Comprehensive Final Report for CDFA Agreement Number 15-0453-000-SA

Title of project
Evaluating Potential Shifts in Pierce's Disease epidemiology

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Abstract
A PD epidemic emerged in Napa and Sonoma counties in ~2013-14. Very high PD prevalence was reported throughout the region, with a large number of stakeholders reaching out to UCCE Farm Advisors. In summer 2015, the project team held a series of joint meetings/field visits with the Farm Advisors. Two observations were made that raised our concern about the problem. First, high prevalence of PD in the North Coast is usually below 1-2% per vineyard; several vineyards visited had over 25% of vines symptomatic. Second, historically PD is closely associated with riparian zones in the North Coast; we have visited several vineyards where PD does not appear to be associated with riparian zones. We have observed these greater rates of disease incidence and dissociation with riparian areas throughout Napa and Sonoma counties—they are not district specific. The goal of this proposal was to determine what factors drove this epidemic, so that ecology-based disease management strategies can be devised and immediately implemented.

Layperson Summary of Project
After a PD epidemic emerged in Napa and Sonoma counties, the project team held a series of joint meetings/field visits with the Farm Advisors. We observed very high prevalence of PD in the North Coast, as well as several vineyards where PD was not associated with riparian zones. The goal of this project was to look at these events using a holistic approach. Our findings confirmed several initial anecdotal observations, and generated a large dataset based on collected field data to study PD epidemiology. While the project had multiple successful outcomes, a main deliverable was the development of new hypothesis on PD spread in Coastal California. The work here allowed for the development of this hypothesis, which is now being formally tested in another project in more systematic manner. This report summarizes our main findings.

Introduction

Pierce's disease of grapevine (PD) has reemerged in Napa and Sonoma counties, where disease incidence has been much higher than usual and the distribution of sick vines within vineyards often does not fall within expectations. These field observations taken together with the very high number of vineyards affected in the region indicated the emergence of a PD outbreak. The goal of this proposal was to determine what factors drove that epidemic, so that ecology-based disease management strategies can be devised and immediately implemented, so that PD management is improvement and hopefully the disease better understood to avoid future outbreaks. In this report we summarize progress made during this project.

List of Objectives as Originally Proposed

Objective 1. Vector, pathogen, and host community surveys to inform the development of a quantitative model to assess future Pierce's disease risk and develop integrated management strategies.

Objective 2. *Xylella fastidiosa* colonization of grapevines and the role of overwinter recovery in Pierce's disease epidemiology.

Objective 3. Determine the role of spittlebug insects as vectors of *Xylella fastidiosa*.

Objective 4. Data mine and disseminate existing information on vector ecology, vegetation management, and efficacy of pruning.

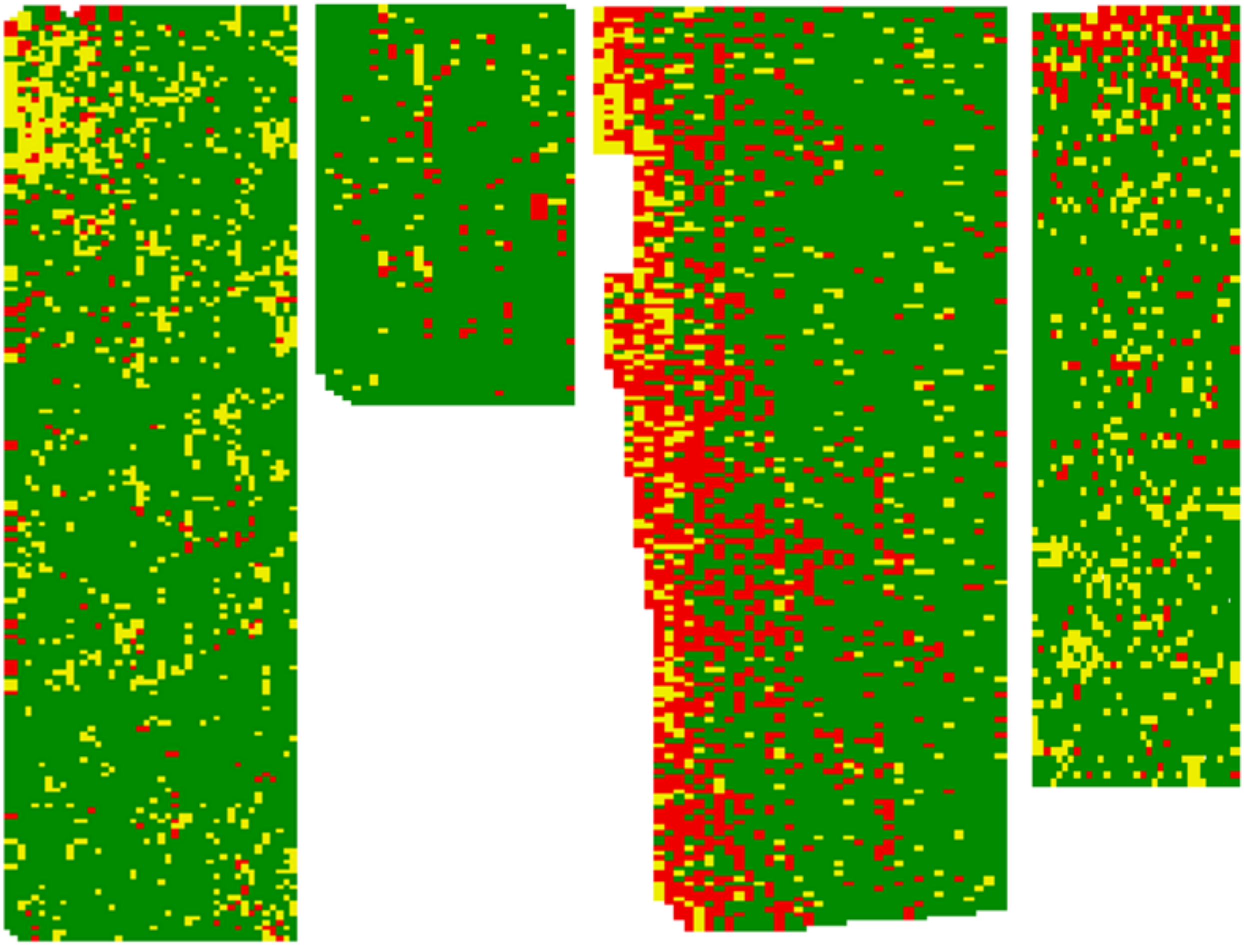
Objective 5. Develop a larger extension and outreach footprint with additional seminars, extended interviews made available on the web, and an update to the *Xylella fastidiosa* website, the main online resource for PD information.

Objective 6. Determine if an emerging strain of *Xylella fastidiosa* was responsible for the PD outbreak. This Objective was added as recommended by proposal reviewers.

Description of Activities

Objective 1. Vector, pathogen, and host community surveys to inform the development of a quantitative model to assess future Pierce's disease risk and develop integrated management strategies.

We conducted three years of Pierce's disease surveys in 32 vineyards throughout Napa and Sonoma Counties. As a first step toward understanding the condition changes that may have triggered the recent PD epidemic in the North Coast, we have initiated a set of spatial analyses to describe the patterns of disease at each site at the outset of the study. Here, we summarize the results of those analyses for four representative vineyards in the Fall of 2016. Two sites are located in Napa County ("CDV" and "TREF"), have no nearby riparian habitat, and were estimated to have less than 5% PD (Table 1). Two other sites located in Sonoma County ("NEWS" and "V7") are adjacent to riparian corridors, with PD prevalence ranging between approximately 8 and 20% (Table 1).



Mapping results for Pierces disease at four representative sites in the Fall of 2016. Red pixels denote vines with PD, yellow are dead missing, or replant vines, and green denotes apparently healthy vines. Sites (L to R) are: CDV, TREF, NEWS, V7. Maps are on the same approximate scale, but each is oriented arbitrarily. For NEWS and V7, riparian habitat is located to the left and above, respectively.

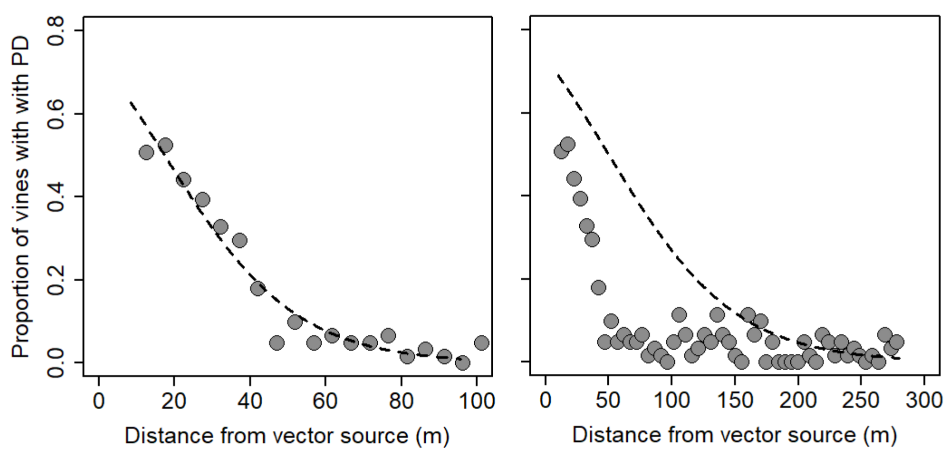
In the Fall of 2016 we surveyed all of the vineyards, inspected each vine in the block, noted the status of each vine as: apparently healthy, PD, dead, replant, or missing, and collected tissue samples from up to 20 PD vines to confirm infection by *X. fastidiosa*. The mapped distributions of initial disease prevalence were then subjected to a suite of analyses to look for 1) non-random distribution (i.e. clustering) of PD cases, 2) spatial association between PD cases and other non-healthy disease categories (i.e. dead, missing, or replant vines), and 3) non-uniform distribution of PD cases over the block (i.e. anisotropic gradients in disease).

For the first two analyses, we used a pair of point pattern analyses to look at the strength and scale of clustering in non-healthy vines (Dale and Fortin 2014). In the first, we used an L means test on just vines showing evidence of PD (Brunson and Comber 2015). The tests were significant for all four of the sites (Table 1). This suggests significant clustering of PD cases at all sites, though the scale of clustering varied from below 5 vine spaces for site TREF to over 15 vine spaces at site NEWS. Next, a similar L means test was used for PD vines versus other non-healthy vines to look for co-clustering (Brunson and Comber 2015). This second set of tests indicated variability among the sites, with three sites showing significant co-clustering while the fourth (TREF) was non-significant (Table 1). In other words, at the three significant sites (CDV, NEWS, V7), PD vines are more likely to be found near dead, missing, or replant vines than expected by chance.

