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Research

Host and Shelter Plants for the Beet Leafhopper, Which Vectors Curly Top Viruses and Phytoplasmas in Southern Idaho

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Abstract

Weeds and crop plants not only serve as reproductive hosts and transitory or shelter plants for the beet leafhopper (BLH; *Circulifer tenellus*) but also as sources of plant pathogens that can then be vectored by the BLH. Thus, the plants that the BLHs are feeding on and infecting are of interest and may be changing over time. Therefore, BLH samples from a recent survey were investigated through DNA barcoding via the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) and maturase K (*matK*) chloroplast gene regions to determine what the BLHs had been feeding on prior to capture on yellow sticky cards in southern Idaho during 2020 and 2021. In June of both years, the first generation of BLHs predominately fed on *Pinus* spp. (59 to 76% of samples), which were likely in mountainous areas, and dispersed approximately 48 to 80 km to crop and sagebrush steppe locations. During July to September, the BLHs predominantly fed on *Salsola* spp. (Russian thistle; 61 to 66% of samples) and *Bassia scoparia* (kochia; 15% of samples). In both years, the BLHs that fed on pine had the highest percentage (55 and 75%, respectively) of samples with beet curly top virus based on primers that can detect both the Worland and Colorado strains. In both years, BLHs that had fed on Russian thistle and alfalfa had the highest percentage of samples with Spinach curly top Arizona virus. These data will be utilized in the development of future curly top management plans.

Keywords: beet curly top, Beet curly top virus, beet leafhopper, *Beta vulgaris*, *Circulifer tenellus*, common bean, *Phaseolus vulgaris*, phytoplasmas, Spinach curly top Arizona virus, sugar beet

Weeds and crop plants not only serve as reproductive hosts and transitory or shelter plants for the beet leafhopper (BLH; *Circulifer tenellus* Baker; syn. *Neoaliturus tenellus*; Hemiptera: Cicadellidae) but also as sources of plant pathogens that can then be vectored by the BLH (Bennett 1971). The BLH has been documented to transmit curly top viruses, phytoplasmas, and spiroplasmas (Bennett 1971; Chen and Gilbertson 2016; Creamer 2020; Crosslin et al. 2006; Strausbaugh et al. 2024; Swisher et al. 2016, 2018). The BLH

and pathogens such as beet curly top virus (BCTV) have been associated with numerous plant species (Bennett 1971). While the BLH can transmit BCTV to over 300 plant species, many of these species are not suitable for reproduction or long-term survival of the BLH and may only be serving as transitory or shelter plants (Supplementary Table S1; Bennett 1971; Cook 1967; Munyaneza and Upton 2005). Such plants may not support BLH reproduction but may still be of importance in curly top virus epidemiology.

In southern Idaho, sugar beet production began in 1912, and by 1919, as acreage expanded to meet sugar shortages associated with World War I, the first severe outbreak of curly top occurred (Bennett 1971). From that time up to 1930, the three factories in the central part of the Snake River Valley in southern Idaho had never run at more than 50% capacity because of curly top (Bennett 1971). Some of the more important BLH host plants in burned, overgrazed, or deteriorated rangeland areas in southern Idaho have been flixweed (*Descurainia sophia* [L.] Webb ex Prant.), perfoliate pepperweed (*Lepidium perfoliatum* L.), and tumble-mustard (*Sisymbrium altissimum* L.) (Cook 1967; Douglass and Cook 1954; Fox 1938). In sagebrush steppe areas, western (green) tansymustard (*Descurainia pinnata* [Walt.] Britt.) was the most important BLH host (Cook 1967; Fox 1938). The most important spring hosts in Idaho have historically been flixweed, perfoliate pepperweed, tumble mustard, and western tansymustard, while the most important summer hosts were Russian thistle (*Salsola kali* L.) and tumbling saltbush (*Atriplex rosea* L.) (Carter 1930; Cook 1967; Douglass and Cook 1954; Fox 1938). The most important holdover host plants in southern Idaho were big sagebrush (*Artemisia tridentata* Nutt.), yellow rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.), and shadscale saltbush (*Atriplex confertifolia* [Torr. & Frém.] S. Watson) (Cook 1967). In northern Utah, BLHs were captured on 108 species of plants, but of these plants, only 36 species were breeding hosts, and 17 were transitory or shelter hosts (Cook 1967; Knowlton 1932). In BLH breeding areas from Washington to central Utah, the important spring and summer weed hosts, except for western tansymustard, are introduced plant species that have become established on abandoned, waste, and deteriorated rangelands (Douglass and Cook 1954).

In southern Idaho, the largest nymphal populations were historically produced on field pennycress (*Thlaspi arvense* L.) in early summer, povertyweed (*Monolepis nuttalliana* [Schult.] Greene) in midsummer, and smotherweed (*Bassia hyssopifolia* [Pall.] Kuntze) in late summer (Douglass and Hallock 1957). Significant nymphal populations in late summer would also develop on hairy nightshade (*Solanum villosum* [L.] Mill.), tumbling saltbush, and Russian thistle (Cook 1967). BLHs can breed on sugar beet (*Beta vulgaris* L.), radish (*Raphanus sativus* L.), spinach (*Spinacia oleracea* L.), and potato (*Solanum tuberosum* L.) but will not breed on several other crops, including common bean (*Phaseolus vulgaris* L.), cantaloups (*Cucumis melo* L.), cayenne pepper (*Capsicum annuum* L.), squash (*Cucurbita* spp. L.), and tomato (*Solanum lycopersicum* L.) (Douglass and Cook 1954; Munyaneza and Upton 2005).

A recent survey of BLH and curly top viruses in southern Idaho identified aspects of curly top virus epidemiology that warranted further investigation to determine the extent to which historical patterns still hold (Strausbaugh et al. 2024). For example, aside from plant resistance, the timing and movement of BLHs were historically considered to be the most important factors for controlling beet curly top in the western United States (Blickenstaff and Traveller 1979; Rojas et al. 2018). The movement of BLHs from weedy sagebrush steppe areas has been associated with above-normal spring temperatures (Cook 1967; Harries and Douglass 1948); however, in recent years, some sagebrush steppe areas near crop fields had few if any winter annual weeds, and local weedy areas near crop fields appeared to be more important sources of the BLHs than plants in the sagebrush steppe (Strausbaugh et al. 2024). Moreover, pathogens such as the pepper curly top strain of BCTV (BCTV-PeCT), spinach curly top Arizona virus (SpCTAV), and phytoplasmas were recently detected for the first time in Idaho (Strausbaugh et al. 2024). The plant hosts for these pathogens are poorly understood, as are the weed hosts. In addition, BLHs seem to be dispersing into crop fields a month earlier than historical timing (Strausbaugh et al. 2024). Thus, the host plants that the BLHs are feeding on and infecting, as well as the prevalence of other pathogens in the system, may differ from historical observations. Therefore, BLH samples from a recent survey were investigated through DNA barcoding via the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) and maturase K (*matK*) chloroplast gene regions to determine what the BLHs had been feeding on prior to capture on yellow sticky cards in southern Idaho and to gain insights into the potential importance of different BLH plant sources and the pathogens they possess.

