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Vector within-host feeding preference mediates transmission of a heterogeneously distributed pathogen

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Abstract. 1. Ecological theory predicts that vector preference for certain host species or discrimination between infected versus uninfected hosts impacts disease incidence. However, little information exists on the extent to which vector within-host feeding preference mediates transmission. This may be particularly important for plant pathogens, such as sharpshooter transmission of the bacterium *Xylella fastidiosa*, which are distributed irregularly throughout hosts.

2. We documented the within-host distribution of two vector species that differ in transmission efficiency, the leafhoppers *Draeculacephala minerva* and *Graphocephala atropunctata*, and which are free to move throughout entirely caged alfalfa plants. The more efficient vector *D. minerva* fed preferentially at the base of the plant near the soil surface, whereas the less efficient *G. atropunctata* preferred overwhelming the top of the plant.

3. Next we documented *X. fastidiosa* heterogeneity in mechanically inoculated plants. Infection rates were up to 50% higher and mean bacterial population densities were 100-fold higher near the plant base than at the top or in the taproot.

4. Finally, we estimated transmission efficiency of the two leafhoppers when they were confined at either the base or top of inoculated alfalfa plants. Both vectors were inefficient when confined at the top of infected plants and were 20–60% more efficient when confined at the plant base.

5. These results show that vector transmission efficiency is determined by the interaction between leafhopper within-plant feeding behaviour and pathogen within-plant distribution. Fine-scale vector and pathogen overlap is likely to be a requirement generally for efficient transmission of vector-borne pathogens.

Key words. Disease spread, heterogeneous infection, host preference, vector behaviour, vector competence.

Introduction

For vector-borne pathogens, vector behaviour can affect disease dynamics in at least three ways. First, at the host community scale, vector preference for certain species may drive pathogen spillover (Malmstrom *et al*., 2005). For example, seasonal shifts in mosquito host species feeding preference explains the timing and severity of West Nile Virus epidemics in humans (Kilpatrick *et al*., 2006). Second, within a given host species, vector preference associated with infection status may have important implications for pathogen spread (McElhany *et al*., 1995). For example, children carrying *Plasmodium falciparum* gametocytes, the transmissible stage of the Malaria parasite, attracted twice as many mosquito vectors as did healthy children (Lacroix *et al*., 2005). Conversely, aphid vectors are less likely to either colonise or feed on Zucchini Yellows Mosaic Virus infected versus healthy plants (Blua & Perring, 1992). Finally, at the individual host scale, vectors may show within-host feeding site preference (Dekker *et al*., 1998; Shaw *et al*., 2003; Marucci *et al*., 2004). This last aspect of vector behaviour, although often overlooked, may be an important determinant of vector transmission efficiency (i.e. vector competence).

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Within-host preference has been documented in many vector taxa. Some ticks, such as the Lyme disease vector *Ixodes scapularis* Say, are distributed irregularly on their hosts, with the highest burdens occurring on exposed, heavily vascularised regions (e.g. ears, neck – Shaw *et al*., 2003). Similarly, *Anopheles* mosquitoes show preference for feeding on certain locations of their human hosts (Dekker *et al*., 1998). The literature on vectors of plant pathogens is replete with similar evidence of feeding site preference. Aphids and psyllids, in particular, are frequently distributed unevenly on their host plants (e.g. Horton, 1999; Tsai *et al*., 2002) favouring new shoots or other regions with easy access to phloem sap (Elliot & Hodgson, 1996). Such vector within-host heterogeneity may be important epidemiologically if the choice of feeding site affects the likelihood of pathogen transmission.

