



## Research

# Weeding them out: identifying noncrop hosts and sources of infectious beet leafhopper, *Neotalitrus tenellus* (Hemiptera: Cicadellidae), in the Columbia River Basin

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Effective pest management requires regular monitoring to assess pest population dynamics and forecast outbreaks. For generalist insects that are vectors of plant pathogens, monitoring can also identify how variation in host plant use affects pathogen transmission. However, movement of vectors among crop and noncrop hosts often makes it challenging to coordinate sampling and identify season-long trends. We addressed this by conducting a 3-yr study monitoring the beet leafhopper (*Neotalitrus tenellus* Baker; Hemiptera: Cicadellidae), a pest of potato and other vegetable and seed crops as a vector of *Candidatus* Phytoplasma trifolii (CPT) and beet curly top virus (BCTV). Specifically, potato crops and adjacent weedy hosts in the Columbia River Basin region of central Washington, USA, were sampled from 2019 to 2021 to identify developmental hosts of beet leafhopper and potential sources of pathogens. We show that adult beet leafhopper commonly overwintered on weeds such as tumble mustard and flixweed, with kochia and Russian thistle acting as summer hosts. Many of these weeds frequently harbored the CPT and BCTV pathogens. While BCTV prevalence peaked in spring, CPT prevalence remained relatively high throughout entire seasons. By assessing a vector and two plant pathogens, we show how pathogens have variable transmission strategies. Our study also shows how leveraging intense monitoring of a vector and pathogens across different host communities can improve risk-prediction and aid growers in making management decisions.

**Keywords:** beet curly top virus, landscape ecology, pest population dynamics, purple top disease, vector monitoring.

## Introduction

Successful integrated pest management relies on a foundation of effective pest monitoring. Coordinated and regular sampling of insect pests within crop fields and across landscapes is used to assess population trends and forecast outbreaks, which ideally allows producers to apply control measures before severe economic damage

occurs (Kogan 1998, Ehler 2006). For some pests, spatiotemporal models incorporating long-term sampling data are integrated into decision support systems to predict pest population dynamics and provide site-specific recommendations, reducing the insecticides applied per field (Brewster and Allen 1997, Jones et al. 2010, Damos 2015, Wohleb et al. 2021). However, effective sampling of insect populations can be difficult because generalist species often

reproduce on uncultivated hosts and disperse into crops after planting and throughout growing seasons (Kennedy and Margolies 1985, Kenis et al. 2016, Rafter and Walter 2020). With such pests, understanding patterns of season-long host plant use and migration into crop fields is key to developing integrated pest management programs.

Dispersal of pests into and out of agricultural environments is especially key in annual crop systems, where the cultivated host is only present for part of the year. Insects colonizing seasonal crops often overwinter on weeds growing near crop plants that serve as a “green bridge” to the crops (Kennedy and Storer 2000, Horton et al. 2015a,b, Cooper et al. 2019a). Monitoring the weedy hosts used by polyphagous species before, during, and after periods when annual crops are present is key to predicting when and where pests will occur in these crop systems. In addition, pests may move among multiple cultivated host species in areas where crop diversity is high. An awareness of how pest and host plant phenology overlap can aid in generating more accurate population models for decision support systems. However, coordinating sampling of insect pests across crop and noncrop hosts throughout seasons can be logistically challenging.

Understanding which uncultivated hosts are used by generalist insect pests across growing seasons is especially important when pests transmit one or more plant pathogens. When pests are vectors, they often acquire pathogens from noncrop hosts before dispersing to and often infecting crop plants (Weintraub and Beanland 2006, Gutiérrez Illán et al. 2020). All major crop systems are affected by insect-borne plant pathogens (Bebber et al. 2014), and it is key to monitor not only vector populations but also pathogen prevalence in those populations and their host species. Molecular screening of pest and plant tissues can reveal sources of infected insects as they move into crop fields (Cooper et al. 2019b, 2022, Reyes Corral et al. 2020, 2021). Identifying which noncrop host plants are common reservoirs of pathogens at different times, and which host plants serve as developmental hosts of vectors, could help predict epidemics of plant diseases and identify areas at risk across landscapes with variable conditions.

In this study, we surveyed potato fields and adjacent weeds in the Columbia River Basin region of Washington, USA to determine seasonality of a key insect vector, the beet leafhopper (*Neoliturus tenellus* Baker; Hemiptera: Cicadellidae). Beet leafhoppers are major pests of potato and other vegetable and seed crops in the Columbia River Basin, primarily because they are the primary vector of pathogens such as *Candidatus* *Phytoplasma trifolii* (CPt; formerly often referred to as “beet leafhopper-transmitted virescence agent” or BLTVA) and beet curly top virus (BCTV). However, management of beet leafhoppers and their associated pathogens has been limited by a poor understanding of the host plants that commonly serve as pathogen reservoirs. Here, we used trapping and molecular screening to identify seasonal temporal dynamics and movement of leafhoppers and their associated pathogens in weedy and crop host plants. Our results provide a framework to predict beet leafhopper dispersal and pathogen transmission into crops as part of a decision aid system to improve grower management outcomes (Wohleb et al. 2021).

## Materials and Methods

### Study System

The beet leafhopper has long been a pest in the Western USA as it is the sole significant vector of multiple pathogens that cause economic losses in vegetable crops (Ball 1907, Munyaneza et al.

