How Can Plant Pathology Help in the Control of Human Pathogens Associated with Edible Crop Plants?

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Abstract

Edible plants have become established as an important vehicle in the transmission of human pathogens. Most pathogens are food-borne and plants that have been implicated are those that are eaten raw or minimally processed. Detailed investigation of the molecular interactions that underpin food-borne pathogens and plant hosts has highlighted many similarities with plant-associated bacteria, including phytopathogens, although important distinctions are also evident. One aspect that draws a useful comparison with plant pathology is in the elicitation of the plant defence response, where there are parallels for human pathogens in PAMP-triggered immunity. However, the extent of the plant immune response on perception of human pathogens is unclear, as is the ability of the pathogens to subvert, overcome or avoid the response. Control of human pathogens on plants has developed under food safety and risk management approaches. Yet, there are important overlaps in crop protection for the control of phytopathogens, where both disciplines can benefit from shared dialogue and research interests.

1. Introduction for human pathogens

1.1 Produce-associated foodborne outbreaks

Foodborne pathogens are frequently associated with consumption of fresh fruits and vegetables. In some countries, e.g. USA, plant-based foodstuffs now account for more than 50 % of foodborne illnesses (Painter et al. 2013). Although it is likely that plant-based foods have always been responsible for proportion of foodborne illness, it was only after large-scale outbreaks in the mid 2000's that the area garnered attention, for example after an outbreak of *Escherichia coli* O157:H7 associated with spinach in the USA in 2006 (Centers for Disease Control and Prevention (CDC) 2006). In 2018, notable outbreaks included an outbreak of *E. coli* O157:H7 from consumption of contaminated romaine lettuce, which resulted in 210 reported cases, 5 fatalities and 27 cases of hemolytic uremic syndrome (CDC 2018); cucumbers contaminated with *Salmonella enterica* serovar Agona resulted in 147 reported cases of salmonellosis centred in the UK, and detected in Finland, Germany and Ireland (Whitworth 2018); parasite infections also occurred in the USA, including a widespread and large outbreak of *Cyclospora cayetanensis* with 761 reported cases arising from contaminated salad sold at fast food restaurants (511 cases) (Centers for Disease Control and Prevention 2018b) and in vegetable trays (250 cases) (Centers for Disease Control and Prevention 2018a).

1.2 Causative organisms

Although a number of different human pathogens are associated with outbreaks from fresh produce, the common factor is that they are transmitted through the food chain during production process, either during plant growth or during post-harvest. All classes of pathogens associated with foodborne illness have be implicated in contamination of foods of plant origin, including viruses, parasites, bacteria and fungi. Many are derived from an animal source, where farmed livestock or humans are the primary reservoir. An important distinction between the pathogens relates to how they interact with plants, and they can be split into those that either actively interact with plants with the potential to use plants as secondary hosts, or those that are passively transmitted into the food chain by plants. These groups can be distinguished by their host requirements for proliferation, so that those in the latter group have a fastidious requirement for an animal host to complete their life cycle. Microbes that undergo an active interaction with plants include most bacterial pathogens, while human pathogenic viruses and parasites cannot replicate on plant material and plants act as fomites in the transmission pathway. A third group of pathogens that are more rarely implicated in human disease from consumption of contaminated produce are those that are normally associated with plant colonisation, either in a commensal non-pathogenic state or as phytopathogens. This group includes

some opportunistic fungal phytopathogens (Dickman and de Figueiredo 2011) and is less frequently reported than the foodborne human pathogens.

Consideration of the role of plants in the life cycle of pathogens leads overlaps with many aspects of plant pathology and plant-microbe interactions. As such, these disciplines can provide valuable insights into mechanisms of colonisation and transmission, and subsequently means for control. Indeed, examination of the molecular basis of the human pathogen-plant interactions serves to highlight the need to consider this area as an extension of plant pathology / plant-microbe interactions rather than a distinct discipline. Furthermore, the interactions are not limited to living plants in their pre-harvest state, but are also valid for post-harvest considerations, where the overlaps are with food-spoilage microbes. Here, the focus is on the bacteria-plant interactions that occur in living, pre-harvest plants, drawing on the extensive body of work within plant pathology.