Table 1. Summary statistics for Pierce's disease at four representative sites in the Fall of 2016, including whether they are adjacent to riparian habitat, total number of vines surveyed, percent of vines showing PD symptoms, L means test for clustering of PD cases, L means test for co-clustering between PD cases and missing, dead, or replant vines, and test for uniformity in the distribution of PD cases across the vineyard block (i.e. no disease gradient).

				PD clustering		Co-clustering		Uniformity		
Site	**Riparian**	**# vines**	**% *PD***	***u***	***P***	***u***	***P***	χ^2	**df**	***P***
CDV	N	7406	2.85	144.17	0.01	6.670	0.01	1.0172	2	0.6013
TREF	N	2220	4.68	37.158	0.01	5.050	0.12	1.7144	2	0.4243
NEWS	Y	6608	20.11	256.4	0.01	17.832	0.01	9.6049	2	0.0082
V7	Y	3355	8.29	107.45	0.01	0.5741	0.01	21.663	2	<0.0001

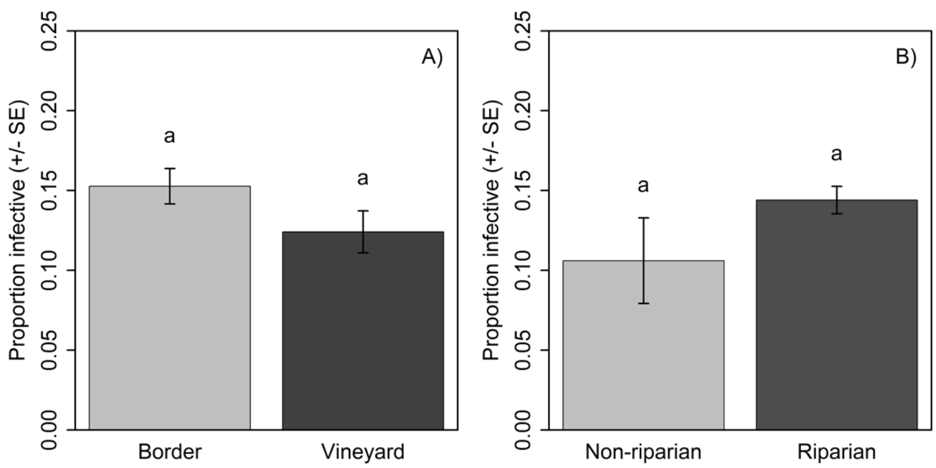
In the third analysis of PD patterns at each site, we used Guan's test for uniformity (package spTest() in the R programming language; Weller 2016) to determine whether there were gradients in PD across the vineyard block. For this test, a significant value (i.e. $P<0.05$) indicates anisotropy, which was followed up with a generalized linear mixed-effects model (GLMM) to quantify the nature of that gradient. Specifically, we used a GLMM binomial error, a fixed effect of distance from potential vector source habitat (i.e. nearby riparian habitat), and a random effect of vine number nested within row number to account for spatial autocorrelation. The results of the test for uniformity showed evidence of significant gradients at the two riparian sites, but not the non-riparian sites (Table 1). For the two riparian sites the likelihood of a vine having PD declined significantly at greater distances, with most cases within approximately 60 m of the riparian corridor but with still a handful of cases at much greater distances.



Gradients in Pierces disease prevalence as a function of distance from riparian habitat. Sites: a) NEWS, b) V7. Points reflect proportions of vines with PD of 50-100 vines at different binned distances. Dashed lines denote model fit.

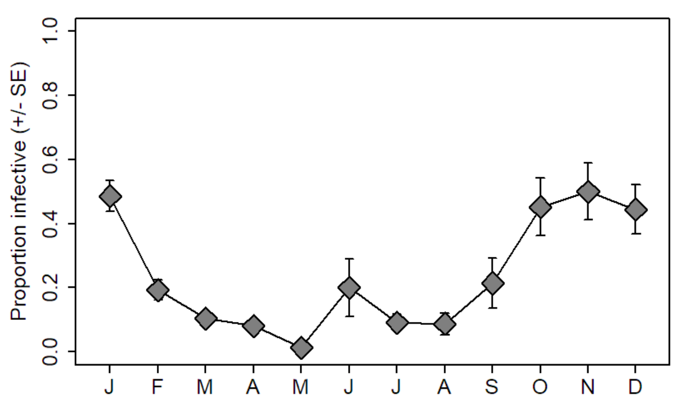
As part of our monitoring activities, we regularly collected BGSS on nearly 400 sticky traps and testing them via qPCR to determine the fraction that are positive for *X. fastidiosa*. Thus far, more than 1800 unique BGSS have been assayed from collections made at more than 30 vineyard sites between December 2016 and April 2018. Of the insects tested, overall, approximately 14% (256 of 1812) were positive for *X. fastidiosa*, with a range between sites of approximately 2% to over 25%. We compared the fraction of samples testing positive in two related analyses. First, we analyzed the overall differences in infectivity in a generalized linear mixed effects model (GLMM), which included fixed effects of site type (i.e. sites with riparian habitat nearby vs. non-riparian sites) and trap location (i.e. traps within the vineyard vs. bordering the vineyard), a random effect of site identity to account for autocorrelation stemming from repeated measurements made at each site over time, and binomial error. A second GLMM was conducted on just those 11 sites at which there were sufficient samples over the season to estimate an effect of time (month irrespective of year; as a fixed effect), a fixed effect of trap location, a random effect of site ID to account for autocorrelation, and binomial error. In both analyses model selection (via AIC rankings) was used to identify the minimum adequate model.

For the first analysis, the preferred model included only a non-significant effect of trap location (χ^2=0.782, *df*=1, *P*=0.3765). Although, overall, the fraction of BGSS collected from traps bordering vineyards (i.e. nearby riparian habitat or other source habitat) testing positive for *X. fastidiosa* was higher than those BGSS collected within vineyards, the difference was not significant. Similarly, although the overall fraction of BGSS testing positive at riparian sites was slightly higher than at non-riparian sites, the difference was not significant. These results suggest that *X. fasidiosa* infectivity within BGSS populations is pretty well mixed, at least with respect to these relatively crude categories of site type and trap location at a site.



Overall proportion of BGSS testing positive for *X. fastidiosa* between A) trap locations, and B) site types

For the second analysis, the preferred model included only a significant effect of time (χ^2=173.67, *df*=11, *P*<0.0001). The fraction of BGSS testing positive varied from a low of approximately 1% in May to a high of 50% in November. These results suggest there is substantial variability in BGSS infectivity, with low infectivity over much of the growing season and far higher infectivity during the late and dormant seasons.



Seasonal variability in the fraction of BGSS testing positive for *X. fastidiosa*.

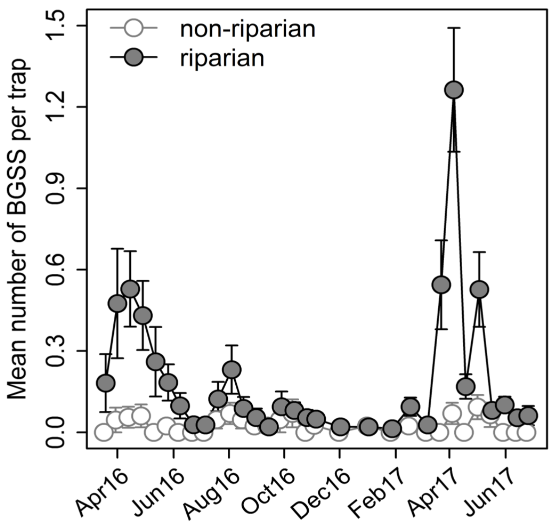
Beginning in late August and continuing through mid-September in 2016 and 2017, incidence of PD was recorded for each vine in all study blocks. Disease incidence was based on the occurrence of a combination of the common visual symptoms of PD: shriveled clusters, leaf scorching, uneven lignification of shoots, matchstick petioles and stunted growth. Two hundred samples were collected from Napa and Sonoma counties, respectively (n=400), to correlate visual assignment of vines as PD-positive with *X. fastidiosa* PCR-based detection in the laboratory (ongoing). Researchers walked every row of each block and recorded incidence of PD symptoms for individual vines on vineyard block maps. These maps were generated using Geographic Information Systems (GIS) to digitize a matrix of points in a spatial environment where each point represents a vine in its exact geographic location. A customized geoprocessing tool was created to generate detailed vine-by-vine GIS files with accurate row and vine spacing. Based on the inputs, the tool generates a new GIS point shapefile representing vine locations within a vineyard block. Data on disease incidence, missing vines, replants and dead vines was recorded. In Sonoma County, incidence of PD symptoms ranged from 1.5 to 33.5% in 2016 and from 0.3% to 28.1% in 2017. In Napa County, incidence ranged from 0.09% to 22.4% and 0.06% to 7.8% in 2016 and 2017, respectively. A portion of replant and missing vines may be due to Pierce's disease in previous years. Spatial analysis of the georeferenced data is ongoing.

Percent vines with Pierce's disease, replanted, missing and dead for 2016 and 2017 in 32 study blocks in Napa and Sonoma counties.

