CHAPTER 15

A Review on the Implications of Interaction Between Human Pathogenic Bacteria and the Host on Food Quality and Disease

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15.1 Human Pathogenic Enteric Bacteria and Their Association With Fresh Agricultural Products

Studies suggest that increasing health awareness has resulted in a significant increase in the demand for ready-to-eat fresh produce. However, several reports indicate the emergence and outbreaks of food-borne illness that have been found to be closely associated with fresh fruits and vegetables; therefore, researchers across the globe have been focusing on identifying microbial contamination of fresh produce (Tomasi et al., 2015; Mir et al., 2018). Until the advent of this century, much research was focused on studying the interaction of enteric pathogens with human and animal hosts and food-borne illness was believed to be result of postharvest microbial contaminations. Recently, the notion has been significantly questioned in the scientific community and, therefore, much research in today's scenario is focused on the ecology of enteric pathogens on plant surfaces. Previously, enteric pathogens were known to colonize human or animal digestive tract, an environment that provides protection from external environmental factors and also provided a variety of easily accessible nutrients. However, recently documented reports suggest that enteric pathogens colonize the phyllosphere and the rhizosphere of plants. In the present section, we shed light on the most important and classical examples of enteric pathogens that are known to be associated with food-borne illnesses of fresh fruits and vegetables.

15.1.1 Escherichia coli

Consumption of contaminated foods, especially raw or undercooked ground meat products and raw milk has been known to be associated with the transmission of *E. coli* O157:H7 into humans. Other sources of infection include fecal contamination of water and other foods,

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as well as cross-contamination during food preparation (from contaminated surfaces and kitchen utensils). *E. coli* O157:H7 has been considered as a serious pathogen because of its high pathogenicity, its ability to infect the host even at very low infective doses, its ability to survive harsh and deleterious environmental conditions, especially frozen conditions (Tilden Jr et al., 1996; Franz et al., 2008; van Elsas et al., 2011; Semenov et al., 2009; Yao et al., 2013; Wang et al., 2014) and what make it even a more serious and dangerous pathogen is its ability to transfer the virulence genes into nonpathogenic *E. coli* strains (Herold et al., 2004). The bacterial pathogen causes hemolytic uremic syndrome that can lead to death, particularly in children, elderly especially the ones who are immunocompromised. Of serious concern is the fact that raw fruits and vegetables, especially fresh-cut leafy greens, are more and more being recognized as the important vehicles for the transmission of *E. coli* O157:H7 (Fremaux et al., 2008). It is pertinent to mention here that *E. coli* O157:H7 was identified as the causal agent of the largest outbreak of bacterial enteric disease in recent times, with more than 6000 cases epidemiologically linked to contaminated radish sprouts in Japan in 1996 (National Institute of Health Infection Disease Control Division, 1998; Watanabe et al., 1999). Recently in 2013, consumption of contaminated, sprouted fenugreek seeds resulted in an outbreak of hemolytic-uremic syndrome (HUS) and hemorrhagic colitis (HC) that started in Germany and subsequently spread throughout Europe and North America. The causative agent was an enterohemorrhagic *E. coli* (EHEC) strain of serotype O104:H4 (European Food Safety Association, 2013). Bielaszewska et al. (2011) and Mellmann et al. (2011) reported that the strain possessed a combination of virulence factors from both Shiga toxin (Stx)-producing *E. coli* (STEC) and enteroaggregative *E. coli* (EAEC) strains. Information on *E. coli* contamination of fresh produce has been compiled and is presented in Table 15.1.

