Invasive Potential of *Xylella fastidiosa*

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ABSTRACT

Evaluating the risks of invasion by the bacterium *Xylella fastidiosa* to geographic regions where this plant pathogen currently does not occur is an important challenge. Various strains of *X. fastidiosa*, differentiated by their plant host range, comprise a formidable variety of serious plant diseases throughout the tropical through subtropical Americas. These diseases do not seem present as significant threats outside the Western Hemisphere, except for Taiwan, which has recorded diseases in pear and grape caused by *X. fastidiosa*. Identifying the factors limiting or even prohibiting the spread of *X. fastidiosa* and their modes of action would be useful in attempts to estimate risks of new invasions by this bacterium and-more importantly-to identify the most effective phytosanitary strategies to prevent the bacterium from establishing in new regions. Although it is clear that cold severity of sub-freezing winter climates limit the geographic spread of *X. fastidiosa*, we lack an understanding of the underlying mechanisms of how freezing eliminates it from plants. Other aspects of climatic temperature regimes, such as limiting high temperatures or sustained cool but above freezing temperatures need to be addressed. For some regions, the lack of suitable insect vectors or suitable alternative hosts of *X. fastidiosa* may prevent introductions of *X. fastidiosa* in infected plant hosts from establishing a permanent presence. It is likely the permanent establishment of *X. fastidiosa* requires a suitable combination of vectors' distribution, abundance, plant preferences, phenology, transmission efficiency, and dispersal behavior in conjunction with the abundance and distribution of plant hosts of *X. fastidiosa* and the characteristics of the plant communities in which they are embedded. The intriguing possibilities of interactions with other bacteria and viruses have only begun to be explored as limiting factors.

Keywords: *Xylella*, Pierce's disease, citrus variegated chlorosis, sharpshooter, quarantine, phytosanitary

INTRODUCTION

Why be concerned about the invasiveness of *Xylella fastidiosa*?

Our practical concerns with the bacterium *Xylella fastidiosa* emphasize the prevention and control of the numerous plant diseases that this plant pathogen causes. Countries without these diseases want to prevent their invasion and establishment. The large diversity of serious diseases in numerous crop and forest species that are caused by *X. fastidiosa* have been reviewed recently [9, 27, 45]. These range from diseases affecting grape, almond, oleander and alfalfa in California and other southwestern parts of North America, to diseases of grape, peach, plum, pecan, blueberry and numerous forest tree species in southeastern North America, to diseased orange, coffee and plum crops in South America. Outside of the Americas, the only confirmed occurrences of diseases caused by *X. fastidiosa* are diseases of pear and grape in Taiwan [9, 30, 52]. .*X. fastidiosa* has also been reported in grape in Serbia (now Bosnia) [4] and a brief report in almond in Turkey [21], but it unclear if the diseases concerned are spreading in Europe.

The theoretically huge list of plant species that support the multiplication of *X. fastidiosa* (considerably more than 50% of those species tested so far) [16, 25, 45, 47] should facilitate the spread of the bacterium through the commercial movements of live plants. Yet there is no convincing evidence that this has contributed to transoceanic of *X. fastidiosa*. The introduction of grapevines unknowingly infected with *X. fastidiosa* may have introduced Pierce's disease (PD) into commercial vineyards in France, where new plantings with PD were removed and insecticides applied to prevent the establishment of PD [7]. Without untreated controls, the subsequent disappearance of PD could not prove the effectiveness of removing suspect plants in conjunction with insecticide applications. Classically, most introductions of exotic organisms fail to establish a permanent presence, but eventually many exotic invaders establish permanently [31]. Plant quarantines by practical necessity are based on logic instead of scientific proof.

Why hasn't *X. fastidiosa* invaded more regions outside of the Americas? Numerous fungal and viral pathogens of grape that are native to North America have become widespread throughout much of the world, beginning in the late 1700s with of the importation of grape species to European botanical collections. Yet PD, another disease of grape indigenous in southern North America, never became established. This was despite the massive importation from the southern United States to Europe of wild grapevines for use as rootstocks against the grape phylloxera[18]. It is inconceivable that *X. fastidiosa* was not present in some of these vines. Species of wild grape native to the southern United States are tolerant of *X. fastidiosa* [22]. We can only speculate about possible explanations to answer the question of why any invasive organism has not established where it is continually introduced.