2010, Greenway 2022). One prevalent pathogen is CPt, which causes purple top disease, leading to symptoms of leaf rolling and purpling and reduced tuber yield and quality (Crosslin et al. 2005, Munyaneza et al. 2006, 2007). BCTV is also transmitted by beet leafhoppers and affects many vegetable crops, causing leaf curling and discoloration and stunted growth (Ball 1917, Bennett 1971, Creamer 2020). Beet leafhoppers are highly efficient vectors of both pathogens: CPt can be acquired in as little as 5 min of feeding time with transmission beginning after a 12-d latent period (Golino et al. 1987), and BCTV is acquired within seconds but requires a 4-h latent period within the insect before transmission occurs (Alkhatib et al. 2024). Beet leafhoppers also transmit several less common pathogens that still can affect many crops, such as the bacteria *Spiroplasma citri* (Lee et al. 2006). Given a lack of plant resistance, control practices for these pathogens have historically relied on frequent insecticide applications targeting beet leafhoppers (Severin 1921a, Campbell 1937, Cook 1943, Douglass et al. 1955).

Beet leafhoppers are intensively monitored by extension specialists in the Columbia River Basin (Jensen 2008, Rondon and Murphy 2016, Foutz et al. 2024). Although adults may feed on hundreds of different plant species, much of this knowledge stems from early-1900s studies (Davis 1927, Carter 1930, Severin 1933, Hills 1937, Cook 1941). The beet leafhopper’s life cycle may have changed little since then, but shifting climates and land use have greatly altered the availability of weed and crop hosts. Moreover, although recent studies have assessed beet leafhopper seasonality and infectivity on crops and weed hosts in other regions affected by this pest (Strausbaugh et al. 2024, Bundy et al. 2025), the role of uncultivated plants in the epidemiology of beet leafhopper-borne pathogens in the Columbia River Basin is largely unknown (Horton et al. 2018).

### Site Selection and Sampling

Sampling was conducted across the Columbia River Basin throughout 2019 and 2020 and in spring 2021 (Table S1; Fig. 1). Most sites were commercial farms in the Washington State University potato pest monitoring network, and the others were research farms. In 2019 and 2020, all sites were in weedy areas adjacent to irrigated potato fields. In 2021, all sites were in locations where potato cultivation occurs, but sampling was conducted before crop planting. Sites were sampled every other week in 2019 and 2020 and weekly in 2021. At each site, potential weedy hosts of beet leafhopper within 100 m of crop fields were visually identified and then sampled using a reversible leaf blower (26cc Gas Handheld Blower Vacuum, Homelite Corporation, Charlotte, NC; Wilson et al. 1993). As there were frequently large stands of a single weed species as well as dispersed individual plants, insects were suctioned from a single species of plant per sample into an organdy bag. Stands of all potential weedy hosts present were sampled for 1 min each, and the contents of each collection were transferred into 3.78 L resealable plastic bags. Nearby potato field edges were also opportunistically sampled in this manner. Additionally, a composite sample of 5 leaves was taken from each stand of plants (weedy hosts and potato) and placed into extraction bags (Bioreba AG, Reinach, Switzerland). Plant tissue samples included both mature leaves and new growth and were taken regardless of apparent plant health, although no obviously symptomatic plants were observed. Live insects and plant tissue samples were kept on ice during transport to the laboratory, where they were immediately frozen at  $-40^{\circ}\text{C}$ .