				Percent vines:			
County	Vineyard	Variety	Acres	PD	Replant	Missing	Dead
Napa	NA 2016	Cabernet Sauvignon	9.07	0.1	0.1	1.1	
	NA 2017			0.2	1.3	0.03	
	NB 2016	Chardonnay	5.0	0.04		70.3	
	NB 2017			22.4	0.03	45.4	0.04
	NC 2016	Merlot	3.03	0.09	2.2	4.2	0.09
	NC 2017			0.06	9.7		
	ND 2016	Cabernet Franc	6.37	2.9	13.1	0.03	0.05
	ND 2017			1.6	12.1	3.4	0.04
	NE 2016	Cabernet Sauvignon	7.44	0.2	10.8	0.1	
	NE 2017			0.1	7.5	0.1	
	NF 2016	Cab. Sauvignon	1.92	0.6	14.3	0.5	0.04
	NF 2017			0.3	11.6	3.6	
	NG 2016	Petit Verdot	0.89	0.9	10.7	9.7	0.1
	NG 2017			0.1	13.8	1.0	
	NH 2016	Cabernet Sauvignon	2.84	1.4	19.0	0.4	
	NH2017			0.2	13.2	0.5	0.04
	NI 2016	Cabernet Franc	2.5	1.5	7.3	0.1	
	NI 2017			2.7	7.1	0.2	
	NJ 2016	Cabernet Sauvignon	4.88	9.3	0.2	3.6	0.3
	NJ 2017			6.7	0.2	3.9	0.1
	NK 2016	Chardonnay	4.6	3.0	19.3	0.1	
	NK 2017			3.2	12.6	0.1	
	NL 2016	Malbec	1.69	0.2	2.6	3.5	0.1
	NL 2017			0.2	2.7	3.7	0.1
	NM 2016	Cabernet Sauvignon	4.42	0.5	0.3	1.2	0.2
	NM 2017			0.6	0.7	0.9	0.4
	NN 2016	Chardonnay	2.6	4.7	2.9	0.2	
	NN 2017			7.8	2.8	0.1	0.1

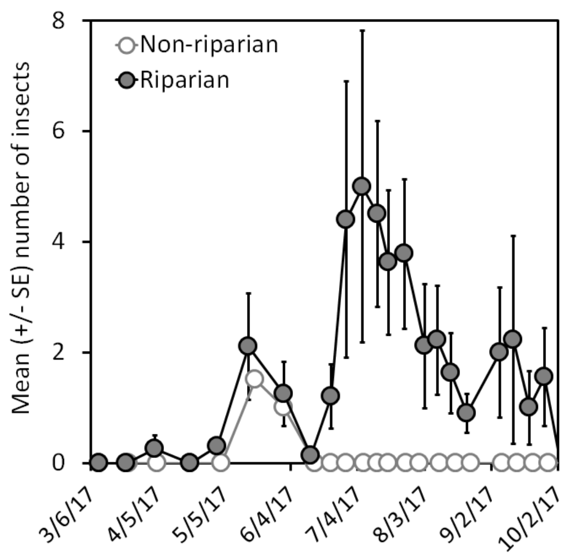
	NO 2016	Cabernet Sauvignon	5.0	10.3	44.0	0.02	
	NO2017			6.9	52.8	0.2	0.04
	NP 2016	Cabernet Sauvignon	7.33	5.6	8.1	0.6	0.6
	NP 2017			0.99	14.8	0.6	0.2
Sonoma	SA 2016	Chardonnay	5.1	17.2	11.1	0.2	1.8
	SA 2017			3.8	18.8	0.7	2.1
	SB 2016	Chardonnay	5.45	7.0	0.6	0.0	0.1
	SB 2017			10.2	0.6	5.0	0.1
	SC 2016	Zinfandel	1.1	1.7	28.8	0.5	3.2
	SC 2017			0.8	23.9	1.8	3.6
	SD 2016	Zinfandel	4.3	7.0	0.0	1.1	3.0
	SD 2017			5.0	0.0	1.5	2.5
	SE 2016	Chardonnay	3.8	6.4	0.4	3.7	0.5
	SE 2017			NA	NA	NA	NA
	SF 2016	Gruner Veltliner	4.93	15.3	3.9	0.3	0.1
	SF 2017			14.8	3.2	0.3	0.0
	SG 2016	Merlot, Cab. Sauv.	5.8	12.9	5.2	0.0	0.7
	SG 2017			9.6	7.9	0.9	0.5
	SH 2016	Pinot Noir	3.97	33.5	5.9	0.0	0.0
	SH 2017			28.1	14.8	0.0	0.1
	SI 2016	Merlot	3.8	1.5	15.6	0.1	0.5
	SI 2017			0.3	9.4	1.1	0.4
	SJ 2016	Chardonnay	7.5	5.9	17.7	0.0	0.0
	SJ 2017			1.6	12.2	0.0	0.1
	SK 2016	Malbec	4.25	20.1	7.6	0.1	0.0
	SK 2017			15.4	7.6	0.9	1.4
	SL 2016	Chardonnay	2.25	3.6	0.2	20.5	0.5
	SL 2017			6.0	24.2	0.0	0.0
	SM 2016	Chardonnay	5.0	22.9	4.2	0.0	1.0
	SM 2017			11.2	3.7	3.2	0.0
	SN 2016	Chardonnay	4.2	8.4	12.7	0.0	0.1
	SN 2017			8.9	7.2	0.2	0.5
	SO 2016	Chardonnay	4.1	8.6	6.9	0.0	0.0
	SO2017			10.2	2.3	0.0	0.2
	SP 2016	Chardonnay	2.8	18.7	2.6	0.0	0.0
	SP 2017			7.7	14.0	2.5	0.1

The BGSS monitoring program indicated vector populations in vineyards were low, with the highest densities primarily in some Sonoma County vineyard blocks between the end of March and mid-May. The leafhoppers species *Draeculacephala minerva*, *Pagaronia* sp., and the spittlebug species *Philaenus spumarius*, and *Aphrophora* sp. were collected from sweeping vegetation at the edge of some vineyard blocks and the leafhopper *Carneocephala fulgida* from Bermuda grass, *Cynodon dactylon* . These vectors were previously reported from this area (Delong & Severin, 1949; 1950). However, few studies have been done on the role these species may play in the spread of the pathogen.



Mean number of BGSS caught on yellow sticky traps in 15 blocks in Sonoma County placed a) at the vineyard edge next to riparian vegetation (riparian) and b) inside the vineyard (non-riparian), from April 2016 through June 2017.

Mean number of vectors (all taxa) collected with sweep nets in 15 blocks in Sonoma County from March to October 2017. "Riparian" are sweeps performed on ground vegetation at the edge of the vineyard adjacent to the riparian vegetation. "Non-riparian" are sweeps taken on the ground vegetation and the canopy inside the vineyard.



Data obtained with the surveys discussed above is now being analyzed and used to parameterize disease spread mathematical models.

Objective 2. *Xylella fastidiosa* colonization of grapevines and the role of overwinter recovery in Pierce's disease epidemiology

The largest component of this work has been published, here we present the PDF proofs of that article, as it is a representative summary of the work done. Note that we chose to publish it in a trade magazine as it has been a topic of interest by stakeholders, and this was a good alternative to reach a large audience (it was peer-reviewed). While our work did not find a relationship between temperature vis-à-vis overwinter recovery, the research performed did not eliminate that possibility.

PRACTICAL Winery&Vineyard

Has Climate Contributed to a Pierce's Disease Resurgence in North Coast Vineyards?

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CLIMATIC CONDITIONS PLAY AN important role in agroecosystems via direct effects on plant performance and indirectly by influencing pest or pathogen dynamics[3]. Differences in temperature, precipitation or humidity may contribute to interannual variability in crop yield, quality, or damage and underlie long-term trends in such effects over longer timescales[12,19].

For grapevines, vine growth and berry quality are sensitive to climatic conditions, with the expectation that climate change is altering which regions are most suitable for premium winegrape production[21]. Climate change may also impact damage to vines, requiring changes to pest and disease management programs[5]. One disease whose epidemiology is strongly tied to climate is Pierce's disease (PD)[16].

Pierce's Disease and the Role of Climate

PD is caused by a strain of the bacterium *Xylella fastidiosa* that causes progressive leaf scorch, desiccation of fruit, defoliation, and vine death (FIGURE 1)[20]. Although there are some differences in symptom expression among cultivars[15], all conventional cultivars of *Vitis vinifera* are considered susceptible to the pathogen. *X. fastidiosa* is transmitted by multiple species of xylem-sap feeding insects, including sharpshooter leafhoppers and spittlebugs[20].

In coastal areas of California, PD is strongly associated with the activity by the native blue-green sharpshooter (BGSS, *Graphocephala atropunctata*), which is efficient at transmitting *X. fastidiosa* to grapevines[13]. Patterns of disease reflect proximity to BGSS reproductive habitats, with clustering of diseased vines typically on the periphery of vineyards near riparian habitats[13].

MATT DAUGHERTY

FIGURE 1. Grapevine in late summer showing characteristic leaf scorch symptoms of Pierce's disease.

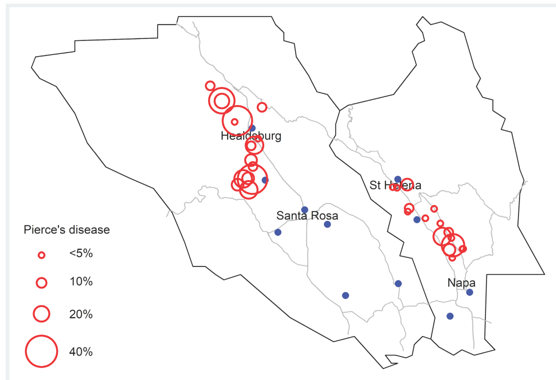


FIGURE 2. Map of the study region, including Sonoma and Napa counties. Open symbols denote the prevalence of Pierce's disease (i.e. percent of infected vines in Fall 2018) at 32 vineyards surveyed as part of other research, some of which have upwards of 30 percent of vines infected. Blue points denote the location of 11 weather stations used in analyses, and gray lines show major roads.

PD in the North Coast, including Napa and Sonoma counties, is episodic—modest in most years, but with occasional periods of high incidence. At least three epidemics have occurred in the region since the 1970s, including an ongoing resurgence in which surveys have documented upwards of 30 percent disease in some vineyards (FIGURE 2)[1]. A comprehensive understanding of the episodic nature of PD in this region, or the cause of the current outbreak, is lacking. Ongoing research by the authors, funded by the Pierce's Disease Control Program (*cdfa.ca.gov/pdcp/*), is evaluating the potential drivers of this resurgence, including whether recent climatic conditions played a role[1].

PD epidemiology has been known to depend on climate for several decades, based on observations that disease incidence was higher following high rainfall years[22]. Many aspects of the PD pathosystem have been linked to temperature or precipitation. In the field, BGSS densities are higher following warm, wet rainy seasons[10], and temperature influences seasonal patterns of BGSS reproductive and flight activity[4].

Experiments confirm that most aspects of sharpshooter performance are strongly related to temperature, including higher feeding rate[18], development[2], overwinter survival[17] and transmission of *X. fastidiosa*[7] at higher temperatures. In addition, *X. fastidiosa* infections depend on climate, particularly temperature. The multiplication rate of *X. fastidiosa* is generally positively related to temperature[9], which results in plants becoming a source of infection sooner and a more rapid disease onset under warmer conditions[8].

