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The beet leafhopper odyssey in North America: a brief overview

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In 2002, a disease in potatoes known as "purple top" emerged as a management issue for Columbia Basin potato growers. The disease was found to be caused by a bacterium-like organism known as a phytoplasma, now known as the *Beet leafhopper transmitted virescence agent* (or BLTVA for short). Symptoms of infection include upward leaf curling and purpling (Fig. 1C-D), swollen nodes and production of aerial tubers, early die-down, yield loss, and reduced tuber quality. BLTVA is moved from plant-to-plant during the feeding activities of a small insect known as beet leafhopper (Fig. 1A-B). In this article, we provide an overview of beet leafhopper and its biology in the Columbia Basin. The leafhopper story in potatoes actually began in a different crop, sugar beets. Outbreaks of a serious virus disease of beets ("*curly top*"; Fig. 1E) later traced to the feeding activities of beet leafhopper prompted a large research effort in the early- to mid-1900s to examine the leafhopper's ecology in western North America. Much of what we know about the insect's field biology stems from that research. Beet leafhopper was found to have a complex life cycle, one that complicates managing purple top for today's potato growers. Our overview will include an historical account of the beet leafhopper in western North America, a discussion of the insect's life cycle, and a look at the role of non-native plant species in allowing residency of the leafhopper in the Columbia Basin. Our overview will end with a discussion of a planned collaborative project between ARS, WSU, and OSU researchers to examine biology of beet leafhopper and the purple top phytoplasma in the Columbia Basin.

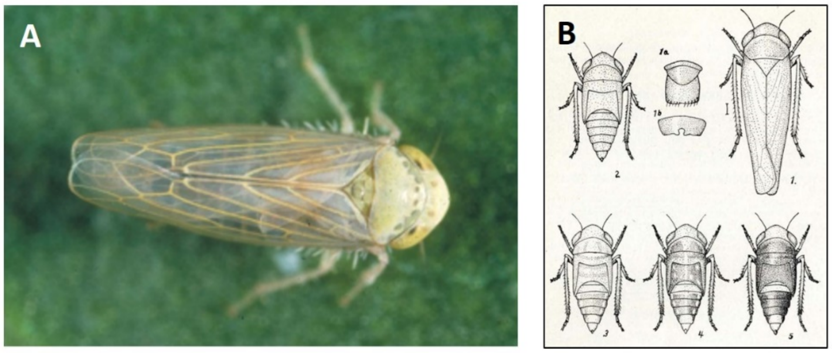

Figure 1. (A) Beet leafhopper adult. (B) Drawings from early 1900s monograph (Ball 1917) showing adult and late-stage immature of beet leafhopper; bottom row of drawings shows the range in color of the late-stage immature. (C-D) Phytoplasma-infected potato with purple top symptoms. (E) Characteristic symptoms of sugar beets infected with *Beet curly top virus*.

WHAT IS BEET LEAFHOPPER?

Beet leafhopper (*Circulifer tenellus*) is in the Family Cicadellidae and Order Hemiptera (e.g., aphids, whiteflies, psyllids, etc.). The adult insect is relatively small (3-3.5 mm in length), somewhat wedge-shaped with body narrowing at the posterior end, and greenish-yellow in color (Fig. 1A) although darker in wintering adults. The insect's head is rounded (not pointed) in front and has no or only faint spotting, unlike many other leafhopper species found in potato fields. Leafhoppers insert their eggs into tissues of their host plants. Newly hatched leafhoppers are wingless and proceed through five stages before becoming adult. The leafhopper is readily monitored in potato fields using sweep nets or sticky cards. Sweep nets are also used regularly to monitor beet leafhopper in non-agricultural settings.

Beet leafhopper feeds by inserting its needle-like mouthparts into plant tissues and sucking up plant juices. The insect develops on a number of plant species, but prefers mustards and amaranths (e.g. Russian thistle, sugar beet). Beet leafhopper also readily feeds on plant species that do not support development. Like many other leafhoppers, beet leafhopper is a vector of plant pathogens, and the insect's willingness to feed on plant species that do not support development means that it transmits pathogens to a variety of non-host crops. Plant pathogens vectored by beet leafhopper include BLTVA; *Beet curly top virus* which causes disease in multiple crops other than potatoes, most notoriously sugar beets (discussed extensively below); and *Spiroplasma citri*, the cause of disease in a number of crops including a disease of carrots in the Columbia Basin known as carrot purple leaf disease.