Materials and Methods

Leafhopper samples

BLH samples were collected during the 2020 and 2021 growing seasons using yellow sticky cards (Alpha Scents, Canby, OR) placed in five southern Idaho counties (Bingham, Elmore, Minidoka, Owyhee, and Twin Falls) where sagebrush steppe areas and sugar beet and common bean fields were in close proximity (Strausbaugh et al. 2024). Yellow sticky cards were collected weekly for 22 weeks from mid-April through mid-September (Strausbaugh et al. 2024). There were three sample sites (sagebrush steppe, sugar beet, and common bean) within a county with three cards per site. The global positioning system (GPS) coordinates for card locations were published previously (Strausbaugh et al. 2024). When retrieved, the cards were placed in a cooler for transportation back to the laboratory. Once back at the laboratory, cards were placed in a –20°C freezer. The BLHs were identified based on morphological characters using a stereomicroscope (Jensen 2008). From each card, up to a maximum of 10 BLHs were sampled and pooled into groups of up to five BLHs in a 2-ml microcentrifuge tube and stored at –80°C for molecular analysis.

Plant identification

Molecular methods had been utilized previously to confirm the morphological identification and evaluate for the presence of curly top viruses and phytoplasmas (Strausbaugh et al. 2024). The DNA had been extracted using Plant DNeasy kits (Qiagen, Valencia, CA) using methods described previously (Strausbaugh et al. 2024). In the current study, these same samples were utilized in PCR assays to amplify a portion of the *rbcL* chloroplast gene region that served as a barcoding marker to identify the plant species the BLHs had fed on prior to capture. A semi-nested PCR assay was utilized using *rbcL*-specific primer pairs P1630F/P1782R (P1630F 5′-ATGTCACCACAAACAGAGACTAAAGC-3′ and P1782R 5′-ATACTTCACAAGCAGCAGCTAGTTCC-3′) followed by P1630F/SI_R (SI_R 5′-GTAAAATCAAGTCCACCRCG-3′) (Inaba et al. 2023; Kress et al. 2009; Levin et al. 2003; Olmstead et al. 1992). The first round of PCR assays was conducted with the P1630F/P1782 primers, Phire Plant Direct PCR master mix (Thermo Fisher Scientific, Waltham, MA), and approximately 10 ng of target DNA. The amplification conditions

were 5 min at 98°C, followed by 35 cycles of 98°C for 10 s, 66°C for 20 s, and 72°C for 60 s, and finally 2 min at 72°C with a holding temperature of 4°C. The second round of reactions were conducted with the P1630F/SI_R primers and a 1/20 dilution of the first-round product as template with these conditions: 5 min at 98°C, followed by 30 cycles of 98°C for 10 s, 59°C for 20 s, and 72°C for 30 s, and finally 2 min at 72°C with a holding temperature of 4°C. The amplification product from the first round was 1.4 kb, and the second round was 0.6 kb. Reactions without template DNA served as negative controls, whereas template DNA from established plant samples served as positive controls. For the *Pinus* (pine) and *Salsola* spp. L. (Russian thistle), the *matK* chloroplast gene region was also amplified to make species identification possible. For the pine species, the *matK* primers 1F_Pt1548F (5′-TAAACGATCCTCTCATTCACGA-3′) and 2R_Pt2567R (5′-GAACTCGTCGGATGGAGTG-3′) were utilized along with the following reaction conditions: 5 min at 98°C, followed by 38 cycles of 98°C for 15 s, 64°C for 20 s, and 72°C for 45 s, and finally 2 min at 72°C with a holding temperature of 4°C (Gernandt et al. 2009; Wang et al. 1999). For the Russian thistle species, the matK primers matK-F-uni (5′-AATTTACGATCHATTCATTCMATWTTTCC-3′) and matK-R-uni (5′-AGTTYTARCACAAGAAAGTCGAARTATATA-3′) were utilized along with the same reaction conditions used for the pine matK primers, except the annealing temperature was 53°C (Schaefer et al. 2011).

Amplification products were visualized on a 1% agarose gel after GelRed (Biotium, Freemont, CA) staining. Amplicons were sent to TACGen (Richmond, CA) for bidirectional sequencing. The sequencing was also conducted in duplicate to achieve 4× coverage. The sequences were evaluated using BioEdit version 7.2.6.1 (Hall 1999), and consensus sequences were generated. The predominant haplotype that occurred for each host was deposited in GenBank (*rbcL* accessions PP374774 to PP374815; *matK* PP374816 to PP374820). The consensus sequences were compared with those on GenBank via BLASTn. The sequences for the *rbcL* and *matK* regions were concatenated prior to evolutionary analysis. The DNA sequences were then aligned using ClustalX 2.1 (Larkin et al. 2007), and the predominant haplotypes for the pine and Russian thistle species were evaluated using evolutionary analyses versus GenBank accessions (Supplementary Table S2) to confirm what was found using BLASTn. The substitution model that best fit the data according to the Bayesian information criterion was T92 + G for both the pine and Russian thistle species. Using this model, evolutionary analyses were conducted by the maximum-likelihood method with MEGA 11.0.13 (Tamura et al. 2021). An initial search (two replicates) was conducted to estimate the model parameters, which were then fixed for a bootstrap analysis of 1,000 replicates.

Data analysis

Comparison of haplotype frequencies between studies was conducted using a contingency test in SAS (version 9.4; SAS Institute, Cary, NC) via the Proc Freq procedure with the χ^2 statistic.

Results

Plant host identification

In 2020, 492 yellow card samples were determined to be BLHs (Strausbaugh et al. 2024), and plant DNA barcoding using the *rbcL* chloroplast gene region was successful on 40% of these samples. In 2021, 854 yellow card samples were determined to be BLHs, and plant DNA barcoding was successful on 60% of these samples. The DNA barcoding determined that the BLHs had fed on 42 different plant hosts (Table 1). Seventeen of the plant hosts mentioned in Table 1 may be the first report of BLH feeding on these hosts since they do not appear on the list compiled from previous studies (Supplementary Table S1). The BLASTn results indicated that all the plant host *rbcL* sequences submitted to GenBank had 98.43% or higher sequence identity with GenBank accessions for that host (Table 1). *Salsola* sp. H1 had 100% sequence identity with more than one species in BLASTn results. Thus, the *matK* region was also sequenced and concatenated with sequencing from the *rbcL* region and used to determine that this haplotype fit into a clade with *S. collina* Pall., *S. praecox* (Litv.) Iljin, and *S. komarovii* Iljin (Fig. 1). Of these three species, *S. collina* is the only one known to be present in the United States (based on United States Department of Agriculture [USDA] Natural Resources Conservation Service [NRCS] Plants Database; https://plants.usda.gov/home). Although *Salsola* sp. H1 fits in a clade with *S. collina*, this sequence also

