Dispersal of *Bactericera cockerelli* (Hemiptera: Triozidae) in relation to phenology of matrimony vine (*Lycium* spp.; Solanaceae)

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ABSTRACT

Bactericera cockerelli (Šulc) (Hemiptera: Triozidae) is a key pest of potato (*Solanum tuberosum*; Solanaceae) in western North America. Native species of *Lycium* (Solanales: Solanaceae) in the southwestern U.S. have been known since the early 1900s to support populations of *B. cockerelli*. These shrubs are adapted to survive arid habitats by entering a summer dormancy characterized by partial or complete defoliation. Summer leaf fall by native *Lycium* in the southwestern U.S. triggers the dispersal of *B. cockerelli* to new seasonally available hosts, including potato. Recently, *B. cockerelli* was found to occur on non-native species of *Lycium* (*L. barbarum* and *L. chinense*), collectively known as matrimony vine in the Pacific Northwest (Washington, Oregon, and Idaho). Monitoring of matrimony vine in previous years suggested qualitatively that these non-native shrubs also entered a summer dormancy with effects on *B. cockerelli* populations. Our study had two principal objectives: 1) document when and under what conditions matrimony vine enters summer dormancy, and 2) determine whether summer leaf fall is associated with dispersal of *B. cockerelli* from these plants. In this report, we demonstrate that matrimony vine exhibits xerophytic phenological traits similar to the *Lycium* species native to the southwestern United States, and we provide evidence that psyllid dispersal from matrimony vine is associated with the onset of the host plant's summer dormancy. These results may be beneficial for the development of predictive models to forecast *B. cockerelli* pressure in potato based upon populations occurring on matrimony vine in early spring.

INTRODUCTION

The potato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae) is a key pest of solanaceous crops (Solanales) including potato (*Solanum tuberosum*) and tomato (*S. lycoperiscum*) in western North America (Munyaneza 2012). This psyllid is a primary vector of *"Candidatus* Liberibacter solanacearum" (=*"Ca.* L. psyllaurous"), the pathogen associated with zebra chip disease of potato (Hansen

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et al. 2008; Liefting *et al.* 2009; Munyaneza 2012). No direct methods currently exist for controlling Liberibacter, so zebra chip disease is managed using prophylactic calendar-based applications of insecticides to suppress populations of the vector. *Bactericera cockerelli* develops on nearly all genera of Solanaceae examined and on many species of Convolvulaceae (Solanales), including many weeds that require management by growers (Crawford 1914; Essig 1917; Knowlton and Thomas 1934; Pletsch 1947; Wallis 1955; Murphy *et al.* 2013; Thinakaran *et al.* 2017; Kaur *et al.* 2018; Cooper *et al.* 2019a). A major challenge in the management of *B. cockerelli* and zebra chip disease is the inability to predict when and in what fields the psyllid is likely to first colonize. The difficultly in making such predications is largely due to uncertainty of the primary weed sources of *B. cockerelli* entering fields of potato.

In the southwestern United States (U.S.), *Lycium* spp. (Solanales: Solanaceae) are important non-cultivated host plants for *B. cockerelli* (Romney 1939). This genus includes about 80 species worldwide with an area of high species richness occurring in the southwestern U.S. (Hitchcock 1932; Chiang-Cabrera 1981; Levin and Miller 2005). *Lycium* species that are native to the southwest exhibit two seasonal intervals during which new foliar growth occurs, separated by a summer dormancy characterized by total or partial defoliation (Hanley and Brady 1977; Ackerman *et al.* 1980). The summer dormancy allows *Lycium* species to survive periods without precipitation by limiting periods of growth and flowering to the spring and autumn when precipitation occurs. Large populations of *B. cockerelli* occur particularly on *Lycium* during the intervals of leaf flush in spring and autumn (Romney 1939) but are thought to disperse when *Lycium* enters summer dormancy, and to colonize seasonally available annual Solanaceae weeds (e.g., *Solanum, Nicotiana, Datura,* etc.) (Wallis 1955; Horton *et al.* 2016). A portion of *B. cockerelli* dispersing from *Lycium* are thought to also colonize commercial plantings of potato or tomato.

Although *Lycium* does not naturally occur in the Pacific Northwest (PNW = Washington, Oregon, and Idaho), herbaria records (http://pnwherbaria.org) indicate that two introduced Eurasian species – *L. barbarum* L. (=*L. halimifolium* Miller) and *L. chinense* Miller – occur in this region. Floral morphology and sequence analyses support the occurrence of both species in the PNW, but evidence also suggests the presence of intermediate forms, possibly due to hybridization (Horton *et al.* 2016). These closely related species are both referred to collectively and without distinction as matrimony vine, wolfberry, or Goji berry (hereafter referred to as matrimony vine) (Horton *et al.* 2016). Matrimony vine has recently been identified as an important host plant of *B. cockerelli* in the PNW, particularly during the spring and summer, when annual host plants of the psyllid are unavailable (Horton *et al.* 2016; Thinakaran *et al.* 2017; Cooper *et al.* 2019a).

