A review of *Erwinia pyrifoliae:* the causal agent of a new bacterial disease on strawberry

Matevz Papp-Rupar, NIAB EMR, East Malling, Kent, ME19 6BJ

Summary

Erwinia pyrifoliae is a bacterial pathogen related to fireblight (*E. amylovora*). It was first described in the 1990s as causing disease on Asian pear in Korea and Japan. It was unexpectedly detected in 2013 as a strawberry flower and fruit pathogen in the Netherlands. On pear, it causes symptoms comparable to fireblight, while on strawberry, its symptoms include black discolouration of flowers, fruits, flower calyx and fruit stems. In this review, we collated all available data on *E. pyrifoliae* to better understand its ecology, control measures and potential risks to UK horticulture.

Summary of main findings

- *Erwinia pyrifoliae* is a bacterial pathogen related to fireblight, a common bacterial disease of apple and pear in the UK
- The bacterial pathogen *E. amylovora*, which causes fireblight, reportedly infected strawberry in Bulgaria in 2005
- The high planting density and typically warm and humid conditions commonly found in UK protected strawberry production can increase the risk of bacterial diseases
- In June and October 2013, *E. pyrifoliae* was found to infect glasshouse crops of Elsanta in several locations in the Netherlands. Other infected cultivars included Selva, Clery, Mallling Opal and Ischia
- Symptoms included blackening of the immature fruits, fruit calyx and attached stems, but no symptoms were observed on the leaves. Blackening was also obvious inside young fruits. Release of bacterial ooze was observed on the surface of the young fruits and their attached stems. In many cases, fruits were malformed
- Similar symptoms had been recorded in 2011 on a commercial production site in Belgium
- As a high proportion of strawberry plants used in the UK are sourced from the Netherlands, it is likely that the pathogen is already present in the UK. However, to date, there have been no reports of related symptoms
- Surveillance for the disease by growers and agronomists is important and samples of plants showing any suspicious symptoms should be sent to a plant clinic for analysis
- *E. pyrifoliae* is not a notifiable or quarantine disease, so no mandatory screening or containment measures are required
- No plant protection products are registered for control of the pathogen on strawberry and none have been tested for their efficacy against this pathogen

- Based on fireblight (*E. amylovora*) data, it is believed that several biological products could provide some protection by competing with the pathogen when it is growing on the stigma in flowers. Examples include *Aureobasidium pullulans* (Boni Protect, approved on apples and pears), *Bacillus subtilis* (Serenade ASO, approved on soft fruit and tree fruit; Solani, approved on strawberry), *Bacillus pumilus* (Sonata, approved on soft fruit) and *Bacillus amyloliquefaciens* (Sentinel and Amylo X, approved on soft fruit and Taegro approved on strawberry)

Introduction

There are few bacterial diseases on strawberry, but the ease with which they are spread and the general lack of plant protection products available to control them means they can cause severe problems. Intensification of strawberry production (Figure 1) in covered soilless systems have improved yields and reduced issues with soilborne diseases. Higher planting density and a more conducive environment under covers, however, can – in turn – increase the risk of bacterial diseases. Currently, the most important bacterial pathogens of strawberry are *Xanthomonas fragariae*, the causal agent of bacterial angular leaf spot of strawberry;[1,2] *Pseudomonas solanacearum* (bacterial wilt), mainly infecting nursery seedlings;[3] and a fireblight pathogen, *Erwinia amylovora,* which was reported to infect strawberries in Bulgaria.[4] The scope of this review is *E. pyrifoliae,* a novel bacterial pathogen of strawberries first reported in the Netherlands in 2013.