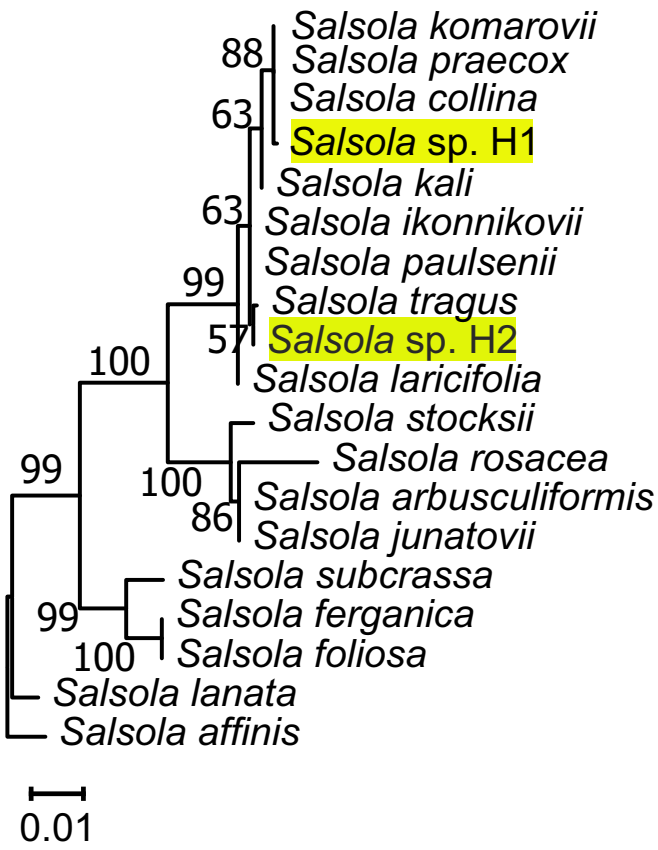

FIGURE 1
Phylogenetic relationships among *Salsola* spp. and the predominant *Salsola* haplotypes (yellow boxes) identified among beet leafhopper samples collected in southern Idaho during 2020 and 2021 based on sequencing from both the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) and maturase K (*matK*) chloroplast gene regions. Concatenated sequences (1,312 bp) from these two regions were evaluated in a maximum-likelihood analysis. Numbers on the nodes of the tree represent the statistical support based on 1,000 replicates. The tree is drawn to scale with the branch lengths measured in the number of substitutions per site and rooted to *Salsola affinis*. The GenBank accessions utilized for each species are in Supplementary Table S2. The *Salsola* sp. H1 accessions are PP374805 and PP374819, and the *Salsola* sp. H2 accessions are PP374806 and PP374820.

falls very close to the *S. kali* clade, which is a species known to be present in Idaho, while *S. collina* only occurs in neighboring states to the east (based on USDA NRCS Plants Database and the Idaho Species Catalog; https://idfg.idaho.gov/). The *Salsola* sp. H2 sequence was in a clade with several other *Salsola* species. However, *S. tragus* L. is the only species in this clade known to be present in Idaho. The *Pinus* sequences were also investigated via both *rbcL* and *matK* sequencing and evolutionary analyses (Fig. 2). The *Pinus* sp. subsection *Contortae* sequence was placed in a clade next to *P. contorta* Douglas ex Loudon (Lodgepole pine), which is a species known to be present in Idaho's mountainous areas. The *Pinus* sp. subsection *Ponderosae* sequence was placed in a clade next to several *Pinus* species. Of the species in this clade, *P. ponderosa* Lawson & C. Lawson (ponderosa pine) is the only species known to be present in Idaho's mountainous areas. The *Pinus* sp. subsection *Strobus* sequence was placed in a clade next to several pine species. Of the species in this clade, *P. albicaulis* Engelm. (whitebark pine) is the only species known to be present in Idaho's mountainous areas.

Timing of feeding

The timing for sample collection in relation to host or shelter plant is presented in Table 2. All hosts or shelter plant samples present in double digit numbers during at least 1 year are presented individually in Table 2, while the remaining host and shelter plants were lumped together and designated "other hosts". DNA barcoding for BLH samples collected in May was poor in both years, which did not allow for trend identification. In June samples in both years, the BLHs' predominant feed plant was pine (76% of samples in 2020 and 59% in 2021; Table 2). The frequency of *Pinus* sequences by subsection was 57% *Contortae*, 38% *Ponderosae*, and 5% *Strobus*. These data suggest that the first generation of BLHs is disseminating into the crop fields and sagebrush steppe from surrounding mountainous areas after having fed on lodgepole and ponderosa pine. Samples from July through September indicate the BLHs had predominantly fed on Russian thistle (76% of 2020 samples and 59% in 2021). The next most frequently identified host was *Bassia scoparia* (L.) A.J. Scott (kochia; 15% of samples in both years). The frequency of Russian thistle sequences was 97% H1 (likely *S. kali*) and

TABLE 1

Plants detected during a 2020 to 2021 survey of beet leafhopper, *Circulifer tenellus*, in southern Idaho based on sequencing from the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) chloroplast gene[a]