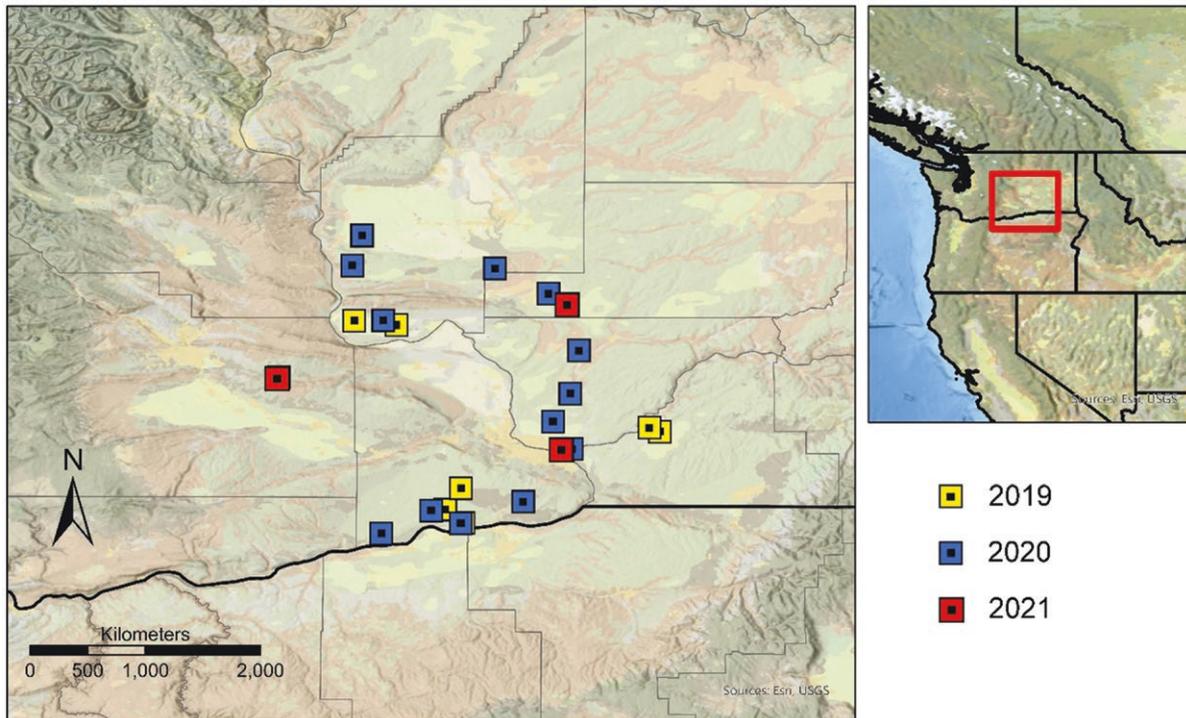


Fig. 1. Map of study sites.

### Beet Leafhopper Identification

Beet leafhoppers are challenging to identify because there are many visually similar species that occupy agricultural environments but are not vectors of pathogens. Adult beet leafhoppers are 3 to 4 mm long, roughly cylindrical with a wide rounded head tapering to a pointed abdomen, and pale yellow-green to tan with no distinct markings (Fig. 2). Overwintering specimens are darker in color and often have irregular pigmentation on the wings or head (Fig. 2). Females have a rust-colored ring around the base of the ovipositor, and males have truncated subgenital plates (Fig. 2). Beet leafhoppers were identified and sexed using these traits under microscope, separated from bycatch, and stored in 1.5-mL centrifuge tubes at  $-40^{\circ}\text{C}$  until processing.

Leafhopper nymphs are especially difficult to identify for several reasons—they are minute in size, many species' unique characteristics are only present in adults, and the traits of nymphs are poorly documented. All leafhopper nymphs collected were examined under magnification, and any that were obviously not beet leafhopper based on their size or coloration were set aside. All remaining nymphs that might be beet leafhopper were microscopically photographed using a focus-stacking procedure in the CellSens imaging software (Olympus Corp., Tokyo, Japan). Nymphs were then stored in 1.5-mL centrifuge tubes at  $-40^{\circ}\text{C}$  until molecular processing.

Some beet leafhoppers collected were visibly parasitized, either with a distended abdomen resulting from endoparasitic species, a thylacium (likely of a Dryinid wasp) protruding from the abdomen or thorax, or Strepsiptera between abdominal sclerites. Although detailed parasitoid identification, either morphological or molecular, was not included in this study, we recorded the number of visibly parasitized beet leafhopper adults and nymphs.

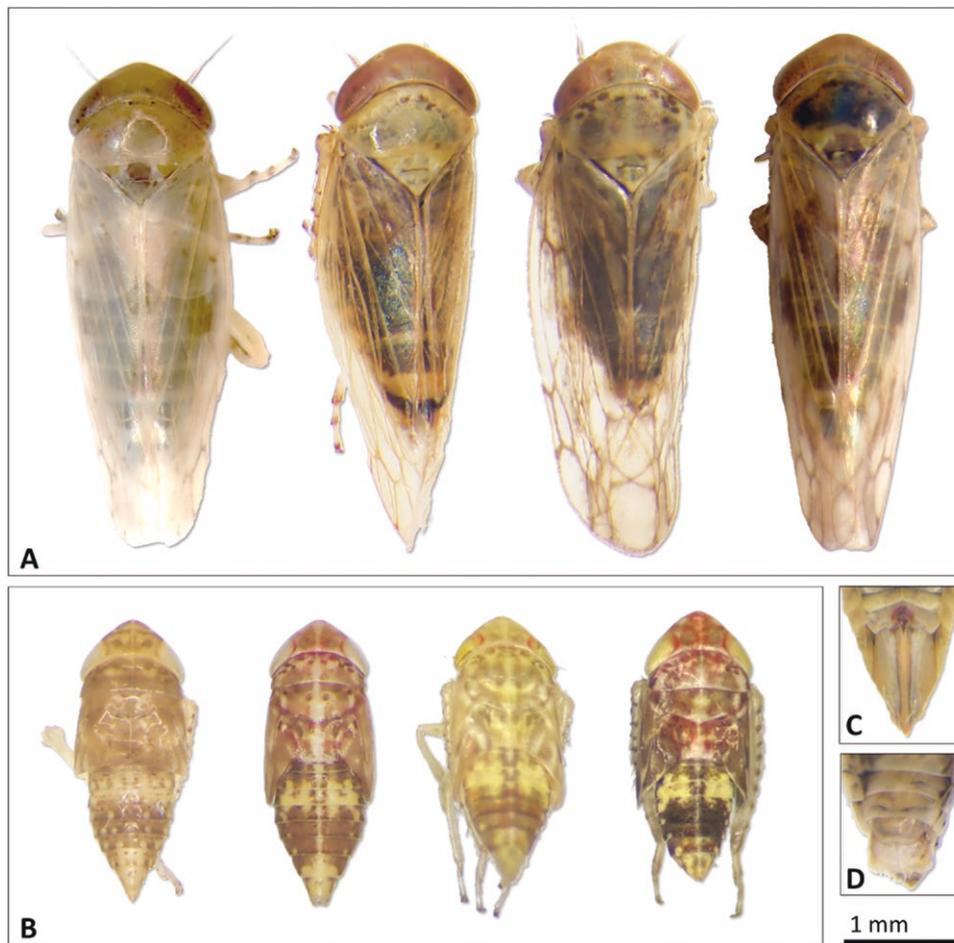
Other leafhoppers were frequently collected in bycatch, but typically not in high quantities. These were not tested for CPt or BCTV, both due to the large number of beet leafhopper samples that took

priority for molecular processing and because other species are not known to be vectors of these pathogens.