1.3 Food-borne pathogens

The most frequently reported foodborne bacteria associated with plants are shigatoxigenic *E. coli* (STEC), non-typhoidal *Salmonella enterica* and *Listeria monocytogenes* (FAO/WHO 2008). Sub-species variants occur in produce-associated outbreaks, including a number of different *S. enterica* serovars, while the most frequent STEC serotype is O157:H7. *L. monocytogenes* is considered to be a soil-associated pathogen, with quite distinct physiology and life cycle aspect to the *Enterobacteriaceae*. It is frequently characterised by its ability to grow at low temperatures, and an ability to form recalcitrant biofilms, which means that it is often associated with post-harvest contamination (Freitag et al. 2009). *E. coli* and *S. enterica* belong to the *Enterobacteriaceae* and share similarities in physiology, metabolic requirements and routes of transmission in the food chain (Neidhardt F C et al. 1996), and their primary reservoirs are farmed animals. They are genetically related to important plant pathogens belonging to the soft-rot erwinia. Genomic comparisons served to highlight the similarities, including potential factors for plant colonisation (Toth et al. 2006; Holden et al. 2009). An important aspect of this family of bacteria is their metabolic flexibility and as mesophiles, their ability to proliferate under a wide range of phyio-chemico environments, which underpins their ability to grow and persist in an astonishingly wide range of hosts and habitats. In contrast, *L. monocytogenes* has more fastidious requirements, which may give rise to a degree of 'niche exclusion' and explain the relative prevalence of the *E. coli* and *S. enterica* in outbreak reports.

2. Plant-microbe interactions

2.1 Localisation of human pathogens on plant tissues

Food-borne bacteria have been reported to associate with all types of plant tissues. In keeping with localisation of endemic plant-associated microbes, the roots and rhizosphere appear to present a

preferential niche (Berg et al. 2005). This ecological habitat is rich in nutrients, relatively buffered from temperature and humidity fluctuations compared to foliar tissue (Bais et al. 2006; Holden 2018). Indeed, apparent die-off or reduction in viable, culturable cells has frequently been reported for food-borne pathogens associated with foliar tissue compared to the roots & rhizosphere (Dong et al. 2003; Kisluk and Yaron 2012; Quilliam et al. 2012).

2.2 Genomic comparisons with plant-associated bacteria

Phylogenomics of human and phytopathogenic bacteria show similar patterns, where species within the shared taxonomic families tend to exhibit a trend towards either clonality or alternatively (but not exclusively) extensive recombination. This is demonstrated by the *Enterobacteriaceae*, where *Escherichia* and *Pectobacterium* species show similar patterns of mosaicism in their genomes, indicative of divergence and multiple recombination events (Pritchard et al. 2016; Dixit et al. 2017). A similar pattern is seen for the generalist pseudomonads, such as the *Pseudomonas fluorescens* species complex (Scales et al. 2014) and the xanthomonads (Jibrin et al. 2018). On the other hand, clonality is more evident for some soil-associated bacteria, such as *Listeria* species (Ragon et al. 2008) or specialist plant pathogens such as *Xylella fastidiosa* (Nunney et al. 2014). However, more detailed examination of any species inevitably reveals a degree of clonality (Tibayrenc and Ayala 2012). The differences in recombination and divergence are a reflection of promiscuity for DNA uptake, selective pressures and different physiological responses to stresses. The result is a wide range of genotypes that enable colonisation of and persistence on plant hosts. Genomic comparisons between different groups of bacteria have been used to identify potential plant colonisation factors, both of the human pathogen *Klebsiella pneumoniae* (Holden et al. 2009) and the phytopathogen *Pectobacterium atrosepticum* (Toth et al. 2006). However, successful colonisation is multi-faceted and undoubtedly dependent on a combination of factors rather than a single genetic component.

2.3 Evolution towards a plant-adapted lifestyle

Pathogens evolve in response to selective pressure, and there are some indications that food-borne human pathogens have evolved in association with plant hosts. For example, phylogeny of STEC shows distinct clades associated with different plant species, such that serotypes normally associated with cattle, e.g. O157:H7, have also been linked to outbreaks from leafy salads like spinach and lettuce, whereas other serotypes e.g. O104:H4 and O111 have been linked to sprout- and flour-associated outbreaks (Hao et al. 2012). Whether these differences are down to selective pressure of the plant-environment, or as a result of differences in the primary reservoir is not yet clear, but does raise the possibility of the plant environment as an evolutionary driver. *E. coli* is widespread in nature and they are prevalent in arable agriculture, although show wide genetic diversity (Holden et al. 2013).