For *X. fastidiosa*, we have evidence for some limiting factors such as winter climate. For regions where freezing temperatures are rare, we must search for explanations, realizing that key limitations may be completely different from one location to another. Finding explanations of factors that limit invasions of *X. fastidiosa* into new locations may not only provide new ideas or improved quarantine measures or other phytosanitary strategies, but may also provide new ideas for control of *Xylella*-caused diseases in areas where this pathogen is native.

POSSIBLE LIMITING FACTORS

Climate

Winter climate is an important feature of the epidemiology of PD in northern California [27, 40] and probably elsewhere [27]. Subfreezing winter temperatures are important for recovery of grapevines with PD [29, 36, 40]. Almond leaf scorch disease has similar results in California [8]. Vector-borne new infections of *X. fastidiosa* in grapevines after the first two months of the growing season in northern California had recovered and were free of *X. fastidiosa* after the next winter [13, 41]. Northern California vines that did not recover overwinter had populations of *X. fastidiosa* that were sufficient for vector acquisition only after June [51]. The overwinter recovery phenomenon, in conjunction with the seasonal changes in *X. fastidiosa* populations, explains why the early growing season is critical for establishing chronic infections (no recovery) of *X. fastidiosa* [27, 43, 45]. They also offer a hypothesis to explain the failures of *X. fastidiosa* to permanently establish in Europe. Europe lacks known or potential vectors of *X. fastidiosa* that overwinter as adults, thus avoiding having flying vectors during the critical early growing season that is so important to establishing chronic infections [42]. Chronically infected plants eventually die of disease, age or other factors. For *X. fastidiosa* to persist in a location indefinitely, the rate of spread of *X. fastidiosa* to new host plants must exceed the rate at which the bacterium disappears from colonized hosts (either diseased or symptomless).

Overwinter recovery has been modeled with regression-based mathematical models based on experimental data [33]. Despite some promising clues [36], an understanding of how freezing temperatures induce recovery is still a mystery. Understanding the mechanism of cold therapy might provide insights in how to develop climate-based models to predict the geographic range of *X. fastidiosa* or provide new ideas for disease control or therapies.

Another way that climatic temperature patterns can influence the potential for the spread of diseases caused by *X. fastidiosa* is the pattern of growing season temperatures. Some temperate regions may lack the subfreezing temperatures needed for environmental therapy of diseased vines, but not have sufficient degree-days to support population growth of *X. fastidiosa* to sustain the development of severe symptoms or to promote rapid plant-to-plant spread. Temperature also may affect vector transmission [11]. It is surprising that a pathogen that is most virulent in tropical climates has a maximum temperature for sustained growth under 34^{o}C [14] and is susceptible to temperatures below 15^{o}C (Fig. 1). Is it possible some climates are too hot to sustain PD? Both of thee possibilities are unexplored.

Diseased Plant Hosts

Hybrids of grapevines that are tolerant or resistant to *X. fastidiosa* nonetheless can harbor populations of *X. fastidiosa* [17] that are adequate for vector acquisition of the bacterium [24]. Illegal importations of new PD-resistant grape varieties could thus introduce plants with persistent populations of *X. fastidiosa* if the winter climate is suitable for survival of the bacterium. This is also true of resistant cultivars of other perennial plants that may harbor populations of *X. fastidiosa* but with mild or no symptoms. Nursery plants of citrus with CVC represent a proven threat for the movement of CVC to new locations, as occurred in Brazil [19]. The use of nursery plants free of *X. fastidiosa* is a fundamental part of the current control methods for CVC in Brazil [19].

The importance of having diseased crop plants as inoculum is quite clear for CVC in Brazil [19, 20, 29, 49] (reviewed in [43]), despite the CVC strains being able to infect many weed species [35]. This is not so apparent for PD in California or Florida, where it has been most extensively studied. The genetic regulation of growth and movement of *X. fastidiosa* in European grape (*Vitis vinifera*) apparently is not adequate to prevent severe symptoms in grape. This may make commercial vineyards with PD especially important as acquisition sources in late summer for adult vectors that inoculate the bacterium into grapevines the following spring.