Scientific name	Common name	BLASTn	*rbcL* accessions
Arabidopsis thaliana (L.) Heynh.*	Wall-cress	100% MK353213	PP374774
Atractylodes sp. DC.*	Atractylodes	99.65% NC_037484	PP374775
Atriplex canescens (Pursh) Nutt.	Fourwing saltbush	100% NC_082104	PP374776
Bassia scoparia (L.) A.J. Scott	Kochia	100% MF065087	PP374777
Bassia prostrata (L.) A.J. Scott*	Forage kochia	99.82% MT931110	PP374778
Beta vulgaris L.	Sugar beet	100% NC_059019	PP374779
Camelina sp. Crantz	False flax	99.83% KX886352	PP374780
Chenopodium sp. L.	Goosefoot	100% NC_034949	PP374781
Chorispora tenella (Pall.) DC.	Siberian mustard	98.96% NC_049622	PP374782
Cirsium sp. Mill.*	Thistle	99.65% AY874436	PP374783
Convolvulus arvensis L.	Field bindweed	100% NC_054224	PP374784
Descurainia sophia (L.) Webb ex. Prant.	Flixweed	100% NC_049631	PP374785
Diplotaxis sp. DC.*	Wallrocket	100% KX282700	PP374786
Elaeagnus angustifolia L.*	Russian olive	99.83% NC_040992	PP374787
Enchylaena tomentosa R. Br.*	Ruby saltbush	99.13% ON756826	PP374788
Equisetum arvense L.*	Field horsetail	98.43% NC_014699	PP374789
Fraxinus sp. L.*	Ash	100% NC_043874	PP374790
Helianthus sp. L.	Sunflower	100% MN602834	PP374791
Juniperus communis L.*	Juniper	99.48% NC_035068	PP374792
Lactuca sp. L.	Lettuce	100% ON550363	PP374793
Linum usitatissimum L.	Flax	100% NC_036356	PP374794
Malva sp. L.	Mallow	99.83% MK860036	PP374795
Medicago sativa L.	Alfalfa	99.83% NC_042841	PP374796
Mentzelia albicaulis (Hook.) Torr. & Gray*	Whitestem blazingstar	100% NC_044830	PP374797
Picea pungens Engelm.*	Blue spruce	100% NC_067714	PP374798
Pinus sp. subsection *Contortae* L.	Pine	100% MH612863	PP374801
Pinus sp. subsection *Ponderosae* L.	Pine	100% NC_067715	PP374800
Pinus sp. subsection *Strobus* L.	Pine	100% MN536531	PP374799
Pottia sp. Ehrh. ex Fürnr.*	Moss in Pottiaceae	99.46% DQ463105	PP374802
Prunus sp. L.	Plum	100% MK634746	PP374803
Quercus sp. L.*	Oak	100% NC_048513	PP374804
Salsola sp. H1 L.	Russian thistle	100% NC_066995	PP374805
Salsola sp. H2 L.	Russian thistle	100% MT931131	PP374806
Sarcobatus vermiculatus (Hook.) Torr.	Greasewood	100% NC_040932	PP374807
Solanum lycopersicum L.	Tomato	99.83% CP023757	PP374808
Solanum nigrum L.	Black nightshade	98.61% NC_028070	PP374809
Solanum tuberosum L.	Potato	100% OP589401	PP374810
Sonchus sp. L.	Sowthistle	100% NC_048510	PP374811
Syntrichia sp. Brid.*	Moss in Pottiaceae	99.82% KC250538	PP374813
Taraxacum officinale F.H. Wigg.	Dandelion	100% MN601479	PP374812
Tragopogon sp. L.*	Goat's beard	100% NC_085463	PP374814
Vitis vinifera L.*	Wine grape	100% MN561034	PP374815

[a] The plant feeding is based on DNA barcoding of chloroplast DNA from the *rbcL* gene region sequenced from beet leafhoppers. Plant species followed by an asterisk are the first report for beet leafhoppers having fed on this species. BLASTn = percent sequence identity for the *rbcL* gene sequencing. *rbcL* accessions = the GenBank accessions from this study for the *rbcL* gene region sequencing.

7% H2 (likely *S. tragus*). Other hosts most frequently identified throughout the 22-week sample period were *Medicago sativa* L. (alfalfa; 2 to 5% of samples), *Beta vulgaris* (sugar beet; 4%), *Helianthus* sp. L. (sunflower; 2 to 3%), and *Lactuca* sp. L. (lettuce; 1 to 2%). Other hosts found less frequently are only mentioned in Table 1 and designated as "other hosts" (when grouped together they represented 7 to 12% of the samples) in Table 2. These data suggest that after the first generation of BLHs disseminates from mountainous areas, the subsequent BLH generations were predominantly feeding on Russian thistle and kochia with a peak in early August in 2020. In 2021, peak feeding on Russian thistle ranged from late July to late August, while the peak for kochia occurred in early September.

Feeding by site

On cards in sagebrush steppe areas and next to sugar beet and bean fields, pine was the predominant host or shelter plant in June both years (Table 3). In July through the end of the summer, Russian thistle and kochia were the main hosts at all sites. However, over the 2 years, 58 to 70% of the Russian thistle samples came from sagebrush steppe sites, while 23 to 35% came from sugar beet sites, and only 6 to 7% came from bean sites. For BLHs that fed on pine, 42 to 50% of the samples came from sagebrush steppe sites, while 26 to 34% came from sugar beet sites, and 24% came from bean sites. For BLHs that fed on kochia, 33 to 62% came from sugar beet sites, and 25 to 45% came from bean sites, while sagebrush steppe sites were only 12 to 22%.

Pathogens associated with feeding

The presence of detectable BCTV coat protein was 54% in 2020 and 70% in 2021, with the percentage ranging from 44 to 75% in 2020 and 50 to 83% in 2021 depending on host (Table 4). The presence of the California/Logan strain of BCTV (BCTV-CA/Logan) was associated with feeding on sugar beet and alfalfa in 2021, but the number of samples in 2020 was too low to determine any trend. The chance of finding the Colorado strain of BCTV (BCTV-CO) in a BLH sample ranged from 11 to 29% across all hosts in 2021, and the positive detections were too low in 2020 to show any clear patterns. Sample numbers for BCTV-PeCT and Severe (BCTV-Svr) strains of BCTV were low in both years, making finding trends difficult to identify. In both years, the BLHs that fed on pine had the highest percentage (55 and 75%, respectively) of positive samples with the BCTV-Wor+ primers (detects both the BCTV-CO and Worland [Wor] strains). The chance of finding BCTV-Wor+ positive samples was lowest