15.1.2 Salmonella enterica

A review on the literature of *Salmonella enterica* shows that the occurrences of *S. enterica* in fresh produce have been associated with surface waters, used commonly for irrigation purposes in agricultural fields. Documented literature also suggests that *S. enterica* is the cause for most frequent outbreaks from fresh produce (Barak and Schroeder, 2012). *S. enterica* serovar Typhimurium DT104 has been reported in cases where contaminated lettuce was consumed (Horby et al., 2003; Takkinen et al., 2005). The survival of the enteric pathogen on fresh produce has been studied in great detail over the last decade. Findings suggest that *S. enterica* has abilities to survive desiccation stress (Davies and Wray, 1995). Studies have shown that small populations of *S. enterica* can survive on crop plants and eventually increase to infectious dose levels once favorable conditions are restored. These characteristics of the pathogen make it a serious contaminant associated with fresh produce (details are presented in Table 15.1). A comprehensive analysis of the documented literature suggests that the reported cases of *S. enterica* outbreak on fresh produce are more on fruits as compared with leaves (Barak and Schroeder, 2012). Reports suggest that *S. enterica*

Table 15.1: Human pathogenic bacteria and their association with fresh agricultural produce

Pathogen	Contaminated Agricultural Produce	References
E. coli O157:H7	Spinach, radish, alfalfa, cabbage, celery, coriander, cress sprouts	Jay et al. (2007), Jay-Russell et al. (2010), Nathan (1997), and Zepeda-Lopez et al. (1995)
E. coli O157 CDC	Leafy greens	California Leafy Green Handler Marketing Board (2012)
E. coli O104:H4	Fenugreek	Buchholz et al. (2011)
E. coli O26	Clover sprouts	http://www.cdc.gov/ecoli/2012/O26-02-12/
E. coli O145	Lettuce	Taylor et al. (2013)
S. enterica	Alfalfa, mung, clover, tomato, cantaloupe, beet leaves, cabbage, cauliflower, chili, green onion, parsley, pepper, spinach	Rimhanen-Finne et al. (2011), Mohle-Boetani et al. (2009), and Orozco et al. (2008)
Clostridium difficile	Ready-to-eat salads; potatoes, onion, mushroom, carrot, radish, cucumber	Bakri et al. (2009) and Al Saif and Brazier (1996)
Bacillus cereus	Ready-to-eat vegetables, potato	Chon (2016) and Luo et al. (2016)
Campylobacter **spp.**	Leafy vegetables, lettuce, parsley, pepper, prepacked salads, spinach	Park and Sanders (1992) and Salaheen et al. (2016)
Listeria monocytogenes	Cucumber, cabbage, carrot, tomato, lettuce	Ajayeoba et al. (2016)
Cronobacter **spp.**	Chinese cabbage, cucumber, carrot, lettuce, strawberry, cabbage	Chen et al. (2016) and Vojkovska et al. (2016)

lacks biochemical assimilatory machinery for sucrose utilization (Lin, 1996), one of the main sugars present in leaf (Lindow and Brandl, 2003). The two most severe serotypes of *S. enterica* Typhi and Paratyphi A, which cause typhoid and paratyphoid fever, are responsible for hundreds of thousands of deaths worldwide every year. Results show that serovars have not evolved independently and recombination plays a key role in the genomic evolution, diversification, and ecological adaptation of lineages of *S. enterica* (Didelot et al., 2011).

15.1.3 Clostridium difficile

Clostridium difficile infection can often result in severe diarrhea. *C. difficile* a spore-forming, Gram-positive anaerobe produces two toxins, viz., toxin A (an enterotoxin) and toxin B (a cytotoxin), which can cause gastrointestinal disease, especially in immunosuppresed patients (Nitzan et al., 2013). A review of the documented literature shows that *C. difficile* has been reported from both animals and humans (Keessen et al., 2011; Songer, 2010). Reports on the occurrence of *C. difficile* in ready-to-eat salads and vegetables have been previously reported by several researchers (documented in Table 15.1). Recent studies have shown that the pathogen has potential of transmission through food supply. Eckert et al. (2013) assessed the prevalence of ready-to-eat raw vegetables contaminated with *C. difficile* and observed that ready-to-eat salads were contaminated. In another recent study, the prevalence of

C. difficile was observed in ready-to-eat foods, indicating food as a reservoir for the pathogen (Rahimi et al., 2015). Soil, fertilizers (manure), water, and processing environments could be the various possible sources of contamination of *C. difficile* in fresh produce (Weese, 2010). The spore-forming abilities of *C. difficile* allows the bacterium to survive environmentally unfavorable conditions, thereby facilitating its transmission.