OUR CURRENT UNDERSTANDING OF LEAFHOPPER BIOLOGY RELIES EXTENSIVELY ON EARLY- TO MID-1900S RESEARCH ON A DISEASE OF SUGAR BEETS

Our understanding of beet leafhopper biology in the U.S. is largely a consequence of the insect's role in the struggles of the sugar beet industry during the late-1800s into the mid-1900s. Figure 2 summarizes notable events during this interval, starting with arrival of the sugar beet industry in the western U.S. in the 1870s, although the story actually begins a century or more earlier with arrival of the leafhopper in North America. Beet leafhopper is an Old World (Mediterranean) import, presumed to have arrived in the Americas with Spanish explorers several centuries ago. The Mediterranean origin of the insect was not realized until the 1940s (Fig. 2). As we show below the leafhopper's Mediterranean origin may help explain its host affinities, life cycle, and residency in the Columbia Basin.

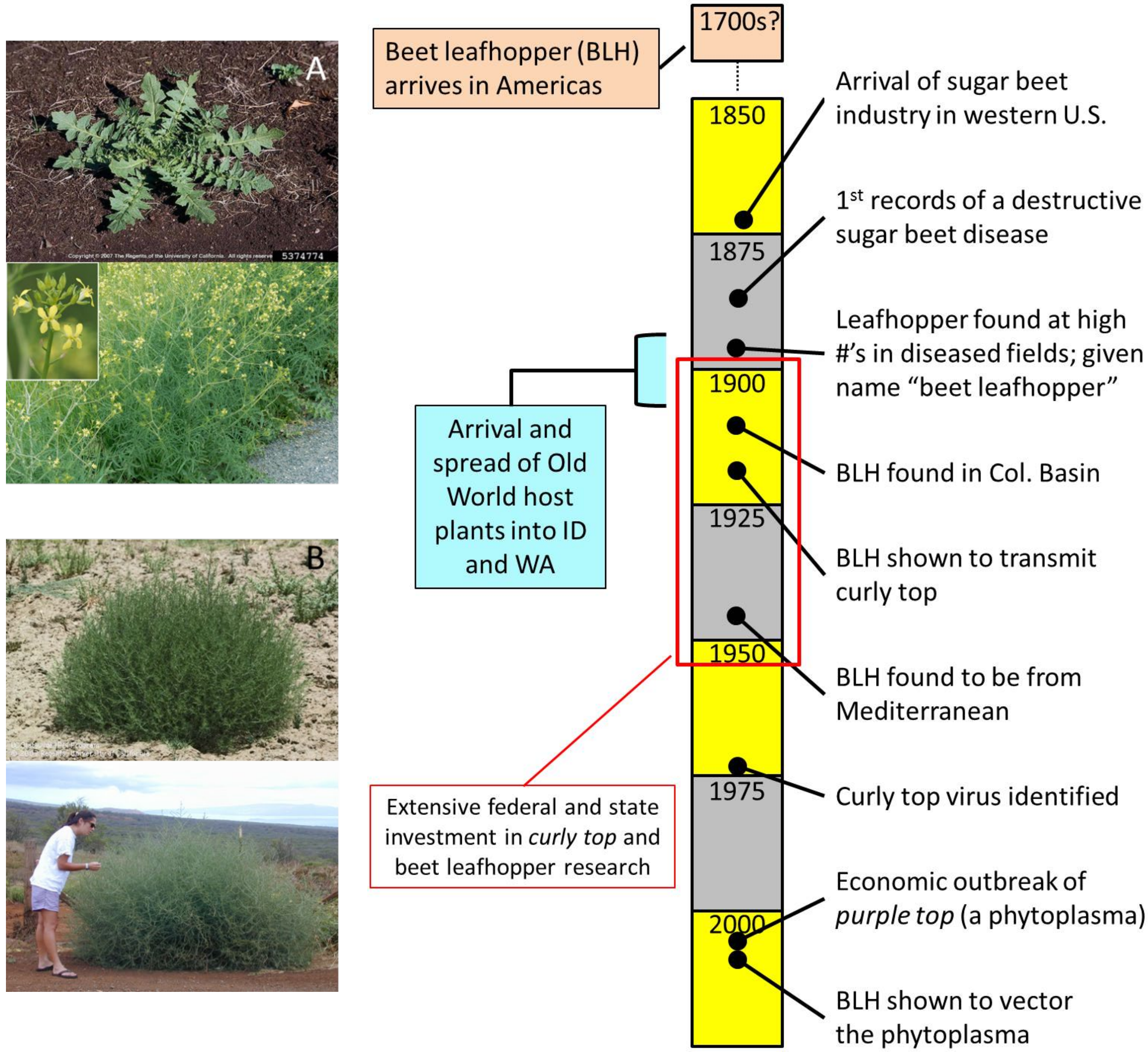

Figure 2. Timeline of events preceding the 2002 outbreak of potato purple top disease in the Columbia Basin. Photographs at left show two important Old World invasive weeds (A - tumble mustard; B - Russian thistle) of critical importance to Columbia Basin populations of beet leafhopper.

The 1870s arrival of the sugar beet industry in the western U.S. was followed soon by outbreaks of a sugar beet disease, originally referred to as California blight or western blight, but now known as curly top disease. Observations in 1895 that a leafhopper was abundant in diseased fields led to speculation that the "blight" disease was caused by the feeding activities of this insect; the leafhopper received the common name "beet leafhopper" due to its association with sugar beets (Fig. 2). Trials in 1915 confirmed that feeding by beet leafhopper led to the disorder, although the pathogen was not