### Molecular and Data Analyses

DNA from each leafhopper was extracted using DNeasy Blood & Tissue Kits, and DNA from plant tissues was extracted with DNeasy Plant Kits (Qiagen, Hilden, Germany). A subset of samples was tested with a Nanodrop spectrophotometer (ThermoFisher, Waltham MA) to confirm the quality and quantity of DNA obtained was suitable. Extractions and subsequent testing also included no-template controls to ensure that contamination had not occurred in any reagents. Extracted DNA was stored at  $-20^{\circ}\text{C}$  until further molecular work was conducted.

Testing for CPt in all insects was done using real-time PCR on a Lightcycler 480 (Roche, Basel, Switzerland) with these conditions: a 5 min hold at  $95^{\circ}\text{C}$ , 20 cycles of  $95^{\circ}\text{C}$  for 10 s,  $65^{\circ}\text{C}$  for 10 s, and  $72^{\circ}\text{C}$  for 10 s, then 20 cycles of  $95^{\circ}\text{C}$  for 10 s,  $55^{\circ}\text{C}$  for 10 s, and  $72^{\circ}\text{C}$  for 10 s, a melting curve to assess primer specificity, and a cooling cycle. Each 20  $\mu\text{L}$  reaction contained 10  $\mu\text{L}$  of SYBR Green PCR Master Mix (ThermoFisher, Waltham MA), 8.2  $\mu\text{L}$  of nuclease-free water, 0.4  $\mu\text{L}$  each of *Ca. P. trifolii* primers “z-R16R2-wfB\_F” (AAA TAT TTC TCG GGG TTT GTA CAC ACC GCC CGT CA) and “BLTVA-int-wfB\_R” (AAT TAT CTC TGA TGA TTT TAG TAT ATA TAG TCC) at 20  $\mu\text{M}$  concentration, and 1  $\mu\text{L}$  of extracted DNA (Cooper et al. 2023, Swisher Grimm et al. 2023). Plant samples were analyzed on a CFX96 real-time PCR system (Bio-Rad, Hercules, CA) with the same CPt primers used for insects. The real-time PCR program had a 5 min hold at  $95^{\circ}\text{C}$ , 40 cycles of  $95^{\circ}\text{C}$  for 10 s,  $65^{\circ}\text{C}$  for 10 s, and  $72^{\circ}\text{C}$  for 10 s, a melting curve to assess primer specificity, and a cooling cycle. Each 10  $\mu\text{L}$  reaction included 5  $\mu\text{L}$  of SYBR Green PCR Master Mix, 3  $\mu\text{L}$  of nuclease-free water, 0.5  $\mu\text{L}$  each of the CPt primers at 10  $\mu\text{M}$  concentration, and 1  $\mu\text{L}$  of extracted DNA.



**Fig. 2.** High definition pictures taken under microscopy that show A) variations in adult beet leafhopper coloration; B) variations in beet leafhopper nymph coloration; C) beetle leafhopper female anatomy; and D) beetle leafhopper male anatomy. These characteristics were used to distinguish beet leafhoppers from other leafhopper species caught in our surveys.

Screening for BCTV in all insect samples was done with conventional PCR. Conditions were: 1 min at 95 °C, 20 cycles of 95 °C for 15 s, 65 °C for 30 s (touchdown,  $\Delta$ -0.5 °C), and 72 °C for 20 s, then 20 cycles of 95 °C for 15 s, 55 °C for 30 s, and 72 °C for 20 s, then 1 min at 72 °C before an infinite hold at 4 °C until samples were removed. Each 20  $\mu$ L reaction had 10  $\mu$ L of Amplitaq Gold 360 Master Mix (ThermoFisher Scientific, Waltham, MA), 8.6  $\mu$ L of nuclease-free water, 0.2  $\mu$ L each of primers “BCTV2-F” (GTG GAT CAA TTT CCA GAC AAT TAT C) and “BCTV2-R” (CCC ATA AGA GCC ATA TCA AAC TTC) at 20  $\mu$ M concentration, and 1  $\mu$ L of extracted DNA (Strausbaugh et al. 2008, Swisher Grimm et al. 2023). BCTV infection was determined by visualizing the ~520-bp PCR products under UV light on a 1% agarose gel stained with GelRed (Biotium, Fremont, CA). Plant samples were tested for BCTV on a CFX96 real-time PCR system with the same primers used for insects. Each 10  $\mu$ L reaction contained 5  $\mu$ L of SYBR Green PCR Master Mix, 3  $\mu$ L of nuclease-free water, 0.5  $\mu$ L each of the BCTV primers at 10  $\mu$ M concentration, and 1  $\mu$ L of extracted DNA. Conditions for the real-time PCR reaction were as follows: 1 min at 95 °C, 34 cycles of 95 °C for 1 min, 54 °C for 1 min, and 72 °C for 1 min, then 5 min at 72 °C before an infinite hold at 4 °C until sample removal.

