants and psyllid hot spots; and molecular detection of plant DNA in psyllid colonists. These approaches will be discussed in more detail below. What is needed for all approaches, however, is that we first have some idea about psyllid numbers and phenology on targeted non-crop species. Our first efforts have looked at species of *Lycium*, perennial plants in the Solanaceae that are widespread in arid regions of North and South America and that are known to host potato psyllid in the southwestern U.S. (Fig. 1). Our studies of *Lycium* began in 2014 with funding support from the Northwest Potato Research Consortium, and the research continues into and beyond 2016 with SCRI support.

In this report, we update our results from 2+ years of monitoring of *Lycium* at locations in WA, ID, and OR. This work suggests that phenology of *Lycium* and potato psyllid in the Pacific Northwest is strikingly similar to what occurs in southern growing regions, and we will suggest that observations from the southern U.S. can be useful in understanding what is happening in the Pacific Northwest. The presence of *Lycium* in the Pacific Northwest, where it is not native, has a very interesting history, and we will discuss that history. Indeed, an understanding of this history provides clues about the geographic distribution of *Lycium* in the potato growing regions of the Pacific Northwest. Finally, our monitoring results provide circumstantial evidence that *Lycium* is a source of potato psyllid arriving in potato fields of the Pacific Northwest. We will show this circumstantial evidence, and then discuss how we are going about testing the evidence.

Figure 2. Multiple species of *Lycium* showing flowers and fruit

What is *Lycium*? There are about 85 species of *Lycium* worldwide, known variously as matrimony vine, Goji berry, desert thorn, and wolfberry. These plants have a perennial life cycle, are generally shrub-like in form (Fig. 2), and are often armored with thorns. The funnel-shaped or tubular flowers have five petals, and are purple, blue, or white in color (Fig. 2). Berries are fleshy and generally red or orange in color (Fig. 2). *Lycium* apparently originated in the deserts of South America, and the plants have important life history traits that allow them to flourish in regions of dry summer conditions. These plant traits in turn affect biology of potato psyllid, as we will show. *Lycium* is particularly common and widespread in the deserts of the southwestern U.S. and northern Mexico, and the plants are widely used as hosts by potato psyllid in these regions (Fig. 1). The two species of *Lycium* that occur in the Pacific Northwest are not native to the region, but are instead introductions from Eurasia. These two species have had an interesting history in colonization of the Pacific Northwest, and we will discuss some of that history in the following sections.

Lessons from the desert southwest. We have known since the early 1900s that species of *Lycium* are important host plants for potato psyllid in northern Mexico and the southern U.S. (Fig. 1). The plants are adapted to the arid conditions of these deserts, inhabiting arroyos, streambeds, or washes generally at elevations below 3000-4000 feet. One important species for potato psyllid is *Lycium andersonii*, known as Anderson's wolfberry or water jacket (Fig. 3). This plant is common in southern Arizona, New Mexico, and northern Mexico, and supports high densities of potato psyllid at certain times of the year (Fig. 3). Observations from the 1900s can be used to illustrate phenology of potato psyllid and *L. andersonii* in the desert southwest (Fig. 4). *Lycium andersonii*, like other *Lycium* species, has evolved an interesting way of surviving the dry summer conditions of its desert habitat. The shrubs have two seasonal intervals in which new foliar growth is put on, with the two intervals separated by leaf fall and 2-3 months of leafless summer dormancy (Fig. 4; see also photographs in Fig. 3). Leaf-drop and dormancy are induced by hot, dry conditions. In fact, artificial irrigation of *Lycium* has been shown to turn these deciduous shrubs into evergreen plants – thus, shrubs that receive irrigation will skip the mid-season leaf-drop and dormancy, and remain evergreen through the heat of the summer.

Figure 3. *Lycium andersonii*. Growth form (lower left), January and October flush, leafless summer dormancy, and flowers (lower right). The upper left panel shows adult, eggs, and nymphs of potato psyllid on *L. andersonii*.