Temperature influences the percentage of vines that lose infection over the winter, with more recovery under colder conditions or at locations with more frequent cold winter days[9,11]. Such effects likely explain why PD appears to be restricted to certain coastal and southern areas of the United States[14]. They also suggest that interannual or longer-term differences in climate may be epidemiologically significant, with disease incidence expected to be highest around relatively wet, warm rainy seasons and warm growing seasons.

Here, we ask whether recent climatic conditions in the North Coast have contributed to the ongoing PD resurgence by using long-term weather station records. Specifically, multiple temperature and associated metrics were analyzed to determine if conditions surrounding the approximate onset of an outbreak were noticeably different than historic observations in a way that is expected to favor PD.

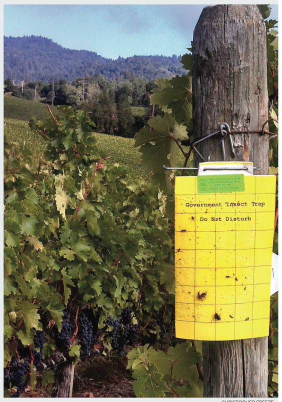
Best Practices for Sharpshooter and Pierce's disease Monitoring

Monitoring is needed to guide when or where vector management should occur. The easiest way to monitor blue-green sharpshooter is with double-sided sticky traps, which are available from several retailers (FIGURE 3). Vary trap number based on block size, from at least a few traps for small blocks (less than two acres), up to one per two to three acres for larger blocks. Spread traps along the periphery of the block, especially nearby vector sources (riparian habitat, ornamental plantings) or other areas with high PD prevalence in the past. Place traps on trellis wires or posts above the trellis, slightly above the canopy, raising them as the canopy develops. Check traps at least monthly from budbreak through leaf fall, particularly during the Spring when weekly to biweekly checks may be justified. Record the number of sharpshooters and replace the trap as needed.

Disease surveys should occur yearly to identify which vines to remove due to lack of vigor or limit sources of infection for vectors. PD symptoms are most apparent later in the growing season. Visually inspect each vine in the late Summer or early Fall, and flag those vines with symptoms for later removal. PD can be highly variable, and may appear similar to other diseases (Esca, Grapevine Leafroll Disease), nutrient deficiencies (magnesium, potassium), and excess soil salinity. Prior to vine removal, if unsure about symptoms, consider sending a sample of one leaf per vine collected from a subset of suspected PD vines to a laboratory for confirmation.

2020 PD/GWSS REFERENDUM

California grape growers will vote in Spring 2020 on extending the Pierce's Disease and Glassy-Winged Sharpshooter (PD/GWSS) Assessment for another five years. The assessment funds research to find solutions to PD, GWSS and additional designated pests and diseases of winegrapes. Every entity that produced and sold winegrapes in 2019 will receive a ballot. Growers who operate multiple entities will receive a separate ballot for each entity; they are not duplications. Each ballot should be voted upon and returned.



CHRISTOPHER FREEZE

FIGURE 3. Double-sided yellow panel trap used in a vineyard to monitor for blue-green sharpshooter and other insects.

Key Points

- Pierce's disease (PD) has affected grape production for as long as commercial vineyards have been present in California.
- Ultimately a large-scale, long-term monitoring program is needed in the region to understand comprehensively the role of climate in triggering a PD outbreak.
- Several PD epidemics have occurred, but their causes have not always been clear.
- Since approximately 2012, vineyards in the North Coast of California have seen a marked increase in PD prevalence, at least the third such outbreak since the 1970s.
- Local climatic conditions are known to affect many aspects of the PD pathosystem, including performance of the pathogen (*Xylella fastidiosa*) and vector (*Graphocephala atropuncata*).
- Analyses were conducted to assess whether the climate in recent years may have contributed to the observed PD resurgence in the region.
- Observed higher temperatures during both the dormant and growing seasons are consistent with elevated PD incidence in some, but not all, recent years.

Analysis of Recent Climatic Conditions in the North Coast

Records were collected from 11 weather stations located throughout Napa and Sonoma counties (FIGURE 2) that are part of the California Irrigation Management Information System (CIMIS) or National Climate Data Center networks (*ipm.ucanr.edu/weather/index.html#weatherdata*). Each included up to 90 years of daily measures of minimum and maximum air temperature, which were used to analyze multiple temperature and associated metrics during two seasons: "dormant" (November to March) and "growing" (March to November). Patterns in precipitation were not explored given the historic drought in the region at the time, which if anything constrained PD incidence[10].

Three temperature metrics were considered for the dormant season: mean daily minimum temperature (°C), number of days with a minimum temperature less than 4°C (i.e. frequency of "cold days")[11] and maximum temperature. For the growing season, three similar metrics were considered: mean daily maximum temperature, number of days with maximum temperatures above 18°C (i.e. frequency of "warm days"), and the time to reach the degree-day requirement for *G. atropunctata* BGSS development (i.e. 162 degree days). This last metric reflects how quickly the offspring of overwintering adults develop to become active in vineyards the following summer, which was calculated starting in January following research from E.A. Boyd and M.S. Hoddle[4].

Prior to analysis, values of each metric were standardized yearly between 2011 and 2016, by dividing by the historic mean for each weather station through 2010. Values greater than 1.0 represent yearly observations that were warmer, more frequent, or slower than observed historically, whereas values less than 1.0 equate to observations that were colder, less frequent, or more rapid than was historically the case.

TABLE 1. Range in historic values among weather stations, and test for overall significant difference between recent years and historic averages (i.e. intercept ≠ 1), for temperature and associated metrics during the dormant or growing seasons. Results are from a set of linear mixed-effects models with a random effect of weather station[6].

		intercept			
	historic values	x^2	df	P	value (se)[1]
Dormant season (Nov-Mar)					
min. temp.	2.1 - 4.9°C	10.214	1	0.0014	0.959 (0.011)
cold days	60 - 98.3 d	13.264	1	0.0003	1.208 (0.043)
max. temp.	15.3 - 16.8°C	17.917	1	<0.0001	**1.029 (0.005)**
Growing season (Mar-Oct)					
max. temp.	23 - 28°C	1.068	1	0.3015	0.993 (0.007)
warm days	184 - 217 d	3.736	1	0.053	**1.023 (0.011)**
d-d requirement[2]	136 - 184 d	2.961	1	0.0853	1.045 (0.026)

[1] **bolded values** are consistent with effects expected to be associated with higher PD incidence.

[2] Number of days required to meet the degree day developmental requirement for blue green sharpshooter.

A set of statistical analyses were conducted to test, overall, whether the standardized temperatures and associated metrics in recent years differed from the historic average (i.e. 1.0)[6]. We then evaluated the following predictions for each year: warmer temperatures than was historically the case (i.e. more than 1.0), fewer cold days during the dormant season (i.e. less than 1.0), more warm days during the growing season (i.e. more than 1.0), and shorter times to reach the degree-day requirement (i.e. less than 1.0).

For the dormant season, historic means of the three climate metrics varied up to two-fold among the coldest and warmest sites, with minimum temperature showing the widest range (TABLE 1). The intercepts for all three metrics differed significantly from 1.0 (TABLE 1), and some years had significant deviations from historic means in a direction that may have contributed to PD incidence. The 2014-15 dormant season had higher minimum temperatures and lower frequency of cold days than historic averages, and both the 2013-14 and 2014-15 seasons had higher maximum temperatures (FIGURE 4).

For the growing season, mean values of the three climate metrics varied up to 35 percent among the coldest and warmest sites (TABLE 1). The frequency of warm days had an intercept that was marginally different from 1.0, whereas the other two were non-significant (TABLE 1). There were significant deviations from historic means for two of the metrics in a direction that is consistent with greater PD pressure—daily maximum temperature was higher in 2015 (FIGURE 5A) and the frequency of warm days was greater in three of the years (FIGURE 5B).

Galley December 2019

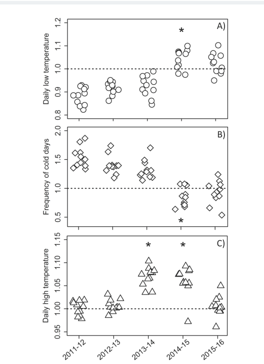


FIGURE 4. Relative A) daily minimum temperature, B) frequency of days with minimum temperatures below 4° C, and C) maximum temperature, November to March – 2011/12 to 2015/16.
"*" denotes seasons significantly warmer than historic means (dotted line).

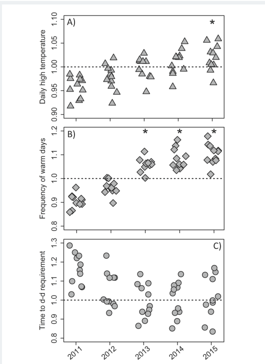


FIGURE 5. Relative A) daily maximum temperature, B) frequency of days above 13.3° C, and C) time to sharpshooter degree-day requirement, March to October – 2011 to 2015.
"*" denotes seasons significantly warmer than historic means (dotted line).

Conclusions and Next Steps

For vector-borne diseases, epidemics may be attributable to a wide range of factors associated with the pathogen, vector, host or environmental conditions. *X. fastidiosa* exemplifies this potential for multiple triggers of disease outbreaks[16], with periods of unusually high incidence that have been ascribed to pathogen introduction, prevalence of nearby reservoir hosts, invasion by a new vector, and with climate likely playing an important role[14].

Multiple lines of evidence indicate that warmer conditions are generally expected to increase sharpshooter populations or activity, and *X. fastidiosa* infection levels and persistence. Long-term datasets are lacking that would allow for explicit tests of the role of climate in presumed increases in vector or pathogen pressure building to outbreak conditions. As a preliminary step toward addressing this hypothesis, contemporary weather station data relative to historic values was compared to determine if they differ in a way that is expected to exacerbate PD incidence.

In the analyses presented, one metric each in the dormant and growing seasons had an overall intercept that differed significantly from historic conditions in a manner that is consistent with greater PD. Moreover, for five of the six metrics in at least one of the contemporary years, there was a significant deviation from historic averages that may favor higher vector populations and activity levels[10,18] or more rapid development and greater persistence of infections[8,9,11]. Thus, it is plausible that these significantly warmer conditions in recent years elevated PD incidence in the North Coast[1].

Yet, the results were also mixed in that all temperature metrics were not significantly different from historic averages in all years. Indeed, by some metrics, the first couple of years (2011 and 2012) during this window of time appear colder than historic averages. Nor is it known definitely how many consecutive years of warmer than typical conditions are required to elevate the risk of a PD outbreak.