identified until 1970. Beet leafhopper was first documented in the Columbia Basin in 1909 "swarming on *Atriplex* in Yakima" (Ball 1917, Davis 1927), while additional surveys in the 1920s found it in Wenatchee, the Okanagan region, British Columbia, and west of the Cascades. Weedy Mediterranean host plants of BLH began to arrive and spread in Idaho and Washington in the late-1800s and early-1900s (Fig. 2: blue shading). These Old World plants were subsequently found to have a key role in the insect's life cycle and presence in the Columbia Basin, as we discuss below.

Outbreaks of curly top beginning in the early 1900s caused extensive and unpredictable losses to the western U.S. sugar beet industry over several decades in the form of yield losses, sharp declines in harvested acres, abandoned fields and farms, and closings of sugar processing plants. The line graphs in Figure 3 show some of the year-to-year fluctuations in sugar beet yields driven by outbreaks of beet leafhopper in 1914, 1919, 1921, 1924, and 1926. Acres of sugar beets lost to the leafhopper in one area of Idaho were estimated to have exceeded 50% during two very bad years in the 1920s (gray bars in Fig. 3). The losses were significant enough to prompt federal and state intervention, notably in the creation and funding of federal research laboratories (USDA-ARS; known then as Bureau of Plant Industry) with the expressed responsibility of conducting research on curly top and beet leafhopper (Fig. 2: red box). Much of what we know today about the biology of beet leafhopper is a product of these research efforts.

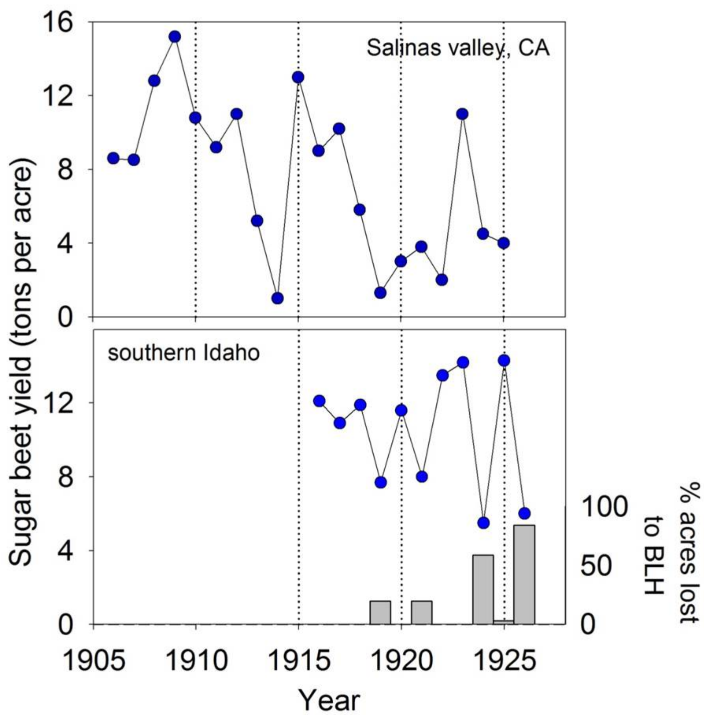

Figure 3. Year-to-year fluctuations in sugar beet yields caused by fluctuations in BLH pressure at fields in California and Idaho. Gray bars show % of planted acres not harvested due to BLH. From Carter (1930) and Carsner (1933).