Potato psyllid is at its highest densities on *L. andersonii* just preceding the plant's summer dormancy (Fig. 4). Summer leaf-drop prompts the psyllid to disperse, and it is at this time that a burst of movement northwards (Fig. 1) is thought to occur. It is also likely that some portion of the dispersing population remains in the region by moving to higher altitude locations where they either colonize stands of *Lycium* at the shrubs' high-elevation limits, or colonize high-altitude host plants of other genera (e.g., *Solanum*, *Physalis*, and *Nicotiana* are common representatives of the higher elevation flora of southern Arizona and New Mexico). Finally, it may be that potato psyllid, like its host plant, becomes quiescent in summer and remains at very low densities on or near the leafless shrub, possibly in leaf litter below the shrub. Once summer dormancy has ended, a new flush of foliage and flowers begins in September, and potato psyllid colonizes this new flush (Fig. 4). The source of these autumn colonists is not known, but could include psyllids returning from higher elevations or quiescent psyllids which had stayed with *Lycium* through the shrub's summer dormancy. A trickle of psyllids then overwinters on the winter-leafless *Lycium*, presumably in a quiescent state, until January when plant flush prompts a new round of egglaying.

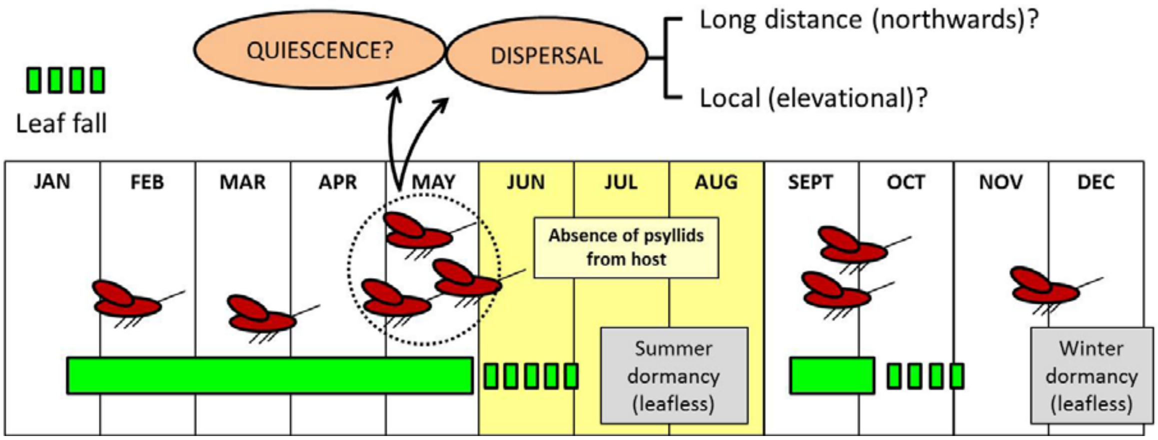

Figure 4. Phenology of *Lycium andersonii* showing timing of spring and autumn flush separated by summer (leafless) dormancy. Potato psyllid disappears from host during the summer dormancy. See Figure 3 for photograph of leafless plant in summer dormancy.

Matrimony vine: its arrival and spread in the Pacific Northwest. In 2014, we began monitoring stands of *Lycium* at multiple sites in WA, OR, and ID (Figs. 5-6). Two observations immediately became apparent during this monitoring. First, stands of *Lycium* are very common and widespread in the dry interior of the Pacific Northwest (Figs. 5-6). We will explore the reasons for this widespread presence in the following paragraphs. Second, phenology of potato psyllid and its *Lycium* host in the Pacific Northwest look very similar to what occurs in the desert southwest. This similarity is all the more striking given that the *Lycium* in the Pacific Northwest is not native to North America, but arrived here from Europe and Asia.

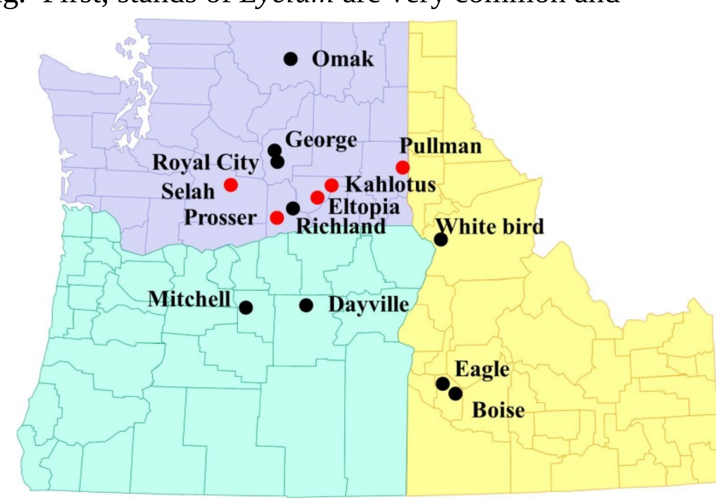

Figure 5. Locations of matrimony vine examined in WA, ID, and OR, all found to host potato psyllid. Red symbols: intensively sampled locations.

