

Xylella fastidiosa; a summary of the threat to the U.K. and the current preparations

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Summary

- *Xylella fastidiosa* has been described by the European Commission as “one of the most dangerous plant bacteria worldwide, causing a variety of diseases, with huge economic impact for agriculture, public gardens and the environment” (1, CR High¹).
- The bacterium *X. fastidiosa* only affects plant health but can be carried by insects who spread the disease (3, CR High).
- Insect-plant-pathogen-environment interactions can be complex. Symptoms of the disease can be extremely varied and are often similar to those of water stress including scorched and wilted leaves (2, CR High). The infection can be difficult to diagnose by eye (3, CR High).
- Trade of plants for planting is considered to be the greatest risk of *X. fastidiosa* entering the UK (CR Medium, 4).
- Multiple strains of the bacterium, originating from different locations, have been introduced into Europe and have caused infections in a variety of plant species (CR High, 5).
- If an outbreak occurs in the UK it could become established due to several native insects that are known to carry the disease and a large range of potential hosts (CR Medium).
- *Xylella fastidiosa*, and the measures that would be taken to eradicate it, are highly likely to have significant impact on agriculture, nurseries and urban trees (CR High, 6).

Context

Xylella fastidiosa is a plant associated bacterium that is pathogenic, and so causes disease, in over 100 plant species (7). It is not known to occur in the UK (5) and there is currently no cure for the infection (6). The pathogen is spread by insects who feed on the water transporting xylem vessels of the plant.

Xylella fastidiosa is native to the Americas (8) where it is known to cause serious disease outbreaks in economically important crops such as coffee and grapevine. Pierce’s disease of grapevine, caused by one subspecies of the pathogen, costs Californian producers over \$100 million per annum in crop loss and replanting expenses (7). An additional \$50 million is spent on preventative measures. Research into controlling the infection has been estimated to save an additional \$189 million per year (7). This has included identifying the late spring as the most effective point in the growing season to apply insecticides (9).

In 2013, the first European recording of the pathogen was made in southern Italian olive trees (10). Since then there have been several separate outbreaks of different subspecies including: multiple

¹ CR = confidence rating. Confidence ratings have been applied to statements in the summary as an indication of the level of evidence that supports the statements.

occasions in France and Spain; further occurrences in Italy; and a confirmed case in Portugal in 2019 (5).

Xylella fastidiosa – the bacterium

The bacterium is unable to survive outside its plant or insect hosts, so spread is dependent on the presence of insect vectors (2) (4). The insect foregut and the plant xylem tissue where it resides are mostly made up of non-living tissue. The xylem vessels are also nutrient poor (11). *Xylella fastidiosa* lacks a Type III secretion system; a classic indicator of pathogenicity which suppresses host plant defence responses and can limit host range (2) (12) (13). This trait is likely unnecessary in *X. fastidiosa* because the bacteria interacts mainly with dead host cells (13).

Biofilms are accumulations of bacteria held together by a mucus like matrix of carbohydrate. *Xylella fastidiosa* is more adhesive (i.e. sticky) than other bacteria, which means it can form biofilms with intricate 3D architecture and withstand the constant high-pressure liquid flow of the xylem vessels (7) (11) .

In plant hosts *X. fastidiosa* uses twitching motility (movement against the flow) to spread around the xylem system while releasing enzymes which damage sections of the xylem walls and allow the bacteria to colonise new vessels (11). The bacterium must change into an adhesive state to be acquired by insects (7).

Too many *X. fastidiosa* cells in one xylem vessel will limit flow and presumably the nutrients the bacterium (and plant) needs to survive (7). In cases where plants are heavily infected biofilms are abundant (7) (11). It is theorised that to control its own virulence the bacterium boosts production of biofilms; controlling its own spread so that parts of the plant are less infected and increasing the number of cells that can be acquired by insects. This benefits the bacterium as its host survives longer and explains how *X. fastidiosa* can exist in some plant species without becoming pathogenic (7).

Taxonomy

A genome is the complete set of genetic material present in a cell. Every cell in an organism contains the same sequence of DNA or genetic ‘directions’. Genotyping involves examining an individual’s DNA sequence to identify small genetic variations compared to other individuals. These small genetic differences can result in major observable characteristic differences.