Vector species often vary in the efficiency with which they transmit a pathogen (Turell *et al*., 2001; Daugherty & Almeida, 2009). Different feeding preferences may contribute to this variation if they affect vector exposure to the pathogen. Infection levels (i.e. pathogen population density or titre) in individual hosts frequently vary through time (Hill & Purcell, 1995; Saracco *et al*., 2006), which can affect vector acquisition efficiency (Hill & Purcell, 1997; Shriram *et al*., 2005). Moreover pathogens, especially some plant pathogenic bacteria, are irregularly distributed within individual hosts (Krivanek & Walker, 2005). For example, both chrysanthemum yellows phytoplasma (Saracco *et al*., 2006) and citrus greening disease pathogen '*Candidatus* Liberibacter asiaticus' (Tatineni *et al*., 2008) show evidence of heterogeneous infections, with up to 10-fold differences in mean pathogen population densities in different vegetative parts of the plant. Such heterogeneous infections should promote vector acquisition when vector feeding site preference coincides with regions of high infection. Conversely, acquisition should be constrained when vectors feed within hosts at low infection sites. This hypothesis, that transmission efficiency is tied to behaviourally mediated differences in vector exposure, has received little attention in the literature (but see Perkins *et al*., 2003).

One system for which both vector and pathogen within-host heterogeneity may be important is in the transmission of the plant pathogen *Xylella fastidiosa*. *Xylella fastidiosa* is a xylem-limited bacterium that is widespread throughout the Americas and causes disease in a wide range of native, weedy, and agricultural plants (Purcell, 1997) – including Pierce's disease in grapevines, almond leaf scorch, and alfalfa dwarf disease in the Western U.S.A. (Weimer, 1937; Davis *et al*., 1978, 1980). Different host-plant species or cultivars vary in their infection level and symptom severity (Almeida & Purcell, 2003; Krivanek & Walker, 2005; Krivanek *et al*., 2005; Lopes *et al*., 2009). In addition, pathogen distribution may be heterogeneous within individual hosts (Hopkins, 1981). For example, *X. fastidiosa* population densities in grapevine stems are up to 10-fold lower than in leaves (Krivanek & Walker, 2005). Given that transmission efficiency depends on infection level in this system (Hill & Purcell, 1997), heterogeneity may be important for pathogen spread if vectors also show feeding site preference.

Xylella fastidiosa is transmitted by several species of xylem-sap feeding insects, the most important being the sharpshooter leafhoppers (Hemiptera: Cicadellidae; Severin, 1949). Within this group, however, there exists substantial variation in transmission efficiency among vector species (Frazier & Freitag, 1946; Hewitt *et al*., 1946; Daugherty & Almeida, 2009; Lopes *et al*., 2009). For example, in the 1940s a collection of studies (Frazier & Freitag, 1946; Hewitt *et al*., 1946) compared the efficiency of the blue–green sharpshooter (BGSS) *Graphocephala atropunctata* Signoret and the green sharpshooter (GSS) *Draeculacephala minerva* Ball to understand which was responsible for coincident outbreaks of alfalfa dwarf and Pierce's disease in California's Central Valley (Weimer, 1937). Although *G. atropunctata* was more efficient at transmitting among grapevines, *D. minerva* was over 25% more efficient at acquiring from infected alfalfa plants than was *G. atropunctata* (502/595 vs. 37/64, respectively). The mechanism behind these differences in transmission efficiency is not known. Given that sharpshooters may show feeding site preference (Marucci *et al*., 2004), it is plausible that differences in preference, combined with pathogen heterogeneity, are important determinants of vector efficiency.

In this study we tested the hypothesis that vector feeding behaviour mediates pathogen transmission, with efficient transmission requiring overlap between pathogen within-host colonisation and vector within-host feeding preference – using *X. fastidiosa* in alfalfa as a model system. First, we documented feeding site preferences of the leafhoppers *D. minerva* and *G. atropunctata* on alfalfa. Then we documented patterns of *X. fastidiosa* infection in plants. Finally, we estimated within-plant variation in transmission efficiency by the two vectors.

Materials and methods

Vector feeding site preference

To estimate vector feeding site preference we confined groups of 10 *D. minerva* or *G. atropunctata* adults on individual potted alfalfa plants (*Medicago sativa* L., cv. WL625 HQ), which were enclosed by 15 cm × 45 cm mesh sleeve cages. Plants in this experiment were approximately 6 weeks old (pre-flowering stage), 40 cm tall, grown in 10 cm pots filled with Supersoil potting soil (Rod Mclellan Company, San Mateo, California), and were free of *X. fastidiosa* infection. Insects were 2-week-old adults reared on sweet basil (*Ocimum basilicum* L.), from laboratory colonies originally established with sharpshooters collected in Sonoma (*G. atropunctata*) or Solano (*D. minerva*) county, California. Prior testing confirmed that both vector colonies were free of *X. fastidiosa*. The vector groups were confined on the caged alfalfa plants for 3 days, during which we counted twice daily the number of insects on the basal, middle, or apical third of the plants. There were 10 replicate caged plants for each vector species.