Two species of *Lycium* occur in the Pacific Northwest: *Lycium barbarum* and *Lycium chinense*. These shrubs are referred to collectively, and often without distinction, as matrimony vine and Goji berry. In popular accounts of *Lycium* in the Pacific Northwest, the common names are regularly used interchangeably

Figure 6. Stands of matrimony vine at multiple locations showing growth forms and surrounding habitat. The stand at George, WA is located in a region of old homesteads and a cemetery; the stone marking the cemetery states "*In memory of the Low Gap homesteaders who "claimed a desert" (1903-1920)"*.

and without accompanying taxonomic details. This practice has led to frustration for us in determining just what species are in the Pacific Northwest, and in determining how the plants arrived in the Pacific Northwest. Additional confusion is caused by difficulties in distinguishing between species. We have used both floral morphology and molecular methods to examine stands of *Lycium* from WA, ID, and OR. While there is both morphological evidence and molecular evidence that both *L. barbarum* and *L. chinense* are present in the Pacific Northwest, the evidence also argues for the presence of intermediate forms, possibly due to hybridization. We use "matrimony vine" and "Goji berry" interchangeably in this report, following the lead of the literature that we will be discussing.

Matrimony vine has had an interesting cultural history preceding and accompanying introduction into North America. Both *L. barbarum* and *L. chinense* are native to Eurasia, despite the New World origin of the genus. *Lycium* arrived in Asia apparently as a colonist from Africa. The African flora, in turn, is a consequence of dispersal from the Americas. The two species were domesticated in China, and have had a long and very important cultural connection with the Chinese people. The berries are popularly known as Goji, and have been used for centuries by the Chinese in teas, as dried condiments, as additions to soups and stews, and for medicinal purposes. Matrimony vine spread worldwide from this Asian locus, including into the Pacific Northwest. What is interesting for us is that matrimony vine has taken two quite different, human-assisted routes as it colonized the Pacific Northwest and spread through the region's dry interior. As we now discuss, these different routes help explain the current widespread distribution of matrimony vine in western North America.

Homesteads, railroads, and the North American gold rush. Matrimony vine is common throughout the dry interior of western North America (Fig. 7; green shading shows county presence). The shrubs colonized western North America through two quite different routes. One source of shrubs was the Euro-American settlers and homesteaders, who planted matrimony vine as they moved into the western U.S. in the 1800s and early 1900s. Stands of matrimony vine are found extensively around abandoned homesteads in the dry interior of northern California, eastern Oregon, and eastern Washington (Figs. 6 and 8). Some of these stands may be over a century old, surviving with continuous reseeding or by clonal growth. In some cases, the only indication that a site was actually the location of homestead is the presence of these old stands of matrimony vine – all other evidence for the homestead having long vanished. A mapping effort in early 2000 at the federal Hanford site in Washington State (Trumbo 2004, King 2015) led to the discovery of 50 or more discrete patches or stands of matrimony vine, many apparently associated with long-departed, pre-World War II homesteads (Fig. 6). The stand of matrimony vine that we monitored near George, WA (Fig. 5) is located in a site that apparently had been occupied in the early 1900s by homesteads and a cemetery (Fig. 6).