December 2019 Galley

Ultimately, a comprehensive understanding of whether recent conditions contributed to the ongoing North Coast PD resurgence will require long-term, large-scale observations of sharpshooter abundance and *X. fastidiosa* infection dynamics in vines beyond what are currently available. Such information is needed to gain insight into the episodic nature of PD in the region, and to eventually be able to predict when an outbreak is likely to occur. In the absence of such predictive tools, it remains especially important for grape growers to monitor regularly for sharpshooters and PD (see sidebar), to identify those areas most at risk and to guide management decisions. WBM

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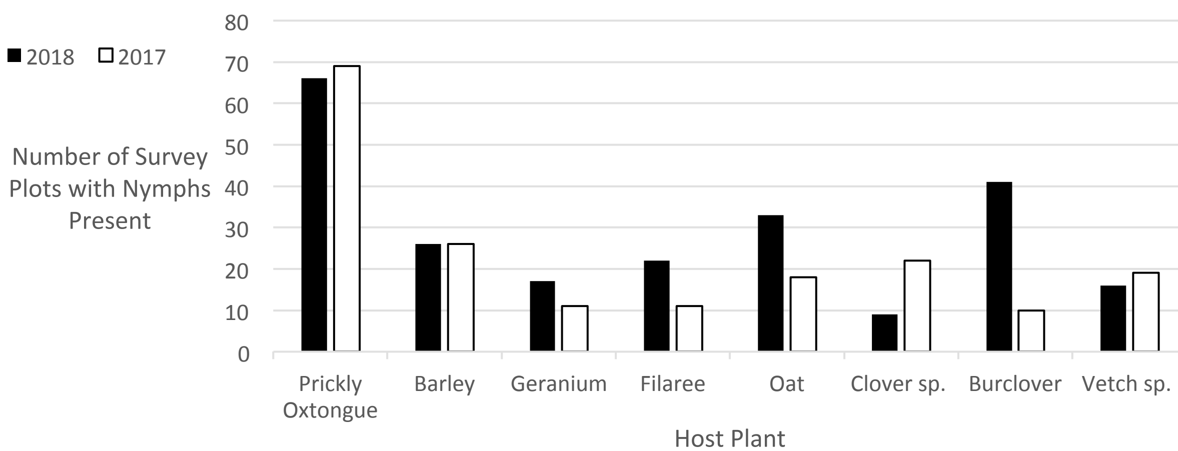
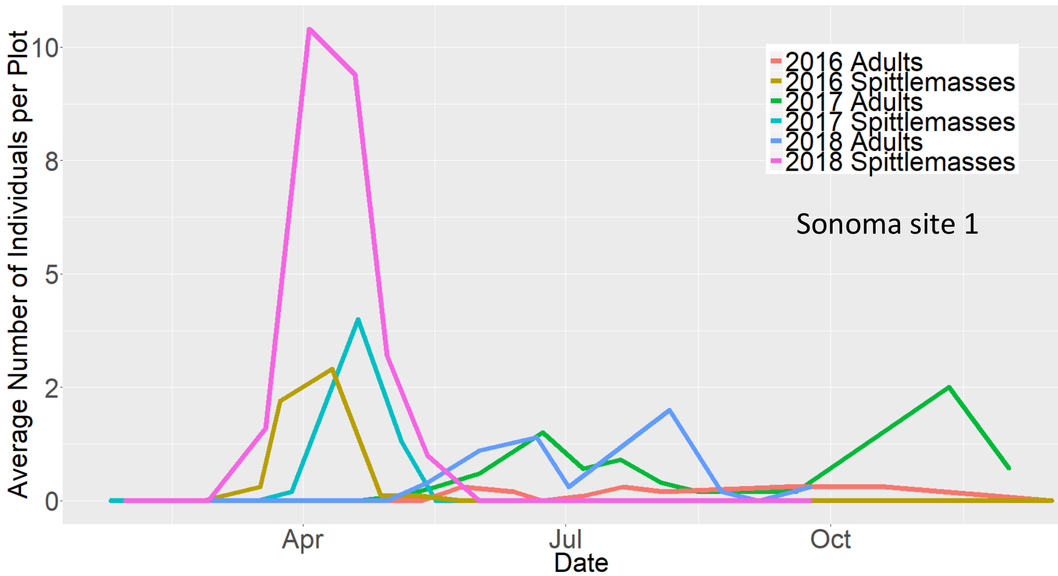
Objective 3. Determine the role of spittlebug insects as vectors of *Xylella fastidiosa*.

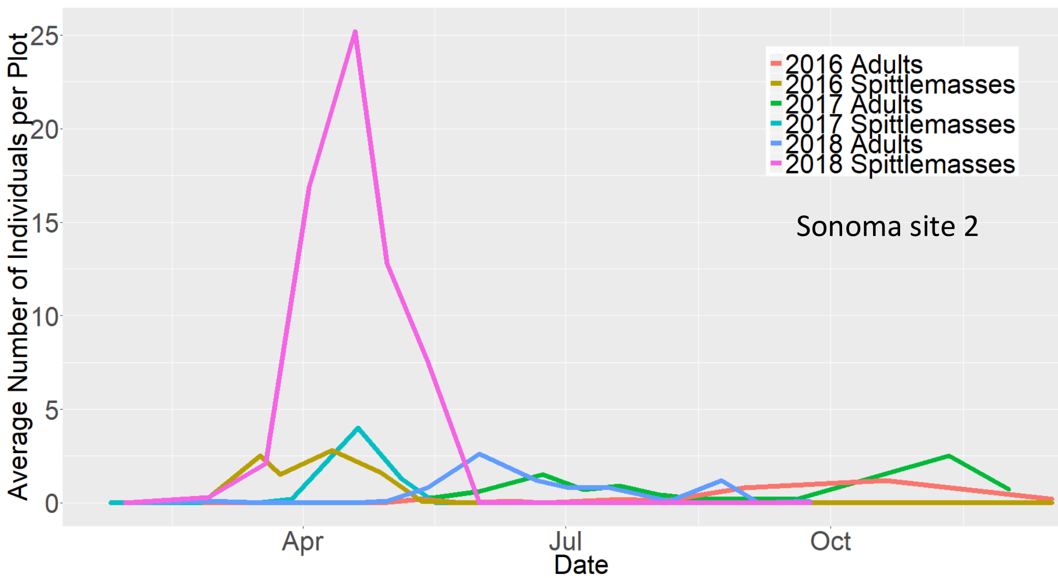
A large amount of data have been collected on the biology, ecology, and infectivity of spittlebugs in the context of *X. fastidiosa* and Pierce's disease in Napa and Sonoma counties. Here we summarize this work by dividing the report into a known vector, *Philaenus spumarius*, and other insect vectors collected with sweep nets, including the *Aphrophora* group.

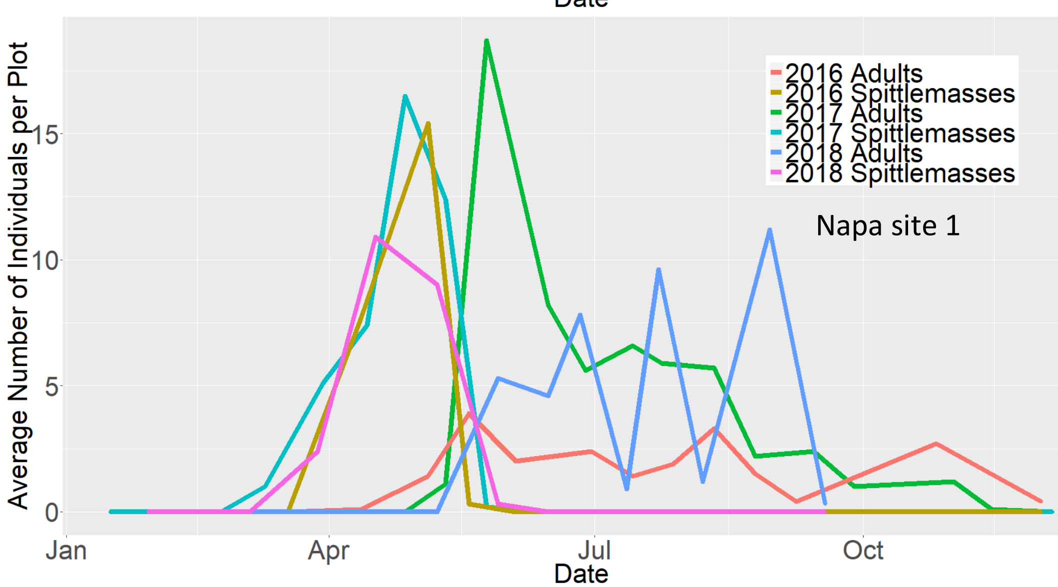
In 2016, 2017 and 2018, we surveyed sites in Napa and Sonoma counties for nymphs of the meadow spittlebug, *P. spumarius*. At the site in Sonoma, two vineyards were surveyed while at the Napa site, only one vineyard was surveyed. Except in cases of extreme weather, the vineyard sites were surveyed biweekly. These surveys consisted of randomly selecting 10 plots in each vineyard during each sampling period. Each plot consisted of two vine-rows and one inter-row and had an approximate area of 7x15 ft^2. Nymph sampling consisted of randomly tossing six 2x2 ft^2 quadrats in each plot and collecting all nymphal spittlemasses within each quadrat. Nymphs were removed from spittlemasses and individually counted back in UC Berkeley. Associated nymphal host plants were identified in the field and any unknown host plants were collected and preserved for identification back at UC Berkeley. For 2017 and 2018, we summarized the most common nymphal host plants across all sites by counting the number of survey plots where *P. spumarius* nymphs were found on a given host plant.