We tested for differences in sharpshooter species feeding site preference by comparing the cumulative proportion of insects found on the basal, middle or top third of the alfalfa plant

over the 3 days. We used one-way MANOVA (Crawley, 2007), with species as a categorical effect and the three cumulative proportions as response variables, arcsine transformed to meet test assumptions. A significant effect in the MANOVA was followed up with three separate one-way ANOVA for the effect of species on the individual basal, middle, or top proportion – while controlling α for multiple tests.

Pathogen distribution

To determine whether *X. fastidiosa* is distributed heterogeneously, we mechanically inoculated alfalfa plants with one of four pathogen isolates, then measured infection in different parts of the plant. No type isolates of *X. fastidiosa* were identified from alfalfa during the California alfalfa dwarf epidemics in the 1930s (Weimer, 1937), and no population genetics studies have been conducted of *X. fastidiosa* in alfalfa fields. Therefore, we used two representative *X. fastidiosa* isolates from each of the two dominant strains of this pathogen in the western U.S.A. (Schuenzel *et al*., 2005). These include the 'Butte' and 'Dixon' isolates that are grouped genetically within the almond strain (*X. fastidiosa* subsp. *multiplex*), and the 'Pavich' and 'Traver' isolates that belong to the grape strain (Almeida & Purcell, 2003; J. Lopes, unpublished; subsp. *fastidiosa*). Given the proximity of alfalfa, grape, and almond plantings in portions of California, it is likely that there is pathogen movement among these crops. The grape strain has been isolated from asymptomatic alfalfa plants in the field, but almond has not. However, almond isolates have been shown in the laboratory to infect alfalfa plants (J. Lopes, unpublished). Thus, given the uncertainty in the relative prevalence of these two pathogen strains in the field, we used isolates from both strains to encapsulate some of the natural variation in disease that may occur due to differences in pathogen lines. The four isolates also offer a natural unit of replication for investigating patterns of infection in alfalfa. Inoculations were made on alfalfa seedlings, 10 days after transplanting to pots. Ten replicate plants per isolate were pin-inoculated on the primary stem, 5 cm above the soil surface, with 5 µl of a 10^8–10^9 colony forming units (CFU) ml^{-1} suspension of one of the *X. fastidiosa* isolates (Hill & Purcell, 1995).

At 5 and 12 weeks post inoculation, we cut plants at 5 cm above the soil surface to mimic natural alfalfa harvesting. During the second harvest we collected approximately 0.15 g of tissue from plants at each of five locations: the base of the axillary stem growing off the original inoculation point, the base of an adjacent (non-inoculated) stem, the top of the axillary stem (approx. 30 cm above soil surface), the top of an adjacent stem (non-inoculated; approx. 30 cm above soil surface), and the taproot just below soil surface. The samples were then plate cultured with serial dilutions to determine both the proportion of samples infected and infection level (i.e. bacterial population) at each plant location (Hill & Purcell, 1995).

We compared infection rates among pathogen isolates for each sampling location separately using a generalised linear model with binomial errors, with adjustment of α to account for multiple tests (Crawley, 2007). As samples were collected at different locations from an individual source plant, they amount to non-independent subsamples. Therefore, we also analysed patterns of infection in the plant using relative metrics, comparing differences in infection rate and infection level between the location nearest the inoculation point, the base of the inoculated stem, and the other locations sampled. For infection prevalence, we calculated the proportion of positive samples for a given pathogen isolate at a given location and used this to calculate the relative difference ($p_{base} - p_x$, where x denotes 'top', 'adjacent base', 'adjacent top', or 'roots'). Thus the four pathogen isolates equate to experimental replicates. Values greater than, less than, or equal to one indicate lower, higher, and equal proportion of infected samples compared with the base of the inoculated stem. These relative differences in prevalence were evaluated with individual one sample t-tests to determine whether they differed significantly from zero, while controlling α to account for multiple tests. We followed a similar procedure for calculating the relative infection level ($cfu_{base} - cfu_x$) for all positive samples for a given plant location.