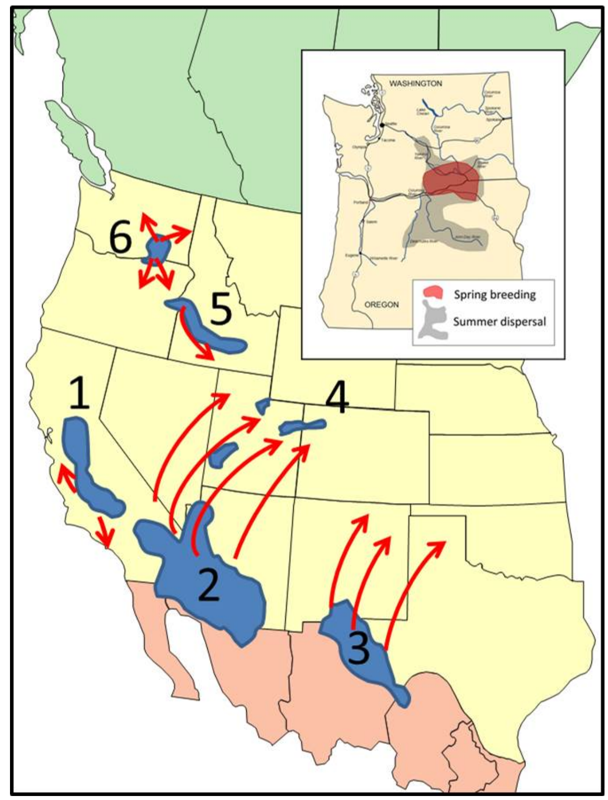

Figure 4. Six primary spring breeding regions of beet leafhopper and directions of summer dispersal (red arrows). Modified from Hills (1937) and Douglass and Cook (1954).

Biology of beet leafhopper in western North America. Beet leafhopper has six primary spring breeding areas in the U.S. (Fig. 4: blue fills) from which it disperses into summer breeding regions (Fig. 4: red arrows). These spring movements may be widespread, such as those originating in the desert regions of Arizona and Texas. Both spring and summer breeding areas occur in desert regions of sparse vegetation, behavior shown by the insect also in its native Mediterranean range. Indeed, preference for these dry, sandy, and sparsely vegetated habitats is perfectly expressed by a quote from a prominent leafhopper biologist of the early 1900s: "*You don't usually find [beet leafhopper] until you begin to get sand in your sweep net*" (cited in Oman 1970). The two major breeding areas in the northwest U.S. are the Snake River plains of Idaho and the lower Columbia Basin of Washington and northern Oregon (Fig. 4). Preferred habitat again comprises dry and often sandy regions of sparse vegetation.

Beet leafhopper has a complicated life cycle in WA, OR, and ID. Adult leafhoppers overwinter on autumn-germinating annual plants, typically Old World species that have colonized North America (Fig. 5: (1)). When these fall-germinating plants resume growth in spring, the overwintered females begin laying eggs and produce a generation on these hosts ("spring brood"). New adults from this generation are produced in spring at about the time the hosts are senescing, causing the leafhoppers to disperse into other habitats in search for summer hosts like Russian thistle and kochia (Fig. 5: (2-3)). At least one generation is completed on these summer hosts ("summer brood"). Leafhoppers will feed upon a variety of non-host species, including potato, during their summer movements (Fig. 5: red oval), and it is at this time that potato is at risk of being infected with the purple top pathogen. As summer hosts die in late summer, leafhoppers return to autumn-germinating hosts for overwintering (Fig. 5: (3-4)). Perennial species such as rabbitbrush may serve as temporary feeding hosts during this autumn movement but do not support overwintering.