15.1.4 Bacillus cereus

B. cereus is a group of free-living bacteria and some strains can cause food-borne illnesses in humans. *B. cereus* is one of the major pathogens associated with raw vegetables worldwide (Park et al., 2013). The two types of gastrointestinal disease (emesis and diarrhea) are caused by *B. cereus* (Ki Kim et al., 2009; Arslan et al., 2014). Ingestion of the toxin cereulide secreted by *B. cereus* causes an emetic type of illness (Takeno et al., 2012), whereas consumption of food contaminated with diarrheal toxin secreted by *B. cereus* causes diarrhea (Kim et al., 2011). Since *B. cereus* is a soil deviling microbe, its wide occurrence in vegetables and other agricultural fresh food is not surprising. Compiled information on the occurrence of *B. cereus* on fresh produce is presented in Table 15.1. Occurrence of *B. cereus* in fresh vegetables depends significantly on whether or not the crops were fertilized with human or animal wastes or irrigated with water containing such wastes. A review on the recent literature indicates occurrence of *B. cereus* in a wide variety of foods (Dzieciol et al., 2013; Li et al., 2016). Recent studies carried out by Kim et al. (2011) and Hwang and Park (2015) have shed light on the molecular characterization of enterotoxin genes in *B. cereus*. Their findings show that four different enterotoxins, viz., hemolysin BL (Hbl), nonhemolytic enterotoxin (Nhe), cytolysin K (CytK), and enterotoxin FM (EntFM), are hypothesized to play key roles in disease.

15.1.5 Campylobacter *spp.*

Recent documented literature suggests that cross-contamination from fertilizers, soil, and irrigation water is among the prime reasons for *Campylobacter* spp. contamination in fresh produce (information on the occurrence of *Campylobacter* spp. on fresh produce is presented in Table 15.1). The pathogen has resulted in a number of food-borne outbreaks associated with raw fruits and vegetables (Khalid et al., 2015; Tang et al., 2016). Chai et al. (2009) also reported *Campylobacter* spp. contamination in vegetable farms. One of the major concerns associated with *Campylobacter* spp. contamination (especially *C. jejuni*) is that of multidrug resistance especially toward quinolones and erythromycin (Ge et al., 2013). Studies carried out by Sheppard et al. (2013) highlight the molecular mechanisms involved in the pathogenicity. Their findings indicate that *C. coli* became progressively adapted to the agricultural niche via genomic introgression with *C. jejuni*. Recent studies by Pascoe et al. (2015) have shown that the mechanism of biofilm production in *Campylobacter* spp. has

considerably evolved and is a result of different genetic backgrounds. These evolved biofilm formation mechanisms are believed to be responsible for the organism's survival and dispersal in agricultural environments. Pearson et al. (2015) have recently carried out studies on *C. coli* and *C. jejuni* isolates in agricultural and nonagricultural systems to evaluate whether phylogenetic relatedness or sharing of environmental niches affects the distribution and dissemination of type II CRISPR (clustered regularly interspaced short palindromic repeats)-Cas (CRISPR-associated) system.