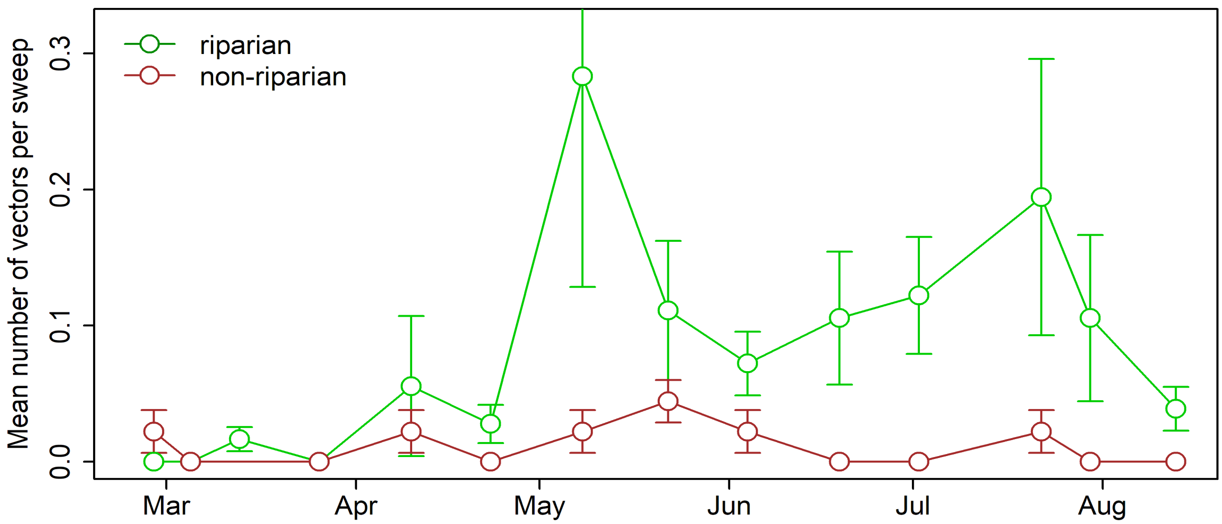
In late March to early April of each field season, biweekly surveys for the adult *P. spumarius* began at our two sites in conjunction with observations of this species' phenological development. In each of the 10 plots, the two vine-rows and the inter-row were each subjected to 25 sweeps with a sweep net. Additionally, a yellow sticky trap (Seabright Labs) was hung on the middle trellis wire of each plot's two vine-rows and checked biweekly (weather permitting) for captured adults of *P. spumarius*. Below we present preliminary data that have not been analyzed.


Average Number of Individuals per Plot
10
8
5
2
0
Apr
Jul
Oct
Date
2016 Adults
2016 Spittlemasses
2017 Adults
2017 Spittlemasses
2018 Adults
2018 Spittlemasses
Sonoma site 1


Average Number of Individuals per Plot
25
20
15
10
5
0
Apr
Jul
Oct
Date
2016 Adults
2016 Spittlemasses
2017 Adults
2017 Spittlemasses
2018 Adults
2018 Spittlemasses
Sonoma site 2

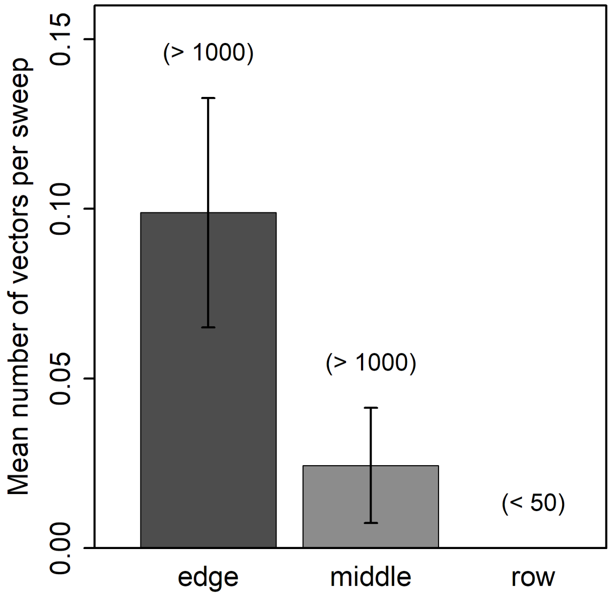

Average Number of Individuals per Plot
15
10
5
0
Jan
Apr
Jul
Oct
Date
2016 Adults
2016 Spittlemasses
2017 Adults
2017 Spittlemasses
2018 Adults
2018 Spittlemasses
Napa site 1

Starting in late February or March of 2018 (and 2019, but those data have not been analyzed), we conducted replicate sweep-net sampling in each of 32 vineyard sites in Napa and Sonoma Counties. This included sampling on the vineyard floor between vine rows, along the edge of vineyards, and in a limited number of cases from underneath vines. Sampling occurred twice a month at Sonoma sites and monthly at Napa sites through at least August, at which point sampling was halted because a substantial portion of plants on the vineyard floor had reached senescence. For each set of sweeps all insects were collected, identified, and counted. We then compared seasonal differences in the abundance of all known vector taxa over the season, among site types (i.e. those near riparian areas versus those not), and among sampling locations (i.e. vineyard edge, between rows, and under vine rows). In addition, we compared the abundance of the most common vector taxa over the season. Thus far these comparisons have been completed for Sonoma sites.



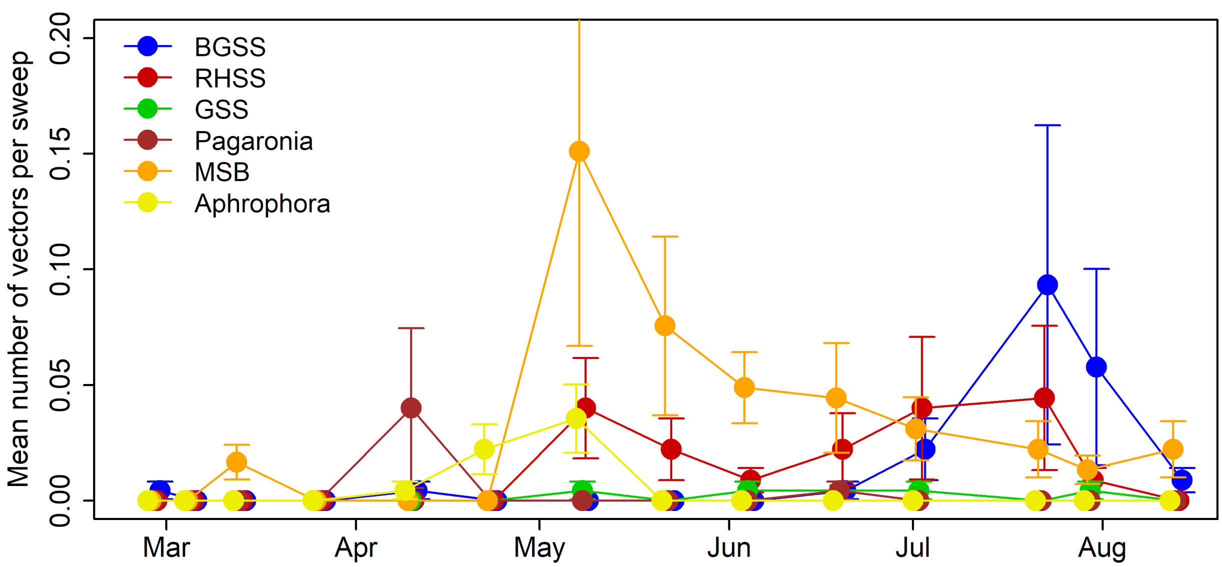
Mean (±SE) total number of all vector taxa collected in sweep-net sampling over the season at riparian versus non-riparian sites in Sonoma County.

A total of more than 400 vectors were collected during sweep-net sampling over the season. Collectively, vector taxa were most common from May through the end of July, and were less common the remainder of the year. On average, vectors were approximately 8-fold more abundant at riparian sites compared to non-riparian sites, particularly during May and July. Within sites, substantially more vectors were collected on the periphery of vineyards compared to between rows, or especially underneath vine rows – though the relatively small number of sweeps conducted underneath vine rows may have influenced this conclusion.



Mean (±SE) total number of vectors over the season in sweep-net sampling at the edge of vineyards, in the middle between rows, and underneath vine rows. Numbers in parentheses reflect the approximate total number of sweeps at each location.

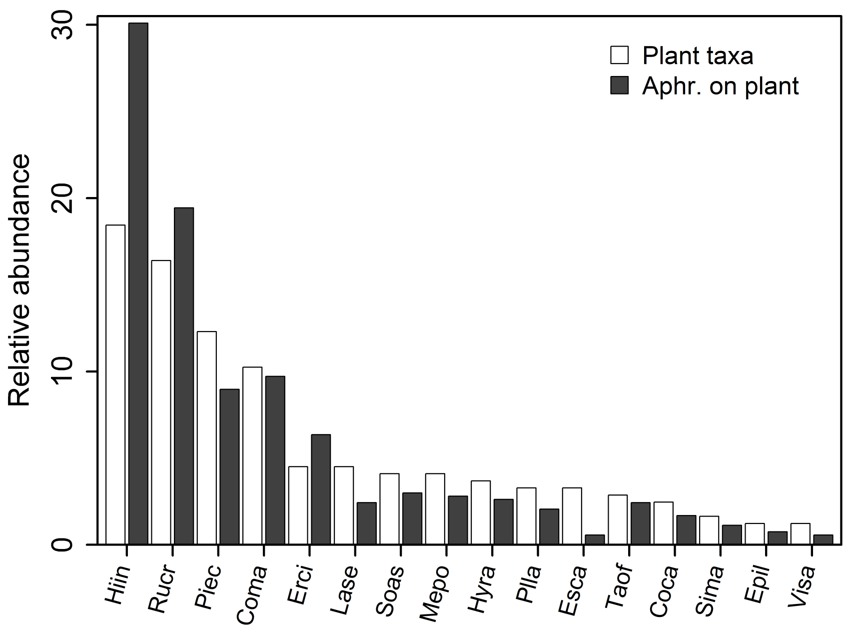
Finally, with respect to vector species, six taxa were relatively common in sweep-net sampling among sites but to varying degrees. These vector taxa include the blue-green sharpshooter, red-headed sharpshooter (RHSS; *Xyphon fulgida*), green sharpshooter (GSS; *Draeculacephala minerva*), another sharpshooter (*Pagaronia* sp.), the meadow spittlebug (MSB; *Philaenus spumarius*), and another spittlebug (*Aphrophora* sp.). Of these, GSS was the least common over the season, while *Pagaronia* and *Aphrophora* were most common briefly in the spring. MSB, RHSS, and BGSS were more common, but showed substantially different seasonal patterns. RHSS was moderately abundant over the Spring and Summer, MSB abundance peaked in May they declined thereafter, and BGSS was common in sweep-net sampling only in July and August – corresponding with the secondary peak of the F1 generation of BGSS that typically is represented in yellow sticky-trap monitoring.



Seasonal abundance of vector taxa in sweep-net sampling at Sonoma County sites.