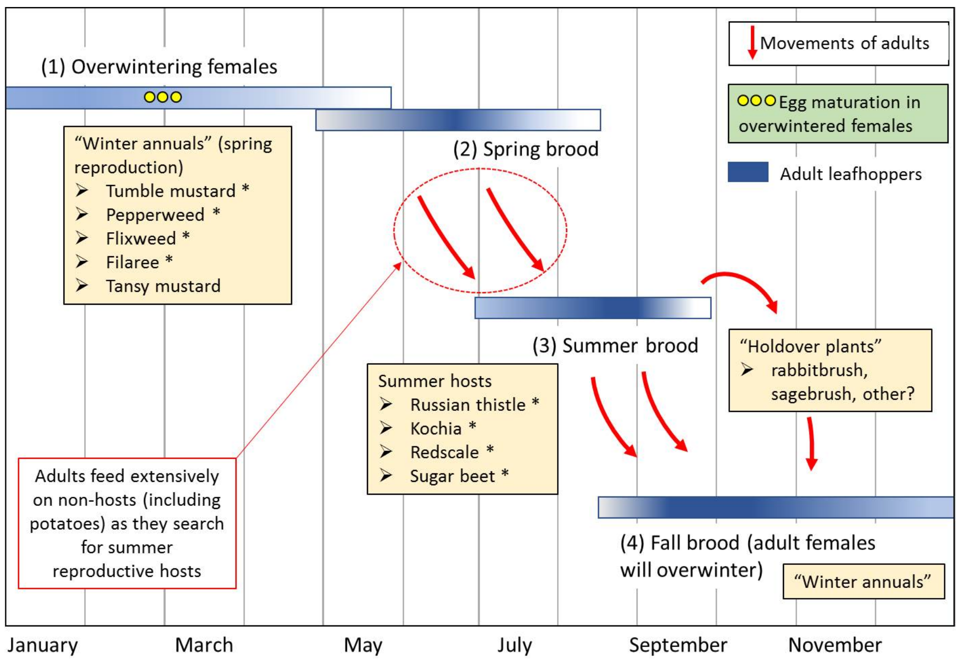

Figure 5. Presumed life cycle of beet leafhopper in the Columbia Basin, showing sequential use of host plants between spring and autumn; most of these host plants are Old World natives (plant species having asterisks). Modified from Hills (1937) and others.

Non-native weeds: a critical resource for Columbia Basin leafhoppers. While beet leafhopper throughout its range requires a sequence of plants to complete its annual cycle, there are differences between northern and southern populations in what plant species fulfill this need. One striking difference is origin of the hosts. Virtually all of the insect's important host plants (both spring and summer) in the Columbia Basin are non-natives that have arrived from Eurasia or the Mediterranean region (Fig. 5: plants with asterisks). As mentioned above, the leafhopper also is a Mediterranean import, and in its native range is known to associate with these hosts. This immediately raises the question of whether the presence of these non-native species helps the leafhopper maintain residency in WA, OR, and ID. Douglass and Cook (1952) noted that of the 16 important spring and summer hosts in southern breeding Regions 1-3 (Fig. 4), 14 are native to North America. This contrasts strikingly with what occurs in Regions 5-6 (Fig. 4) where only tansy mustard is native, and the other 8 or so plant hosts of the spring and summer broods are native to the insect's home in Eurasia and the Mediterranean.

One important way these non-native species may contribute to leafhopper residency in the Columbia Basin is through the life cycles of plants used by the spring brood (Fig. 5). These non-native autumn/spring hosts are known as “winter annuals” and with correctly timed precipitation will germinate in autumn, providing beet leafhopper with needed wintering hosts. The leafhopper is thought to feed on these plants during warm intervals of winter. In years that these winter annuals fail to be readily available, due to poor germination of autumn seed, beet leafhopper apparently suffers winter mortality leading to low spring counts. These “winter annuals” also are spring reproductive hosts, allowing overwintered leafhoppers to complete a spring generation before moving onto summer hosts.