15.1.6 Listeria monocytogenes

Among the six known species of *Listeria* (*L. monocytogenes, L. ivanovit, L. seeligeri, L. innocua, L. welshimeri, and L. grayi*), *L. monocytogenes* is considered to be the most deleterious food-borne pathogen. Its detection in vegetables, fruits, and dairy products has been widely reported (Kasalica et al., 2011; Ajayeoba et al., 2016). The pathogen is a Gram-positive, facultative anaerobe that is a nonsporulating motile bacterium capable of causing listeriosis (Bayoub et al., 2010). Recent studies have suggested the involvement of previously uncharacterized cellobiose PTS system in central nervous system infections (Grad and Fortune, 2016). The occurrence of the pathogen in ready-to-eat vegetables has been a matter of serious concern (details in Table 15.1), considering the high demand of such products in the market. The primary source of contamination of agricultural fresh produce has been associated with the contaminated water from sewage sludge for the purpose of irrigation (Oranusi and Olorunfemi, 2011). A comprehensive detailed overview has been recently documented in a review on the fresh farm produces as a source of pathogens by Mritunjay and Kumar (2015). They highlight that a major source of contamination of fresh agricultural produce is because of the use of contaminated water (used for sprinkling purpose in order to keep the vegetables fresh) and contaminated containers (used for transportation purposes). Recent report by Stea et al. (2015) highlights the prevalence and diversity of *L. monocytogenes*, in an urban and a rural municipal source. The study documents important findings that can go a long way in order to understand the ecology and occurrence of the pathogen under agriculturally diverse environments.

15.1.7 Cronobacter *spp.*

Cronobacter spp. was formerly described in the literature as *Enterobacter sakazakii*. The recent literature based on whole-genome sequencing and multilocus sequence typing (MLST) targeting 7 genes (atpD, fusA, glnS, gltB, gyrB, infB, ppsA) has resulted in the identification of seven species in the *Cronobacter* genus viz. *C. sakazakii, C. malonaticus, C. turicensis, C. muytjensii, C. dublinensis, C. universalis, and C. condiment* (Forsythe et al., 2014). Studies on the virulence factors associated with the pathogenicity of *C. sakazakii* have been recently published from our laboratory (Singh et al., 2016). The authors highlight that in addition to

different virulence factors viz. outer membrane protein A (ompA), plasmid-associated genes such as filamentous hemagglutinin (fhaBC), *Cronobacter* plasminogen activator (cpa), and genes responsible for iron acquisition (eitCBAD and iucABD/iutA), several biophysical growth factors such as the formation of biofilms and resistance to various environmental stresses also contribute to the pathogenic potential of this pathogen. Recent studies carried out by Chen et al. (2016) have focused on analyzing a large number of vegetables in an attempt to find the source for this pathogen. Similar studies have been carried out in our laboratory that have been focusing on the isolation of *C. sakazakii* from a wide variety of food sources (for details please refer to Singh et al., 2015a, b). From our laboratory studies, it is evident that out of the 219 food samples have been evaluated, a total of 45 *Cronobacter* spp. were isolated. *Cronobacter* spp. in a food sample category of herbs and spices accounted for 34.3% of total samples, whereas 26% were from vegetables and fruits. In another recent study, Vojkovska et al. (2016) detected *Cronobacter* spp. in vegetables, fruit, and environmental samples collected from local farms and supermarkets in the Czech Republic. They further reported that environmental isolates of *Cronobacter* spp. create the capsule more often than the isolates of clinical origin. The capsule formulation facilitates enhanced desiccation resistance of the bacterium and increases its ability to attach to surfaces and create biofilms.

15.2 Entry of Human Pathogenic Bacteria into the Food Chain: Tracking the Point of Origin

A review on the literature, in an attempt to track the point of origin of entry of human pathogenic, enteric bacteria into the food chain (with special reference to fresh produce) shows that the entire process can be divided into two broad categories: first, the point of entry of enteric pathogen is at the site where the agricultural produce is being raised. The contaminating sources include water (used commonly for irrigation purposes) and raw or inadequately amended manure. Second, the enteric pathogen can enter the food chain during postharvest processing. In the following section, we review the potential sources of contamination of enteric pathogens in fresh agricultural produce.