Matrimony vine appears to enter a period of summer dormancy marked by defoliation much like the native *Lycium* species of the southwestern U.S. (Horton *et al.* 2016; Thinakaran *et al.* 2017), but the relationship between matrimony vine phenology and *B. cockerelli* dispersal is still unclear. Anecdotal evidence suggests that leaf fall of matrimony vine in the PNW does indeed trigger dispersal of *B. cockerelli* to annual herbaceous hosts, including potato. This evidence includes observations that populations of *B. cockerelli* are highest

during the intervals of leaf flush and begin arriving in fields of potato at about the same time they begin declining on matrimony vine (Horton *et al.* 2016; Thinakaran *et al.* 2017). Further evidence is provided by results of gut content analysis that indicated that at least some *B. cockerelli* present on matrimony vine had arrived there from potato following harvest (Cooper *et al.* 2019b). A long-term goal of our research is to develop a model to predict *B. cockerelli* pressure in potato fields during summer based upon populations of *B. cockerelli* occurring on matrimony vine during spring (Cooper *et al.* 2019c). For this model to be effective, there is a need to document when and under what conditions matrimony vine enters summer dormancy and to determine whether summer leaf-fall is associated with dispersal of *B. cockerelli* from these plants. For this study, we monitored both wild and propagated stands of matrimony vine in Washington State (WA) and used canonical correlation analysis to identify associations among weather events, plant phenology, and presence or dispersal of *B. cockerelli*.

MATERIALS AND METHODS

Seasonal phenology of naturalized stands of matrimony vine

Psyllid presence and plant phenology were monitored weekly in naturalized stands of matrimony vine (two stands in 2017, three in 2018) located in central WA (Table 1). Sampling took place from spring until autumn to include both periods of leaf flush and the period of summer dormancy. These three stands were chosen because they were known to harbor large populations of *B. cockerelli* in previous years (Thinakaran *et al.* 2017).

Table 1. Locations and characteristics of matrimony vine stands used to examine the relationship between plant phenology and dispersal of *B. cockerelli*. Sampling dates are also provided.

Location	GPS coordinates	Approx. stand size	Months sampled
Prosser, WA, Gap Road	46° 13′ 24.8″ N 119° 47′ 24.5″ W	20 x 5 m	20 Apr. to 29 Sep. 2017 2 May to 7 Nov. 2018
Richland, WA, Port of Benton Blvd.	46° 20′ 57.4″ N 119° 16′ 10.8″ W	20 x 25 m	18 May to 29 Sep. 2017 2 May to 7 Nov. 2018
Richland, WA, Horn Rapids Road	46° 21′ 3.2″ N 119° 17′ 36.9″ W	8 x 8 m	2 May to 7 Nov. 2018

Bactericera cockerelli populations were monitored by dislodging adults from branches onto a 0.5-m^2 beat sheet by tapping the branches with a 0.2-m rubber hose at five locations from each stand. Dispersal of adult *B. cockerelli* from the matrimony vine stands was monitored by placing three yellow sticky cards (30 cm x 23 cm, Alpha Scents Inc., West Linn, OR) attached to metal stakes at a height of 1.5 m about 3 m from the edge of each stand.

Variables associated with foliar growth and senescence included leaf drop, leaf density, and chlorophyll content. Leaf drop was monitored by placing three 45 x 30 cm pans filled with water at the base of each stand and counting the

number of leaves dropped in each pan (Horton *et al.* 1993, 1994). Leaf density was monitored by counting the number of leaves per centimetre of shoot length on five 15–20 cm shoots from each stand. Chlorophyll content was estimated from 25 leaves per stand using a chlorophyll meter (Opti-Sciences, Model CCM-300) (Gitelson *et al.* 1999).

Abiotic variables included soil moisture, air and soil temperature, and precipitation. Soil moisture was estimated by collecting three 15-cm-deep soil plugs from each stand and measuring the difference in weight between freshly collected soil plugs and soil that had been air-dried in a detached greenhouse. The samples were weighed weekly until the dry weight was unchanged. The greenhouse was not cooled and achieved high temperatures with low humidity in the eastern WA summer climate. Daily weather data (minimum, maximum, and average temperatures, average soil temperature, and precipitation) were obtained from the Washington State University AgWeatherNet (www.weather.wsu.edu) "WSU Prosser" (5 km from the Prosser stand of matrimony vine) and "WSU Tri Cities" (2–3 km from the two Richland stands) weather stations. The data for each abiotic variable were averaged over the week preceding each weekly sampling.

Correlations among variables were assessed with three independent canonical correlation analyses using PROC CANCORR of SAS 9.4 (SAS Institute Inc. 2013). This method identifies and measures associations among two sets of variables by determining orthogonal linear combinations of variables within each dataset that best explain the variability within and between datasets. The number of orthogonal linear combinations, called canonical variates, is equal to the number of variables in the smaller of the two datasets. The canonical variates are then interpreted in terms of the original variables by inspecting canonical structures where larger values indicate greater correlations between variables, and opposite signs indicate inverse relationships. Data were averaged by week at each location, and each sampling week in 2017 and 2018 was ordinally categorized with the reference 'week 1' being the first week of January. Both years were included in each of the three analyses. The first analysis assessed correlations between weather variables (mean air temperature, mean soil temperature, soil moisture, and precipitation) with plant growth characteristics (leaf drop, chlorophyll content, and leaf density). The second analysis assessed correlations between plant growth characteristics and presence or dispersal of *B. cockerelli* (numbers on plants and numbers on sticky traps). The third analysis assessed correlations between weather variables and *B. cockerelli* movement variables. In each analysis, the Wilks' Lambda statistic was used to determine overall significance, and correlations among variables were estimated by canonical loadings.