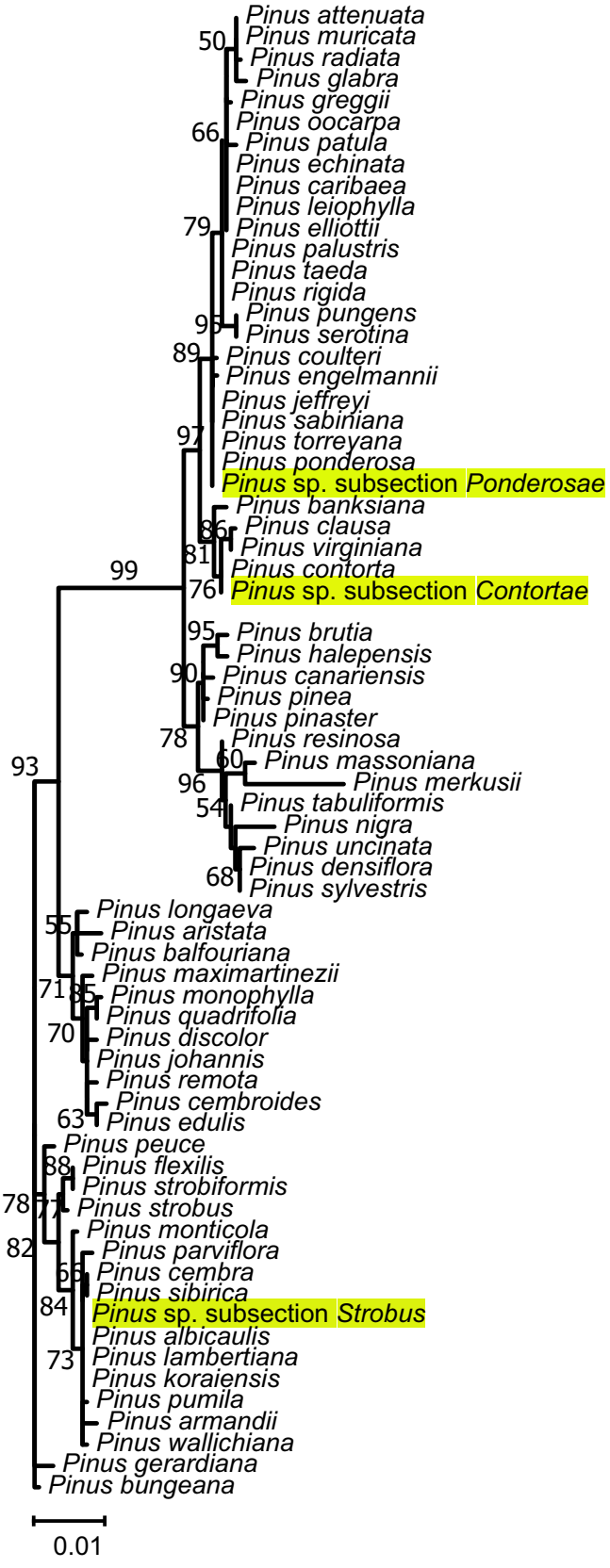

FIGURE 2

Phylogenetic relationships among *Pinus* spp. found in the United States and the predominant *Pinus* haplotypes (yellow boxes) identified among beet leafhopper samples collected in southern Idaho during 2020 and 2021 based on sequencing from the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) and maturase K (*matK*) chloroplast gene regions. Concatenated sequences (1,536 bp) from these two regions were evaluated in a maximum-likelihood analysis. Numbers on the nodes of the tree represent the statistical support based on 1,000 replicates. The tree is drawn to scale with the branch lengths measured in the number of substitutions per site and rooted to *P. bungeana*. To find the GenBank accessions utilized for each species, consult Supplementary Table S2. The accessions for *Pinus* sp. subsections in Idaho samples were PP374801 and PP374816 for *Contortae*, PP374800 and PP374817 for *Ponderosae*, and PP374799 and PP374818 for *Strobus*.

(11 to 25%) with BLHs that fed on sugar beet and sunflowers in 2020, while BLHs feeding on other plants ranged from 42 to 55%. In 2021, the chance of finding BCTV-Wor+ was again lowest (36 to 38%) on BLHs that fed on sugar beet and sunflowers, while BLHs feeding on other plants ranged from 51 to 75%. In both years, BLHs that had fed on Russian thistle and alfalfa had the highest percentage of detectable SpCTAV. The sample numbers for hosts with detectable phytoplasma were low in both years, which did not allow for trend identification.

BLH haplotype associated with feeding

Previous work had identified two dominant haplotypes within the BLH population (Strausbaugh et al. 2024). Thus, the distribution of these two haplotypes with regards to feeding is shown in Table 5. In 2020 and 2021, the contingency tests comparing the distribution within a host versus the distribution seen for the whole population did not differ significantly (P ranged from 0.0937 to 0.9113). The comparison between the 2020 and 2021 haplotype distribution was also not significant ($P = 0.9919$). Thus, the BLH haplotype frequency did not vary with host feeding or year.

Discussion

Historically in sagebrush steppe, sagebrush was frequently codominant with perennial bunchgrasses in southern Idaho (Connelly et al. 2004). In the 1960s, in southern Idaho Snake River Plains sagebrush plant communities with minimal disturbance, the number of plant species ranged from 13 to 24 (Tisdale et al. 1965). However, plant dynamics in sagebrush habitats has changed with domestic herbivory, the introduction of exotic plants, changes in disturbance regimes (e.g., fire), and atmospheric CO_2 (Anderson and Inouye 2001; Connelly et al. 2004; DiTomaso 2000). Irrigation systems were also developed in the early 1900s, which put much of the more fertile land into agricultural use (Blickenstaff and Traveller 1979; Hironaka et al. 1983; Scott et al. 2001). The estimate of potential sagebrush habitat in southern Idaho is 88,084 km^2, but, currently, there is 49% in sagebrush habitat, 25% in agriculture, and 26% in other habitats or uses (Connelly et al. 2004). Given all these changes and dynamics, the distribution of BLHs and their hosts may be changing as well.

Historically, BLH overwintering on mustards such as flixweed, tumblemustard, tumbling saltbush, perfoliate pepperweed, and western tansymustard in sagebrush steppe areas were considered the primary source of the first generation of BLHs in southern Idaho (Carter 1930; Douglass and Cook 1954; Fox 1938; Haegele 1927). As mustard hosts begin desiccating each spring or summer, the BLHs moved to summer hosts such as halogeton (*Halogeton glomeratus* [M. Bieb.] C.A. Mey.), kochia, Russian thistle, and smotherweed (Carter 1927, 1930; Douglass and Hallock 1957; Fox 1938; Haegele 1932). Historically, the breeding grounds in Idaho and eastern Oregon lie on the Snake River Plains at elevations below 1,372 m, and the movement of BLHs into crop fields was thought to be from local breeding grounds and not long-distance flight (Carter 1930; Douglass and Cook 1954; Fox et al. 1945). However, in the current study, BLH feeding suggests that the first generation of BLHs are dispersing from high elevation mountainous locations in late spring/early summer in southern Idaho, which has not been documented previously. In Elmore County, the yellow cards were surrounded by Russian thistle at the time the cards were initially deployed in both years, yet BLHs in Elmore County predominantly fed on pine species when captured up through June. These data support that the first generation of BLHs are dispersing in from long distances and not from local sources. Just prior to migration, the host data suggest the BLHs most frequently fed on lodgepole and ponderosa pine prior to flight. Feeding on pine had not been suggested or documented previously, except for a recent study by Cooper et al. (2022). They found that BLHs in few of their May to June samples from the Yakima area in Washington state had also fed on pine.

TABLE 2

The beet leafhopper, *Circulifer tenellus*, fed on these plants based on DNA barcoding with leafhopper samples collected for 22 weeks in 2020 and 2021 in southern Idaho[a]

		May		June		July		August		September	
Host	Total number	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late
2020											
Russian thistle	110	0	0	0	2	13	24	36	20	12	3
Pine	42	2	0	16	16	8	0	0	0	0	0
Kochia	24	0	0	0	0	1	5	8	7	3	0
Sugar beet	9	0	0	1	0	1	2	0	0	3	2
Alfalfa	4	0	0	0	0	2	1	0	0	0	1
Sunflower	4	0	0	0	0	0	1	3	0	0	0
Lettuce	2	0	0	0	0	0	0	1	0	0	1
10 other hosts	15	0	0	3	6	2	0	1	0	3	0
Total	210										
2021											
Russian thistle	231	0	0	3	9	25	52	47	53	42	0
Pine	102	0	3	28	63	4	2	1	0	1	0
Kochia	55	0	0	1	0	1	1	9	18	25	0
Alfalfa	28	0	0	5	8	3	2	2	7	1	0
Sugar beet	21	3	1	2	3	3	2	3	3	1	0
Sunflower	14	0	0	0	0	2	3	5	2	2	0
Lettuce	13	0	0	2	1	1	4	1	1	3	0
30 other hosts	66	3	4	14	16	10	3	1	2	13	0
Total	530										

[a] Only the predominant host or shelter plants detected using DNA barcoding with the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) gene region are listed in this table, but the full list of host or shelter plants detected is given in Table 1 along with their scientific names. Early = during the first 15 days of the month. Late = during day 16 or later in the month.