15.2.1 The Potential Role of Water in the Contamination of Fresh Agricultural Produce

As a general practice in agricultural farms, groundwater is used for irrigation purposes. However, it is well-established and a well-known fact that irrigation water could be a potential source of enteric pathogen contamination, since it is often contaminated by effluents from municipal waste (Pachepsky et al., 2011). The problem is highly reported in underdeveloped and developing countries. A recent report by Akinde et al. (2016) highlights that fresh vegetables could be an easily available transmission vehicle for human pathogens, because of poor irrigation water quality at vegetable farms in southwestern Nigeria.

Contamination of agricultural produce in fields irrigated with contaminated waters is easily possible when the produce is in close contact with the soil matrix. Contaminated water can lead to the colonization of enteric pathogens into aerial tissues and root systems of fruit and vegetable plants (Martínez-Vaz et al., 2014). The consumption of raw agricultural produce by humans can eventually lead to the transmission of enteric pathogens and therefore has been identified as the most likely cause of disease outbreak as discussed in detail earlier, in Section 15.2.

Contamination of irrigation waters in agricultural fields as a result of municipal waste is only one of the possible means of transmission of enteric pathogens. Water can also be contaminated by livestock (cattle or sheep) defecation, especially if they use rivers for drinking or as crossing points. Runoff from animal pastures into artificial or natural water bodies can also create havoc. A review of the documented literature in this context shows interesting reports and reviews on the contamination of water sources by *E. coli* O157 (Quilliam et al., 2011). Recently, Hamm et al. (2016) documented a first report on cattle being an important reservoir of an unusual, highly virulent EHEC O104:H4 strain. As discussed previously in Section 15.2.1, the pathogen resulted in a serious outbreak in early May 2011.

The development of quick and reliable methods for the detection of enteric pathogens in water samples is the need of the hour. In this regard, recently researchers have been focusing on developing accurate and less time-consuming methodologies. Recently, Banting et al. (2016) described a most probable number (MPN)-qPCR assay for molecular-based detection of *Campylobacter* spp. especially in irrigation water samples. Henao-Herreño et al. (2017) evaluated *Salmonella* contamination in Bogotá River water that was being used for irrigation purposes for lettuce, broccoli, and cabbage. Based on the *Salmonella* concentration, the authors developed a qPCR-based quantitative microbial risk assessment model. Their results emphasized the presence of wastewater treatment, before Bogotá River water is used for irrigation purposes.

15.2.2 The Potential Role of Noncomposted or Improperly Composted Manure in the Contamination of Agricultural Fresh Produce

Organic fertilizer inputs in agricultural fields in the present scenario has significant environmental benefits over the use of chemical fertilizers and the practice has gained much importance. Organic matters such as animal manure, sewage sludge, and food wastes are decomposed using the anaerobic digestion process which has been reported to be an effective measure in controlling enteric pathogens (Horan et al., 2004). However, it has been observed that there are reports on the occurrence of food-borne pathogenic bacteria on crops, which were grown in soil that contained contaminated manures. A recent study in this regard carried out by Biswas et al. (2016) suggests that there exists significant variations in the survival of pathogens (the authors carried out their study with three enteric pathogens viz. *E. coli*, *Salmonella* spp., and *Listeria monocytogenes*) with temperature and environmental conditions, that is, liquid dairy manure in anaerobic and limited aerobic storage conditions.

Another important aspect of enteric pathogens in manure, which eventually contaminate the fresh produce, is the ability of these pathogens to be able to develop resistance against antibiotics. A review of the documented literature shows that there is a significant rise in antibiotic-resistant bacteria in animal feces, which can enter into the food chain since the animal manure is extensively used in farmlands (da Costa et al., 2013). A recently documented report by Takemura et al. (2016) indicates that because of extensive use of veterinary antibiotics, there is high persistence and survival of antibiotic-resistant bacteria in livestock manure. Similar studies on the prevalence and persistence of potentially pathogenic and antibiotic-resistant bacteria during anaerobic digestion treatment of cattle manure have been reported by Resende et al. (2014).