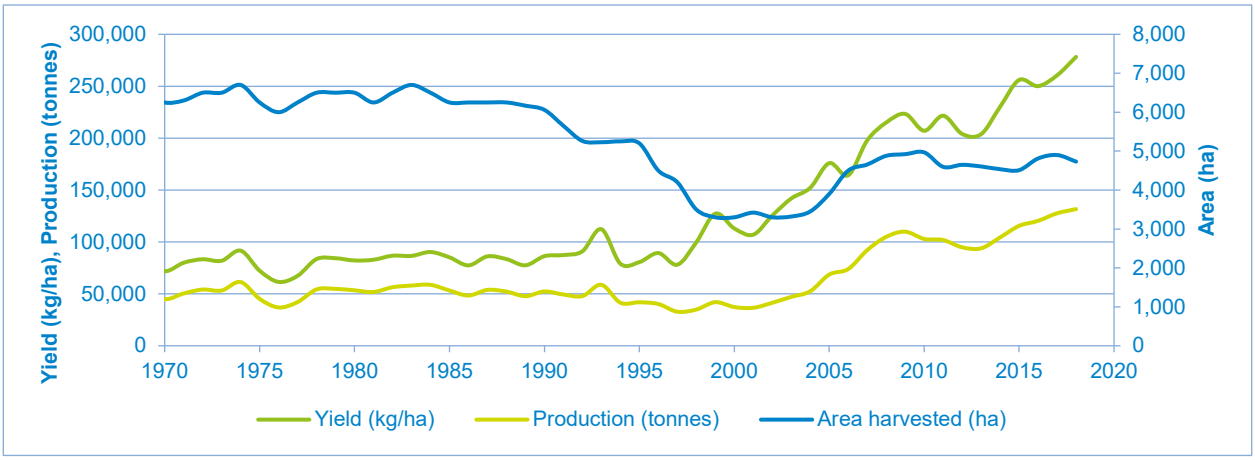

Figure 1. Intensification of strawberry production in UK in the last 50 years. Yields per hectare and total production volume have been increasing, while at the same time the production area has been similar or decreasing

Source: FAO[5]

Pathogen characteristics

Scientific name: *Erwinia pyrifoliae*[6]

Common name(s): Asian pear blight, bacterial shoot blight of pear

Taxonomic position: Class: Gammaproteobacteria, Order: Enterobacteriales, Family: Erwiniaceae

E. pyrifoliae cells are motile, Gram-negative, straight rods, non-spore-forming and flagellated all over the surface (peritrichous) and respiration is aerobic and facultative anaerobic. Strains grow on yeast extract peptone dextrose agar (YPDA) medium, producing colonies that are 2 mm in diameter after 48 hoursat 28°C. Colonies are circular, white, well-domed and opaque. Glucose (dextrose) is fermented without gas production.[6] The genome size of *E. pyrifoliae* is between 3.9 and 4 Mbp.

First description and characterisation of disease on pear

E. pyrifoliae was first described as a pathogen on Asian pear trees (*Pyrus pyrifolia* Nakai) in South Korea.[6] Symptoms on Korean pear trees resembled those of fireblight (*E. amylovora*), with black-brown stripes and spots on the leaves and necrotic petioles, blossoms and fruitlets. The bark tissue below the black-brown surface remained green, in contrast to the red-brown colouration seen with fireblight.[6] Symptoms spread to entire branches and a high proportion of trees in the orchards were affected.[7]

Bacteria isolated from necrotic branches of Asian pear trees in Korea formed white colonies on Luria-Bertani (LB) agar and slightly yellow mucoid colonies on minimal agar medium MM2Cu. Koch postulates with *E. pyrifoliae* were validated on pear seedlings (*Pyrus pyrifolia*) and immature pear fruit (*P. communis*), where ooze typical of *Erwinia* infection was produced in 3–7 days. In two-dimensional electrophoresis analysis, *E. amylovora* and *E. pyrifoliae* had similar, but not identical protein patterns. No similarity was found in the plasmid profiles and, consequently, no signal was obtained in polymerase chain reaction (PCR) testing with primers from the *E. amylovora* plasmid pEA29. Repetitive element PCR (REP-PCR) also produced bands that differed between the two organisms.[7] Based on a comparison of 16S rDNA, a combination of biochemical tests and DNA hybridisation, *E. pyrifoliae* was suggested to be a new species, closely related to *E. amylovora*.[6]

First report and description of disease on strawberry

The pathogen was found in the Netherlands in June and October 2013, where it infected greenhouse-grown strawberries (cv. Elsanta) in several locations.[8,9] Symptoms included intense blackening of immature fruits, the fruit calyx and attached stems (Figure 1), with no symptoms on the leaves. The discolouration was also obvious inside the young fruits. At the edge of infected fruit, an intense darkening of the tissue was observed and there was intense shining of the tissue in the middle of infected fruits. Release of bacterial ooze was observed on the surface of the young fruits and their attached stems (Figure 2). In many cases, fruits were heavily malformed (Figure 3). In most cases, these symptoms were present throughout the whole greenhouse and incidence was high: about 50% of plants in the greenhouses had at least one symptomatic fruit.[8] All infected fruit was rendered unmarketable.[9] Depending on the exact time of infection, economic losses varied greatly, from very high in early season infections to very low in late season infections.