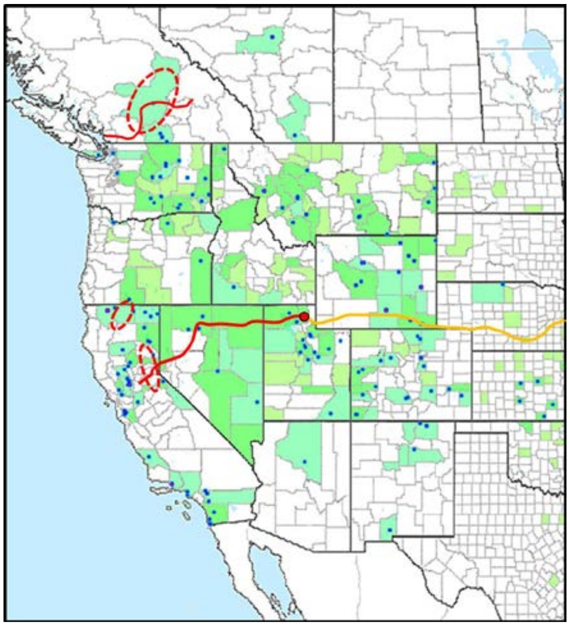

Figure 7. County-distribution of matrimony vine (green shading). Red and yellow lines show route of Transcontinental Railroad (U.S.), with red dot showing location east and west branches were joined (Promontory Summit, UT); red line in Canada shows route of Canadian Pacific Railroad. Red ovals in California and Canada show locations of 1850s-1860s gold rushes.

Figure 8. Matrimony vine growing along kitchen wall of the remnants of an old Oregon homestead (from Jackman and Long 1964).

Matrimony vine is actually more of a shrub than a vine, and was often trained to grow in an upright form along walls or the front and back porches of homesteads (Fig. 8). It has been suggested that these shrubs were planted by homesteaders as a source of something green in otherwise vegetation-poor regions, as well as a source of shade near the home itself. The following, from an article published in the 1940s, describes this history for a desert region (Silver Lake) in central Oregon (History of the Fremont National Forest 1940): *"This station [Silver Lake, Oregon] is located in one of the most desert-like valleys in the state of Oregon. Because it is dry and exposed to drifting sands, it is difficult to keep things growing, and the station well is not up to any very extensive irrigation. Hence anything that will grow without much water or attention and produce a spot of green is doubly welcome. Trumpet, or matrimonial vine as it is sometimes called, meets these specifications. With its abundance of small purple flowers and green leaves, this plant is a prominent feature of the desert country, growing wild about abandoned homesteads long after every other living thing, plant, or animal has given up the struggle"*. Shrubs growing next to houses may have received water as dishwater was disposed of through kitchen windows (Jackman and Long 1964). Some folklore has it that newlyweds planted matrimony vine on new homesteads to bless the marriage. Matrimony vine has been called a "pass-along plant", species in which "small rooted portions are lifted and gifted", often from mother to daughter, and this tradition helped the species spread between homesteads (Todt and Hannon 2016).

A vastly different route of arrival drove the colonization and spread of what is popularly referred to as Goji berry, a common name often used interchangeably with "matrimony vine". Waves of Chinese immigrants began arriving in San Francisco in the 1850s, and with these immigrants came components of their native culture, including traditional Chinese foods such as Goji berry. These immigrants arrived in the tens of thousands, escaping poverty and civil war in China, initially bound for the gold fields of California (Fig. 7). They were known as "Celestials" (with China as the "Celestial Kingdom"), and they made their way to California, traveling first to Hong Kong in junks, and from there jammed into the holds of sailing vessels in passage to San Francisco. Their hopes were to accumulate a few hundred dollars from the California gold rush, sufficient to provide for return home to China and a retirement of relative ease.

From San Francisco, the Celestials filtered not only into the gold fields of California, but became also a virtually indispensable source of labor in the completion of the section of the Transcontinental Railway between Sacramento and Promontory Summit in Northern Utah (the site that the western and eastern sections met and became joined; see red dot in Fig. 7). As large camps of Chinese workers became established in the gold fields or along railway lines, camp inhabitants spread Goji berry into these regions as they planted seed brought from China and as they disposed of their garbage in moving from work site to work site. Goji berry continued to spread as the Chinese moved opportunistically into other regions of North America, often fueled by additional immigration. The 1850s'-1860s gold rush in the Fraser River Valley of British Columbia led to substantial levels of Chinese immigration into British Columbia, and these regions now support populations of Goji berry (Fig. 7). In the 1880s, the western portion of the Canadian Pacific Railroad was built (Fig. 7), substantially with the help of Chinese immigrants. An estimated 17,000 Chinese came to work on the railroad, living often in tent cities along the planned route much as they did when working on the Transcontinental Railroad in the U.S. Goji berry spread with the Chinese laborers. The photographs in Figure 9 show a Chinese cemetery from the 1800s located near Kamloops, B.C., overgrown with Goji berry plants from seed apparently buried with occupants of the graves (Goad 2016). Swathes of Goji berry plants continue to expand in these regions as the seed is spread by rain, birds, and humans.