Seasonal phenology of experimental stands of *Lycium*

Cuttings collected from a naturalized stand of *Lycium* near Selah, WA, in June 2014 were propagated in soil within a greenhouse and transplanted into experimental plots (n=4) located at the USDA experimental farm near Moxee, WA, in July 2014. Each plot consisted of four plants separated from one another by ~0.5 m. Adjacent plots were separated by 3–5 m of fallow ground. Each plot was enclosed in a 2x2x2-m organdy cage from 2014, when the plots were

established, until spring of 2017. By 2017, the plants had spread to fill the 2x2-m space of each cage, with many new shoots from spreading rhizomes. A pyrethrum fogger (Doktor Doom 70ml, Ultrasol Industries Ltd., Edmonton, Alberta) was used to treat the plots in late March 2017 to eliminate resident insects prior to the study. Pyrethrum was chosen because it is an effective contact insecticide with a residual activity limited to only several hours. Each cage was then infested with 500 *B. cockerelli* of the northwestern haplotype (Swisher *et al.* 2012) obtained from a laboratory colony on 17 April 2017 and again on 26 April 2017, 2–3 weeks after the pyrethrum treatments. Cages were removed from plants on 20 May 2017, when eggs were present on leaves and shoots. Weekly sampling of *B. cockerelli* presence and dispersal and foliar characteristics began on 5 June 2017. All four plots received weekly irrigation until late June.

Plant characteristics, soil moisture, and *B. cockerelli* populations were estimated as described for the naturalized stands, except that four sticky cards were placed at each cardinal direction around each plot. Weather variables were obtained from the WSU AgWeatherNet station "Moxee East", located about 10 km from the USDA experimental farm. The relationships between weather variables, plant characteristics, and *B. cockerelli* dispersal were assessed using canonical correlation analysis as described for naturalized stands.

Simulated drought using potted plants

Shoot cuttings collected from a stand of *Lycium* located near Richland, WA, (Horn Rapids Rd) were propagated in 10-cm pots within a greenhouse maintained at 24° C and with supplemental lighting to ensure a 16:8 (L:D) hour photoperiod. All plants received weekly watering before the start of the experiment until the plants had established roots, new shoots, and new foliage (about 6 weeks).

Chlorophyll, leaf density, and soil moisture were measured for each plant (n=12) for seven weeks. Plants were either watered weekly or were water-stressed during weeks 2, 3, and 4 of the study. Plants were arranged in six blocks, with each block consisting of one plant of each treatment. Plants received ~250 ml of water weekly immediately after plant and soil variables were recorded: these included chlorophyll meter readings from five leaves per plant, and leaf density with counts of the number of leaves on a 10-cm section of stem from each plant. The stem sections were marked at the beginning of the study so that the same section was assessed each week. Soil moisture was recorded using a soil probe (Spectrum Technologist Inc., Aurora, IL, U.S.; model TDR300). Each variable (chlorophyll, number of leaves per centimetre of shoot, and soil moisture) was analyzed using PROC GLMMIX of SAS 9.4 (SAS Institute Inc. 2013). In each analysis, week, treatment (watered versus dry), and the week by treatment interaction were included as fixed effects, and block and treatment by block interaction were included as random effects. When the overall univariate analysis indicated a significant main effect interaction, differences between treatments were assessed using a Tukey adjustment for multiple comparisons (ADJUST=TUKEY of the LSMEANS statement) while including the SLICE option of the LSMEANS statement to limit comparisons within each week.