Isolates from the Netherlands were analysed by 16S rDNA sequencing and quantitative PCR (qPCR), which revealed the species to be *E. pyrifoliae*.[10] Further microbiological analysis revealed Gram-negative bacterial cells that were able to utilise sorbitol but not gelatine, esculin or D-raffinose – similar to the *E. pyrifoliae* reference strain LMG 25888. Pathogenicity of isolated strains was confirmed on strawberry cv. Elsanta. Inoculation of young fruitlets with isolated strains and an *E. pyrifoliae* reference strain (LMG 25888) resulted in similar symptoms to those observed on the original field samples.[8,9]

After initial detection of disease, all affected crop was removed. Pathogen surveillance was conducted in subsequent years and the disease was found in four different provinces in the Netherlands.[11]

The origin of strawberry pathogenic strains in the Netherlands is unclear and molecular comparison with strains from Korea and Japan is ongoing.

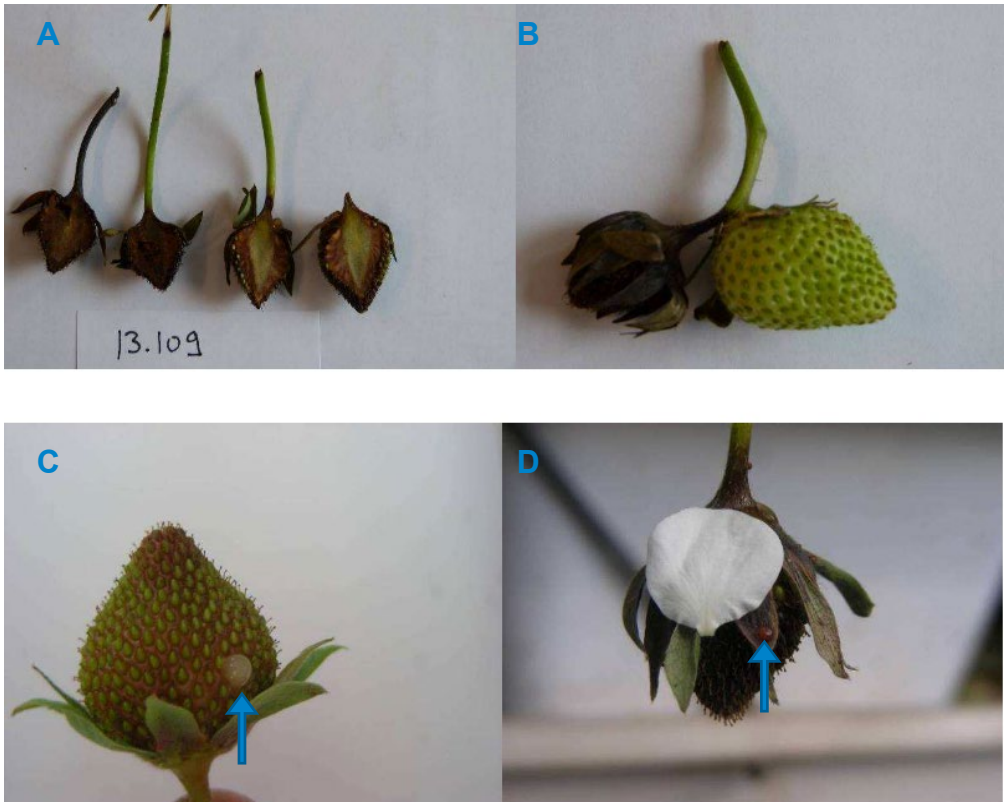

Figure 2. Intense blackening of the fruit, calyx and stems infected with *Erwinia pyrifoliae* (A, B). Bacterial ooze on infected fruit (C, D arrowheads)

Source: National Plant Protection Organization[6]

Figure 3. Heavily malformed strawberry fruit in infected greenhouses

Source: Wenneker and Bergsma-Vlami[9]

Pathogen distribution and hosts

Erwinia pyrifoliae has been detected in:

- 1995 in South Korea, on Asian pear (*Pyrus pyrifolia*)
- The 1970s in Japan, on Asian pear
- 2013 in the Netherlands, on commercial indoors-grown strawberry

A case of possible detection was also reported in 2011 in Belgium, in field-grown strawberry. See Figure 4.