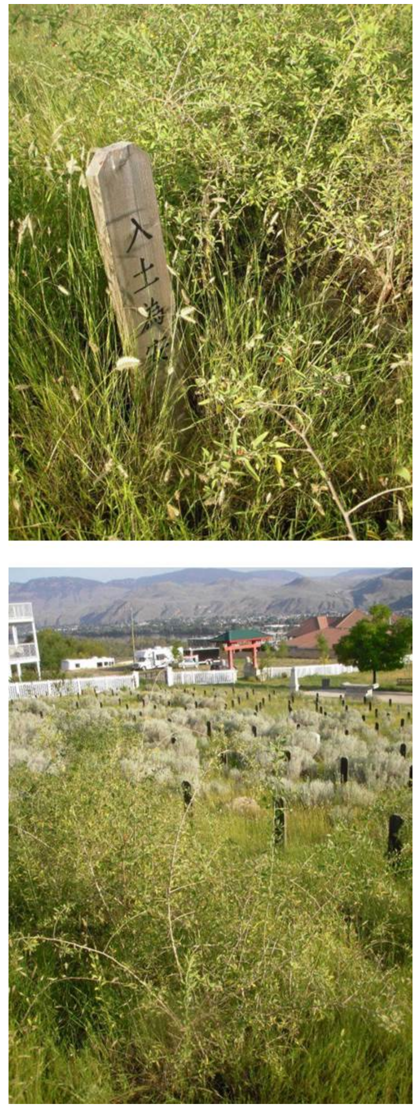

Figure 9. Cemetery for Chinese immigrants of the 1800s, Kamloops, B.C. Cemetery is overgrown with Goji berry plants (Goad 2016).

Matrimony vine as source of potato psyllid in the Pacific Northwest. All 14 stands of matrimony vine that we examined in WA, ID, and OR (Fig. 5) were found to be infested with potato psyllid. These populations are distributed over a broad geographic range, extending as far north almost to Canada and at least as far southwards into the Boise region of Idaho. These results suggest that association of potato psyllid with matrimony vine in the Pacific Northwest is common and widespread. At five locations (Fig. 5: red symbols), we sampled matrimony vine at 2-4 week intervals over the course of two years, to learn about phenology of potato psyllid in relation to phenology of matrimony vine. Sampling at these locations began in summer and autumn of 2014 and extended into late June 2016 (Fig. 10). Potato psyllid was monitored using a beating sheet (Fig. 6: see Prosser photograph). Over 8000 adult psyllids were collected during the two years summed across the five locations. Psyllid numbers sometimes reached quite high levels, exceeding 10 per tray at one location (Kahlotus) on several sample dates (Fig. 10). Psyllid phenology was characterized by two well-defined seasonal peaks, separated by intervals in which few or no adult psyllids could be collected. These peaks occurred fairly simultaneously across locations, and included a late spring peak in May and early June (Fig. 10: blue shading), and a mid-autumn peak in October (Fig. 10: red shading). The May/June peak in adult numbers was preceded by large numbers of eggs and nymphs on spring flush (Fig. 11). Population trends at the Pullman location were somewhat different from the other sites, in that psyllids remained visible on matrimony vine even in mid-summer, possibly because precipitation in the Pullman region is sufficiently high to keep the shrub green through the growing season (see next paragraph).

Population trends of potato psyllid on matrimony vine in the Pacific Northwest are strikingly similar to phenology of the psyllid on *Lycium* in the desert southwest. Potato psyllid often increased to high numbers in May and June (although not at all sites both years), but then seemingly disappeared from the host plant at all locations except Pullman during the hot and dry conditions of late-June through August and into September. Matrimony vine exhibited the same response to hot, dry summer conditions as shown by its relatives of the desert southwest (Fig. 12). Except at the higher-precipitation location (Pullman), leaves began turning yellow in mid- to late-June, and then dropped from the plant either partially or completely (Fig. 12). At the Pullman site, shrubs remained mostly green during the summer. Following the summer interval of shrub dormancy, new growth began in September and October, and potato psyllid increased to often large numbers on this new growth preceding winter – just as what is observed on *Lycium* in the desert southwest (Fig. 4). The source of these autumn psyllids is unknown.