For summer reproduction, Russian thistle seems to be critically important in the beet leafhopper life cycle in WA, OR, and ID. This idea was especially shown by results of a 1949 sampling study of Russian thistle (Fig. 6). At a site in southern ID (King Hill), Russian thistle was found to cover >50% of the monitored region (~46,000 acres). Sampling beet leafhoppers in these stands led Douglass and Hallock to estimate that there were upwards of 60 billion leafhoppers in Russian thistle in the region. This weed became a focus of leafhopper control efforts in ID in the 1940s and 1950s. One strategy employed in these efforts was to reduce Russian thistle density by managing the dryland regions that the plant prefers. This included efforts to reduce overgrazing of habitats and seeding of damaged regions with perennial grasses. A second strategy adopted during the mid-1900s was to kill the summer brood of the leafhopper by targeted spraying of Russian thistle with pyrethrum and with DDT (Fig. 7).

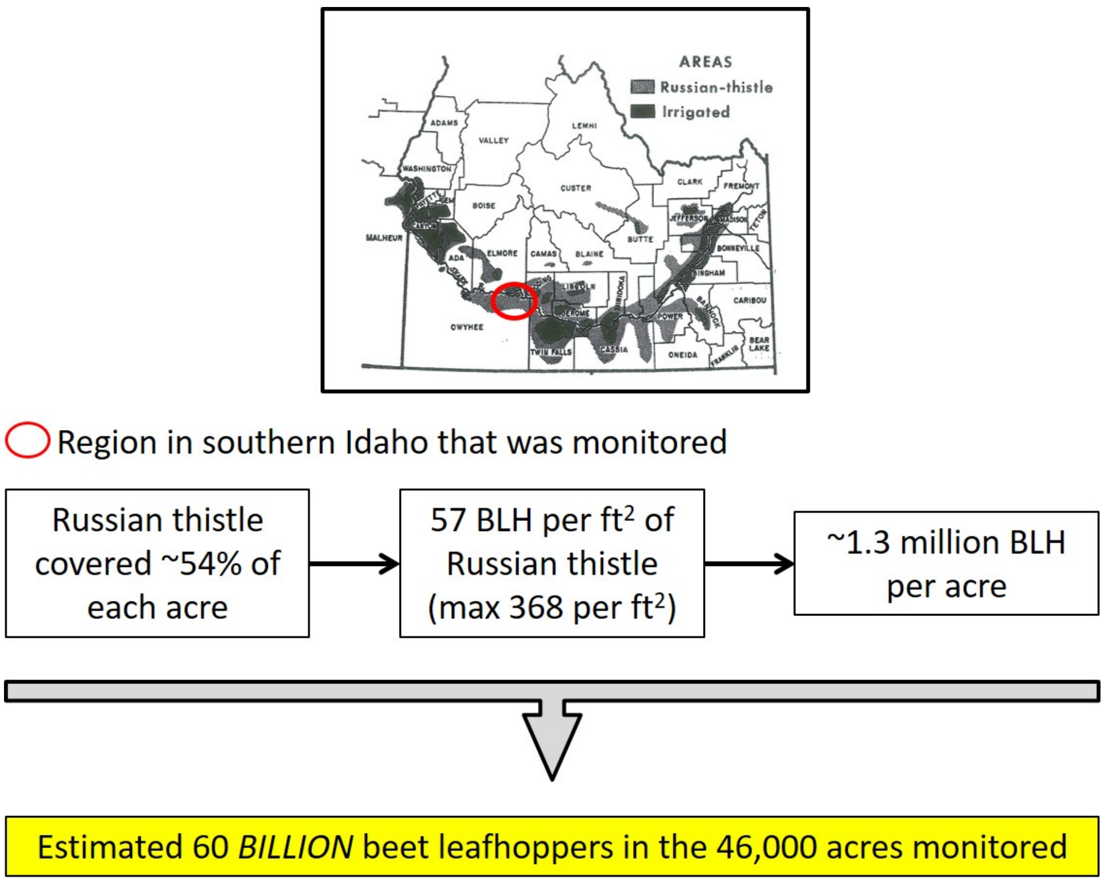

Figure 6. Late 1940s demonstration of the importance of Russian thistle as summer host plant of beet leafhopper. Modified from Douglass and Hallock (1958).