All leafhopper adults from 2019 and 2020 were also tested for *S. citri* using conventional PCR. Thermocycler conditions were identical to those for BCTV, except each 20  $\mu$ L reaction contained 10  $\mu$ L of Amplitaq Gold 360 Master Mix, 8.6  $\mu$ L of nuclease-free water,

0.2  $\mu$ L each of primers “*S.citri*-1” (GGT CTG CTG CTT TAA TTT CTA C) and “*S.citri*-2” (TGC AGC ACC TGC AAC TGT AG) at 20  $\mu$ M concentration, and 1  $\mu$ L of extracted DNA (Cooper et al. 2023, Swisher Grimm et al. 2023). *Spiroplasma citri* infection was determined by visualizing the ~350-bp PCR products under UV light on a 1% agarose gel with GelRed staining.

To confirm species identity, all nymphs were tested with beet leafhopper-specific primers “A-BLH356-F” (TCT TGC AGG GAT CTC ATC AAT CC) and “A-BLH419-R” (GGT CCA AGG TTA TAC CCT TAG GC), which are CO1 sequences that distinguish them from other leafhoppers (Folmer et al. 1994, Ye et al. 2012). Nymphs were tested with real-time PCR on a Lightcycler 480, with a 5 min hold at 95 °C, 40 cycles of 95 °C for 10 s, 65 °C for 15 s, and 72 °C for 15 s, a melting curve to confirm specificity, and a cooling cycle. Each 20  $\mu$ L reaction contained 10  $\mu$ L of SYBR Green PCR Master Mix, 7.5  $\mu$ L of nuclease-free water, 0.75  $\mu$ L of each of the beet leafhopper primers at 5  $\mu$ M concentration, and 1  $\mu$ L of extracted DNA.

Due to the seasonal nature of the sampling, data collected includes information about both the presence and absence of beet leafhopper and its associated pathogens in crop-adjacent environments. As a result, formal statistical analyses are not provided. Instead, data were examined to inspect the seasonality and infection status of beet leafhopper and its host plants in the Columbia River Basin. We identified seasonal patterns in the landscape-level movements of both beet leafhopper and the pathogens it transmits. The mean

proportions of infectious beet leafhopper and infected tissues from each plant sampled at each site per month were also calculated for each year of sampling.

## Results

### Plant Seasonality and Infection Prevalence

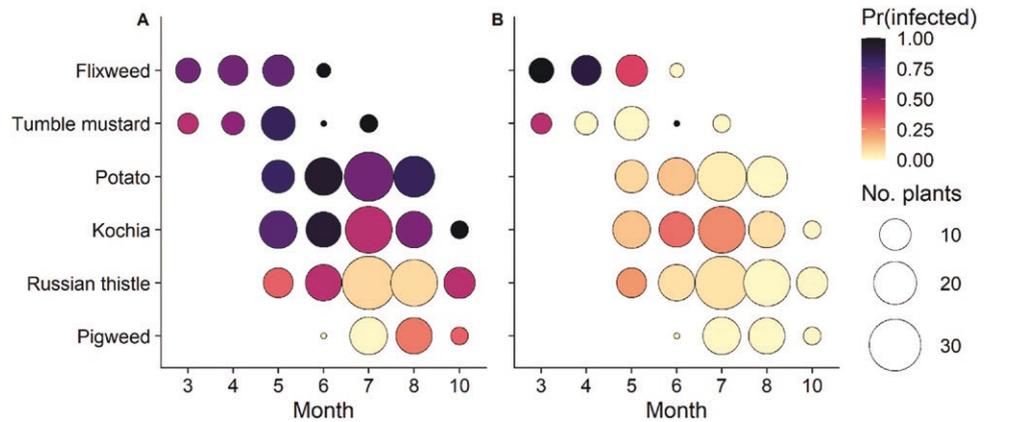
We sampled 11 plant species in 2019 from June to October, 22 species in 2020 from April through October, and 5 species in 2021 from March to June (Table S2). Beet leafhoppers were found on 87% (20 of 23) of species, with some hosts available only in spring and others all year. The most common spring hosts were tumble mustard (*Sisymbrium altissimum* L.) and flixweed (*Descurainia sophia* L.) (Table S2). Hosts that overlapped with potato included Russian thistle (*Salsola tragus* L.), kochia (*Bassia scoparia* L.), and redroot pigweed (*Amaranthus retroflexus* L.). These, along with pitseed goosefoot (*Chenopodium berlandieri* Moq.) and hairy nightshade (*Solanum physalifolium* Rusby), remained in the landscape following potato harvest (Table S2).