Considering the above problems of persistence and survival of enteric pathogens in noncomposted or improperly composted manure, we must (a) understand the factors the can help in the reduction of enteric pathogens in manure and (b) develop biotechnologies for improvement of dairy manure treatment. The physical character of the manure (i.e., liquid manure, slurry manure, or solid manure) can significantly influence the survival of enteric pathogens, which in turn depends on the farm management practices and also on the livestock. In manure which is in slurry or liquid form, survival of the enteric pathogens is high because of the presence of favorable moisture and alkaline pH (Cools et al., 2001). In case of solid/dried manure, the temperature is an important factor that determines the persistence of enteric pathogens in the manure. Recent reports published by Park et al., 2016, specifically focus on the role of temperature in the survival of manure-borne generic *E. coli*, *E. coli* O157:H7, and fecal coliform in soils. Erickson (2016) carried out studies on the survival of *Salmonella* or *E. coli O157:H7* during the holding of manure-based compost mixtures at sublethal temperatures (20–40°C). They simultaneously interrogated the influence of carbon amendment to the compost mixtures. An environmental concern which has recently received much attention is that agricultural facilities having storage of large quantities of manure especially in dried form, may serve as a source of airborne contamination of leafy greens being cultivated in nearby fields. Dehydrated animal manure, results in the generation of dust-like particles that can be small enough to become readily airborne (Berry et al., 2015). Research in regard has been initiated and Oni et al. (2015) has recently documented a report that focuses on the characterization of parameters that focus on the survival of *S. enterica* in or on dust particles of dried turkey manure and litter that could be aerosolized during handling and survive on leafy greens in the fields.

Biotechnologies for the reduction of survival and persistence of enteric pathogen in manure are highly advocated. Anaerobic digestion of cattle manure is one of the most environmentally favorable biotechnologies for managing enteric pathogen microbial load (Manyi-Loh et al., 2013). Recently Manyi-Loh et al. (2014) documented a 1-log reduction of *E. coli* and *Campylobacter* spp. (i.e., 90% decay rate) as opposed to a 2-log reduction of *Salmonella* spp. that occurred between day 9 and 14, but a similar 1-log reduction of these cells during the rest of the process indicating a 90%–99% kill rate was achieved in mesophilic

anaerobic digestion. A detailed review on the use of anaerobic digestion technology for reducing the persistence and survival of enteric pathogens has been recently documented in a review by Manyi-Loh et al. (2016).

15.2.3 Enteric Pathogen Can Enter the Food Chain During Postharvest Processing

Contamination of fresh produce during the postharvest processing is one of the most significant points of entry of enteric pathogens into food chain. The contamination can be due to injury to the plants during the harvesting or during storage and transportation of the fresh produce. Mechanical means to harvest the fresh produce at times result in injury to the plant tissue. Such injuries are an open invitation for the enteric pathogens to colonize the plants, since the nutrients available are easily accessible to the bacterium. Similar problems arise during storage and transportation of fresh produce. Washing of the fresh produce, is a common practice, however, the presence of pathogenic bacterium in contaminated water can easily result in entry of the bacterium into the agricultural produce. Good manufacturing practices (GMPs) can play a significant role in preventing the risk of contamination. A recent review article by Gil et al. (2015), highlights the strategies that can be employed to prevent microbial contamination in fresh leafy vegetables during pre- and postharvest processes.

15.3 Interaction Between Enteric Pathogens and Plant Hosts

Previously, it had been believed that enteric bacterial pathogenesis on humans was defined by their ecological niche. However, reports on the outbreak of disease that have been caused as a result of consumption of contaminated fresh produce have challenged the traditional view point (recent reports are discussed in Sections 15.2 and 15.3). It is now a well-established fact that enteric pathogens colonize plant tissues and thereby uses the plant host as a transmission vehicle to gain eventually entry into the human host. In an attempt to understand the dynamics of the interaction between enteric pathogens and plant hosts, we must first understand (a) fitness of plant surfaces as host, (b) factors influencing the survival and growth of enteric pathogens on fresh produce, and (c) molecular/genomic capabilities of enteric pathogens that allows them to use plants as vehicles for the transmission. These aspects have been discussed in the following sections.