Environmentally persistent *E. coli* are termed 'naturalised' and have been identified in water (Walk et al. 2007) and soil (Brennan et al. 2010), and could act as donors for animal-derived isolates via recombination and genetic exchange. Therefore, is it less straight-forward, especially for the generalist bacteria, to assign pathogen features to non-pathogenic interactions in one host or another. Retrospective pathogen characterisation can occur only after the advent of symptomatic disease, and then generally informs on the features relating to (human) pathogenicity. The ability to persist in secondary hosts such as plants must then be defined by experimentation or chance occurrence from surveillance.

2.4 Attachment

Attachment to host tissue is considered to be a pre-requisite for colonisation. Multiple mechanisms of attachment are employed by bacteria, from non-specific interactions to specific recognition of host-derived targets. Attachment to plant hosts is covered in more detail elsewhere (Holden et al. 2012), but in general adherence mechanisms are better described for the interactions of human pathogens with animal tissue than for plant-associated bacteria with plant tissue, since adherence is considered a virulence factor for human pathogens, linked to development of infection in humans. Although there are some overlaps between mechanisms of binding between biological kingdoms, they appear to be restricted to non-specific mechanisms of attachment, e.g. via flagella (Rossez et al. 2015). On the other hand, adherence mechanisms based on specific interactions are only shared between biological kingdoms when the target receptors and ligands are shared. An example of this are mannans presented as polysaccharides, oligosaccharides or glyco-proteins of mannose, which are a target for the Type 1 fimbriae adhesin, FimH, encoded by *E. coli*, *Klebsiella pneumoniae* and *S. enterica*. Although different glycosidic linkages occur for mannans derived from animal or plant kingdoms, both forms can be recognised by *E. coli* FimH, albeit with differences in specificity (Marshall et al. 2016). On the other hand, some adhesins can only function for plant hosts since the target glycans are not present in the animal kingdom, such as *E. coli* common pilus (ECP), which binds to arabinans (Rossez et al. 2014). This functional specificity is coupled with regulatory control that is appropriate for plant-relevant temperatures. Together, these data point to a model of adherence for bacteria interacting with plants, starting with a form of non-specific adherence, which may be sufficient for proliferation and development of colonies and biofilms, as seen with soil-associated *Bacillus* species on the rhizosphere (Beauregard et al. 2013). For some species, the initial interaction is then followed by a more robust mechanism of binding, via adhesins, which provides a secure interaction (Rossez et al. 2014), and thus a starting place for colony establishment in the rhizosphere. Attachment to phyllosphere has not be investigated to the same extent, but the human pathogens also exhibit elicitation of adherence factors to facilitate biofilm formation, such as curli fibres (Wright et al. 2017).

Fimbrial attachment for plant pathogens has been described for *Erwinia amylovora* in xylem tissue (Koczan et al. 2011) and unipolar polysaccharide fimbriae have been described for *Agrobacterium tumefaciens* (Fritts et al. 2017), although these appear to be involved in biofilm formation rather than attachment to plant surfaces *per se*.

2.5 Defence response

Since the general mechanisms of the initial plant-microbe interactions are shared between plant-associated bacteria and human pathogenic bacteria, it follows that there are similarities in the plant defence response, in particular in the pathogen / microbe-associated molecular pattern (PAMP / MAMP) response. Human pathogens can colonise both foliar and root tissue, and although the plant defence response has been most widely described for leaves, similar responses have been reported for roots e.g. in *Arabidopsis thaliana* (Millet et al. 2010). Key elicitors of PAMP-triggered immunity (PTI) are molecular patterns that are abundant, widespread and well conserved in microbes. Indeed, they can induce innate immune responses in both animal and plant kingdom eukaryotes, highlighting the shared heritage of basal defence. These include the surface-expressed organelles of flagella (Gomez-Gomez and Boller 2000) and lipopolysaccharide (LPS) (Zeidler et al. 2004), and the cytosolic proteins elongation factor (EF-Tu) (Kunze et al. 2004) and cold shock proteins (CSP) (Felix and Boller 2003). Recognition of the molecular patterns by the host report on either intact bacterial cells or cellular components from lysed / disrupted cells. Recognition occurs via well-established pathways, starting with binding of the molecular pattern by the cognate plant pattern recognition receptor (PRR) in concert with co-factor proteins (Segonzac and Zipfel 2011), triggering signalling cascades (Bigeard et al. 2015) and induction of defence responses that strengthen cell walls (Voigt 2014) or produce antimicrobials (Qi et al. 2017). While 'professional' plant pathogens can deliver effector proteins that subvert PTI and hence reduce its impact on microbial clearance by the plant host (Boller and He 2009), whether the same occurs for human pathogens is less clear.