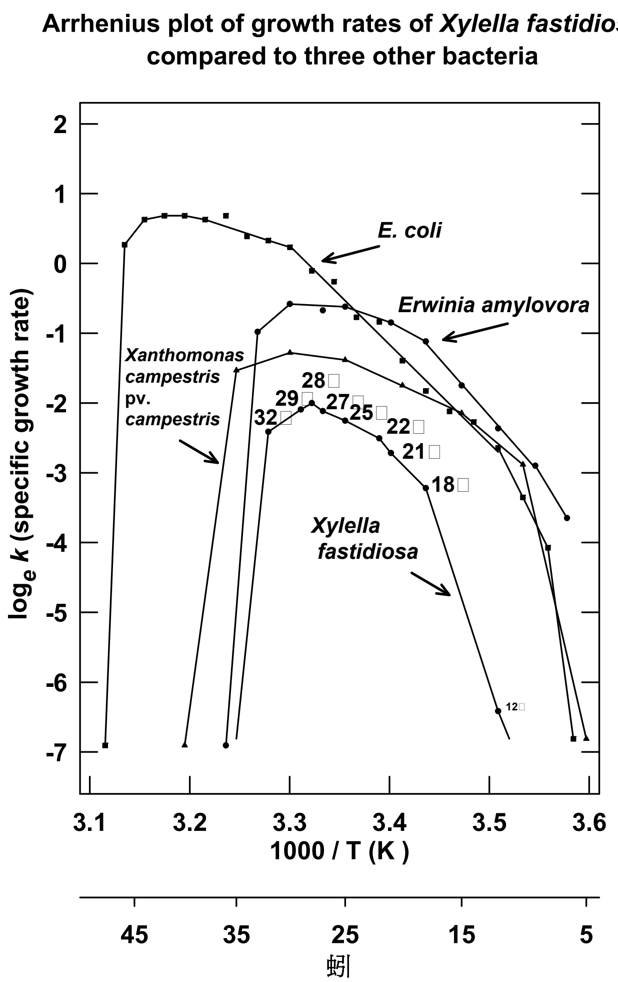

Fig. 1. The response of growth rates of *Xylella fastidiosa* and 3 other bacteria to temperature (Arrhenius plot). Note the narrower range of temperatures suitable for *X. fastidiosa* compared to two other plant pathogenic bacteria (*Erwinia* and *Xanthamonas*). Adapted from [14].

Symptomless Plant Hosts

Current evidence suggests that the cell signaling system of *X. fastidiosa* directs gene expression in ways that minimize host injury by slowing its population growth and increasing adhesion (immobility) to retard systemic movements and spread within the host plant [10, 38]. In the experiments [46] to identify the host status of plants that were favorable for an important vector for PD, recoveries of *X. fastidiosa* were attempted only after an incubation period of about 2 to 3 months. In later repetitions of these experiments for plants in which no growth of *X. fastidiosa* had been detected, populations of inoculated *X. fastidiosa* increased for several weeks, then rapidly decreased to undetectable levels [46]. It appears that xylem elements in which *X. fastidiosa* completely fills the vessel, most of the bacterial cells are dead [10]. This emphasizes the importance to *X. fastidiosa* of systemic movement within a host plant. The bacterium dies out in the plant if it completely packs the host cell and cannot move to new xylem cells [46].

The most common disease syndrome caused by infections of *X. fastidiosa* begins with the progressive decline and eventual death of foliar tissue, usually beginning at the leaf margins and progressing toward the leaf base before spreading further to woody tissues and fruit. PD of grapevine, which is the first described disease now attributed to *X. fastidiosa*, exemplifies this "leaf scorch" syndrome (Fig. 2). However, we can describe two other categories of syndromes. A second symptom type includes the dwarfing or stunting diseases such as alfalfa dwarf [54], phony peach [55], and citrus variegated chlorosis (CVC) [32]. These three diseases have a slower decline than the leaf scorch diseases and without leaf "burn" symptoms (Figs. 3-4). For example, the distinctive foliar lesions (Fig. 4) on citrus with CVC do not resemble the marginal decline and death of leaf tissues characteristic of PD. Like phony peach disease, the most damaging aspect of CVC is the dwarfing of fruits and new stem growth (Fig. 4). These diseases typically take longer to appear following inoculation via insect vector transmission. A third symptom group includes the "symptomless infections", where *X. fastidiosa* multiplies within the host plant and may or not may not move systemically [16, 25, 46]. This third group may differ from the dwarfing syndrome group only in the rapidity and degree to which stunted growth results from colonization of the plant by *X. fastidiosa*. Most experimental evaluations of symptoms are made within a year of inoculation or even shorter, so chronic stunting that causes substantial reductions in growth may not be seen for many months or years. The most difficult potential sources of *X. fastidiosa* to detect for plant quarantines are plants that have small and scattered populations of the bacterium and have a long incubation period before they develop symptoms, although these may be the least important for introducing *X. fastidiosa* because the bacterium is most likely to die out in such plants and they are poor sources for vector acquisition. The persistence of *X. fastidiosa* in and symptomless hosts varies with plant species [3] and probably with winter climate.