The prevalence of CPt and BCTV in plants varied based on seasonality and the host species sampled (Table S2; Fig. 3). Pooling across all host samples by month, CPt prevalence remained relatively high from March to October (Range = 36% to 80% positive per month, Mean = 53.4%, SE = 5.78) (Table S2). In contrast, BCTV prevalence peaked in spring and quickly tapered off, with

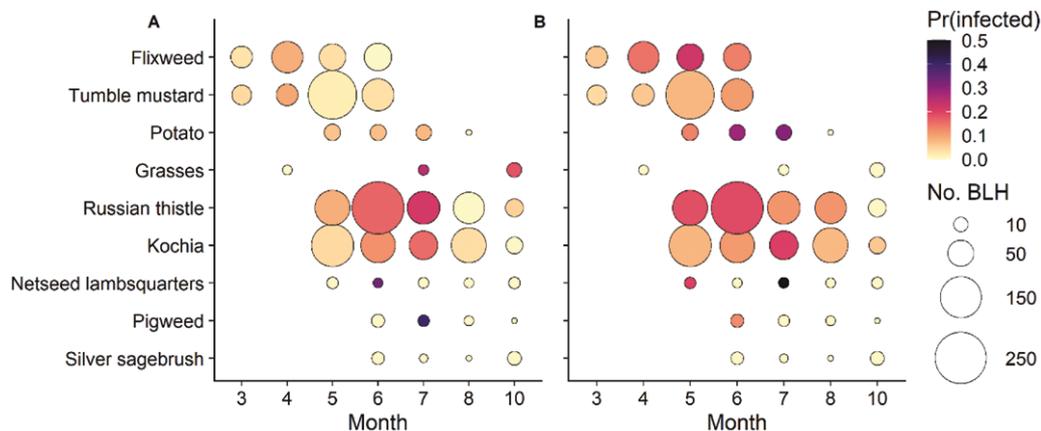
the percentage of positive samples declining from 83% in March to 50% in April, 16% in May, 20% in June, 9.1% in July, 1.1% in August, and 0% in October (Table S2). The prevalence of co-infected samples similarly peaked in spring and quickly tapered off, declining from 33% in March to 27% in April, 13% in May, 19% in June, 5% in July, and 0% in August and October (Table S2). Tumble mustard, flixweed, Russian thistle, and kochia were the most common hosts and were present before, throughout, and following the period when potato was present (Table S2; Fig. 3). These hosts had the highest prevalence of CPt and BCTV, while less common hosts had low prevalence (Table S2; Fig. 3). Potato plants consistently tested positive for CPt for the duration of time they were available but were rarely infected with BCTV (Fig. 3).

### Beet Leafhopper Adult Seasonality and Infection Prevalence

In 2019, 208 beet leafhopper adults were collected from 9 plant species, although 80% were collected from 4 plant species: Russian thistle (40%), kochia (28%), senescing tumble mustard (7.2%), or potato (5.3%) (Table S3; Fig. 4). The remaining 20% of leafhopper adults in 2019 were collected from various less-common or less-preferred hosts (Table S3). In 2020, 833 adult leafhoppers were collected from 17 plant species, with 90% from Russian thistle



**Fig. 3.** Number of host samples collected in each month sampling was conducted for the 6 most common plant species, representing 70% of plant samples collected. The size of the circles represents the number of host samples taken each month, and the colors represent the percentage infected with the A) CPt and B) BCTV pathogens.



**Fig. 4.** Number of beet leafhopper adults collected in each month sampling was conducted on the nine most common host species, representing 97% of adults collected. The size of the circles represents the number of nymphs on each host each month, and the colors represent the percentage infected with the A) CPt and B) BCTV pathogens.

(57%), kochia (23%), tumble mustard (5.6%), or potato (3.8%) (Table S3; Fig. 4). The remaining 10% came from less-common or less-preferred host plants (Table S3). In 2021, 724 beet leafhopper adults were collected from March to May on 5 early-season weed species, with 98% captured on tumble mustard (43%), flixweed (28%), or kochia (27%) (Table S3; Fig. 4). Beet leafhoppers from weedy hosts in March and April were almost exclusively female and had characteristics of overwintering insects. Across all years, the beet leafhopper populations peaked in May and again in July or August. Visible parasitism was observed in 1.5% of all adult leafhoppers collected.

Across all beet leafhopper adults from 2019, 11% were positive for CPt, 8.7% for BCTV, and 1.4% were co-infected. In 2020, 11% of leafhopper adults were infected with CPt, 16% with BCTV, and 3.0% with both pathogens. Across both years, fewer than 0.01% of leafhoppers were positive for *S. citri*. In 2021, 3.7% of leafhopper adults tested positive for CPt, 9.3% for BCTV, and 0.01% were co-infected. Most infected insects were found on tumble mustard, Russian thistle, or kochia, with 74%, 91%, and 100% of CPt-infected insects found on these hosts, respectively, and 83%, 87%, and 99% of BCTV-infected insects from these hosts (Table S3; Fig. 4). Across all years, the majority of infected beet leafhoppers with either CPt or BCTV were collected in the months of May and June (Table S3; Fig. 4). Few infected insects were collected from potato plants at any time point in any of the years of the study (Table S3; Fig. 4).