In addition to sweep-net sampling, we monitored spittlebug abundance each Spring via visual surveys at a subset of sites in Napa and Sonoma. For each census, transects were established that included recording the number of nymphal spittle masses present, the most common plant species on the vineyard floor, and the plant taxa on which nymphs were present. These surveys, in addition to other studies documenting spittlebug development rates, are being used to understand which host plant species are most important for spittlebug populations. Below are the results for *Aphrophora* abundance at the Sonoma County sites.

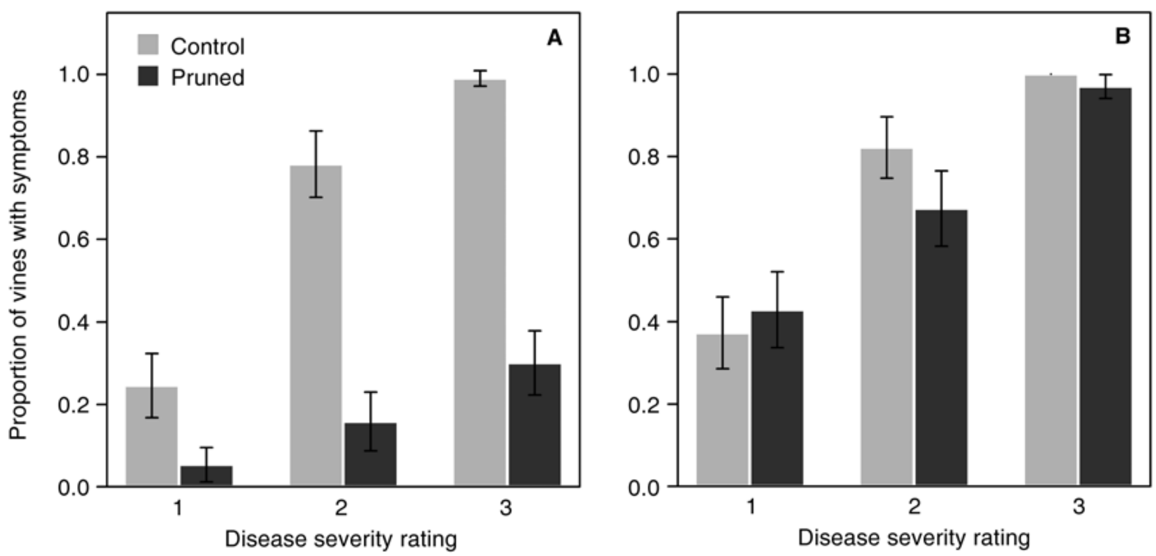
Among sites, *Aphrophora* nymphs were found on more than 20 plant taxa. Among the most common hosts at these sites were weedy or naturalized exotic species (Fig. 4, white bars) such as: shortpod mustard (*Hirschfeldia incana*; Hiin), curly dock (*Rumex crispus*; Rucr), bristly oxtongue (*Picris echioides*; Piec), poison hemlock (*Conum maculatum*; Coma), prickly lettuce (*Lactuca serriola*; Lase), filaree (*Erodium cicutarium*; Erci), burclover (*Medicago polymorpha*; Mepo), sowthistle (*Sonchus* sp.; Soas), catsear (*Hypochaeris radicata*; Hyra), buckhorn plantain (*Plantago lanceolata;* Plla), and dandelion (*Taraxacum officinale*; Taof). In general, *Aphrophora* spittle mass abundance was strongly correlated with the relative abundance of these hosts, but with shortpod mustard and curly dock showing a greater spittle abundance than expected based on plant abundance.



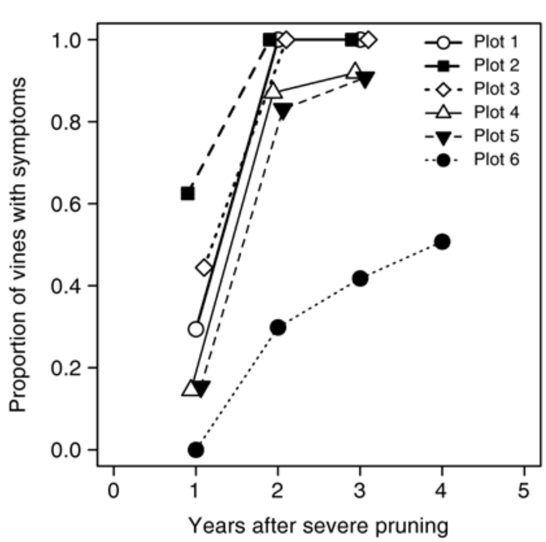
Relative abundance of the most common 16 plant taxa (white bars; % of all plants) and corresponding fraction of *Aphrophora* nymphs on those plants (dark bars). Most plant names listed in the text above.

Objective 4. Data mine and disseminate existing information on vector ecology, vegetation management, and efficacy of pruning.

Our efforts focused on one particular project (others were pursued but had limited success), which asked if severe pruning of *X. fastidiosa*-infected grapevines would cure plants from infection. This has remained a major question for vineyard managers, where the practice is still attempted, primarily because there were no studies available on the topic demonstrating the fact the concept is likely not viable. A large effort to mine data associated with 20-year old experimental data led to a publication: "Daugherty, M.P., Almeida, R.P.P., Smith, R.J., Weber, E.A. and Purcell, A.H. 2018. Severe pruning of infected grapevines has limited efficacy for managing Pierce's disease. American Journal of Enology and Viticulture 69: 289-294." The conclusion of that work was: "These results suggest that severe pruning does not clear *X. fastidiosa* infection from grapevines to an extent that would justify its adoption for disease management."



Graphics showing return of Pierce's disease symptoms in severely pruned or control (conventionally pruned) vines from three disease-severity categories after A) one year or B) two years. Each column represents the average proportion of vines with symptoms, for groups of 101 to 133 vines spread among six vineyard blocks. Error bars denote 95% confidence intervals.



Return of Pierce's disease symptoms after severe pruning of vines in the most severe disease category, for the six vineyard plots. Some plot symbols offset slightly for clarity. Points represent the overall proportion of vines that showed symptoms for up to 67 replicate severely pruned vines per block.

Objective 5. Develop a larger extension and outreach footprint with additional seminars, extended interviews made available on the web, and an update to the *Xylella fastidiosa* website, the main online resource for PD information.

A large extension footprint was developed with this project, some of the outputs included seminars, talks, workshops, newsletters, and other means of information dissemination. Some of those are summarized later in this report.

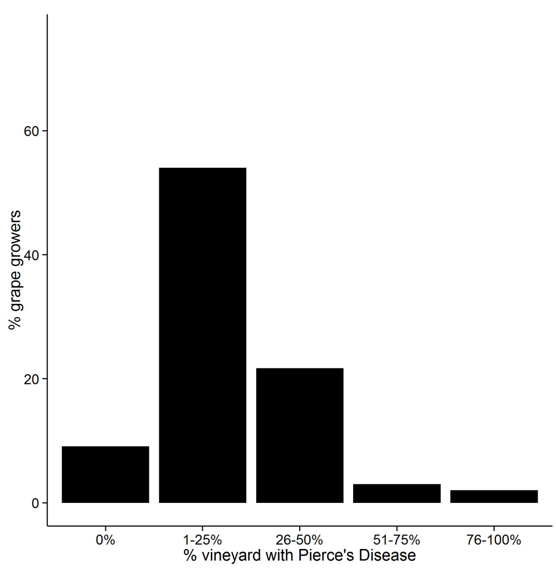
In an attempt to better understand the role of winter conditions on PD epidemiology as well as how growers and managers view the threat of PD and manage the disease, we performed two surveys during extension events conducted on January 13, 2016 (Napa) and February 11, 2016 (Sonoma). In total, 198 growers/managers participated in our surveys: 147 from Napa and 51 from Sonoma. The survey included questions on past and present experiences with PD, management actions, and demographic characteristics.

Two other observations from this survey were interesting. First, 73% of respondents said that PD was one of their top 3 management problems. Second, we gained an understanding of management practice commonly employed for PD with the following question:

Percent of managers responding that they relied mostly on the following management actions:

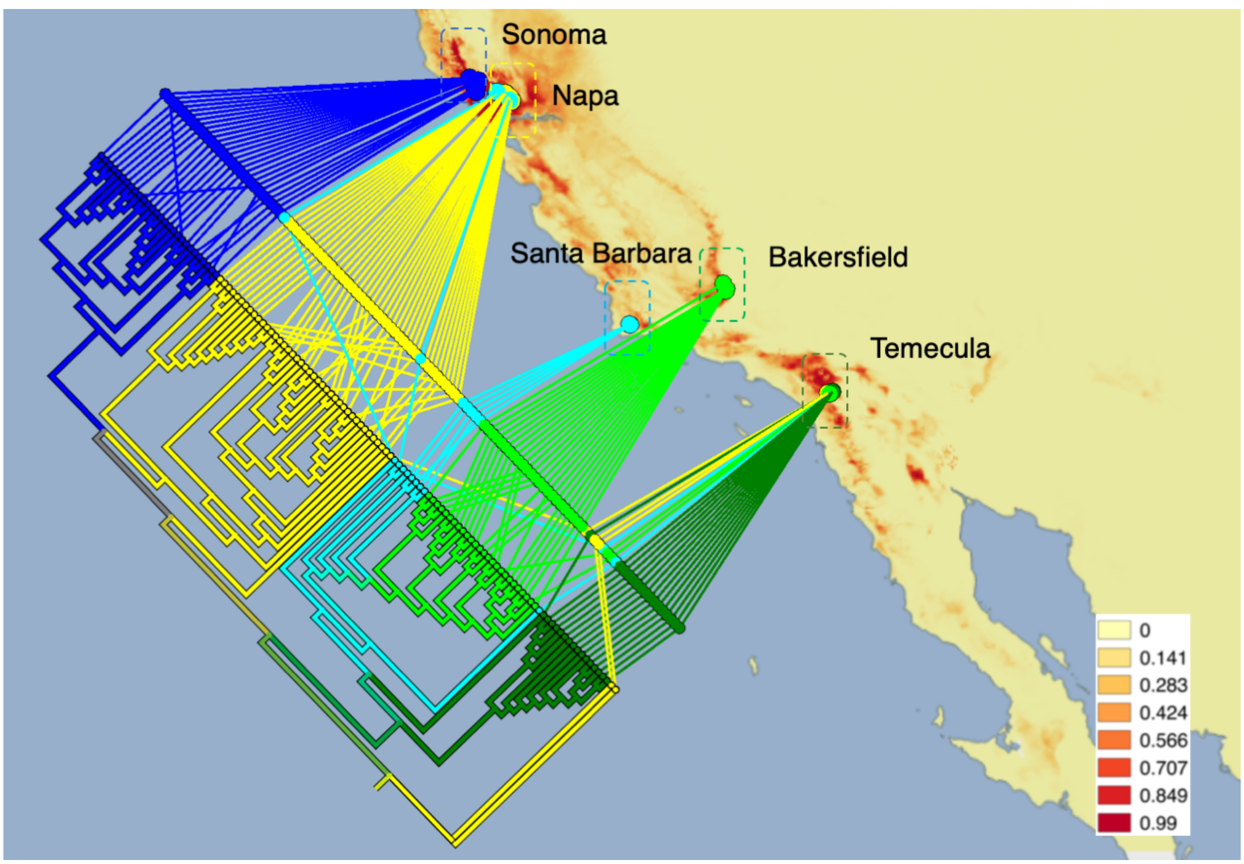
Management action	% growers
Insecticides in vineyard	17.67
Insecticides outside vineyard	1.51
Roguing	38.88
Severe pruning	3.53
Weed control	3.53
Riparian management	8.58
Vector or Disease Monitoring	14.64

Lastly, we attempted to estimate current losses due to PD (see figure below). We note that losses appear to be larger than those attributed to PD in the past decade.