A sub-species is a group within a species known for its distinct traits. Six sub-species of *X. fastidiosa* are named in the literature. The subspecies *fastidiosa*, *multiplex* and *pauca* are well documented (6) (7) (5) (8) (14) (15). They are genetically distinct and appear to have developed in geographical isolation. Their differences reflect the estimated divergence date of at least 15,000 years ago (14). They are recorded as having a distinct and largely non-overlapping set of plant hosts (14).

The remaining three sub-species; *morus*, *sandyi* and *tashke* appear less in the literature and their status as sub-species are disputed (8) (16).

Sub-species (Well known disease)	Status	Origin	Geographical Distribution	Hosts

<i>fastidiosa</i> Pierce's disease of grapevine	Validly accepted (15)	Central America (14)	USA, Mexico, Costa Rica (15), Spain (6), Israel (17), Taiwan (17)	33 host species (15) including grapevines and almonds (7)
<i>multiplex</i> Leaf scorching diseases (various)	Validly accepted (15)	North America (14)	USA – including northern states. (8) Brazil (15) France, Spain Portugal, Italy (5)	117 host species (15) including almond, peach, plum and oak trees (7)
<i>pauca</i> Citrus variegated chlorosis	Well-described subspecies (15)	South America (14)	Brazil, Argentina Costa Rica, Ecuador. (15) France, Italy, Spain (6)	43 host species (15) including citrus, coffee and olive. (8)
<i>morus</i> Mulberry leaf scorch	Not formally accepted. (15) Possible strain of <i>fastidiosa</i> .	South USA – recombination of <i>multiplex</i> and <i>fastidiosa</i> (14)	USA (15)	4 host species (15) including Mulberry (8)
<i>Sandyi</i> Leaf scorch of Oleander	Not formally accepted. (15) Possible strain of <i>fastidiosa</i> .	USA (15)	California and Eastern USA, France, Brazil (15)	7 host species (15) including coffee, oleander (8)
<i>Tashke</i> Leaf scorch of chitalpa	Not formally accepted. No reference strains (15).	USA (15)	New Mexico, Arizona (14)	1 host species, chitalpa (15)

Introductions of *X. fastidiosa*

Different strains of the sub-species *pauca*, *multiplex* and *fastidiosa* have all been identified in Europe; indicating multiple routes onto the continent from varied sources including California, Costa Rica and Brazil (6). It is unclear how long *X. fastidiosa* may have been present, undetected, in Europe. Epidemiological models, based on surveillance from after the Corsica outbreak, suggest the disease may have been present since 2001, 1985 or earlier (3).

Xylella fastidiosa was identified a 2017-2018 survey of Israel in symptomatic almond trees and subsequently eradicated. More recently the bacterium was identified in three adjacent commercial orchards in north-eastern Israel. The origin of the disease in the country is unknown and despite collections in the infected orchards no insects have been found to be infected (18).



FOLLOWING THE DETECTION OF OUTBREAKS OF

Biased Dataset

The current taxonomy of *X. fastidiosa* is based on a limited and biased data set resulting from:

- The strain or sub-species not being recorded when the infection is identified (19). This was particularly true in the past when molecular techniques were less developed, and for native ranges where diagnosis is often based on visual symptoms as a lack of cure makes exact identification pointless.
- Important crop plants being genotyped/diagnosed more often than other plants (19).
- An incomplete sampling of affected plants due to the bacterium presence being difficult to identify (2).

An Evolving Pathogen

Xylella fastidiosa can evolve through genetic material being 'donated' from one strain of the bacterium to another allowing for a novel genetic recombination to form (11). This transfer of genes is recognised to be the major driver behind the development of new diverse strains of *X. fastidiosa*: potentially allowing the bacterium to infect new plant hosts (8) (19). This key ability of the pathogen to evolve and adapt to new environments is helped by its restriction to xylem vessels and the foregut of insects where it can easily encounter other bacteria in very confined spaces (11).

Xylella fastidiosa subsp. *multiplex* appears to be the subspecies most prone to this process and has a large collection of genes which are not present in the other sub-species (19). The more extensive genetic material of *multiplex* is likely a reason for and a product of its wide host range (19).