### Beet Leafhopper Nymph Seasonality and Infection Prevalence

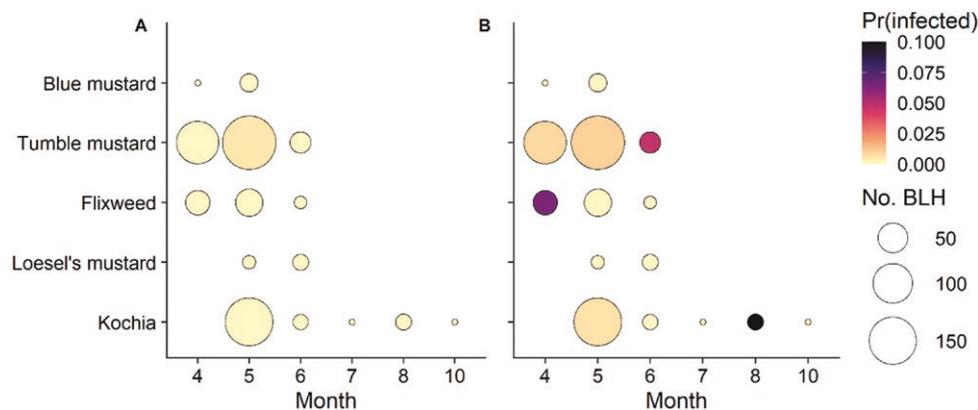
Leafhopper nymphs were only collected in 2020 and 2021, with 30 beet leafhoppers out of 32 total nymphs in 2020 (94%) and 601 beet leafhoppers out of 608 total nymphs in 2021 (99%) (Table S4). Nymphs were collected on fewer hosts than adults (Tables S3 and S4). In 2020, nymphs were collected mainly on kochia and Russian thistle, and in 2021, nymphs were collected from tumble mustard, kochia, and flixweed, primarily in April and May (Table S4; Fig. 5). No beet leafhopper nymphs in 2020 tested positive for CPt (0.0%), and only 1 was positive for BCTV (3.3%) (Table S4; Fig. 5). Only 1 nymph collected in 2021 tested positive for CPt (0.2%), and only 7 tested positive for BCTV (1.1%) (Table S4; Fig. 5). Of the nymphs collected across 2020 and 2021, 16.2% were visibly parasitized.

### Discussion

Outbreaks of pathogens spread by beet leafhoppers are variable within and across years, making them difficult to assess and predict (Stakman 1957, Wintermantel and Kaffka 2006). While fluctuation in pathogen prevalence is due in part to abiotic factors, variation in host plant communities also affects leafhoppers (Novotný 1994). Leafhoppers have high motility at all life stages, and frequently move between agricultural crops and adjacent weedy areas (Waloff 1973). Effective management of pathogens spread by leafhoppers thus requires precise information about vector life history and host plant use. Our understanding of beet leafhopper host use and seasonality stems largely from studies from the early 1900s (Ball 1917, Davis 1927, Hills 1937). Our study supplements these prior surveys by providing information on the crop and noncrop hosts that play a role in the epidemiology of CPt and BCTV in the Columbia River Basin.

The beet leafhopper is endemic to the Mediterranean region (Oman 1948, Frazier 1953). Many of their weedy hosts are invasive from Europe and had become prevalent in agricultural environments and rangelands of the USA by the late 1800s (Piemeisel 1932, Horton 2018), such as Brassicaceous weeds that are hosts in the winter and spring and Amaranths in the summer (Douglass and Cook 1954, Cook 1967). We focused on sampling nonnative plants suspected to support beet leafhopper and found the vast majority on four species: Russian thistle, flixweed, tumble mustard, and kochia. These hosts (and adult leafhoppers from them) were also the most commonly infected with both BCTV and CPt. In contrast, native plants such as sagebrush and rabbitbrush were not key leafhopper or pathogen hosts, and very few beet leafhoppers—infected or not—were collected from potato plants despite the high prevalence of CPt in potato leaf tissue samples. Interestingly, beet leafhopper nymphs had very low rates of infection for both CPt and BCTV, although they were frequently collected alongside infected adult leafhoppers from infected plants. While beet leafhopper nymphs can transmit BCTV, they are highly inefficient vectors when compared with adults (Severin 1921b). Nymphal transmission of CPt does not appear to have been studied. It is unclear why infection in field-collected nymphs was so low in this study despite short acquisition times for both pathogens, but this pattern was also observed in prior surveys using traps (Foutz et al. 2024).

Plants were frequently infected with CPt throughout the season. However, while prevalence of BCTV was high in March and April, it



**Fig. 5.** Number of beet leafhopper nymphs collected in each month sampling was conducted on the 5 most common host species, representing 98% of nymphs collected. The size of the circles represents the number of nymphs on each host each month, and the colors represent the percentage infected with the A) CPt and B) BCTV pathogens.

declined rapidly after May. These results could stem in part from our sampling design, with most sampling conducted near potato fields. While BCTV infects potatoes, it does so less severely than in other crops (Bennet 1971). It is possible that viral infection rates would be higher in weedy plants adjacent to beets, beans, tomatoes, or other more susceptible crops. Similarly, low infection levels of *S. citri* may be because this pathogen is most associated with citrus, horseradish, and carrots (Lee et al. 2006, Swisher Grimm et al. 2023). Many plant samples were co-infected with CPt and BCTV, especially in fall-germinating weed species sampled in March and April. It is likely these plants are infected by beet leafhoppers in fall, letting pathogen titers increase over the winter and allowing the hosts to serve as a pathogen reservoir in the spring. Mixed infection could lead to synergistic interactions between pathogens (Renteria-Canett et al. 2011) and might have effects on vector fitness, behavior, or host preferences (Eigenbrode et al. 2018). Further investigation of the effects of coinfection may provide insights about the transmission of CPt and BCTV across diverse landscapes.

Although identifying parasitoids found in beet leafhoppers was outside the scope of this study, it may be worthwhile to do so. Multiple parasites of beet leafhopper have been noted in literature, including dryinid and other wasps (*Gonatopus* spp., *Polynema* spp., and *Anagrus* spp.), big-headed fly (*Pipunculus* spp.), Strepsiptera, parasitic mites, and hairworms (Severin 1933, Douglass and Cook 1954). Beet leafhopper nymphs collected in this study were much more frequently parasitized than adults, and rates would likely be higher if insect samples were molecularly screened for parasitoids rather than relying on visual inspection. Parasitism may play a role in controlling beet leafhopper populations and merits further investigation.