Is there support for the idea that these introduced plant hosts contribute to beet leafhopper residency in northern regions? Douglass and Cook (1952) proposed that the leafhopper in the U.S. likely once was confined to the southwestern U.S. and spread northwards only as its non-native hosts arrived and spread into ID and WA. Yensen (1981) examined old photographs housed at the Idaho Historical

Society for evidence of Russian thistle and tumble mustard in Idaho and concluded that these hosts began arriving in southern ID just before the turn of the century (late 1890s; see blue-shaded portion of timeline in Fig. 2). While we do not know when beet leafhopper arrived in the Columbia Basin, the first documented record for the insect was in the early 1900s, about the time these non-native hosts arrived. Curly top disease arrived in Regions 5 and 6 several decades after it had shown up in more southern regions, which also supports the idea that leafhopper presence in WA, OR, and ID was due to range expansion from the southwest U.S. following arrival of highly suitable host plants into these northern regions.

Figure 7. Spraying of Russian thistle (Idaho) in the 1950s to control the summer brood of beet leafhopper. From Douglass et al. (1955).

BEET LEAFHOPPER AND POTATO PURPLE TOP DISEASE: LESSONS FROM THE 1900S

Managing purple top disease of potatoes currently relies exclusively on controlling beet leafhopper. This in turn requires an understanding of the leafhopper's biology in the Columbia Basin. The life cycle of beet leafhopper in the Columbia Basin today likely has not departed extensively from what was learned about the insect in the early- to mid-1900s. Changes in the Columbia Basin landscape since the 1940s have probably led to changes in distribution and availability of spring and summer hosts (as well as the insect), but the insect's life cycle as far as we know is similar to what is shown in Figure 5. These changes in landscape include especially large upticks in urbanization, modifications in grazing practices, changing crop types, and arrival of an extensive agricultural irrigation system, all of which likely have affected availability of the leafhopper's important weedy hosts.

One question not answered by 1900s research was the exact role of weed hosts in epidemiology of curly top disease, either as reservoirs of *Beet curly top virus* or as sources of infective leafhoppers. Incidence of curly top was extremely variable geographically and year-to-year in the early 1900s (Fig. 3; Carsner 1926) and remains so today. It still is unclear how (or if) weedy hosts of the leafhopper contribute to this unpredictability. This same question bedevils contemporary efforts to understand potato purple top. Over a three-year sampling period, estimates of percent of leafhoppers carrying BLTVA in the Columbia Basin varied between 6-35% (Munyaneza et al. 2010). The source of this variation is unknown. In particular, we do not know which plant species in the Columbia Basin are reservoirs of the phytoplasma or sources of infected leafhoppers. It is possible that variation in percentages of leafhoppers carrying BLTVA could be explained by year-to-year variation in presence of a specific leafhopper host. Based upon what we know of the leafhopper's life cycle, sources of infective leafhoppers could include (Fig. 5): winter annuals, summer hosts, plants temporarily colonized and fed upon by dispersing adults, autumn "hold-over" plants, or possibly unknown host plants that have arrived in the Columbia Basin since the research of the 1900s.

Purple top is a chronic problem for Columbia Basin growers managed by controlling the leafhopper vector, either incidentally with at-planting applications of neonicotinoids, or directly by May, June, and sometimes July applications of insecticides. We believe that growers would benefit from a better understanding of when and where leafhoppers acquire BLTVA, and in knowing how weedy habitats in potato growing regions contribute to arrival of infective leafhoppers in potato fields. Such knowledge could be incorporated into management practices:

- Scheduling insecticide applications to times when plant protection is most needed (i.e., target only the most threatening leafhopper flights);
- Reducing unwarranted sprays when purple top threat is low;
- Implementing weed control practices to lower the availability of plants important to BLH or to BLTVA, thereby reducing overall purple top risk.