Transmission efficiency

To understand whether heterogeneous infection levels affect transmission, we conducted no-choice acquisition experiments with *D. minerva* or *G. atropunctata* adults confined at different plant locations. The source plants used were approximately 40 cm tall potted alfalfa plants that were pin-inoculated on one stem with *X. fastidiosa* (Traver isolate) 12 weeks prior. For *G. atropunctata* we confined three adults, using plastic clip cages, on the basal or apical third of the axillary stem growing off the inoculation point. For *D. minerva* we confined three adults on each of the same four aboveground locations as in the pathogen distribution experiment. There were 10 replicate plants at each location for *G. atropunctata*, and 15 replicates for *D. minerva* (except $n = 10$ at the top of axillary stem). After a 2-day acquisition access period, vector groups were transferred to caged healthy grape (*Vitis vinifera* L., cv. Cabernet Sauvignon) seedlings for a 2-day inoculation access period. An additional nine grape plants not exposed to sharpshooters served as controls. Ten weeks later, all grape test plants were assayed by culture for infection by *X. fastidiosa* to estimate the proportion of sharpshooter groups that had acquired the pathogen from alfalfa source plants. Grape seedlings were used instead of alfalfa plants throughout, because they are consistently susceptible and develop strong symptoms, and they were a standard test plant in earlier studies of *G. atropunctata* and *D. minerva* transmission (Frazier & Freitag, 1946; Hewitt *et al*., 1946).

We tested for effects of vector species and feeding location on transmission rate. As *G. atropunctata* transmission was evaluated after confinement at the base and top of the inoculated stem only, we compared *G. atropunctata* and *D. minerva* transmission at these two sites using a 2×2 generalised linear model with binomial errors. We compared *D. minerva* transmission among all four feeding locations (i.e.

base and top of inoculated and adjacent stems) with a one-way generalised linear model with binomial errors. Both tests were evaluated at $\alpha = 0.025$ to control for multiple tests. For the *D. minerva* analysis, a significant main effect of feeding location was followed-up with pairwise Fisher's exact tests of the proportion of plants infected among the four locations.

Results

Vector distribution on the plant was relatively consistent among censuses, but patterns were different between the species. The cumulative proportion of vectors on the basal, middle, or apical third of the alfalfa plants differed significantly between the species (Pillai's trace = 0.88, d.f. = 1.18, $P < 0.0001$). Significantly more *G. atropunctata* were found at the top of the plant than were *D. minerva* ($F_{1,18} = 177.80$, $P < 0.0001$), which were rarely found there (Fig. 1). Both vectors showed relatively low preference for the middle of the plant, although *D. minerva* was significantly more prevalent than *G. atropunctata* ($F_{1,18} = 10.55$, $P < 0.0045$). Also, significantly more *D. minerva* were found on the basal portion of the plant than were *G. atropunctata* ($F_{1,18} = 177.80$, $P < 0.0001$), which were rarely found there.

Patterns of *X. fastidiosa* infection at different plant locations were consistent among the four pathogen isolates in the aboveground portion of the plant, with no significant differences in infection rate at the top ($\chi^2_3 = 2.301$, $P = 0.5124$), base ($\chi^2_3 = 5.069$, $P = 0.1668$), adj.top ($\chi^2_3 = 4.704$, $P = 0.1948$), or adj.base ($\chi^2_3 = 3.613$, $P = 0.3064$) sampling sites. Only the roots showed differences in infection rates ($\chi^2_3 = 13.586$, $P = 0.0035$), with the 'Butte' isolate having lower prevalence than the two grape isolates ('Pavich' and 'Traver'; 0% vs. 60% and 67%, respectively). However, there were clear differences in infection among the plant sites. The overall proportion of samples collected from the base of the adjacent stem tested positive for infection at least twice as frequently as the other plant locations, with less than 8% positive for samples from the top of the adjacent stem (Table 1). The difference in infection rate relative to the base of the inoculated stem was significant for all of the other locations (Table 1). For those samples that tested positive, the highest infection levels were in samples collected at the base of inoculated or adjacent stems, with up to two orders of magnitude lower pathogen populations recovered at the other locations (Table 1). Differences in infection levels relative to the base of the inoculated stem were significant for the top of the inoculated stem and in the roots, only (Table 1).