So, is matrimony vine a source of psyllids colonizing potato fields in the Pacific Northwest? We end this article with some discussion of how our SCRI-funded project is addressing this question. We pooled the matrimony vine data from all locations except the Pullman site, and show these phenology data (Fig. 13: gray shading) overlain on the psyllid data from the WSU trapping network (Fig. 13: solid circles and lines). The WSU data show percentage of potato fields in which potato psyllid was trapped, with the data taken directly from graphs shown in the weekly WSU-Potato Pest Alerts (http://us13.campaign-archive2.com/home/?u=2eff8714011ff4bfba18a0704&id=9dc1a6349a). Psyllids began showing up in potato fields at virtually the same time that they were disappearing from matrimony vine, coinciding with the onset of summer defoliation. We show visually what we think is happening by use of a simple (and highly speculative) model (Fig. 14), basing the model on our 2015 sampling results. Yellowing and deterioration of the matrimony vine host in June prompts movement off of matrimony vine and into potato (Fig. 14: red shading). This interval is followed by in-field reproduction and spread of the psyllid among potato fields (Fig. 14: blue shading), possibly supplemented by arrivals of psyllids from other non-crop plants such as bittersweet nightshade. Vine kill in late summer likely prompts psyllids to disperse from potato fields, and it is possible that this dispersal may contribute to the autumn build-up of psyllids on newly flushed matrimony vine. Psyllids then overwinter in low numbers on matrimony vine, followed by at least one generation on new spring foliage in March-May preceding movement into potato fields.

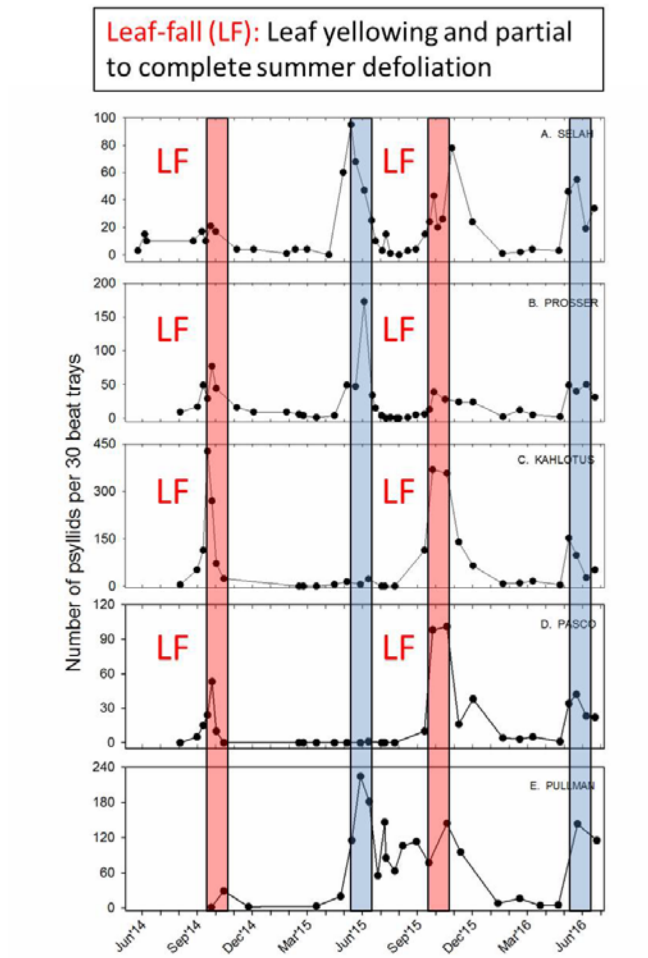

Figure 10. Beat tray counts of potato psyllid on matrimony vine showing spring (blue shading) and autumn (red shading) peaks in numbers, separated by intervals of very low psyllid numbers. "D. Pasco" is the Eltopia location of Figure 5.

Figure 11. Eggs and nymphs on new growth of matrimony vine, Selah WA.