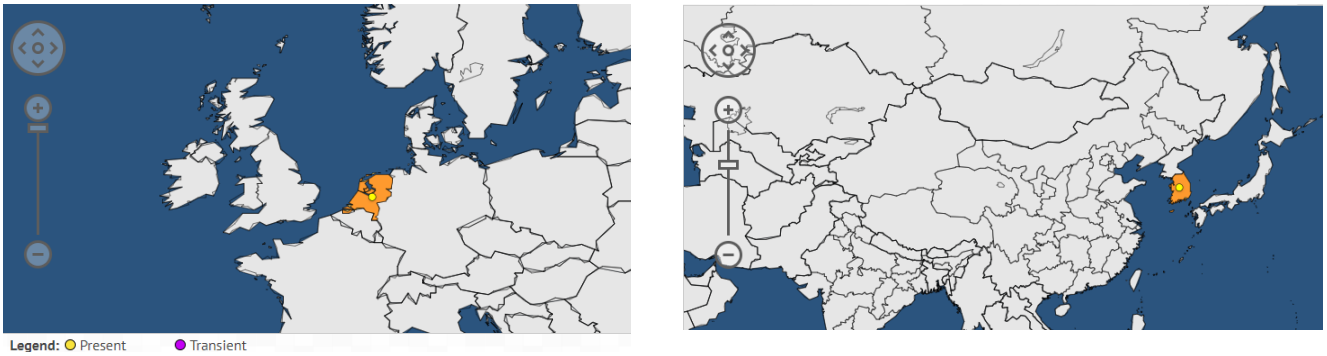

Figure 4. Distribution of *Erwinia pyrifoliae* in Europe and Asia

Source: European and Mediterranean Plant Protection Organization[12]

Between 1995 and 1998, *E. pyrifoliae* was detected in samples from Asian pear orchards in South Korea, but between 1999 and 2000, it was not in the necrotic tissue. Despite extensive surveys, this pathogen has not been found in South Korea since 1998. Strict phytosanitary measures initiated in the area of the original outbreak seem to have eradicated this pathogen in Korea. The host range has been assessed in experimental conditions. Susceptible European pear cultivars include 4703/78, Bartlett, Conférence, Doyenné du Comice, Harrow Sweet, INRA hybrid, Old Home and US 65.063.13.[13,11] Experimentally susceptible apple cultivars include Empire, Fortune, Idared and McIntosh.[13,]

In 2009, Geider et al.[15] re-examined some bacterial isolates, which in Japan in the 1970s, were previously thought to be infection of pear trees with *E. amylovora*.[14] A detailed study concluded that they were also *E. pyrifoliae*.[15,16] There have been no recent reports of this disease outbreak in Japan.

In 2013 and 2014, *E. pyrifoliae* was detected in four different provinces in the Netherlands, from the most northern to the most southern province. Most cases reported were in the southern part of the Netherlands. The most commonly infected strawberry cultivar was Elsanta. However the cultivars Selva, Clery, Malling Opal and Ischia were also found to be infected.[11]

In 2011, during a survey for *Xanthomonas frageriae*, similar symptoms were seen on immature strawberry fruits in one cultivated site in Belgium.[8] The isolates reacted with *E. amylovora* antibodies, but molecular tests (TaqMan PCR) came back negative for *E. amylovora* (TaqMan PCR). Furthermore, in pathogenicity tests, the isolates did not cause typical symptoms on immature pear fruits. A PCR assay and sequencing of the *recA* gene attributed the isolates to the *E. pyrifoliae* taxon. Pathogenicity tests on strawberry were inconclusive.[17] Infected leaves, petioles and immature strawberry fruits did not show typical symptoms. Epicalyx inoculation of immature strawberry fruits, however, resulted in necrosis with exudates.[18] There have been no further reports from Belgium.