Activation of PTI by bacterial flagella has been extensively studied and in plants requires binding of a conserved peptide of flagella to the PRR receptor FLS2 in concert with BAK1 (Chinchilla et al. 2007). Flagella derived from human pathogenic bacteria, e.g. *S. enterica*, are also recognised by FLS2 and lead to a defence response in *A. thaliana* (Garcia et al. 2014). However, in an effort to identify bacterially-associated PAMP responses in *A. thaliana*, inoculation with a flagellin mutant of *E. coli* O157:H7 did not result in significant PAMP-induced gene expression changes compared to a flagellin wild type strain (Thilmony et al. 2006). Occurrence of a similar pattern for a pair of *Pseudomonas syringae* flagellin +/- strains lead to the speculation that flagella organelles in the context of bacteria have a minor PTI impact and are only one of several PAMPs responsible for triggering basal immunity. It does appear however, that the site of inoculation influences the response, with stronger flagellin

perception on leaf surfaces compared to the intracellular spaces (Thilmony et al. 2006; Zipfel et al. 2004).

Identification of the receptor, CORE for the CSP peptide indicates that there is some taxonomic specificity in the plant response, as CORE only appears to be present (to date) in the *Solanaceae* family (Wang et al. 2016). However, its expression in *A. thaliana* resulted in a functional immune response and with concomitant reduction of phytopathogens used in a challenge assay. CSP are ubiquitous in bacteria across diverse taxonomic lineages (Fig. 1) and normally present in multi-copy. Moreover, they are abundantly expressed at temperatures relevant to colonisation of plant hosts (Phadtare and Inouye 2008). Therefore, it is perhaps unsurprising they are perceived as PAMPs in plants. It is notable, however that they are not detected in an analogous manner in animal hosts. The same appears true for the PAMP EF-Tu. In animals, perception of PAMPs/ MAMPs occurs via Toll-like receptors, which share functional and structural similarities to plant PRR. Animal PAMP perception of LPS and flagellin occurs via TLR-4 and TLR-5, respectively (Takeda et al. 2003). It is possible that differences in the repertoire of cross-kingdom in PAMP perception is as a result of PAMP expression differences in association with the different hosts. For example, five of the *E. coli* O157:H7 *csp* genes were substantially differentially induced (> 9-fold) on exposure to spinach leaf extracts, while the genes encoding EF-Tu (*tuf*) were also induced (~ 1.5-fold) (Crozier et al. 2016).

Bacterial effector proteins that supress basal immunity do so by targeting components of the signalling cascade or transcription factors. Since basal immunity in eukaryotes is ancestrally shared, there is the potential for cross-kingdom functional activity of bacterial effectors (Brunner and Fraiture 2014; Zipfel and Felix 2005). A clear example was demonstrated for the *S. enterica* serovar Typhimurium effector, SpvC, which functions in animal hosts to suppress basal immunity and was shown to similarly supress a flagellin-dependent PAMP-response in *A. thaliana* protoplasts (Neumann et al. 2014). Like the *Ps. syringae* effector AvrPto, *S.* Typhimurium SpvC inhibited *FRK1* expression, although its range of inhibition was not as extensive as the phytopathogen effector counterpart. SpvC was shown to act in plant hosts in the same manner as animal hosts (Mazurkiewicz et al. 2008), by dephosphorylating activated MAP-kinases, a central component of the signalling cascade. Furthermore, its deletion resulted in a decreased ability of *S.* Typhimurium to proliferate in infiltrated *A. thaliana* leaves (Neumann et al. 2014).