RESULTS AND DISCUSSION

As observed in previous years (Horton *et al.* 2016; Thinakaran *et al.* 2017), *Lycium* introduced to the PNW underwent leaf flushes in spring and autumn separated by a period of senescence (leaf yellowing) and leaf fall during summer (Fig. 1). The degree of defoliation varied among stands, from complete defoliation at the Richland Port of Benton stand to partial defoliation at the Richland Horn Rapids Road and Prosser Gap Road stands. Populations of *B. cockerelli* were considerably low on matrimony vine and in potato fields throughout the Columbia Basin in 2017 and 2018, relative to previous years (Thinakaran *et al.* 2017; Cooper *et al.* 2019c). Populations were low not only in wild stands of matrimony vine but also in experimental plots that were infested with colony-reared *B. cockerelli* in the spring of 2017. Factors responsible for the low populations 2017 and 2019 remain unknown.
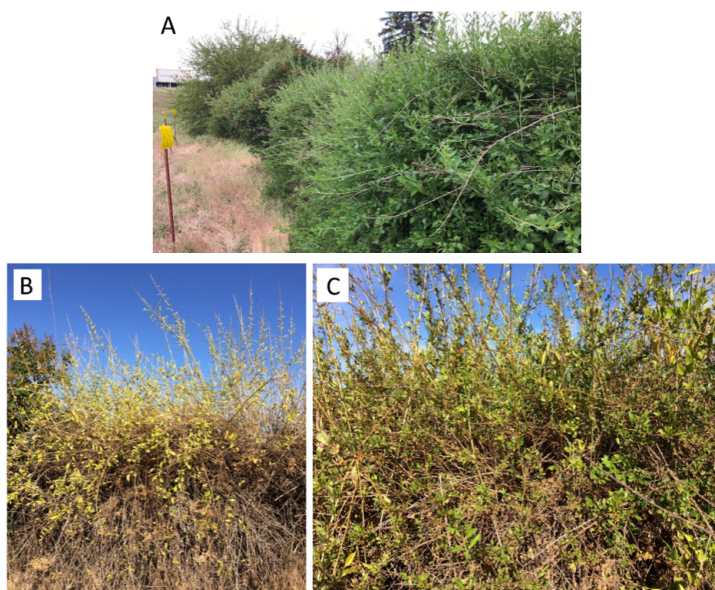

Figure 1. Appearance of matrimony vine during the spring leaf flush in mid-May (A), leaf senescence in mid-July (B), and the autumn leaf flush in late-September (C). Location=Prosser, Gap Road.

Similar trends in weather, plant phenology, and psyllid numbers were observed on the naturalized stands in 2017 (Fig. 2) and 2018 (Fig. 3). Although the 2017 and 2018 datasets were analyzed together, they are presented separately in Figs. 2 and 3 to visually show correlations between weather events and plant phenology. The canonical correlation analysis of plant variables with weather variables from naturalized stands indicated that the first canonical variate was significant, but the remaining variates were not (Table 2A). Since only the first variate was significant, only the first pair of variables need to be identified from the canonical structures. The weather dataset was associated primarily with air and soil temperatures (Table 2A; 0.98 and 0.86, respectively) and was negatively associated with precipitation (Table 2A; –0.37). The plant dataset was negatively

associated with leaf density (Table 2A; –0.90), and positively associated with leaf fall (Table 2A; 0.35). From these results, we can conclude that leaf growth was associated with cooler temperatures and precipitation, and that leaf fall is associated with warmer temperatures and decreasing precipitation. Plants began to visibly decline on 22 June 2017 and 6 June 2018, when maximum air temperatures the week prior to sampling were >25° C and soil moisture was <5% (Figs. 2 and 3). Late summer/early autumn precipitation elicited marked increases in leaf density and chlorophyll content in plants (2017, Fig. 2; 2018, Fig. 3). These late-season precipitation events followed 6–7 weeks without recorded precipitation. Autumn leaf growth occurred from mature stems without growth of new shoots, and leaf densities typically surpassed those observed during the spring interval of leaf flush, when new leaves grew from elongating shoots (2017, Fig. 2B; 2018, Fig. 3B).
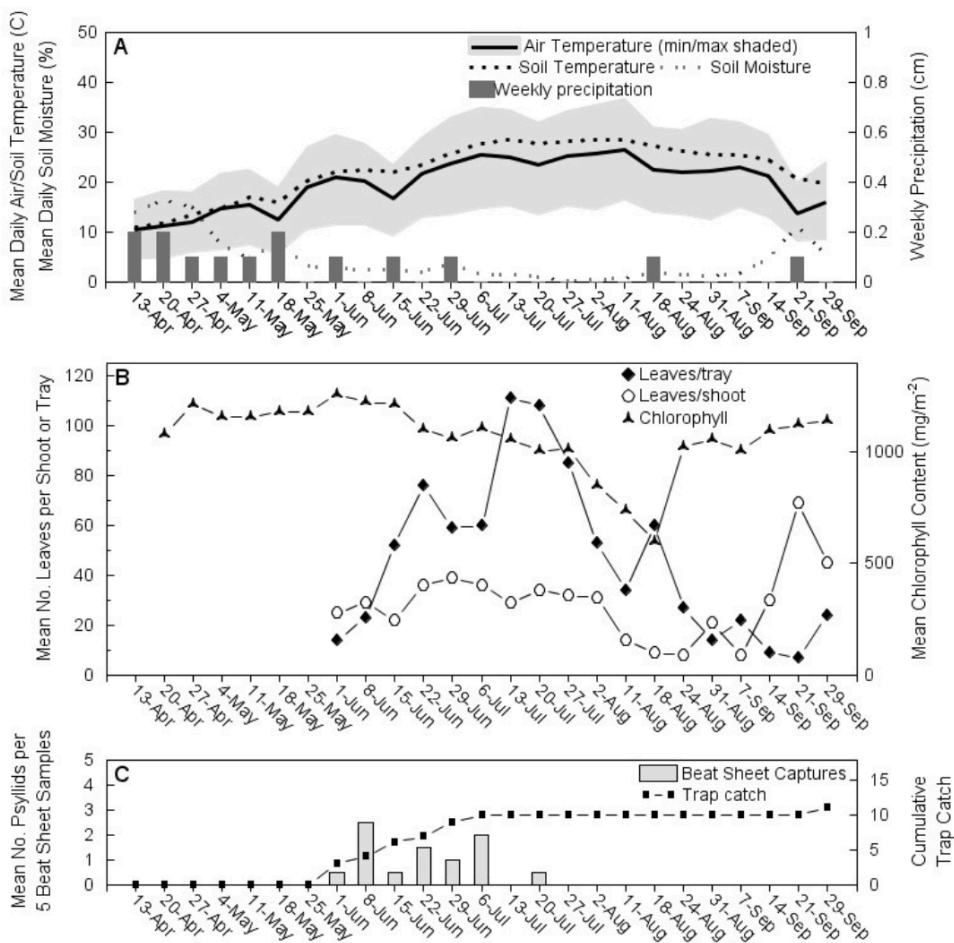