Lodgepole pine is normally only found in the higher elevation mountainous areas from 1,828 to 3,353 m (areas with at least 100 frost-free days; https://csfs.colostate.edu/colorado-trees/colorados-major-tree-species/) in elevation, while the yellow sticky cards capturing BLHs in Idaho (Strausbaugh et al. 2024) were in the middle of the valley at 746 to 1,412 m and approximately 48 to 80 km by air from locations with lodgepole pine. Ponderosa pine is typically found at elevations of 1,920 to 2,896 m. These BLHs appear to have dispersed to sagebrush steppe locations and crop fields with little or no feeding on other hosts along the way. Mountainous areas were investigated in the 1920s, but BLHs were only found on weed hosts and not pine species (Haegele 1927). Even on the weed hosts such as tumbling saltbush, black nightshade (*Solanum nigrum* L.), and knotgrass (*Polygonum aviculare* L.), BLHs were rare in mountainous areas from samples collected April through October (Haegele 1927). Historical reports from other areas mention BLHs dispersing 320 to 482 km or more (Annand 1931; Annand and Davis 1932; Dorst and Davis 1937; Fulton and Romney 1940; Romney 1939; Severin 1933).

The BLH samples collected from yellow sticky cards were not surface sterilized prior to DNA extraction. Thus, the possibility of detecting pollen such as pine pollen cannot be completely ruled out. Although the surface of the BLHs was not purposely sterilized, the BLHs would have been subject to considerable UV light given that some BLHs may have been on the sticky cards close to 7 days. Most pine detections in this study occurred in June samples when numerous grass species and other plants would have also been producing pollen. Most cards were very close to grassy weeds and large acreages of corn, barley, and wheat, yet none of the BLH samples were positive for grass DNA. In some of the sagebrush steppe sites, sagebrush were the only green plants, and we did not detect DNA from pollen or plant tissue from these sites. These negative data suggest that we were not detecting just pollen. Also, the sequencing for most samples only detected one plant species, which also suggests we were detecting DNA from feeding activity and not pollen from numerous species. Since corn, wheat, and barley were common near collection sites, these data suggest that BLHs did not feed on these crop plants or did so very sparingly since no grass DNA was detected.

During dry autumns in southern Idaho (25 to 30 cm of annual rainfall; mostly November through May), precipitation may not be sufficient to establish annual weeds (Cook 1967; Fox 1938). Thus, BLHs will have to spend at least a month or more on what are described as holdover or shelter hosts; however, high mortality tends to occur on these hosts (Cook 1967; Fox 1938). In northern Utah, BLHs were captured from 108 species of plants, but of these plant species, only 36 were considered to be breeding hosts, and 17 were holdover hosts with BLHs being found only during dispersal events on the remainder of the plants (Cook 1967; Knowlton 1932). Cook (1967) lists 14 plant species as holdover hosts: big sagebrush, big saltbush (*Atriplex lentiformis* [Torr.] Watson), California broomsage (*Lepidospartum squamatum* [A. Gray] A. Gray), California sagebrush (*Artemisia californica* Less.), cattle saltbush (*Atriplex polycarpa* [Torr.] Watson), creosote bush (*Larrea tridentata* [DC.] Colville), false tarragon (*Artemisia dracunculus* L.), fourwing saltbush (also chamiso; *Atriplex canescens* [Pursh] Nutt.), mat saltbush (*Atriplex corrugata* Watson), perennial pepperweed (*Lepidium alyssoides* A. Gray), shadscale saltbush, snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby), spinescale saltbush (*Atriplex spinifera* J.F. Macbr.), and yellow rabbitbrush. Historically, some of the most important BLH holdover host plants in southern Idaho sagebrush steppe areas are big sagebrush, rabbitbrushes (*Chrysothamnus* spp. Nutt.), and spinescale saltbush, yet the BLHs disseminating in this study were not detected to have fed on any of these hosts except fourwing saltbush before being collected on the yellow sticky cards (Cook 1967; Douglass and Hallock 1957; Fox 1938). These data suggest that sagebrush is definitely not a favored host, since sagebrush was the only live vegetation at the sagebrush steppe sites in Owyhee and Twin Falls at the time of card placement in mid-April. Even though sagebrush is mentioned as a holdover host, in the 1920s, BLHs could not be found on sagebrush (Haegele 1927). In Washington, sagebrush was not ob-

TABLE 3

The beet leafhopper, *Circulifer tenellus*, fed on these plants based on DNA barcoding with leafhopper samples collected for 22 weeks in 2020 and 2021 in southern Idaho from yellow sticky cards located in sagebrush steppe, sugar beet, and common bean sites[a]

		Sagebrush steppe					Sugar beet					Bean				
Host	Number	May	June	July	August	September	May	June	July	August	September	May	June	July	August	September
2020																
Russian thistle	110	0	2	27	37	11	0	0	8	13	4	0	0	2	6	0
Pine	42	1	16	4	0	0	0	8	3	0	0	1	8	1	0	0
Kochia	24	0	0	0	2	1	0	0	6	7	2	0	0	0	6	0
Sugar beet	9	0	0	3	0	3	0	0	0	0	2	0	1	0	0	0
Alfalfa	4	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0
Sunflower	4	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0
Lettuce	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
10 other hosts	15	0	3	2	0	0	0	5	0	0	2	0	1	0	1	1
Total	210															
2021																
Russian thistle	231	0	7	51	51	25	0	4	20	42	16	0	1	6	7	1
Pine	102	3	37	2	1	0	0	32	2	0	1	0	22	2	0	0
Kochia	55	0	1	0	3	8	0	0	2	10	6	0	0	0	13	12
Alfalfa	28	0	5	0	2	0	0	1	3	4	1	0	7	2	3	0
Sugar beet	21	2	1	1	2	1	1	3	1	2	0	1	1	3	2	0
Sunflower	14	0	0	1	3	1	0	0	4	4	0	0	0	0	0	1
Lettuce	13	0	2	1	1	2	0	0	2	1	1	0	1	2	0	0
30 other hosts	66	3	8	5	0	8	0	15	1	1	6	3	8	6	2	0
Total	530															

[a] Only the predominant host or shelter plants detected using DNA barcoding with the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) gene region are listed in this table, but the full list of host or shelter plants detected is given in Table 1 along with their scientific names. Number = the number of samples.

served to harbor significant populations of crop pests (James et al. 2018). The only pest trapped was a small number of *Empoasca* leafhoppers (James et al. 2018). However, sagebrush and other native sagebrush steppe species do support beneficial arthropods and should be reintroduced into sagebrush steppe areas around crop fields and other areas where the natural ecosystem has been disturbed (James et al. 2018; Wenninger and Inouye 2008).