One study considered the genetic make-up of wild strains of the bacterium and found that the more recently acquired parts included genes involving regulation and signalling, host colonization, nutrient acquisition, and host evasion. These are all fundamental traits of how *X. fastidiosa* bacteria deal with one-another as well as their surroundings. As global trade brings formerly geographically isolated sub-species into proximity, there is a serious risk of genetic advances producing strains with different host ranges (11).

A study of the genomes of 72 strains of *X. fastidiosa*, the largest assembled data set so far, showed the frequency of recombination between subspecies differs among strains, even within subspecies. This could reflect geographic isolation, where recombination between subspecies has occurred only as strains have been introduced to new regions where other subspecies have already established (19).

Subspecies *morus*, found in mulberry in the USA, developed from a recombination of subspecies *multiplex* with a strain of *fastidiosa* from Central America rather than with one from North America (14) (which had been in proximity for far longer). Very little genetic variability was observed within the *morus* strains despite its wide geographical range and evidence of large-scale recombination in its DNA. This suggests plant host specialisation can be a severe constraint and that all but a narrowly defined set of genes, which allowed for mulberry to be colonised, were eliminated (14).

This was disputed in a different study which found a link between the genetic similarity of different strains and the extent to which they infected and damaged the same plant host. If some subspecies exist in a wider selection of hosts but are weakly pathogenic they may remain undiagnosed, creating a false impression of host specificity for the different sub-species (2).

Potential Geographical Distribution

Xylella fastidiosa is known to occur over a wide range of climatic zones. Two studies examined the potential distribution of sub-species *fastidiosa*, *pauca* and *multiplex* in Europe. Minimum winter temperatures were theorised to be the main limitation of potential spread. Since *multiplex* has been identified much further north in the USA it was found to pose the greatest threat to the UK, predominantly in the south-east (6) (8). Sub-species *fastidiosa* had a small risk of establishment in the UK and the threat of *pauca* was not significant (8).

Air temperatures below -5°C were found to be associated with reduced bacterial viability in sycamore shoots but not the plant's roots (20). It has been suggested that in regions with particularly cold winters, *X. fastidiosa* may lie dormant in woody tissue including roots (20). Infection occurrence could be underreported in colder climes due to the bacterium only affecting non-economically important hosts or having a limited impact (6).

The UK has much milder winters and cooler summers than those at the northernmost limits of its distribution in North America. Climate change will alter the distribution of suitable areas for *X. fastidiosa* in Europe as minimum winter temperatures might increase (6).

Hosts



FIGURE 2 DISEASED OLIVE TREE © APHA



FIGURE 3 DISEASED CHERRY TREES © EPPO

Xylella fastidiosa has been reported to infect a wide range of plant hosts including ornamentals (e.g. oleander, lavender), crop plants (e.g. grapevine, peach) and native flora (e.g. oak, elm, plane) (15).

A systematic review of the total number of plants reported to be infected by *X. fastidiosa* included over 500 species (7). This falls to 312 host plant species, from 61 botanical families, when only records with multiple or highly accurate detection methods are considered (7). This extensive host range means its establishment in the UK would have significant impact for horticulture, forestry, crop production and natural ecosystems.

French lavender, almond, myrtle-leaf milkwort, oleander, olive and rosemary have been highlighted as plants of concern by the UK government as *X. fastidiosa* has been found in traded plants of each within the EU (21). There is also a large trade of each species into the UK from the EU. They also appear to be particularly susceptible to infection as multiple sub-species of *X. fastidiosa* have been recorded as pathogenic for each at different locations within the EU trading block.

Asymptomatic Hosts

The asymptomatic period (when the host carries infection but experiences no symptoms) can vary significantly from 1 month in ornamental plants to potentially 3-4 years for *multiplex* in certain hosts (6). This variable and potentially long asymptomatic period can limit successful detection and control, particularly where surveillance is based upon visual inspection (6). Asymptomatic plants can still serve as a source of inoculum for insects (22).

Visually healthy leaves collected from *X. fastidiosa* infected trees tested positive for the bacterium. This suggests that pruning only visually infected branches will not always eliminate *X. fastidiosa* although it may reduce the amount of inoculum available to vectors (23).