Figure 2. Relationships among weather variables (A), matrimony vine phenology (B), and occurrence and dispersal of *Bactericera cockerelli* (C) on matrimony vine stands located in Washington State in 2017.

Canonical correlation analysis also indicated significant associations between psyllid movement and plant growth characteristics for both canonical variates (Table 2B), but no associations between psyllid movement and weather (Table 2C). The first canonical variate suggested an inverse relationship between psyllid trap catch and leaf density (2017, Fig. 2; 2018, Fig. 3). The second canonical variable suggested a correlation between leaf drop and detection of psyllids on the plants (Table 2B), likely because adult populations peaked on plants at about the same time that leaf fall began, and psyllids were largely absent from plants after rates of leaf fall declined (2017, Fig. 2C; 2018, Fig. 3C). Overall, these results are consistent with the hypothesis that summer leaf drop triggers dispersal of *B. cockerelli* from stands of introduced matrimony vine in the PNW (Horton *et al.* 2016).
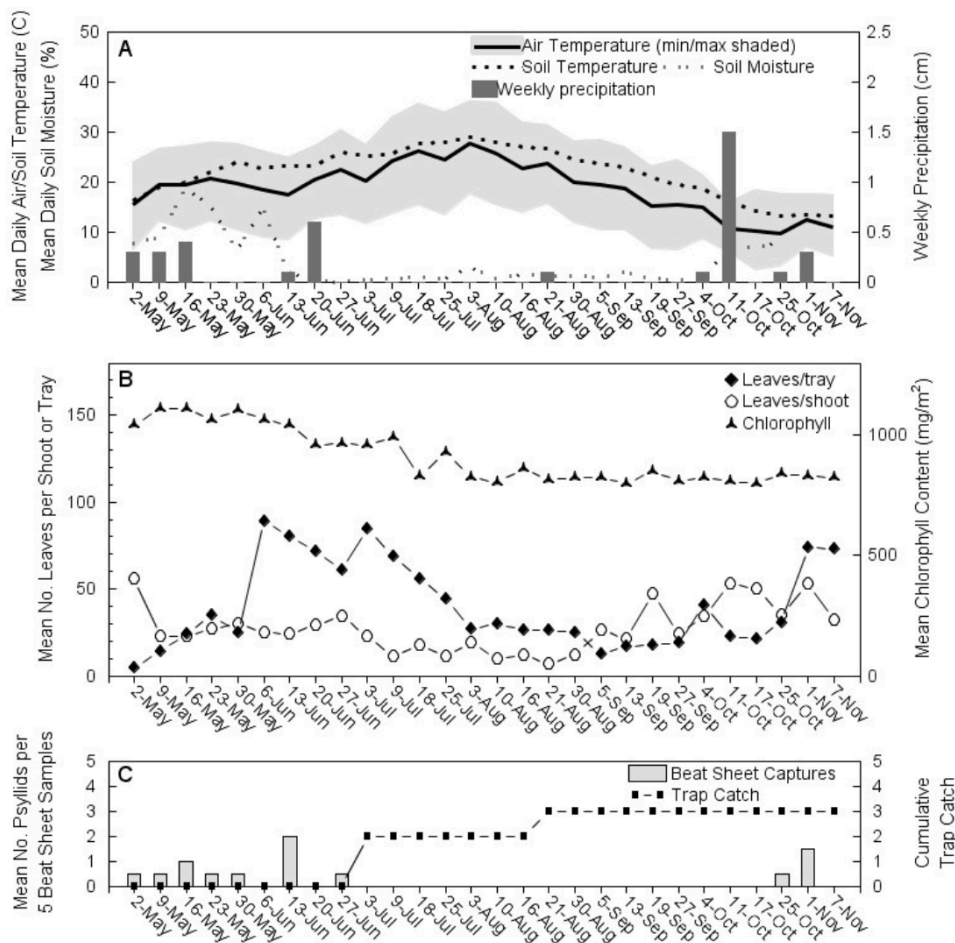

Figure 3. Relationships among weather variables (A), matrimony vine phenology (B), and occurrence and dispersal of *Bactericera cockerelli* (C) on matrimony vine stands located in Washington State in 2018.