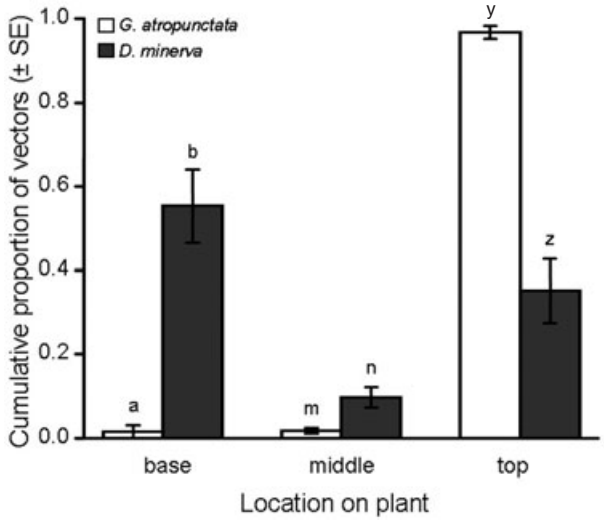

Fig. 1. *Graphocephala atropunctata* and *Draeculacephala minerva* mean prevalence (± standard error) on the basal, middle, or top third of alfalfa plants. Comparisons were made only between species for a given plant location. Bars with different consecutive letters denote significant differences between species in the cumulative proportion of vectors at that location over 72 h.

Across treatments *D. minerva* transmitted *X. fastidiosa* to 24% of grape test plants (13 of 55), whereas *G. atropunctata* transmitted to 10% (2 of 20). None of the control plants were infected. When vectors were confined at the base versus top of the inoculated stem, there was a significant difference between vector species ($\chi^2_1 = 6.71$, $P = 0.0096$) and feeding site ($\chi^2_1 = 11.55$, $P = 0.0007$), but the interaction was not significant ($\chi^2_1 = 0.24$, $P = 0.62$). Plant infection rates were higher when vectors were confined at the base, with *D. minerva* being more efficient than *G. atropunctata* (Fig. 2a). *Draeculacephala minerva* transmission efficiency varied significantly ($\chi^2_3 = 19.86$, $P = 0.0002$) among the four locations, with 6–7-fold higher infection rates occurring when confined at the base of the inoculated stem compared with the other three locations, which were similarly low (Fig. 2b).

Discussion

The transmission process is a fundamental determinant of disease dynamics (Jeger *et al.*, 1998). An understanding of the numerous biological factors involved with transmission is critical for mitigating the effects of disease in natural and managed ecosystems (Almeida *et al.*, 2005). In this study we have shown that vector behaviour, specifically fine-scale feeding preference, can play an important role in the transmission of a widespread plant pathogen.

Phytophagous insects use a variety of chemical and physical cues during the stages of host selection and acceptance (Schoonhoven *et al.*, 2005). For vectors, differential response to these cues may cause innate differences in competence among vector species. Although we found differences in transmission efficiency between *D. minerva* and *G. atropunctata* that may reflect innate differences in host preference or acceptance (i.e. a significant 'species' effect on transmission rate), feeding site had at least as strong an effect on transmission efficiency. Confinement at the base of infected alfalfa plants increased acquisition rates by more than 20% and 50% relative to confinement at the top for *G. atropunctata* and *D. minerva*, respectively, corresponding with an average of 100-fold higher infection levels at the base compared with the top of the plant. *Graphocephala atropunctata* failed to acquire in all cases when confined at its preferred feeding site, the top of

Table 1. Summary statistics for alfalfa infection in different locations and test results for the difference in infection of locations relative to the base of the inoculated stem. Test significance evaluated at $\alpha = 0.0125$.