This study supports historic ideas about beet leafhopper ecology in the Columbia River Basin (Fig. 6). Beet leafhopper females

overwinter as adults on fall-germinating invasive weeds such as tumble mustard and flixweed. Eggs are laid in spring, and a first generation develops on overwintering hosts. As these plants senesce, adults disperse in search of summer hosts and often “sample” many nonhost plant species, including potato and other crops. A second generation is completed on summer weeds such as Russian thistle and kochia, with overlap between the spring and summer generations. As host plants become woody and unpalatable to leafhoppers in late summer and autumn, a third brood returns to fall-germinating hosts to overwinter. Improving the general understanding of beet leafhopper ecology and phenology may promote more successful management of beet leafhoppers and the pathogens they spread in the Columbia River Basin.

Currently, beet leafhoppers are heavily monitored in the Columbia River Basin region for increases in population and infection rates, but forecasting outbreaks remains a challenge. Beet leafhopper sampling is typically conducted only during the crop growing season, from May to September, with sticky card traps placed near crop fields (Wohleb et al. 2021). Extending the duration of beet leafhopper monitoring so that it begins in the early spring and continues into the late fall may provide more accurate estimations of beet leafhopper populations. Sampling outside of crop fields in weedy areas with high concentrations of beet leafhopper hosts could also allow for more informed monitoring outputs, predicting when and where pest and pathogen pressure are amassing. Data from this study suggest that potato and other crops are most at risk of infection when fall-germinating invasive weeds senesce in the late spring, forcing beet leafhopper dispersal. Incorporating this knowledge into pest monitoring networks and decision aid systems will generate more precise models to forecast beet leafhopper populations and incidence of pathogens, ideally allowing for improved local control of vectors and infection.

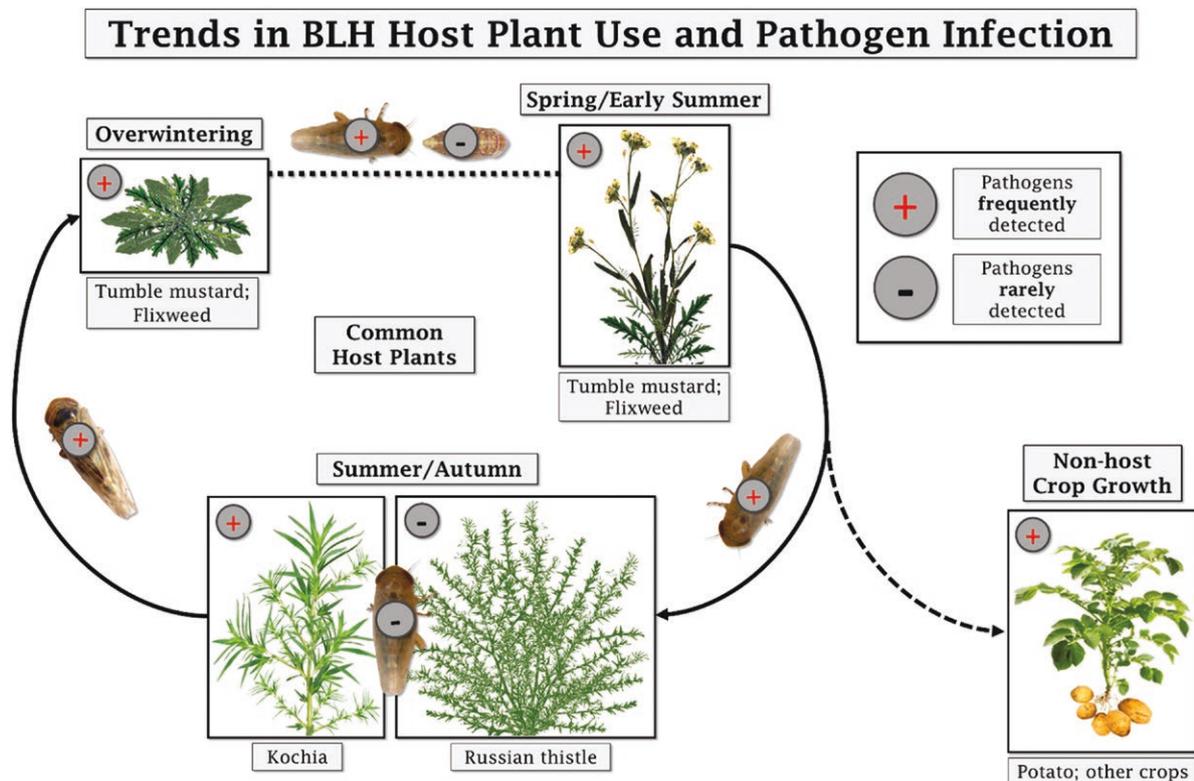


Fig. 6. Trends observed in beet leafhopper host plant use and infection.

## Supplementary material

Supplementary material is available at *Annals of the Entomological Society of America* online.

## Disclaimer

Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the United States Department of Agriculture. USDA is an equal opportunity provider and employer.

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## Conflicts of interest

The authors have no conflicts of interest.

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