Table 2. Canonical correlation analyses of multivariate datasets obtained from naturalized stands of matrimony vine in Washington State.

Canonical comparisons	Canonical correlation	Likelihood ratio	Proportion of model variance	First dataset canonical structures[4]	Second dataset canonical structures[4]
A. Plant[1] versus weather variables[2]					
Can. variate 1	0.51	$F=3.8$; $df=12, 291$; $P<0.001$	0.80	Air temp: 0.98	Leaf fall: 0.35
				Soil temp: 0.86	Chlorophyll: 0.16
				Precipitation: −0.37	Leaves/shoot: −0.90
				Soil moisture: −0.26	
Can. variate 2	0.26	$F=1.6$; $df=6, 222$; $P=0.14$	0.17	—	—
Can. variate 3	0.12	$F=0.75$; $df=2, 112$; $P=0.47$	0.03	—	—
B. Psyllid[3] versus plant variables					
Can. variate 1	0.28	$F=3.1$; $df=6, 222$; $P=0.006$	0.52	Leaf fall: 0.18	Trap catch: 0.96
				Chlorophyll: 0.77	Beat trays: 0.31
				Leaves/shoot: −0.64	
Can. variate 2	0.27	$F=4.5$; $df=2, 112$; $P=0.01$	0.48	Leaf fall: 0.93	Trap catch: −0.29
				Chlorophyll: −0.42	Beat trays: 0.95
				Leaves/shoot: −0.09	
C. Psyllid versus weather variables					
Can. variate 1	0.21	$F=0.9$; $df=8, 232$; $P=0.51$	0.79	Air temp: −0.23	Trap catch: −0.58
				Soil temp: 0.01	Beat trays: −0.80
				Precipitation: 0.46	
				Soil moisture: 0.43	
Can. variate 2	0.11	$F=0.51$; $df=3, 117$; $P=0.67$	0.21	—	—

[1]Plant variables included leaf drop (no. leaves per tray), chlorophyll content (mg/m2), and leaf density (no. leaves per cm of shoot)

[2]Weather variables included avg. daily air temperature, avg. daily soil temperature, soil moisture, and weekly precipitation.

[3]Psyllid variables included no. of psyllids collected from matrimony vine and no. of psyllids captured on traps.

[4]Larger values indicate greater correlations between variables, and opposite signs indicate inverse relationships.

In addition to monitoring naturalized stands of matrimony vine, we used experimental plots to correlate weather patterns, matrimony vine phenology, and psyllid dispersal. The use of experimental plots allowed us to replicate plots at a single location and to corroborate observations at wild stands. Analysis of plant

and weather variables suggested that chlorophyll content was positively correlated with soil moisture and negatively correlated with soil temperature (Table 3A; Fig. 4). Analysis of psyllid and plant variables from the experimental plots did not indicate significant patterns (Table 3B), but the upper bound statistic, Roy's Greatest Root, warranted assessment of canonical structures (F=2.3; df=3, 48; P=0.09) which suggested a positive relationship between the presence of psyllids on plants and leaf density (Table 3B; Fig. 4). Finally, analysis of the psyllid and weather variables suggested that the capture of psyllids on traps was negatively correlated with precipitation and soil moisture and positively correlated with air and soil temperatures (Table 3C; Fig. 4). Overall, results from the experimental plots were consistent with those from the naturalized stands by suggesting that senescence and leaf fall in matrimony vine are triggered by hot and dry conditions (average and maximum air temperature was 22° C and 31° C respectively, and soil moisture below 5%) and is associated with dispersal of *B. cockerelli* from these plants (Fig. 4).

Table 3. Canonical correlation analyses of multivariate datasets obtained from experimental stands established at the USDA experimental farm near Moxee, WA.

Canonical comparisons	Canonical correlation	Likelihood ratio	Proportion of model variance	First dataset canonical structures[4]	Second dataset canonical structures[4]
A. Plant[1] versus weather[2] variables					
Can. variate 1	0.72	F=5.9; df=12, 119; P<0.001	0.64	Air temp: –0.31	Leaf fall: –0.07
				Soil temp: –0.62	Chlorophyll: 0.97
				Precipitation: 0.47	Leaves/shoot: 0.34
				Soil moisture: 0.89	
Can. variate 2	0.57	F=4.4; df=6, 92; P<0.001	0.29	Air temp: 0.75	Leaf fall: 0.66
				Soil temp: 0.65	Chlorophyll: –0.25
				Precipitation: –0.86	Leaves/shoot: 0.47
				Soil moisture: –0.26	
Can. variate 3	0.31	F=2.5; df=2, 47; P=0.09	0.06	—	—
B. Plant versus psyllid[3] variables					
Can. variate 1	0.36	F=1.5; df=6, 94; P=0.18	0.75	Leaf fall: –0.78	Trap catch: –0.28
				Chlorophyll: 0.59	Beat trays: 0.93
				Leaves/shoot: 0.70	
Can. variate 2	0.22	F=1.2; df=2, 48; P=0.31	0.25	—	—
C. Psyllid versus weather variables					

Can. variate 1	0.59	$F=3.2$; $df=8$, 100; $P=0.003$	0.96	Air temp: −0.76	Trap catch: 0.95
				Soil temp: −0.81	Beat trays: −0.18
				Precipitation: 0.92	
				Soil moisture: 0.91	
Can. variate 2	0.15	$F=0.4$; $df=3$, 51; $P=0.77$	0.04	—	—

[1]Plant variables included leaf drop (no. leaves per tray), chlorophyll content (mg/m²), and leaf density (no. leaves per cm of shoot)

[2]Weather variables included avg. daily air temperature, avg. daily soil temperature, soil moisture, and weekly precipitation.