Figure 12. Spring flush of matrimony vine followed by summer deterioration and partial to complete leaf loss at two WA locations.

How are we testing this model? Our SCRI-funded work includes three approaches. First, we are using population genetics to examine psyllid movement between non-crop and crop hosts. These methods look for similarity in genetic composition of populations in different habitats. If populations are highly similar genetically across host species, we infer that there is psyllid movement between hosts. Second, we are examining landscape-scale patterns in distribution of host plants, psyllid hot spots, and potato fields, looking for spatial patterns in non-crop species that might explain spatial patterns in what fields are being infested. Are fields that are rapidly colonized also those that are near large stands of matrimony vine? Lastly, we have developed a molecular approach to detect and identify plant DNA in potato psyllids. By collecting psyllids as they arrive in potatoes, and then assaying them, we are able to determine what species of plants the psyllids had been feeding on before arriving in potato. A consistently strong signal of matrimony vine in these arrivals would be good evidence for movement from matrimony vine into potato fields.

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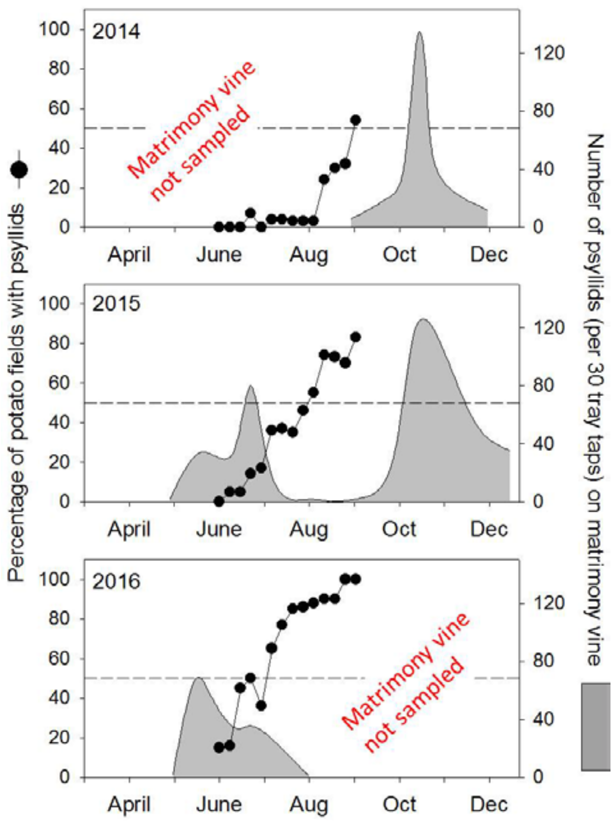

Figure 13. Psyllid numbers on beat trays in matrimony vine averaged over 4 locations (gray shading), in relation to seasonal progression of infestation of potato fields (lines plus black circles; from WSU-Potato Pest Alerts).

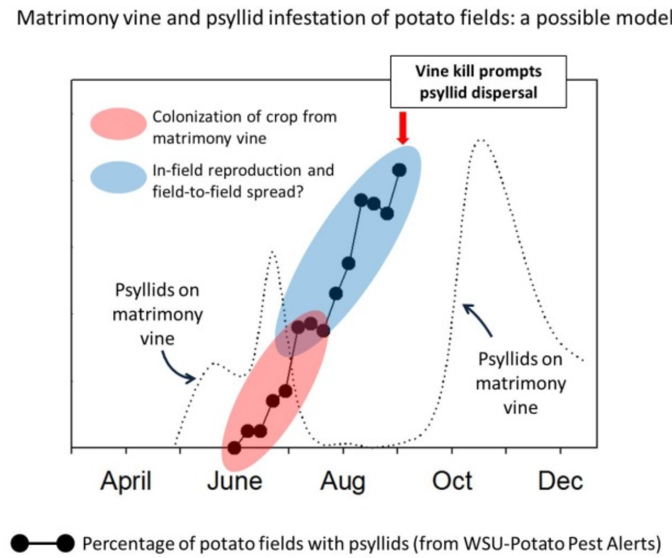

Figure 14. Hypothetical involvement of matrimony vine in the infestation of potato fields by potato psyllid, WA-OR-ID.