BLHs do not have to remain on holdover plants in the sagebrush steppe areas and have been noted to move up canyons in the fall. Dyed BLHs were released at the mouth of a canyon in central California in the fall of 1941 and moved as far as 18 km (11 miles) up the canyon in 2 weeks (Cook 1967). The BLHs likely used upslope winds to aid their movement. Data from the current study suggest the BLH spring dispersal in Idaho likely utilized downslope winds (Stewart et al. 2002) to aid in migration over 48 to 80 km from pines at the top of surrounding mountains to crop fields in the valley. Flights of BLHs have previously been documented to occur in the crepuscular period near sunrise or sunset when temperatures reach a threshold of 16 to 18°C (Lawson et al. 1951). Upslope winds in the fall may aid the BLHs to disseminate back to mountainous area.

When using the rbcL primers, detecting the plant species present was successful in 40% of the BLH samples in 2020 and in 60% of the samples in 2021. Plant detection was par-

TABLE 4

The percentage of beet leafhopper, *Circulifer tenellus*, samples collected for 22 weeks in 2020 and 2021 in southern Idaho associated with curly top viruses and phytoplasmas[a]

			BCTV strains (%)						
Host	Sample number	Coat protein (%)	CA/Logan	CO	PeCT	Svr	Wor+	SpCTAV (%)	Phyto (%)
2020									
Russian thistle	110	55	0	8	2	2	46	21	2
Pine	42	62	0	12	2	0	55	7	0
Kochia	24	46	4	4	0	0	42	17	0
Sugar beet	9	44	0	0	0	0	11	11	0
Alfalfa	4	50	0	0	0	0	50	25	0
Sunflower	4	75	0	0	0	0	25	0	0
Lettuce	2	50	0	50	0	0	50	0	0
10 other hosts	15	47	0	20	0	0	47	13	0
Total	210	54	0	9	1	1	46	16	1
2021									
Russian thistle	231	77	3	15	2	0	65	68	2
Pine	102	83	6	26	1	4	75	36	1
Kochia	55	60	2	11	0	0	51	42	0
Alfalfa	28	82	18	29	4	0	61	54	0
Sugar beet	21	81	14	24	0	0	38	29	0
Sunflower	14	50	7	21	0	7	36	50	0
Lettuce	13	62	0	15	0	0	54	31	15
30 other hosts	66	77	5	26	2	0	65	44	6
Total	530	76	5	19	1	1	63	52	2
Overall totals	740	70	4	16	1	1	58	42	2

[a] Only the predominant host or shelter plants detected using DNA barcoding with the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) gene region are listed in this table, but the full list of host or shelter plants detected is given in Table 1 along with their scientific names. BCTV = beet curly top virus. The BCTV strains included California/Logan (CA/Logan), Colorado (CO), Pepper curly top (PeCT), Severe (Svr), and Worland (Wor). Wor+ = the primers detected both the CO and Wor strains of BCTV. SpCTAV = Spinach curly top Arizona virus. Phyto = phytoplasma detected in this sample. The pathogens present in the beet leafhopper samples were established in a previous study (Strausbaugh et al. 2024). Total = the total number of samples followed by percentage data for coat protein or pathogens detected in those samples. Overall totals = the total number of samples over both years followed by percentage data for coat protein or pathogens detected in those samples.

TABLE 5

The percentage of beet leafhopper (BLH), *Circulifer tenellus*, samples collected for 22 weeks in 2020 and 2021 in southern Idaho and arranged by BLH haplotype[a]

	2020				2021			
Host	Sample number	H1	H2	Prob	Sample number	H1	H2	Prob
Russian thistle	110	53	23	0.2508	231	45	21	0.5140
Pine	42	38	26	0.8636	102	44	24	0.8213
Kochia	24	46	33	0.7450	55	44	25	0.9113
Sugar beet	9	44	25	0.7155	21	25	25	0.1601
Alfalfa	4	NC	NC	NT	28	50	31	0.8865
Sunflower	4	NC	NC	NT	14	64	21	0.0937
Lettuce	2	NC	NC	NT	13	38	38	0.1178
Overall	195	48	25	0.5543	464	44	23	0.7312

[a] Only the predominant host or shelter plants detected using DNA barcoding with the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) gene region are listed in this table, but the full list of host or shelter plants detected is given in Table 1 along with their scientific names. H1 and H2 are the two BLH haplotypes identified previously (Strausbaugh et al. 2024), and the numbers in the table represent the percentage of samples with this haplotype. H1 and H2 were 45 and 29% of the population in 2020 and 44 and 26% of the population in 2021, respectively. Prob = probability for the chi-square statistic for a contingency test conducted to determine if the host population differed from what was found for the whole population. NC = no comparison due to low sample numbers. NT = not tested due to low sample numbers.

ticularly poor in the early season May samples. Plant detection in a sample was considered negative, and no sequencing was conducted if the PCR product could not produce a visible band on the gel. When PCR product produced a band on the gel, some of the product was sent for sequencing. Most sequencing was of very good quality, and no mixture was evident as only less than 1% of the sequences were unusable. A previous study with rbcL primers found they could detect the plant species present in 46% of lanternfly nymphs (Avanesyan and Lamp 2020). Thus, the overall percentage of plant detection in this study was similar to previous work.

Based on BLH feeding in this study, the most important summer hosts in July and August were Russian thistle and to a lesser extent kochia. Historically, if distribution and abundance are considered, flixweed, perfoliate pepperweed, tansy mustard, and tumblemustard were the most important spring hosts, and Russian-thistle and tumbling saltbush were the most important summer hosts (Bennett 1971; Carter 1930; Douglass and Hallock 1957; Haegele 1927, 1932). However, historically, the presence or absence of Russian thistle largely determined the distribution and size of overwintering BLH populations (Bennett 1971). Given the BLH feeding observed in this study, Russian thistle still appears to be the host that drives BLH populations in the summer and early fall in southern Idaho.