15.3.1 Enteric Pathogens in Plant Habitats

The enteric pathogens survival in the plant habitat is subject to its point of contact with the plant tissue. Ideally, the pathogenic bacteria can interact with the plant host at three points, viz. in the rhizosphere, at the leaf surface, that is, plyllosphere and finally in the spermosphere (the zone surrounding the seeds). In the following sections, we discuss the fitness of these three regions as host for enteric pathogens.

15.3.1.1 Plant rhizosphere as a habitat for enteric pathogens

The rhizosphere has been long considered as a hot spot for microbial interactions because of the influence of the below-ground system of the plants, which are known to release large amounts of nutrient-rich root exudates. In the rhizosphere, diverse microbial communities both beneficial and deleterious coexist and interact (Mahajan and Shirkot, 2014). More light on this has been shed because of the recent developments in metagenomics (Hirsch and Mauchline, 2012). Recent studies using metagenomic analysis on the rhizosphere microbiome show evidence for plant species-specific microbiomes (İnceoğlu et al., 2012) and existence of plant genotype-specific rhizosphere microbiomes (Weinert et al., 2011). Recent studies carried out in field-grown potato rhizosphere show that the rhizosphere microbiome is affected by the growth stage of the plant (İnceoğlu et al., 2012).

Organic materials (e.g., farm-yard manure and slurry) have been considered as the most economically viable option for improving soil quality (Semenov et al., 2009). With the increasing demand of organic fertilizer application in fields, it is often observed that immature manure is often used in the farms. This problem often results in enteric bacterial contamination of fruits and vegetables (as discussed in detail in Section 15.3.2). Several reports on the persistence and survival of enteric pathogens in organic manure have been documented. Recently, Yao et al. (2015) studied the survival of *E. coli* O157:H7 in different organic fertilizers (vermicompost, pig manure, chicken manure, peat, and oil residue).

Raw fruits and vegetables, especially cut-leafy greens grown in soils amended with enteric pathogen-contaminated organic fertilizers are highly prone to food-borne contamination, since the below-ground plant system is in direct contact with pathogens. The primary step involved is the attraction followed by colonization. It is believed that rhizobacteria and enteric pathogens both preferentially colonize root tips and/or at the root base where lateral roots emerge (Jablasone et al., 2005; Cooley et al., 2003). The associations might correlate with the fact that the nutrient-rich rhizosphere is commonly available for both pathogenic and nonpathogenic microbes. Distinct and localized spatial patterns of sucrose, amino acids, and nitrate abundance have also been mapped in the rhizosphere (DeAngelis et al., 2005; Jaeger et al., 1999). *S. enterica* is an enteric human pathogen that has been reported by Barak and Schroeder (2012) to colonize crop plants as secondary hosts. Similar findings have also been reported in lettuce by Klerks et al. (2007). It is believed that the movement of *S. enterica* in lettuce rhizosphere is because of the chemotaxis toward the sugar compounds in lettuce root exudates. In a detailed review by Barak and Schroeder (2012), the authors highlight that enteric pathogens especially *S. enteric* prefer to colonize specific leafy greens radicchio and endive compared with lettuce. The researchers are of the opinion that this specificity is primarily due to the difference in nature of root exudates. Following colonization, the survival of the enteric pathogens in plant rhizosphere is believed to be favored by the nutrient-rich rhizosphere. In the rhizosphere, the enteric pathogens are challenged by environmentally

unfavorable conditions; therefore they tend to colonize the internal regions of the plant tissue. A recent report has shown that *E. coli* O157:H7 endophytically colonize spinach and lettuce plants Wright et al. (2013). High-resolution microscopic examination and O-antigen labeling have shown that the food-borne enteric pathogen colonization occurred within the apoplast, between the plant cells.