Forest and Urban Trees

Introduction or spread of *X. fastidiosa* to forest areas within the UK could lead to impact on oaks, elms, maples and other tree species known to be affected in the USA. It is difficult to predict the susceptibility of tree species that are native to Europe but absent in the USA (15).

In *X. fastidiosa* related dieback and decline diseases of ornamental trees like oak, the bacterium has been reported to collect in the trunk and stems particularly in sections with typical symptoms (20).

The impact on urban trees is significant because of their aesthetic importance and the high cost of removing and replacing them (6). In several Maryland and New Jersey municipalities, the cost for maintaining and removing bacterial leaf scorch affected oak trees has been estimated to exceed \$1 million over a period of 5-10 years (23).

Open Questions

The BRIGIT project (24) is investigating the distribution and rate of colonisation of the pathogen in different plants. Six key hosts of concern, including lavender and rosemary, have been selected for controlled environmental studies in licenced containment facilities where they will be inoculated with the bacterium and the spread monitored in two environments; ambient (including seasonal changes) and 25°C.

The pressure level required for enough bacterium to pass from the feeding insect may differ between plants (23). If each tree species has a different pressure threshold required for infection, the amount of inoculum available to insect vectors within their habitat may control which trees become infected.

Vectors



FIGURE 4 - *PHILAEUNUS SPUMARIUS* SHOWING THE EXTENSIVE COLOUR VARIATION IN ADULTS PHOTO BY GERNOT KUNZ

X. fastidiosa is exclusively transmitted by xylem sap-feeding hemipteran insects in the suborder Auchenorrhyncha, which includes insects commonly known as spittlebugs/froghoppers, leafhoppers, sharpshooters and cicadidae. *X. fastidiosa* transmission by insects has these key elements:

- Nymphs lose the pathogen through molting and thus newly emerged adults are *Xylella* free. (25)

- Females that are infected do not transfer the bacterium to their offspring (26).
- It is extremely difficult to predict which xylem-feeding species will or will not transmit *X.fastidiosa* (6).
- Insect species who carry *X. fastidiosa* appear to carry all strains of the bacterium (27).
- Bacteria do not systematically infect the body of the insect, instead being restricted to parts of the foregut where they form a biofilm in insect species which can act as vectors. (25)
- Transmission of *X. fastidiosa* by adult insects is peculiar in that it does not require a latent period and can be transmitted within hours (25)
- Persistent in insects – they are able to transmit the pathogen likely until they die/molt. (26)

Philaenus spumarius – meadow spittlebug

In the Americas, most diseases caused by *X. fastidiosa* are vectored by sharpshooter leafhoppers. In Europe, spittlebugs are much more abundant and diverse than sharpshooter leafhoppers. The meadow spittlebug is considered the main vector in the outbreak of *X. fastidiosa* in Italy (22) (25) (28) (29). Prior to this outbreak it was not viewed as a pest and so biological, ecological and ethological data are missing and rather scattered (22).

Philaenus spumarius is ubiquitous, common and locally very abundant across Europe, including in the UK (22), and inhabits altitudes ranging from sea level to over 2000m. It is considered to be the main potential vector of *X. fastidiosa* in the UK.

The species has one generation per year; nymphs hatch in the spring and adults are mostly seen from late spring until autumn (22). While nymphs feed on a wide range of herbaceous plants, adults have a broader host range and will feed on numerous woody tree species (22).

Researchers have difficulties rearing *P. spumarius* in the lab indicating a lack of understanding of some of their environmental requirements. Despite clear preference for moist environments (e.g. foam production by the nymphs) the meadow spittlebug colonises nearly all habitats (22).



FIGURE 5 - SPITTLE FROM *PHILAENUS SPUMARIUS* NYMPHS © BRIGIT PROJECT

The natural spread of *X. fastidiosa* by *P. spumarius* has been recorded as 1km a year (6), although the insects are potentially capable of long-distance migration. Greater spread is made possible by wind currents and human activities including hitchhiking on cars (22).