Fig. 2. Leaf scorch symptoms of Pierce's disease (PD) in grape in a Florida experimental vineyard. Note the young and missing vines in the background in this resistance screening planting – the result of high rates of infections with *X. fastidiosa* and favorable conditions for severe symptom development. Photo by A. H. Purcell.

Fig. 3. Citrus variegated chlorosis disease (CVC) symptoms in orange fruit (dwarfing) and leaves (stunting, chlorosis). Photo by A. H. Purcell.

Fig. 4. Symptoms of alfalfa dwarf (left)-stunting of leaves and stems, darker leaf color-after 9 months in greenhouse conditions. Photo by A. H. Purcell.

Vector abundance and distribution

Vector transmission is an essential part of the disease cycle for *X. fastidiosa*. It is clear that the types and numbers of vectors are important requirements to sustain the presence of PD. For example, the invasion of a new vector species can cause major changes in the incidence of PD. The successful invasion of southern California in the 1990s by the sharpshooter leafhopper *Homalodisca vitripennis* (formerly *coagulata*) caused major outbreaks of PD where PD previously had not been a major problem [(6)]. In California, PD occurs primarily near vector breeding habitats [(23)]. In Napa Valley, California, the sharpshooter *Graphocephala atropunctata* is the major vector [(23, 39)]. The spatial pattern of populations of *G. atropunctata* during the early growing season is very similar to spatial gradients of the incidence of PD in vineyards, with the proportion of vines with PD decreasing with distance from the sharpshooter's overwintering habitat.

Other vector characteristics are also influential. The following comments address characteristics of vectors that are known to be important for the spread of *Xylella* diseases.

Transmission efficiency

Not every individual vector that has acquired *X. fastidiosa* transmits it to all plants on which the insect feeds. Vector transmission efficiency is the proportion of plants infected per insect access period. Vector species vary greatly in transmission efficiency, depending on the combination of vector species and plant species (reviewed in [48]). For example, the grass-feeding sharpshooter *Draeculacephala minerva* is more efficient in transmitting *X. fastidiosa* to alfalfa than *G. atropunctata*, which prefers woody plants, whereas the reverse is true for transmission to grape [50]. The differences in distribution and anatomy between grasses and dicotyledonous plants may require differences in feeding behavior to respond to the different cues found among various plant species.

Although it has been long hypothesized that all xylem sap-feeding, sucking insects are potentially vectors of *X. fastidiosa* [15], there are strains of this bacterium that differ in transmission efficiency depending on the vector and plant species [34]. This makes it difficult to predict how a certain strain of *X. fastidiosa* will be transmitted in a new location with different vectors and plant communities.

Plant and habitat preferences

Xylem feeders often have wide plant host ranges (reviewed in [48]), but all species demonstrate strong preferences when they have a choice of hosts. The condition of the plant can also be as important as the species in feeding preferences. Xylem feeders generally prefer more succulent, fast-growing plant tissues [37]. The most important native vectors (*Draeculacephala minerva* and *Xyphon fulgida*) in central California are two grass-feeding sharpshooters [23, 44]. Because they prefer succulent plants, they reach their highest populations during California's dry summers where grasses are irrigated [23, 44] Both of these two species are rarely found feeding on grape; their importance as vectors is deduced from their consistent association with PD outbreaks in vineyards next to habitats harboring these sharpshooters [23, 44].