Most strawberry plants grown in the UK are imported from the Netherlands. This, coupled with the lack of surveillance in the UK to date, means that the pathogen is likely to already be present in the UK. However, so far, there have been no reports of *E. pyrifoliae*-related symptoms in the UK. This may be because most UK-grown strawberries are produced in table-top polytunnel systems and not in glasshouses. Polytunnel environments might be less conducive to the disease than glasshouse environments. There is, however, no evidence to confirm this hypothesis.

Disease biology and spread

The biology of *Erwinia pyrifoliae* is largely unknown. The lack of research and information could be attributed to the sporadic and limited distribution of this disease, as well as its low impact thus far. The relatedness of *E. pyrifoliae* and *E. amylovora* suggests their biology may be similar.

E. amylovora, which causes fireblight, infects its hosts through flowers early in the season and, later in the season, through small wounds on young leaves and shoots. After infection, it migrates through the xylem and other tissues, spreading the infection. It overwinters in annual cankers that were formed on diseased branches during the previous season. *E. amylovora* can also reside as an endophyte within apparently healthy plant tissue, such as branches, limbs and budwood.[19] It survives epiphytically on the stigmatic surfaces of the flowers, but not on the leaves.[20] Similarly, *E. pyrifoliae* seems to infect strawberry flowers and fruits, subsequently spreading to adjacent calyces and petioles. No symptoms on the leaves have been reported.[8]

We speculate that the favourable climate for infection might be similar for both pathogens. Spring temperatures above 15°C, with high humidity, rain and wind, usually result in devastating fireblight outbreaks. Similarly, *E. pyrifoliae* outbreaks in the Netherlands have all been reported from glasshouse production, where mild and constant temperature and relative high humidity provide a more conducive environment for the disease than outdoor field conditions. There is, however, no reliable study to confirm this.

E. amylovora has been shown to survive for up to 5 weeks in untreated soil.[21] It is unclear whether *E. pyrifoliae* can survive without a strawberry host.[8]

E. amylovora can disperse short distances in the air.[21] It is also transmitted mechanically by insects including *Aphis pomi* (green apple aphid) and *Chrysoperla carnea* (green lacewing), surviving for up to 12 days after contact with aphids.[22] It was shown that *E. pyrifoliae* can be transported on the hair of honey bees (*Apis mellifera*); the pathogen was also detected in greenhouse-introduced bee colonies before symptoms were visible on the fruit.[11,23]

Detection

The first and most important detection method is surveillance of nursery and production sites by growers and agronomists. Any suspicious symptomatic material (Figure 1) detected early in the season should be collected and sent to a plant clinic for analysis. Pocket Diagnostics® offer an easy-to-use, rapid field test for fireblight (caused by *Erwinia amylovora*), which may or may not *also* detect *E. pyrifoliae*. Given the lack of evidence, we do not recommend its use for screening purposes until its efficacy is confirmed.

Potential *E. pyrifoliae* bacteria can be isolated from symptomatic tissue on rich medium (LB agar), where they form white colonies. When transferred onto MM2Cu medium (4.0 g/L L-asparagine, 2.0 g/L K_2HPO_4, 0.2 g/L, $MgSO_4 \cdot 7H_2O$, 3.0 g/L NaCl, 0.2 g/L nicotinicacid, 0.2 g/L thiamin hydrochloride, 10 g/L sorbitol, 2 mM $CuSO_4$) they form slightly yellowish, mucoid colonies.[13] In contrast, *E. amylovora* produces clear yellow colonies on MM2Cu medium.

There are several published molecular diagnostic methods for *E. pyrifoliae*. Kim et al.[6] originally identified the species by nucleotide sequencing the 16S rRNA genes and the 16S–23S rRNA intergenic transcribed spacer region, as well as biochemical and physiological tests and DNA hybridisation.

Kim et al.[13] developed a classification of *E. pyrifoliae* strains according to their pulsed-field gel electrophoresis (PFGE) pattern after a *Spe*I digestion of their DNA. The same authors also reported two primer pairs for specific detection of *E. pyrifoliae* from necrotic tissue.