The introduction of the Glassy Winged Sharp Shooter in California worsened the spread of Pierce's Disease in the region. As unlike the native species the insect can feed on woody stems and fly further (7). The introduction of this insect, and others, to the EU is possible, and could increase the spread of *X. fastidiosa* (30).

Open Questions

The majority of studies on European insect vectors have concentrated on *P. spumarius* in Italy. Although useful the situation in the UK will likely be very different due to a different climate and landscape including less extensive monocultures. Other UK insects could also play an integral role in the spread of the bacterium.

The BRIGIT project (24) aims to address some of these uncertainties through:

- A widespread standardised sampling project of potential vectors across several regions of the UK at different times of the year and in different habitats to determine local populations.
- Mark-release-recapture experiments to map the dispersal of adult *P. spumarius* in the UK and the distance they can fly.
- Generating genome sequence resources of the potential vectors to discover how genetically different regional and habitat populations of the insects are. This will indicate whether these different populations share habitat and so spread the infection between them.

Managing the Risk

The epidemic of subspecies *pauca* in Italy is unlikely to be eradicated due to the abundance of vectors in the region and the proximity and links between olive groves (31). Italian olive groves can be centuries old and their cultural significance has hampered implementing EU law (7). So the infection appears established in Europe.

Infections can be asymptomatic or produce disease symptoms which range from minor leaf scorch to extensive die-back and plant death. *Xylella fastidiosa* and its vectors have an exceptionally large host range and it is difficult to predict which potential UK plant host species may be susceptible to infection if the pathogen was to establish in the UK.

Difficulties in Detection and Surveillance

Symptoms are similar to those caused by other diseases and lack of water (3). There are complex vector-plant-pathogen-environment interactions and *X. fastidiosa* can remain unseen for a long time (3). It is possible that the pathogen is present but undetected in other locations in Europe (32).

The potential existence of undetected reservoirs of infection in Corsica was considered using mechanistic statistical models (3). The simulations suggested these reservoirs of infection would have a weak effect initially but if not controlled could have a large impact on infection dynamics and increase prevalence (3). Effective surveillance and control strategies should consider the existence of potential hidden reservoirs.

Seasonal fluctuations in *X. fastidiosa* detectability and density have been observed in studies of sweet orange, grapevine and red oak meaning successful detection can be inconsistent (20). The infection can also be localised within a plant so that if a leaf from one branch is uninfected the plant may still carry the bacterium (20).

Diseases caused by *X. fastidiosa* vary by plant host and are often classified by the types of symptoms they cause. Symptom expression has been linked to both host type and tissues in which bacterial multiplication occurs (20).

Insects can also be analysed to detect *X. fastidiosa* and should preferably be collected with sweeping nets (adults) or aspirators (33). This can be a complimentary activity to visual inspection.

New Research into Detection and Management

There have been several studies into different remote sensing methods from robots (34) to hyperspectral and thermal image data taken on flights over olive groves (35). There was a high success rate with the latter with detection occurring before visual symptoms appeared. Experiments are also ongoing into the use of “spy plants” which show symptoms sooner than other plants and could be a useful indicator of the infection existing in a location. (36)

A new online resource, MEDISYS, has been built as a media monitoring system for the surveillance of plant pests. This can be used as a supplementary method to more traditional bio-surveillance to help with early warning, awareness and rapid response (37).

Plant Health Australia organised an exercise involving a scenario where *X. fastidiosa* subsp. *multiplex* had been identified in the country in order to investigate their response capability (38). Visually diagnosing *X. fastidiosa* was raised as a significant issue as was understanding the likely host list.

Since management and regulations of *X. fastidiosa* outbreaks should take account of subspecies, a freely available bioinformatics software tool has been developed to quickly extract information from genomic datasets (16). The three main sub-species were accurately identified while *morus* and *sandyi* were attributed to *fastidiosa*.

Open Questions

The BRIGIT project (24) is currently working on improving procedural preparedness by:

- Developing safe, reliable and precise tools for diagnosis and a stream-lined response in the event of an outbreak that is consistent across devolved territories and between organisations.
- Investigating pathways of *X. fastidiosa* spread including human behavioural implications.
- Modelling how the pathogen may arrive and spread through the UK through the horticulture trade.

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