The professional phytopathogens are well equipped to manipulate immune responses with a suite of effector proteins, where they induce effector-triggered immunity (Jones and Dangl 2006). Specificity in the interaction for this group of pathogens results in differences in the outcome for compatible host or non-host interactions (Senthil-Kumar and Mysore 2013). Phytopathogen effectors are secreted via

a type 3 secretion system (T3SS) (Grant et al. 2006), and although human pathogens similarly secrete their effectors via the T3SS in animal hosts, there are structural and potential regulatory differences between the two groups of bacteria (Roe et al. 2003). This raises the question about the potential cross-kingdom scope of human pathogen-derived effectors, and how they are expressed in plant hosts. It appears then, that the extent of plant immunity in response to human pathogens occurs at the PAMP-level. This is borne out by the observation for *E. coli* O157:H7, where induction of the PAMP-response in infiltrated *A. thaliana* leaves overlapped with a non-pathogenic *Ps. syringae* strain lacking a T3SS (*hrp*-) (Thilmony et al. 2006). As such, human pathogens lend themselves to more detailed investigation of innate immunity in plants, without the masking effect of ETI.

2.6 Establishment and metabolism

Following initial attachment and successful avoidance or countering of the host defence, bacterial colonies become established. The patterns of colonisation of human pathogens on plants bear some similarities with plant-associated bacteria, e.g. between *E. coli* O157:H7 and *P. atrosepticum* (Wright et al. 2013). Differences are also evident, for example *E. coli* O157:H7 on spinach roots accumulates on the surface and in natural crevices, i.e. between cells or surrounding the base of root hairs, while *P. atrosepticum* on potato roots tends to invade root epidermal cells, with less density of bacteria evident on the cell surfaces (Fig. 2). This is presumably down to the invasive phenotype conferred by the activity of plant cell wall degrading enzymes in *P. atrosepticum* (Toth et al. 2006). *E. coli* O157:H7 also has the ability to internalise without the benefit of extracellular enzymes, and has been found to enter plant cells, or can be present in the extracellular apoplast space in roots (Wright et al. 2013) and leafy tissue (Wright et al. 2017). The basis to entry into plant cells is unknown but could be exploitation of senescent cells. On the other hand, the ability to enter into the apoplast of either root or foliar tissue is widely reported for human pathogenic bacteria, admittedly mostly demonstrated under laboratory conditions (Deering et al. 2012; Hirneisen et al. 2012), where it appears that human pathogens, like plant-associated bacteria, take advantage of natural openings such as stomatal pores (Wright and Holden 2018) or emergence of lateral roots (Wright et al. 2013).

Successful establishment and development of colonies on plant host tissue necessitates appropriate metabolism. The role of metabolism as a central facet of adaptation to host or habitat is well accepted and is covered in more detail elsewhere for human pathogens (Alteri and Mobley 2012; Rohmer et al. 2011) and for plant-associated bacteria (Holden 2018; Hugouvieux-Cotte-Pattat 2016; Lodwig and Poole 2003; Price-Whelan et al. 2006). Wholescale transcriptional changes occur for human pathogens on contact with plant tissue or plant-derived substrates (Goudeau et al. 2013; Kyle et al. 2010; Mark et al. 2005), with specificity for different plant tissues from the same species, e.g. differential responses of *E. coli* O157:H7 to root exudates, leafy lysates or leaf cell wall polysaccharides of spinach

(Crozier et al. 2016). Such differences in metabolic pathways can be mapped and linked to available substrates (Holden 2018) and for the pseudomonads, has been shown to be associated with a generalist or specialist life-style on plant hosts (Mithani et al. 2011). Therefore, for human pathogens, much like their plant-associated counterparts, metabolic flexibility and capacity is a key factor in successful colonisation on plant hosts.