Recently, new PCR and qPCR primers were developed for four *Erwinia* species, including *E. pyrifoliae* (Table 1). The primers were validated with Matrix-assisted laser desorption ionisation–time-of-flight mass spectrometry (MALDI–TOF MS).[10] These primers were used in 2013 by Wenneker and Bergsma-Vlami[9] to identify *E. pyrifoliae* infecting strawberry in the Netherlands. The genome sequences of several strains of *E. pyrifoliae* were also published.[16]

Table 1. Primer pairs for specific detection of *Erwinia pyrifoliae*. Amplicon length denoted here is specific to *E. pyrifoliae*

Target gene	Primer name	Primer sequence (5'-3')	Amplicon length (kb)	Reference
16S rRNA	EP16A	AGATGCGGAAGTGCTTCG	0.7	13
	EPIG2c	ACCGTTAAGGTG GAATC		
cps	CPS1	CGCGGAAGTGGTGAGAA	1.2	
	CPS2c	GAACAGATG TGCCGAGTA		
***pstS—glmS* region**	EPPSGL1646	CAGCGCATCATAAGTGTACC	Not available	10
	EPPSGL2698c	TCTGGAATATCGGCTCCGTA		
	EPPSGS1089Q	GGTTACCGCGTTCGTATGAT	0.1	
	EPPSGS1228Qc	TTGTTGTCGTGAGCGCATAG		

Reported control and containment measures

Erwinia pyrifoliae is not listed as a quarantine disease, so no mandatory screening or containment measures are required. The initial outbreaks on pear and strawberry seem to be contained by eradication of all symptomatic plants and subsequent monitoring. In the case of woody tissue, the best way to eradicate the pathogen is to burn the infected plant material at or near the outbreak site to prevent unintended spread through transport of infected material. All tools and personnel outfits involved in the removal of plants should also be disinfected. We were not able to find the exact procedure used in the Netherlands to eradicate infected glasshouse-grown strawberry. We suggest sealing off the infected area, switching the irrigation off for 2–3 weeks to dry the plants and growing media, before proceeding with incineration – preferably without transporting infected material off site. The irrigation system pipes and drippers should either be disinfected or replaced. All glasshouse surfaces and equipment should be disinfected as well. Steam, Jet-5 (Certis) or other disinfectant licensed for horticultural use can be used. Following an outbreak, increased biosafety measures and surveillance are required to prevent potential spread. Overshoes and single-use personnel overcoats are recommended in each separate glasshouse, together with baths for disinfecting shoes on entry and exit to prevent unintended spread.

No plant protection products are currently registered for control of *E. pyrifoliae* in the UK. Moreover, the efficacy of plant protection products currently registered for use on strawberry has not been determined for *E. pyrifoliae* control. Copper-based or antibiotic (streptomycin) treatments are not currently permitted on strawberry in the UK. Based on *E. amylovora* (fireblight) control data, biological products containing *Aureobasidium pullulans*, *Bacillus subtilis*, *Pantoea agglomerans* or *Pseudomonas fluorescens* could provide some protection by competing with the pathogen for space and nutrients when it is growing on the stigmatic surface (flowers).[24] Registered products containing the abovementioned organisms include Serenade ASO and Sonata (Bayer CropScience), Serifel (BASF), Amylo X WG (Certis), Solani (Russell IPM) and Taegro (Syngenta UK).[25] The efficacy of these products in the control *E. pyrifoliae* is unknown.

BlossomProtect (Bio-Protect), with *Aureobasidium pullulans* as an active ingredient, was shown to protect pear blossom against fireblight.[26] It is registered in Germany, Austria and Switzerland for use against fireblight and might also be effective against *E. pyrifoliae*. Another product not registered in the UK but which has shown promising results for the control of fireblight is the plant activator Bion/Actigard (Syngenta). Its active ingredient acibenzolar-S-methyl (ASM) was shown to stimulate the expression of pathogenicity-related proteins in apple, suggesting that resistance was induced through a systemic acquired resistance (SAR) pathway.[27]

Lytic bacteriophages have often been reconsidered as a tool for the biological control of bacteria. Bacteriophages infect very specific target bacteria and are harmless to all non-target organisms. They replicate in their host before killing it to release more phages. A recent *in vitro* study in Korea reported bacteriophages for the control of both *E. amylovora* and *E. pyrifoliae*.[29] No field data on their efficacy have been reported.