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http://climbers.lsa.umich.edu/wp-content/uploads/2013/07/LycibarbSOLAFINAL.pdf (discusses common names of *Lycium*, biology, cultural aspects of Goji berry)

http://1-2.cnhwildflowers.appspot.com/map?Lycium_barbarum (distribution map for matrimony vine used in Figure 7)

http://bonap.net/NAPA/TaxonMaps/Genus/County/Lycium (U.S. distributions maps for native and introduced *Lycium*)

http://www.phoenixtearsnursery.com/virtual-tour.html (discusses Chinese laborers and Goji berry at Promontory Summit, where the eastern and western branches of the Transcontinental Railroad were joined)

http://www.westcoastplacer.com/top-ten-gold-rushes-of-bc-part-1 (discusses the Canadian gold rushes of the 1850s and 1860s)

https://en.wikipedia.org/wiki/First_Transcontinental_Railroad (discusses Chinese immigrants and the Transcontinental Railroad)

Photographs

Web-links to photographs used in this article are provided here. Unless other stated, permission for use of photographs is authorized under Creative Commons license or Fair Use provision of U.S. Copyright law. Photographs in **Figures 11 and 12** were taken by co-authors of this manuscript.

Figure 2. Clockwise from top left. (1) *Lycium fremontii*; photograph by Mike (https://commons.wikipedia.org/wiki/File:Lycium_fremontii_az.jpg). (2) *Lycium chinense*/*L. barbarum*; photograph of authors. (3) *Lycium chinense* flower; photograph by Pancrat (https://commons.wikimedia.org/wiki/File:Lycium_chinense_jd_plt_fleur2.jpg). (4) *Lycium andersonii*; photograph by Max Licher (http://swbiodiversity.org/seinet/imagelib/imgdetails.php?imgid=216075). (5) berries of *Lycium andersonii*; photograph by Thomas Van Devender (http://swbiodiversity.org/seinet/taxa/index.php?taxon=3873).

Figure 3 *Lycium andersonii*. Clockwise from top left. (1) Potato psyllids on *Lycium andersonii*; photograph by Alice Abela, used with permission of A. Abela (http://www.flickriver.com/photos/44150996@N06/26236279211/). (2) January flush; photograph by Keir Morse (http://calphotos.berkeley.edu/cgi/img_query?enlarge=0000+0000+1215+2904). (3) Summer defoliation; photograph by Jean Pawek (http://calphotos.berkeley.edu/cgi/img_query?enlarge=0000+0000+0813+1498). (4) Flowers; photograph by Steve Matson (http://calphotos.berkeley.edu/cgi/img_query?enlarge=0000+0000+0510+2399). (5) October flush; photograph by Jason E. Willand, used with permission of J. Willand (http://calphotos.berkeley.edu/cgi/img_query?enlarge=0000+0000+1207+1607). (6) Growth form; photograph by Br. Alfred Brousseau, Saint Mary's College, used with permission of Saint Mary's College (http://calphotos.berkeley.edu/cgi/img_query?enlarge=6205+3041+0703+0025).

Figure 6 Matrimony vine. (1) Top left: photograph by Merel R. Black (UW-System WisFlora. 2016. http://wisflora.herbarium.wisc.edu/imagelib/imgdetails.php?imgid=17491). (2) Bottom left: photograph by Danny S. (https://commons.wikimedia.org/wiki/File:Lycium_barbarum-46.JPG). All other photographs taken by co-authors.

Figure 8 Matrimony vine adjacent to abandoned homestead. Photograph by Merrit Parks; downloaded from Oregon State University Special Collections & Archives Research Center (http://oregondigital.org/sets/osu-scarc/oregondigital:df70cq97c).

Figure 9 Goji berry and cemetery for Chinese immigrants. Photographs by Janis Goad, used with permission of J. Goad (http://hubpages.com/health/Goji-Berries-a-Traditonal-Chinese-Herb).

Illustrations

Figure 7. Map showing distribution of *Lycium barbarum* was created by Steven K. Sullivan (http://1-2.cnhwildflowers.appspot.com/map?Lycium_barbarum) and modified by co-authors of this paper to show railroads and regions of the North American gold rushes. The records for *L. barbarum* used in creating the distribution map were obtained from a number of herbaria (summarized at http://wildflowersearch.com/general_credits).