3. Control and management approaches

3.1 Transmission pathways

The primary reservoir for most foodborne human pathogens is farmed animals, while others, such as *Listeria monocytogenes* are considered to be soil saprophytes. Regardless of primary source the main transmission routes onto plants during the pre-harvest stage are shared: from contaminated soil or contaminated irrigation water. Irrigation water is seen as the most important route of transmission (Allende and Monaghan 2015). Outdoor grown plants are subject to other inputs, e.g. direct manure contamination, prior contamination of the soil from manure, or contamination from wild-animals or birds, as was the case for the large-scale outbreak of *E. coli* O157:H7 from spinach plants in 2006 (Jay et al. 2007). Another potential source is from contaminated seeds, which was a possibility for the large-scale outbreak of *E. coli* O104:H4 from fenugreek in 2011 (Buchholz et al. 2011). This isolate and other human pathogens have been shown to persist for prolonged periods on seeds (Knodler et al. 2016; Van der Linden et al. 2013), and analysis of endemic seed microbiomes shows the potential for this route of transmission of human pathogens (Nelson 2018).

3.2 Geographical differences

Most of the causative organisms of foodborne illnesses are reportable in wealthy countries, which together with detail epidemiological questionnaires for food source attribution have resulted in detailed databases that allow decision making and implementation of control measures. A clear example of this arose out of the very large-scale outbreak of *E. coli* O104:H4 from fenugreek in the EU, in 2011 (Buchholz et al. 2011), with implementation of EU legislation for microbiological criteria ((EU) No 209/2013) and traceability ((EU) No 208/2013) of sprouted seeds. Many countries do not have the infrastructure or systems for reporting foodborne illness in such detail, which has resulted in a somewhat skewed picture of where the problem occurs. However, given that the main routes of transmission are from irrigation water (Allende and Monaghan 2015) and animal manure (FSA 2009), the burden of disease from consumption of contaminated fresh produce crops is likely to be equally high or even higher in these countries. Furthermore, diarrhoeal disease is one of the major causes of ill health worldwide, with an estimated 600 million (almost 1/10 people) worldwide falling ill after

eating contaminated food (WHO 2018), of which a significant proportion presumably arises from plant-based foods.

An emerging aspect of foodborne illness is regional differences between Northern America and European countries. These areas are within the Northern hemisphere geographical temperate zone and have similarities in their primary production requirements and approaches. However, there appears to be a significant difference in the incidence of foodborne illness arising from plant-based food items. Although directly comparable datasets are not available, food source attribution data show that in the USA for the period 1998 – 2008 46 % of outbreaks and 23 % of death were associated with produce (Painter et al. 2013), while in EU member states 17 % of outbreaks were attributed to produce for the year 2015 (EFSA 2016). The basis to this difference is unknown but could stem from a number of factors including distribution systems, irrigation strategies and weather impacts. Proximity to livestock farming has been identified as an important risk factor, although is unlikely to be a major driver for the geographical differences since livestock densities are similar between the regions, e.g. the USA reported 90 M cattle for the year 2012 (USDA 2018) while the EU (28 member states) reported were 87 M for the year 2013 (Eurostat 2018).

3.3 Management of human pathogens on edible crops

Control of human pathogens on plants relies heavily on risk management and implementation of HACCP principles (EFSA BIOHAZ Panel (EFSA Panel on Biological Hazards) 2014). Given the role of irrigation in transmission of pathogens, various guidelines and regulations are in place for microbial quality of the water. In addition, farm management practices are put in place to protect edible crops from wildlife (Gil et al. 2015). Plant age appears to be an important factor for the ability of human pathogens to colonise plants, with sprouted seeds or young plants marketed as micro-leaf at higher risk of colonisation (Wright and Holden 2018), incurring regulations to be put in place for sprouted seeds ((EU) No 209/2013; (EU) No 208/2013). Contamination can also occur post-harvest, during the production process, requiring application of food safety risk management systems pre- and post-harvest and appropriate control procedures to mitigate the risk (CFA 2007; ICMSF 2002). One aspect currently under investigation for control of plant pathogens that could also aid in food safety is in exploitation of the plant defence response. Elicitors that prime a defence response have been shown to control bacterial and fungal pathogens on plants (Wiesel et al. 2014), and appropriate targeting of the defence response could be extended to include human pathogens.