Assessment of risk to the UK industry

Should another outbreak occur in the Netherlands, the risk of introducing *Erwinia pyrifoliae* to the UK would be very high, given that a high proportion of UK strawberry plants are currently sourced from nurseries in the Netherlands. However, there have been no recent reports of *E. pyrifoliae* outbreaks in the Netherlands.

Should it be introduced, the impact of *E. pyrifoliae* on the UK strawberry industry is uncertain. It is possible that in a year with very wet and warm spring and early summer conditions, infections could spread rapidly from a few imported infected plants to large areas, causing considerable losses. It is also very likely that the pathogen is already present in the UK and is not causing any problems because of our different growing practices and climatic conditions. Should the UK strawberry industry move towards all-year-round production in glasshouses, extra vigilance would be advised.

The fact that *E. pyrifoliae* can also cause disease in apple and pear poses additional risks to the pome fruit industry, especially where strawberry and pome fruits are grown side by side.

Knowledge gaps and future research

The following knowledge gaps should be addressed to accurately assess the potential impact of *Erwinia pyrofoliae* in the UK and facilitate its control.

- The presence and distribution of *E. pyrifoliae* in the UK strawberry and pome fruit industry should be surveyed. Small-scale surveillance studies could be carried out among strawberry/pome fruit growers, with different sources of planting material to establish whether and to what extent the pathogen is present. Pollinator sampling could be used for improved coverage of larger areas
- Efficacy of current products registered for strawberry should be assessed against *E. pyrifoliae in vitro* and *in vivo* to offer an immediate protection strategy if necessary. Also, products not currently registered in the UK and alternative strategies could be investigated
- Susceptibility of commonly grown strawberry and pome cultivars to *E. pyrifoliae* in UK conditions should be investigated to assess the potential host range, spread and impact
- Overwinter survival of the pathogen in wild plants and in soil must be assessed to develop an effective containment plan, should the pathogen start to cause economic losses

References

1. King, T. H., Kennedy, B. W. (1986). *Xanthomonas fragariae*. EPPO Bulletin 16: 17–20.

2. Kastelein, P., et al. (2014). *Development of Xanthomonas fragariae populations and disease progression in strawberry plants after spray-inoculation of leaves*. Plant Pathology 63: 255–263.

3. Hayward, A. C. (1991). *Biology and epidemiology of bacterial wilt caused by Pseudomonas solanacearum*. Annual Review of Phytopathology 29: 65–87.

4. Atanasova, I., et al. (2005). *New host plants of Erwinia amylovora in Bulgaria*. Zeitschrift für Naturforschung C Journal of Biosciences 60:892–898.

5. Food and Agriculture Organization of the United Nations (FAO). *FAOSTAT. Crops.* Available from: http://www.fao.org/faostat/en/#data/QC.

6. Kim, W., et al. (1999). *Erwinia pyrifoliae sp. nov., a novel pathogen that affects Asian pear trees (Pyrus pyrifolia Nakai).* International Journal of Systematic Bacteriology 49: 899–906.

7. Rhim, S., et al. (1999). *Erwinia pyrifoliae, an Erwinia species different from Erwinia amylovora, causes a necrotic disease of Asian pear trees*. Plant Pathology 48: 514–520.

8. National Plant Protection Organization (NPPO). (2014). *January 2014 Pest Report – the Netherlands. Findings of Erwinia sp. 'assigned to the E. pyrifoliae taxon' in two production greenhouses of strawberry fruits (Fragaria).* Utrecht: Netherlands Food and Consumer Product Safety Authority, Ministry of Economic Affairs. Available from: https://english.nvwa.nl/documents/plant/plant-health/pest-reporting/documents/pest-report-findings-of-erwinia-sp-assigned-to-the-e-pyrifoliaetaxon-in-two-production-greenhouses-of-strawberry-fruits-fragaria.