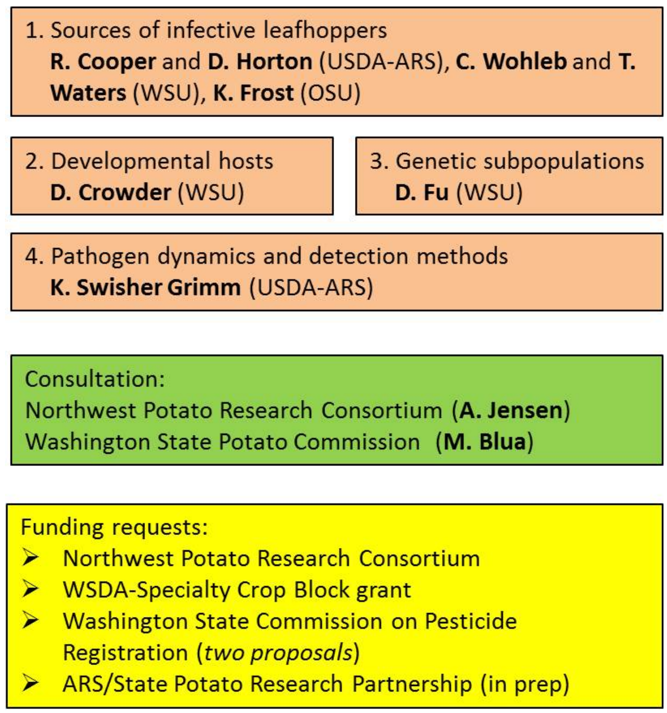

Figure 8. Objectives 1-4 of a multi-institution project to examine beet leafhopper and potato purple top disease in the Columbia Basin.

To this end, a group of researchers from USDA-ARS, Washington State University, and Oregon State University, in consultation with research staff of the Northwest Potato Research Consortium and the Washington State Potato Commission, have initiated a multidisciplinary project to examine important shortcomings in our understanding of potato purple top disease (Fig. 8). Our group includes many of the same individuals who collaborated in the SCRI- and industry-funded potato psyllid/zebra chip project. That project led to large gains in our understanding of potato psyllid and zebra chip. Objectives and approaches overlap between the psyllid and leafhopper projects, and in fact certain technological advances made during the psyllid project will be employed in the leafhopper project. Funds are being requested from multiple sources to support the work (Fig. 8: yellow). Objectives include:

1. **Determine sources of infective leafhoppers arriving in potato fields (USDA-ARS, WSU, OSU).** We will use molecular methods developed in part in the psyllid project to determine dietary histories of leafhoppers entering potato fields, to identify what weedy plants are sources of the insects. By simultaneously examining insects for dietary history and for presence of the phytoplasma (PCR), we will additionally look for association between presence of the pathogen and specific plant species.
2. **Determine what plant species are actual developmental hosts of beet leafhopper in the Columbia Basin (WSU).** We know that beet leafhopper feeds readily on plant species that nonetheless are not used for reproduction. We have a partial list of plant species that support actual reproduction and development (headed by the ubiquitous Russian thistle), but the list is likely to

underestimate the insect's true reproductive breadth. A WSU graduate student will examine this question by sampling plants in the field and conducting rearing assays in the lab.

3. **Determine whether beet leafhopper exists as genetically unique subpopulations (WSU).** One of the more important results of our psyllid project was finding that the potato psyllid population in the Columbia Basin comprises genetic subpopulations that differ in host use and in tendency to colonize potato fields. Discovery of these subpopulations has substantially advanced our understanding of psyllid movement between weedy hosts and potato fields. Beet leafhopper populations in the southern U.S. include genetic subpopulations that may also differ in biology. Similar information is not yet available for Columbia Basin leafhoppers.
4. **Improve methods to detect the BLTVA pathogen in infected potato plants (USDA-ARS).** We will use molecular methods to examine pathogen movement in potato plants, while also developing methods to improve PCR approaches used in detecting the pathogen in plants (current methods are problematic). An improved detection tool will assist purple top researchers studying BLTVA epidemiology and will allow more reliable monitoring of commercial potato fields for presence of the pathogen.

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Title page photograph of potato purple top symptoms by Carrie Wohleb.

Figure 1. (A) Beet leafhopper adult; photograph by G. Oldfield (https://www.forestryimages.org/browse/detail.cfm?imgnum=0746029); (B) Line drawings of beet leafhopper from Ball (1917); (C-D) Potato purple top; photographs by Carrie Wohleb; (E) curly top disease of sugar beet (https://www.ars.usda.gov/ARSUserFiles/oc/graphics/photos/mar16/d3567-1.jpg).

Figure 2. (A) Tumble mustard autumn rosette and mature spring plant; photographs by Joseph M. DiTomaso and Jim Kennedy (https://www.ipmimages.org/browse/detail.cfm?imgnum=5374774; https://www.flickr.com/photos/nature80020/14268313999/in/photostream/); (B) mature plants of Russian thistle; photographs by Forest and Kim Starr, and Jack Kelly Clark (https://en.wikipedia.org/wiki/Kali_tragus; http://ipm.ucanr.edu/PMG/WEEDS/russian_thistle.html)