4. Conclusions

Investigation of the molecular basis underpinning the interactions of human pathogens on plants has developed to provide quite a detailed picture over the last 10 years or so. It shows some striking

similarities with plant-associated bacteria, including phytopathogens, but some important differences that impact the outcome of the interaction. There are still important questions, e.g. relating to the extent and subversion of the plant defence response by human pathogens; the use of non-model, relevant edible crop species for examination of the immune response; the focus on just two or three key species of food-borne pathogens, with little or no data for the less common pathogens. There are also important gaps relating to the wider ecology of human pathogens in the plant environment, and in relation to endemic plant microbiota. Geographical differences have also emerged and at this point, it is unclear why this has occurred and how widespread it is, which necessitate a requirement for international networks. Finally, control has focused on achieving sufficient levels of microbiological food safety criteria, which sets the field apart from plant pathology, where the aim is for crop protection. However, there are important overlaps here that could be exploited for the dual purpose of crop protection and food safety. Therefore, both disciplines can continue to benefit from a shared dialogue and research interests.

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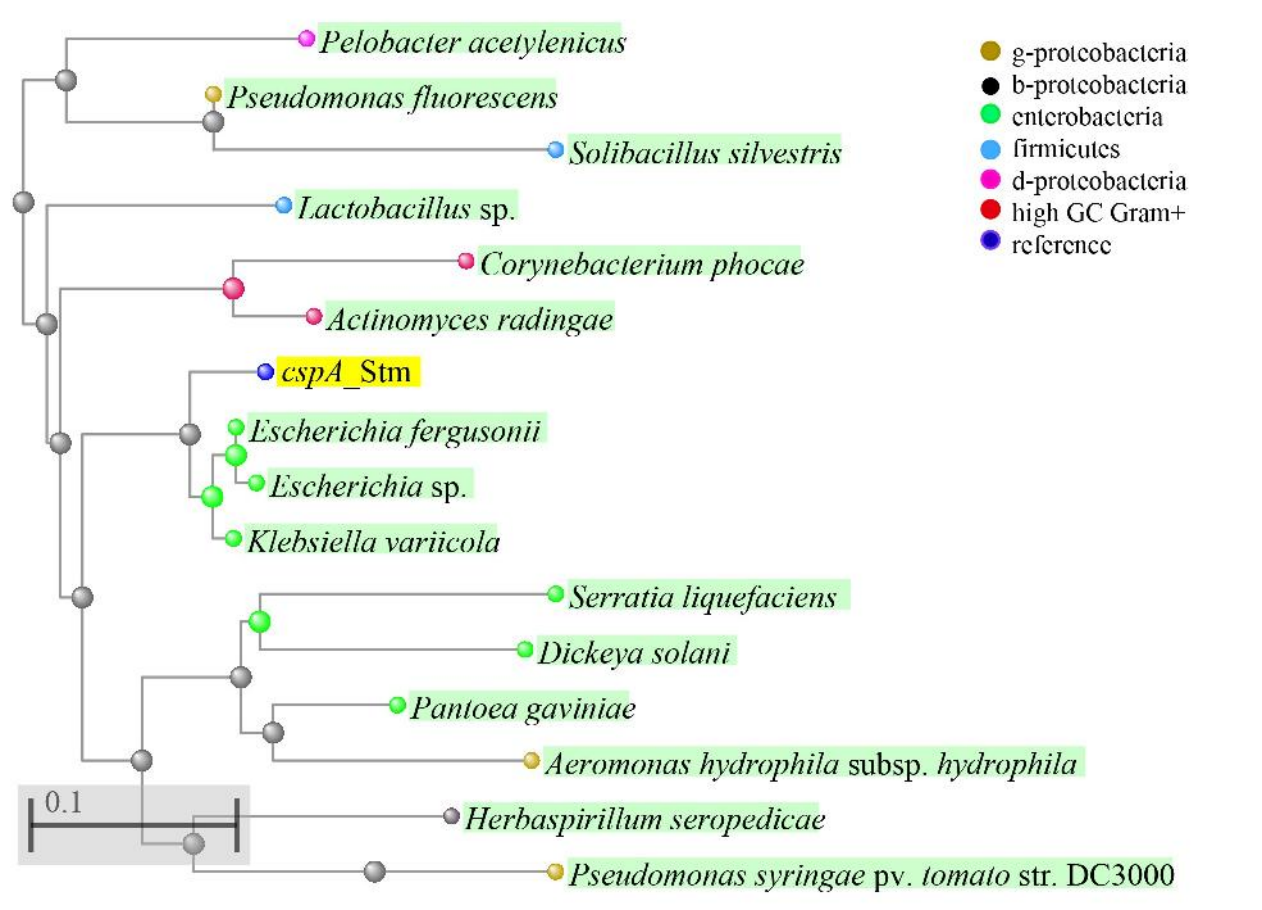
Figure legends