			Relative infection rate				Relative infection level			
Location	Infection rate*	Infection level†‡	Difference§	*t*	d.f.	*P*	Difference§	*t*	d.f.	*P*
Base	0.864 ± 0.141	8.156 ± 0.969	–	–	–	–	–	–	–	–
Top	0.321 ± 0.131	6.035 ± 1.208	0.543 ± 0.127	8.349	3	0.0036	2.347 ± 0.569	8.180	11	<0.0001
Adj.base	0.319 ± 0.153	8.381 ± 0.822	0.544 ± 0.094	11.392	3	0.0015	0.329 ± 0.590	1.074	10	0.3082
Adj.top	0.078 ± 0.097	7.115 ± 0.317	0.786 ± 0.147	10.482	3	0.0019	1.476 ± 0.686	4.219	2	0.0519
Roots	0.400 ± 0.303	6.557 ± 1.329	0.464 ± 0.173	5.257	3	0.0134	1.822 ± 0.803	4.448	14	0.0006

*Proportion of samples testing positive via plate culturing.
†Pathogen population in sample; log(no. colony forming units g^{-1} plant).
‡Positive samples only; mean ± SD.
§Mean ± 95% CI.

the plant. Conversely, *D. minerva* acquired at least 66% of the time when confined at its naturally preferred feeding site near the plant base. These results are important because they explain the outcomes of previous transmission experiments that showed *D. minerva* to be a more efficient vector in alfalfa fields (Frazier & Freitag, 1946; Hewitt *et al*., 1946). Specifically, *D. minerva* feeds preferentially in regions on alfalfa that maximise its exposure to *X. fastidiosa.*

Alfalfa is unique compared to other *X. fastidiosa* host plants because it is repeatedly harvested throughout the growing season. Given the higher infection levels at the base of infected plants, regular harvesting can be expected to reinforce vector acquisition by maintaining proportionately more plant biomass at high infectivity. Such harvesting may also limit variability among vector species by constraining the availability of different preferred feeding sites. These predictions have not been tested and may be an idiosyncrasy of alfalfa disease epidemiology. Regardless, such a scenario is interesting given the documentation of similar context-specific effects of alfalfa harvest stage on predator–prey dynamics (Snyder & Ives, 2001).

Patterns of pathogen distribution are usually considered at the population level, for which clustering of infected hosts can affect rates of disease spread (McElhany *et al*., 1995). Based on our results, the distribution of infection within the individual host scale is also important. There were differences of 80% in *X. fastidiosa* infection rate and up to 100-fold differences in infection level in different parts of host plants – infection declined dramatically away from the base of the plant. The uneven distribution of infection within hosts was associated directly with sharpshooter efficiency, with the highest acquisition rates occurring where vector feeding site overlapped with areas of high infection level. This phenomenon is likely to occur for other vector-borne pathogens, as long as the pathogen is distributed heterogeneously within a host. Conversely, homogeneously distributed infections should promote homogeneous exposure of vectors to the pathogen, and therefore transmission rates,