In contrast, grape is a highly preferred host of the major vector (*G. atropunctata*) in coastal California vineyards [23, 44]. Surprisingly the incidence of PD in central California vineyards compared to Napa Valley vineyards can be very similar, despite only rarely observing vectors on grape in central California vineyards [45]. In addition, the central California vectors are much less efficient transmitters of *X. fastidiosa* to grape. The feeding of *D. minerva* and *X. fulgida* on grape is hypothesized to occur in the evenings, as these two species fly mostly in early evening, when they may drift or wander into nearby vineyards from their normal habitats [44].

Vector dispersal

Vector mobility can compensate for inefficient transmission, as exemplified by the sharpshooter *H. vitripennis*. The transmission efficiency of *X. fastidiosa* to grape by *H. vitripennis* is relatively low, about 5% to 15% per day per insect, [1], but the longer range dispersal and frequent daily movements or over longer time periods by *H. vitripennis* compared to more traditional vectors created epidemic spread of PD [5, 6].

It is the combination of vector traits that determines its overall effectiveness and importance as a vector, not just a single trait. This can be illustrated with a simple mathematical model. The probability of transmission by *n* vectors per plant per time interval (P_{nt}) depends on how many vectors (*n*) and the number of time intervals (*t*) they are present on a plant, as well as the fraction of vectors that are infective with the pathogen (*i*) and that transmit per time interval (transmission efficiency *E*). The relationship is

$$P_{nt} = 1\text{-}P^{-niEt}$$ [41]

In this equation, all four determinants (*n, i, E, t*) are mathematically equivalent. Thus an abundant (high *n*) but inefficient (low *E*) vector can be very damaging as a vector if it has frequent plant to plant movements (high *t*) or a high rate of infectivity (high *i*). Host preferences can affect the frequency of vector movements. As already discussed, transmission efficiency (*E*) by a single vector species can vary with host plant. Thus the mix of plant host species can affect how important any vector species will be.

Phenology

Recall that in temperate climates with almost all grapevines inoculated with *X. fastidiosa* after the early growing season recover completely. Thus overwintering adult vectors that are infective with *X. fastidiosa* establish most of the infections destined to be chronically diseased. This is one possible explanation as to why PD never established in Europe, where most xylem sap-feeders found in vineyards overwinter in the egg stage[42]. Another explanation for the increase in PD accompanying the establishment of *H. vitripennis* in southern California is that this sharpshooter is able to transmit *X. fastidiosa* to dormant vines during winter [2]. *H. vitripennis* overwinters in California as an adult, so this characteristic could be important.

Antagonists of *Xylella fastidiosa*?

There is not yet much to be said about microbial antagonists of *X. fastidiosa* because of a lack of research in this area. Bacteriophages that attack *X. fastidiosa* have been identified [(53)], as well as a number of prophages in the genome of *X. fastidiosa* identified from genome sequencing [(12)] (reviewed in [(43)]).

Strains of *X. fastidiosa* that do not cause disease in grape but protect against PD strains of *X. fastidiosa* have been reported in Florida [(26)]. Other xylem inhabiting bacteria have shown some antagonism but are not yet been proven to be effective as protective agents against *X. fastidiosa* [(28)].

It would be unexpected to find that antagonistic interactions with other microbes would completely inhibit the invasion of *X. fastidiosa* into a new geographic region, but relatively few studies of microbial antagonism to *X. fastidiosa* have been made. This is an area that may have potential for control.

CONCLUSION

The persistence of *X. fastidiosa* in a given environment depends on a combination of suitable conditions at the proper times, not just the introduction of the bacterium in a plant or insect. Climate, host plants, suitable vectors and the vegetation and habitats needed to support them are all essential requirements to sustain the spread *X. fastidiosa* from plant to plant.

Xylella fastidiosa may be present in some geographic regions but unrecognized because it is causes no or very subtle symptoms or if any severely affected plants are not common. PD was not recognized in the southeastern USA until the 1950s, yet is one of the limiting factors for growing grapes there [(22)].

Taiwan is unique in being the only location outside the western hemisphere with documented established diseases caused by *X. fastidiosa*. If we can discover the explanation for the success of *X. fastidiosa* in Taiwan, it might provide new ideas on how to prevent invasions by *X. fastidiosa* from occurring in other countries.

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