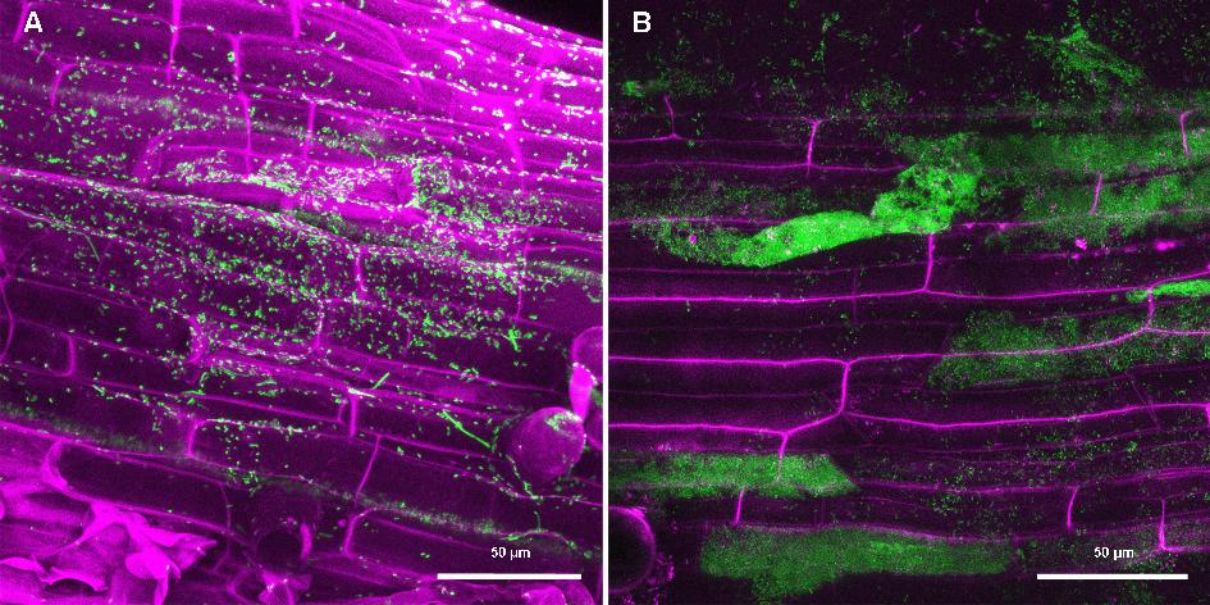
Figure 1 Phylogenetic alignment of *csp* gene sequences

Representative *csp* gene sequences from a sub-set of divergent bacteria (indicated by coloured nodes) were selected by BLASTn alignment to a reference sequence (*cspA*_Stm – highlighted yellow: *cspA* gene from *S.* Typhimurium), and a phylogenetic tree generated using a fast, minimum evolution algorithm (Desper and Gascuel 2004).

Figure 2 Patterns of root colonisation by human pathogenic or phyto-pathogenic bacteria

Spinach plants inoculated with *E. coli* O157:H7 (isolate Sakai) (A) and potato plants inoculated with *P. atrospecticum* (isolate SCRI-1043) (B) were collected 6 days after inoculation, and the roots imaged by laser scanning con-focal microscopy. Plant tissue was labelled with Texas red to stain the cell walls (magenta) and both bacterial isolates are expressing plasmid-borne GFP markers (green). The experimental set-up was part of the study described previously (Wright et al. 2013).


Pelobacter acetylenicus
Pseudomonas fluorescens
Solibacillus silvestris
Lactobacillus sp.
Corynebacterium phocae
Actinomyces radingae
cspA_Stm
Escherichia fergusonii
Escherichia sp.
Klebsiella variicola
Serratia liquefaciens
Dickeya solani
Pantoea gaviniae
Aeromonas hydrophila subsp. hydrophila
Herbaspirillum seropedicae
Pseudomonas syringae pv. tomato str. DC3000
0.1
g-proteobacteria
b-proteobacteria
enterobacteria
firmicutes
d-proteobacteria
high GC Gram+
reference


A
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