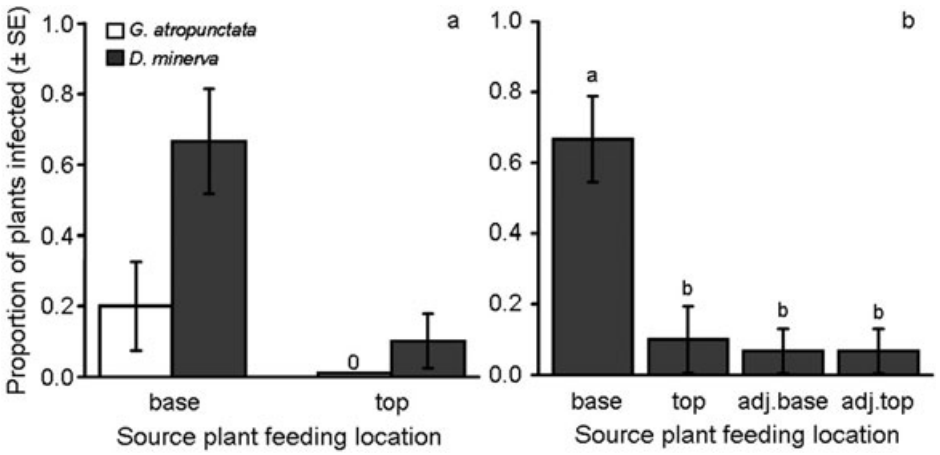

Fig. 2. Transmission rate of *Xylella fastidiosa* by (a) *Graphocephala atropunctata* and *Draeculacephala minerva* when confined on the basal or apical portion of inoculated alfalfa stems, or (b) *D. minerva* when confined at one of four locations on source plants: the basal or apical portion of the inoculated stem ('base' vs. 'top'), or the basal or apical portions of the adjacent stem ('adj.base' vs. 'adj.top'). Different consecutive letters denote significant differences in the proportion of grape test plants infected following a confined 2 days acquisition access period at the different source plant locations. Standard errors of proportions were calculated as: $\sqrt{\{[p^*(1-p)]/n\}}$, where p is the overall proportion of plants infected, and n is the number of replicates.

regardless of feeding site preference. Similar levels of within-host infection heterogeneity have been described for other plant pathogens (Saracco *et al*., 2006; Tatineni *et al*., 2008), although explicit measures are lacking for feeding site preference as it relates to transmission efficiency.

Xylella fastidiosa is notable for its high degree of genetic variation, which stems apparently from host-plant specific adaptations (Schuenzel *et al*., 2005). Given uncertainty regarding the strain or host-plant origin of alfalfa dwarf in the field, we used in the current study four isolates that represent both of the main *X. fastidiosa* strains in western U.S. agriculture (*X. fastidiosa* subsp. *fastidiosa* and subsp. *multiple*x). Strain differences may be important epidemiologically because of differences in multiplication rate (Almeida & Purcell, 2003), which determines transmissibility (Lopes *et al*., 2009). We conducted the transmission tests with the grape strain only. Thus, inferences regarding quantitative estimates of transmission rate at different host-plant sites should be limited to this strain. Nonetheless, patterns of infection were consistent among the four isolates in the different aboveground sampling locations of the plant – only the roots showed strain specific infection. Thus, although transmission rates may differ quantitatively among pathogen strains, it is plausible that patterns of vector acquisition at different alfalfa locations will be qualitatively consistent among isolates. Additional studies are needed that document within-host heterogeneity in infection and vector efficiency among strains for both this pathosystem and other vector-borne diseases.

Behaviourally mediated differences in vector efficiency is not well described for animal pathogens, but there is some evidence that it is important. For example, tick feeding on an individual host may be highly aggregated. This is noteworthy because highly aggregated co-feeding groups can result in efficient tick to tick transmission of the virus (Perkins *et al*., 2003). Thus, close proximity of non-infectious vectors to infectious vectors increases their pathogen exposure, even in the absence of systemic host infection. An additional mechanism by which vector behaviour may be important for transmission has been described for mosquito vectors associated with temporal variability in dynamics of the pathogenic nematode *Wuchereria bancrofti* in humans (Shriram *et al*., 2005). Peaks in the periodic production of the transmissible parasite stage coincide with peaks in mosquito vector biting activity (Vanamail & Ramaiah, 1991). Thus, temporal synchrony of pathogen and vector is considered important for transmission of the pathogen, in a manner that is equivalent to the requirement for spatial overlap that we observed for *X. fastidiosa* and sharpshooter feeding site.

Effects of vector behaviour on disease dynamics can manifest at the community, population, or individual host scale. The first two of these scales have received much attention with respect to the potential for pathogen spillover (Kilpatrick *et al*., 2006) and disease spread (McElhany *et al*., 1995). Here we show that fine-scale vector feeding site preference, within individual hosts, has important consequences for pathogen transmission. These results help to explain observed differences in efficiency among vector species in the *Xylella*–sharpshooter disease system. More generally, the results indicate that an overlap in both pathogen distribution and vector position on hosts is required for efficient transmission – issues deserving of more attention in other disease systems.

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