Objective 6. Determine if an emerging strain of *Xylella fastidiosa* was responsible for the PD outbreak. This Objective was added as recommended by proposal reviewers.

To test if a novel strain of *X. fastidiosa* causing PD swept through California, we sequenced 122 genomes of isolates collected from symptomatic grapevines in five grape-growing regions in the State. The data associated with these genome sequences are all available freely at public databases routinely used to deposit and store genomic data. A total of 5,218 single-nucleotide polymorphisms (SNPs) were found in the dataset. Strong population genetic structure was found; isolates split into five genetic clusters divided into two lineages. The core/soft-core genome constituted 41.2% of the total genome, emphasizing the high genetic variability of *X. fastidiosa* genomes. An ecological niche model was performed to estimate the environmental niche of the pathogen within California and to identify key climatic factors involved in dispersal. A landscape genomic approach was undertaken aiming to link local adaptation to climatic factors. A total of 18 non-synonymous polymorphisms found to be under selective pressures were correlated with at least one environmental variable highlighting the role of temperature, precipitation and elevation on *X. fastidiosa* adaptation to grapevines in California. Finally, the contribution to virulence of three of the genes under positive selective pressure and of one recombinant gene was studied by reverse genetics. We note that the structuring of populations based on the geographical location of populations is a strong indicator that no novel strain swept through the State, and that no novel PD strain drove the epidemic. However, analyses performed have not allowed us to determine why populations are structured geographically. We also do not know if these populations are biologically distinct. Work by our group and collaborators (independently or not) is attempting to address these questions; of particular relevance is ongoing research at the USDA-ARS Parlier testing strains from these populations in grapevines for phenotypic differences.



Publications Produced (major contributions, not complete)

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Daugherty, M.P., Almeida, R.P.P., Smith, R.J., Weber, E.A. and Purcell, A.H. 2018. Severe pruning of infected grapevines has limited efficacy for managing Pierce's disease. American Journal of Enology and Viticulture 69: 289-294.

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Daugherty, M.P., Cooper, M., Smith, R., Varela, L., and R. Almeida. 2019. Has climate contributed to a Pierce's disease resurgence in North Coast vineyards? Practical Winery & Vineyard (Wine Business Monthly), in press

Sicard, A., Zeilinger, A.R., Vanhove, M., Schartel, T.E., Beal, D.J., Daugherty, M.P. and Almeida, R.P.P. 2018. *Xylella fastidiosa*: Insights into an emerging plant pathogen. Annual Review of Phytopathology 56: 181-202.

Vanhove, M., Retchless, A.C., Sicard, A., Rieux, A., Coletta-Filho, H.D., De La Fuente, L., Stanger, D.C. and Almeida, R.P.P. 2019. Genomic diversity and recombination among *Xylella fastidiosa* subspecies. Applied and Environmental Microbiology 85: e02972-18.

Presentations Produced (major contributions, not complete)

Date	Meeting, *Organizer*	Topic	Location	No. Attendees
2/7/2018	Sustainable Vineyard Practices, *Napa Valley Grapegrowers & Napa Vineyard Technical Group*	Emerging pest and disease concerns for grape growers	Napa, CA	153
6/27/2018	Tailgate Meeting, *Santa Rita Hills Grower Group*	Strategies for Pierce's Disease management in coastal wine grapes	Lompoc, CA	55
2/6/2019	Sustainable Vineyard Practices, *Napa Valley Grapegrowers & Napa Vineyard Technical Group*	Addressing knowledge gaps in Pierce's disease epidemiology & Gel baits for Argentine ant management	Napa, CA	161
2/27/2019	Current Wine and Wine grape research symposium *Foundation Plant Services, UCD Extension*	Addressing knowledge gaps in Pierce's disease ecology: implications for management; *presenter: A. Adams, Research*	Davis, CA	180

Date	**Meeting, *Organizer***	**Topic**	**Location**	**No. Attendees**
		Associate		
4/16/2019	Napa Viticultural Society Workshop, *Silverado Farming Company*	Breaking news: the latest in Pierce's Disease, red blotch and vine mealybug management	St Helena, CA	130
12/3/2019	Current Issues in Vineyard Health, *Foundation Plant Services & UC Davis Extension*	Pierce's disease: studies of disease ecology reveal new perspectives on a persistent problem	Davis, CA	

"Understanding the effects of climate on Pierce's disease epidemiology", Pacific Branch meeting of the Entomological Society of America, San Diego, CA 4/2019

"Revisiting our understanding of Pierce's disease epidemiology in the North Coast", Sonoma County Grape Day, Santa Rosa, CA 2/2019

"Pierce's disease epidemiology and management in North Coast vineyards", Sustainable Ag Expo, San Luis Obispo, CA 11/2018

"*Xylella fastidiosa* diseases: tales of a generalist plant pathogen", International Lilac Society, Riverside, CA, 04/2018

"Understanding what is driving the Pierce's disease epidemic: an update", Sonoma County Vineyard Technical Group, Santa Rosa, CA, 03/2018

"Understanding what is driving the Pierce's disease epidemic: an update", Napa County Vineyard Technical Group, Napa, CA, 03/2018

"Understanding what is driving the Pierce's disease epidemic: an update", UCCE Sonoma County, Sebastopol, CA, 01/2018

"Sharpshooter and Pierce's disease management in California vineyards", Sustainable Ag Expo, San Luis Obispo, CA, 11/2017

"Pierce's disease epidemiology in the North Coast: what's behind the recent resurgence?", Current Issues in Vineyard Health, UC Davis Extension, Davis, CA, 11/2016

"Pierce's disease biology and management in California vineyards", UCCE San Luis Obispo, San Luis Obispo, CA, 11/2016

Field tour on scouting for Pierce's disease. Temecula Vineyard Technical Group, Temecula, CA, 09/2017

Workshop on PD monitoring and management. Temecula Small Winegrowers Association, Temecula, CA, 09/2017

Interview, Recent resurgence in Pierce's disease. Western Farm Press, 11/2016

Workshop on developing a sharpshooter sampling plan for Rutherford grapegrowers, 03/2016

Workshop on developing a sharpshooter sampling plan for Napa grapegrowers, 01/2016

Interview, Current status of Pierce's Disease. Wines and Vines, 01/2016

Workshop on sharpshooter monitoring, biology, and management for Napa grapegrowers, 11/2015

Interview, Trends in vineyard IPM. Vineyard and Winery Management, 07/2015

Sonoma Grape Day, One seminar on PD focusing on management strategies. February 10 2016 - ~200 attendees.

Sonoma Vineyard Technical Group, One seminar on PD focusing on management strategies. February 11 2016 - ~75 attendees.

Oak Knoll PD Task Force formed (35 members); have held 3 meetings since early December. We are working closely with this group on insect detection and disease management.

Presentation by M. Cooper, on Pierce's Disease epidemiology (in Spanish) to 220 attendees, at ROOTSTOCK (11/12/2015), organized by Napa Valley Grapegrowers, and held in Napa, CA.
Napa Valley Vineyard Technical Group; Jan 13, 2016; 234 attendees. Two lectures on PD and PD management followed by Q&A.
"Factors affecting Pierce's Disease outbreaks", presented by M. Cooper to Rutherford Dust Society (45 attendees), Feb. 4, 2016, Rutherford, CA.
Pierce's Disease Vector ID workshop, Feb 18, 2016 (English (37 attendees) and Spanish(18 attendees)), Napa, CA.
Outreach
Rhonda Smith, Monica Cooper, and Matt Daugherty have given interviews to several trade publications (e.g. Practical Winery and Vineyard, Wines and Vines). Rhonda Smith was featured in a The Press Democrat article about PD as well.

Relevance Statement
PD is a disease with complex ecology. This work tested a range of hypotheses in an attempt to explain why a devastating PD epidemic emerged in Coastal California during the last decade. Some hypotheses were rejected, others were tested but questions remain. However, a leading hypothesis was developed during this work, suggesting that the established paradigm for PD spread may have been incorrect. In other words, it is possible that we had the basics of PD spread wrong. The relevance of the work done here was three fold, i) hypotheses on disease emergence were robustly tested (and mostly rejected), ii) novel insights on PD ecology and management were obtained as a consequence of this research, and iii) ongoing work is testing if a novel hypothesis explaining PD spread. The later, if demonstrated to be correct, will lead to significant changes to recommendations for PD management.

Layperson Summary of Accomplishments
This project allowed our group to answer some of the pending questions related to the drivers of the recent PD epidemic in Coastal California primarily through the systematic testing of a range of hypotheses. One of the remaining hypotheses is, succinctly, that insect vectors acquire *X. fastidiosa* from infected grapevines at the end of a growing season, prior to migrating to riparian zones to overwinter as adults. The current paradigm proposes that insects acquire *X. fastidiosa* from alternative hosts in the riparian zone. If correct, this new hypothesis would result in significant differences in disease management. Our group is currently analyzing data generated in this project to evaluate this hypothesis, as well as pursuing ecological models with similar goals. Finally, we are communicating to stakeholders the information we have available, what it means in terms of management, and what are the remaining questions currently being pursued.

Status of Funds
Funds were used as proposed.

Summary of Intellectual Property
Not applicable.