9. Wenneker, M., Bergsma-Vlami, M. (2015). *Erwinia pyrifoliae, a new pathogen on strawberry in the Netherlands.* Journal of Berry Research 5: 17–22.

10. Wensing, A., Gernold, M., Geider, K. (2012). *Detection of Erwinia species from the apple and pear flora by mass spectroscopy of whole cells and with novel PCR primers.* Journal of Applied Microbiology 112: 147–158.

11. Wenneker, M., Bergsma-Vlami, M., Van Der Steen, J. J. M. (2017). *Epidemiology of Erwinia pyrifoliae, a new pathogen on strawberry in the Netherlands.* Acta Horticulturae 1156: 721–726.

12. EPPO Global Database. (2017). *Erwinia pyrifoliae (ERWIPY).* Available from: https://gd.eppo.int/taxon/ERWIPY/distribution.

13. Kim, W. S., et al. (2001). *Molecular comparison of pathogenic bacteria from pear trees in Japan and the fire blight pathogen Erwinia amylovora*. Microbiology 147: 2951–2959.

14. Beer, S.V., et al. (1996). *Characterization of bacteria that cause 'bacterial shoot blight of pear' in Japan*. Acta Horticulturae 411: 179–182.

15. Geider, K., et al. (2009). *A polyphasic approach assigns the pathogenic Erwinia strains from diseased pear trees in Japan to Erwinia pyrifoliae*. Letters in Applied Microbiology 48: 324–330.

16. Thapa, S. P., et al. (2013). *Comparative genomics of Japanese Erwinia pyrifoliae strain Ejp617 with closely related erwinias (J Bell, Ed,).* Genome 56: 83–90.

17. Mackesy, D. Z., Sullivan, M. (2017). *CPHST Pest Datasheet for Erwinia pyrifoliae*. USDA-APHISPPQ-CPHST 1–11.

18. National Plant Protection Organization. (2014). *Quick scan number: QS. Bac.2014.01: 1–6.* Utrecht: Netherlands Food and Consumer Product Safety Authority, Ministry of Economic Affairs. Available from: https://pra.eppo.int/getfile/abcbf3d3-47c1-41be-b7f9-dff73f58b5f3

19. Johnson, K. B. (2000). *Fire blight of apple and pear.* The Plant Health Instructor (updated 2015). Available from: doi.org/10.1094/PHI-I-2000-0726-01.

20. Thomson, S. V. (1986). *The role of the stigma in fire blight infections.* Phytopathology 76: 476.

21. Hildebrand, M., Tebbe, C. C., Geider, K. (2001). *Survival studies with the fire blight pathogen Erwinia amylovora in soil and in a soil-inhabiting insect.* Journal of Phytopathology 149: 635–639.

22. Hildebrand, M., Dickler, E., Geider, K. (2000). *Occurrence of Erwinia amylovora on insects in a fire blight orchard.* Journal of Phytopathology 148: 251–256.

23. Van Der Steen, J. J. M., Bergsma-Vlami, M., Wenneker, M. (2017). *The perfect match: simultaneous strawberry pollination and bio-sampling of the plant pathogenic bacterium Erwinia pyrifoliae by honey bees Apis mellifera.* Sustainable Agriculture Research 7: 25.

24. CABI International. (2008). *Invasive species compendium. Erwinia amylovora (fireblight) – datasheet.* Available from: https://www.cabi.org/isc/datasheet/21908#tobiologyAndEcology.

25. Health and Safety Executive. *Plant protection products with authorisation for use on strawberry in the UK*. Available from: https://secure.pesticides.gov.uk/pestreg/ProdSearch.asp, crop = strawberry. Accessed on 15.2.2019

26. Kunz, S., Schmitt, A., Haug, P. (2011). *Development of strategies for fire blight control in organic fruit growing*. Acta Horticulturae 896: 431–436.

27. Maxson-Stein, K., et al. (2002). *Effect of treating apple trees with acibenzolar-S-methyl on fire blight and expression of pathogenesis-related protein genes*. Plant Disease 86: 785–790.

29. Park, J., et al. (2018). *Characterization of the lytic bacteriophage phiEaP-8 effective against both Erwinia amylovora and Erwinia pyrifoliae causing severe diseases in apple and pear.* Plant Pathology Journal 34: 445–450.