BLHs can breed and survive on sugar beet, radish, potato, and spinach but will only feed and not breed on many other crops, including common bean, cantaloups, cayenne pepper, squash, and tomato (Douglass and Cook 1954). BLHs landing on common bean and tomato plants move off them within 5 to 7 h, whereas sugar beet, radish, potato, and carrot have been found to be acceptable hosts (Munyaneza and Upton 2005). Although potato is considered to be an acceptable host, BLH reproduction on potato has been documented to be lower when compared to BLH reproduction on sugar beet and radish (Munyaneza and Upton 2005). In Washington, BLHs suffered high mortality after 4 days of exposure to common bean and tomato, suggesting these plants are not suitable hosts for the BLH (Munyaneza and Upton 2005). In another study, BLHs confined to tomato began dying after 12 to 16 h, and few were alive after 72 h (Thomas and Boll 1977). Only in seasons when BLHs are abundant and movements occur at critical periods in the development of the crop can severe damage be produced on susceptible cultivars of these crops (Bennett 1971; Hudson et al. 2010; Munyaneza and Upton 2005). When we have clip-caged BLHs onto common bean or cayenne pepper plants to screen for resistance (Bosland and Strausbaugh 2010; Soler-Garzón et al. 2023), the BLHs were all dead after 1 day but did transmit BCTV before they died. Thus, even though some plants may be rather toxic, BLHs will still have time to transmit BCTV before they move on to another plant or die. Even though large amounts of BLHs were captured next to the bean fields in Owyhee and Bingham counties and common bean plants had curly top symptoms, none of the BLHs in Idaho samples were found to have fed on common bean prior to capture on the sticky cards. These data suggest that BLHs are not likely to make it out of a common bean field once they start feeding.

One of the biggest challenges for sagebrush steppe regions occurred in 1861 with the introduction of Eurasian annual grasses such as cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski) (Connelly et al. 2004; DiTomaso 2000). These grasses changed the fire interval in the sagebrush steppe from 60 to 110 years before their introduction to less than 5 years today (DiTomaso 2000; Whisenant 1990). In southern Idaho, much of the cheatgrass region is well defined by fires that have burned since 1960 (Connelly et al. 2004). Rangeland improvement in Idaho began in the 1940s with efforts to replace sagebrush steppe weed hosts with grasses such as crested wheat grass (*Agropyron cristatum* [L.] Gaertn.) and desert wheatgrass (*Agropyron desertorum* [Fisch. ex Link] Schult.) (Blickenstaff and Traveller 1979; Cook 1967). Rangeland management efforts continued up through 1972 but were only partially successful since many seedlings did not become established and remained as weed host areas (Blickenstaff and Traveller 1979). Also, some important weed host areas did not get seeded for various reasons, and new weed host areas developed due to range fires and abandoned land-clearing efforts (Blickenstaff and Traveller 1979). The most important host plants for BLHs in burned areas have historically been flixweed, perfoliate pepperweed, and tumblemustard (Douglass and Hallock 1957), yet of these hosts, BLHs were only detected to have fed on flixweed in this study.

BLHs will stay on any perennial or annual that is succulent at the time they are forced from their summer hosts (Cook 1967). Fertilized female leafhoppers overwinter on annuals, and those that survive the winter lay their eggs in March or early April in southern Idaho (Cook 1967). This first generation normally matures in May or June (Cook 1967). The percentage of spring-generation BLHs carrying BCTV into cultivated areas has varied from 4 to 80% (Douglass and Cook 1954; Strausbaugh et al. 2024). Giddings (1938) was the first to clearly differentiate strains of BCTV, but recently, as many as 11 strains of BCTV have been acknowledged (Strausbaugh et al. 2017). The hosts infected by different strains can vary in not only crop plants but also weed hosts (Bennett 1971). For example, *Chenopodium murale* has been shown to be immune to the strains of BCTV that are highly virulent on sugar beet but can be infected by some of the less-severe strains (Bennett 1971; Giddings 1950). Thus, BLH feeding on weed hosts resistant to severe stains of BCTV may lead to mild strains becoming prevalent in weedy breeding grounds (Bennett 1971; Carsner 1925; Lackey 1929, 1932, 1937; Melgarejo et al. 2024; Wallace and Murphy 1938). This reasoning may explain why a shift in strains occurred in southern Idaho that coincided with the introduction of neonicotinoid seed treatments for use in sugar beet (Strausbaugh et al. 2006, 2008, 2012, 2014, 2017). With neonicotinoid seed treatments able to protect sugar beet plants for at least the first 77 days after planting, the reproduction of BLHs and transmission of curly top viruses during this time has shifted to other crops or weeds (Strausbaugh et al. 2016). Thus, a shift from the BCTV-Svr strain to milder strains such as BCTV-Wor and BCTV-CO occurred in southern Idaho (Strausbaugh et al. 2017). BLHs were detected to have fed on sugar beet in this study, but such samples were detected only later in the season after neonicotinoid seed treatments had lost their effectiveness. Samples were positive 42 to 55% of the time in 2020 when Wor+ primers (which detect both BCTV-Wor and BCTV-CO strains) were used, except when the samples came from BLHs that had fed on sugar beet or sunflower (11 to 25%). A similar trend occurred in 2021, since Wor+ samples were positive 51 to 75% of the time across hosts other than sugar beet and sunflower samples, which were only 36 to 38% positive. Pine samples were positive for Wor+ primers 55% in the time in 2020 and 75% in 2021. Samples with detectable virus with the BCTV-CO primers were similar (11 to 29%) across all hosts in 2021. Thus, the data suggest the presence of the BCTV-Wor strain is common in many hosts but must be present at lower titer levels in sugar beet and sunflower, making it more difficult for the BLHs to acquire the virus. BLHs feeding on sugar beet and alfalfa were associated with the presence of the BCTV-CA/Logan strain in 2021.

Very little is known about the SpCTAV virus, which was present in 16% of BLH samples in 2020 and 43% of the 2021 samples (Strausbaugh et al. 2024). When investigating relation-

ships with host feeding, the presence of SpCTAV was highest when the BLHs had fed on Russian thistle and alfalfa in both years. The responses of sugar beet and other crops to this virus remain to be explored.

Given the changes in BCTV strains, the presence of curly top viruses newly documented to be widespread (such as SpCTAV), and changes in BLH hosts and/or dispersal patterns, controlling curly top in crop fields will continue to be a challenge (Melgarejo et al. 2024; Strausbaugh et al. 2017, 2024). In sugar beet and common bean, curly top management centers around host resistance and the use of neonicotinoid seed treatments (Rojas et al. 2018; Soler-Garzón et al. 2023; Strausbaugh et al. 2017, 2024). However, neonicotinoid seed treatments have both environmental and regulatory concerns, and host resistance in sugar beet is only low to intermediate at best (Panella et al. 2014; Strausbaugh et al. 2017, 2024). Thus, alternative control measures need to be found, and host resistance needs to be improved. Some areas in the western United States still spray sagebrush steppe areas to control BLH numbers. Data from this report suggest researchers may need to investigate controlling BLHs in mountainous areas and not just sagebrush steppe areas. In the future, the importance of *Pinus* spp. to BLH populations and curly top virus epidemiology should be investigated further to determine if management is warranted in mountainous areas.

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