[3]Psyllid variables included no. of psyllids collected from matrimony vine and no. of psyllids captured on traps.

[4]Larger values indicate greater correlations between variables, and opposite signs indicate inverse relationships.
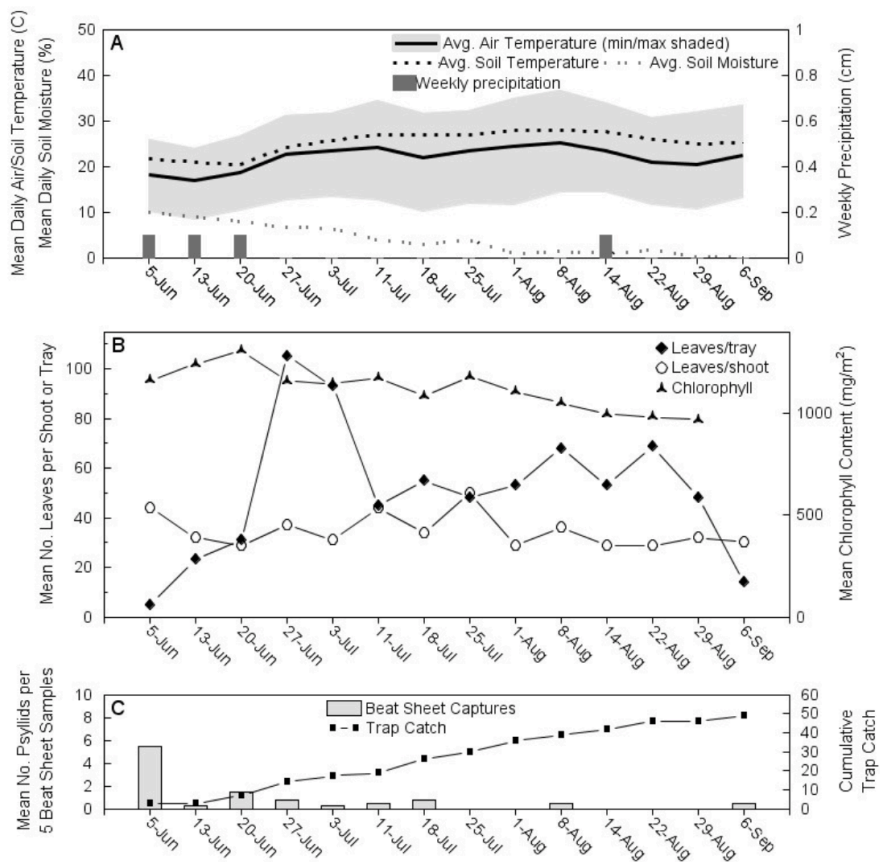

Figure 4. Relationships among weather variables (A), matrimony vine phenology (B), and occurrence and dispersal of *Bactericera cockerelli* (C) on experimental matrimony vine stands located at the USDA experimental farm in Moxee, WA in 2017.

Soil temperature, air temperature, and soil moisture are related (precipitation declines during the hottest part of summer), making it difficult to discern which weather variables are most responsible for eliciting changes in seasonal phenology of matrimony vine. In addition, the difference between wet and dry soil weights served only as an indirect estimation for soil moisture under stands of matrimony vine. We therefore performed a controlled greenhouse experiment to assess the effects of soil moisture on matrimony vine phenology while keeping air temperature relatively constant. Analysis of soil moisture indicated a significant week by treatment (watered versus dry) interaction (F=9.6; df=6, 34; P<0.001). As expected, soil moisture content dropped in the dry treatment between weeks 2 and 5 when plants were not watered (Fig. 5A). Analysis of leaf density also indicated a week by treatment interaction (F=2.5; df=6, 31; P=0.04; Fig. 5B). Statistical differences were not observed between treatments during the dry weeks, but leaf density increased sharply during week 5 on plants that were previously deprived of water (Fig. 5B). There was also a week by treatment interaction for chlorophyll content (F=5.8; df=6, 42; P<0.001). Statistically significant differences in chlorophyll content were observed in weeks 4 through 7 (Fig. 5C). The lack of water was associated with a decrease in chlorophyll content, but chlorophyll increased sharply when watering resumed on week 5 (Fig. 5C). In fact, chlorophyll content was significantly higher during weeks 5 through 7 in previously water-stressed plants compared with plants that received weekly watering (Fig. 5C). These results demonstrate that matrimony vine rapidly recovers from water deprivation with a hyper-response that leads to higher leaf density and chlorophyll content when compared with unstressed plants. Based on this greenhouse study, we conclude that soil moisture likely has a larger role in eliciting changes in matrimony vine phenology – and therefore dispersal of *B. cockerelli* – than air or soil temperature.

Results of our study demonstrate that the introduced matrimony vine in the PNW is ecologically similar to native *Lycium* species that occur in the southwestern United States. Like native species of *Lycium* (Hanley and Brady 1977; Ackerman *et al.* 1980), the introduced matrimony vine undergoes a summer dormancy triggered by low soil moisture and rapidly recovers after even modest rainfall in autumn. This trait presumably allows these plants to survive in the arid regions of inland PNW. Native *Lycium* species are an important seasonal host plant for *B. cockerelli* in the southwest, where psyllid populations peak on these plants just preceding the plants summer dormancy (Wallis 1955). This was also the trend we observed on matrimony vine in WA, where psyllid populations peaked prior to or during summer leaf fall and were undetectable during summer dormancy. Results of our study confirm that matrimony vine serves as a host for *B. cockerelli* during the spring and autumn when annual host plants are not available (Thinakaran *et al.* 2017) and demonstrate that summer dormancy of matrimony vine triggers the dispersal of *B. cockerelli* to new host plants, which likely includes potato. By documenting the relationship among abiotic factors, matrimony vine phenology, and *B. cockerelli* dispersal, this report should aid in developing prediction tools with which to forecast *B. cockerelli* pressure based upon psyllid populations occurring on matrimony vine in early spring (Cooper *et al.* 2019c).
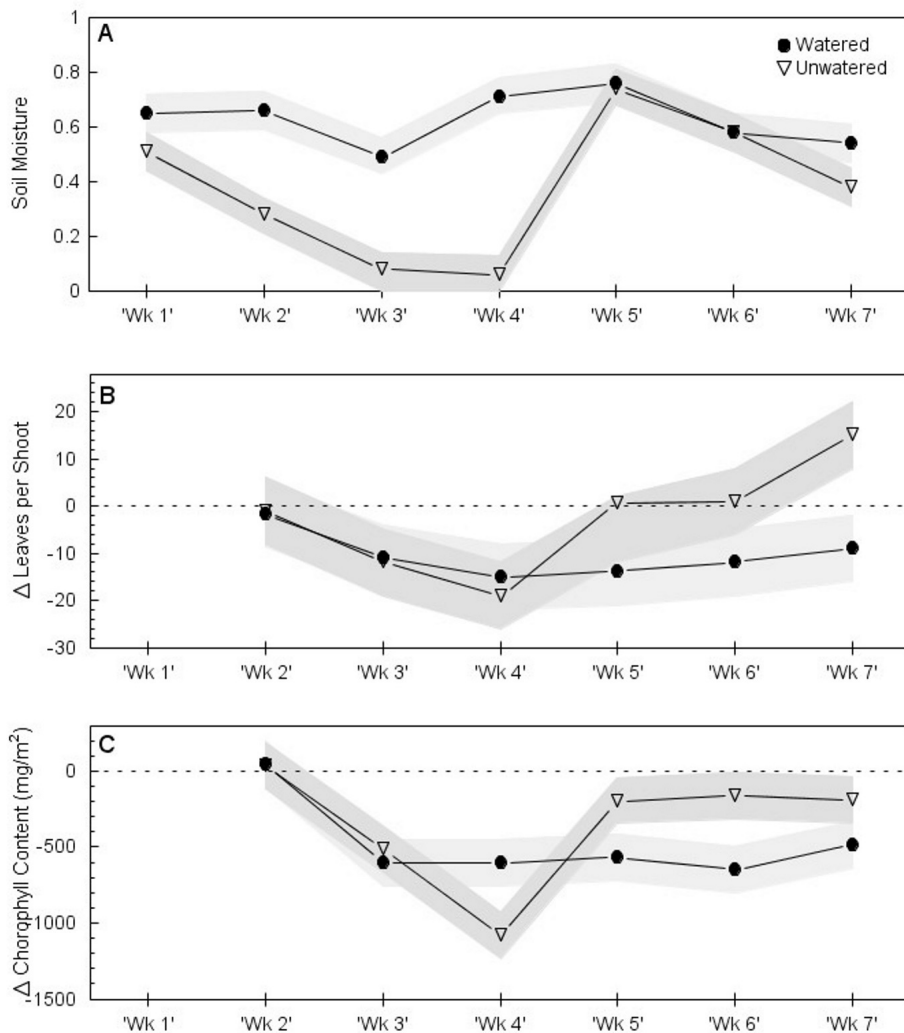
Figure 5. Soil moisture (A), change in leaf density (B), and change in chlorophyll content (C) in a simulated drought study performed in a greenhouse. The dotted lines in B and C indicate the starting variable; values below the dotted lines indicate decreases in leaf density or chlorophyll content while and values above the dotted lines indicate increases in these measurements. The shaded areas denote the standard errors of the mean.

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DISCLAIMER

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