15.3.1.2 Phyllosphere as a habitat for enteric pathogens

The above-ground regions of the plant are physically more easily accessible to the enteric pathogens. Soil splashing, irrigation, and insect transmission (as discussed in Section 15.3) are easy modes available for the transmission of pathogens. The phyllosphere accounts for the aerial parts of plants, which are dominated by leaves. A recent review by Vorholt (2012) on the microflora associated with the phyllosphere shows that the global bacterial population present in the phyllosphere could comprise up to 10^{26} cells.

In spite of the large leaf surface area offered to the microbes, their colonization is subject to several environmental challenges such as limited nutrient availability, high ultraviolet radiation, and fluctuating water availability. It is surprising that in spite of such stringent environmental pressure, the microbial populations survive on the phyllosphere. Several documented reports on the occurrence of enteric pathogens on the leaf surface have been documented. Recently, Han and Micallef (2016) reported *S. enterica* colonization on tomato plant surface. Their findings have shown that tomato surface compounds and exudates play an important role in colonization by the enteric pathogen. Documentation of previous reports indicates that *S. enterica* colonization on phyllosphere is a result of chemotaxis. Furthermore, the colonization by the enteric pathogen in phyllosphere is highly concentrated in type 1 trichomes, which happen to be an area on the phyllosphere in the genus *Solanum* where maximum exudates are synthesized and accumulated (Barak et al., 2011).

In an attempt to understand the risk associated with irrigation water as a potential source of enteric pathogen contamination especially in the phyllosphere, Wood et al. (2010) studied the survival behavior of enteric pathogen (*E. coli*). They introduced the enteric pathogen into agricultural systems during irrigation in the spinach phyllosphere and observed declines in their culturable *E. coli* populations on spinach leaf surface under open environmental conditions. The possible reason associated could be the ability of enteric pathogenic bacteria to colonize the internal regions of the phyllosphere. Recent documented literature have indicated that enteric pathogens are also known to internalize the leafy green phyllosphere tissue, in order to avoid the harsh environmental conditions, as discussed earlier in this section. Erickson et al. (2014) reported internal colonization by *E. coli* O157:H7 into the spinach tissue. They reported that the mobilization of enteric pathogen cells into the leaf surface and its further survival were not influenced by virulence factors of Shiga toxin since they used Shiga toxin-negative *E. coli* O157:H7 isolates in their study.

15.3.1.3 Spermosphere as a habitat for enteric pathogens

Spermosphere is an extremely small zone (2–12 mm) around the seed, where interactions between soil, microbial communities, and germinating seeds take place (Schiltz et al., 2015). The spermosphere has a very short-lived interface, that is, only during the seed germination, yet it is highly significant. This is the first point of contact between the plant and the microbial community in the soil, which can be beneficial microbes, plant pathogenic microbes, or enteric pathogens (in the context of the present book chapter). These associations are known to influence the future microflora in the rhizosphere, which in turn influences the future plant growth and yield (Singh et al., 2011). Once the seed imbibes, it is believed that a number of compounds are exuded into the spermosphere (Schiltz et al., 2015). Several reports are well documented in literature that report on the characterization of the exudates during germination. A few recent reports by da Silva Lima et al. (2014), Scarafoni et al. (2013), and Kamilova et al. (2006) have shown that the exudates during germination process include (a) carbohydrates, viz. arabinose, fructose, galactose, glucose, maltose, mannose, lactose, raffinose, rhamnose, ribose, sorbose, sucrose, xylose; (b) amino acids viz. alanine, glutamic acid, glutamine, glycine, homoserine, leucine/isoleucine, methionine, phenylalanine, pyroglutamic acid, serine, threonine, tryptophan, tyrosine, valine; (c) organic acids, viz., acetic acid, citric acid, formic acid, malonic acid, oxalic acid, succinic acid; (d) fatty acids viz. hexadecanoic acid, octadecanoic acid isomers, tridecanoic acid; (e) proteins, viz., chitinases, cysteine-rich protein, galactosidases, glycosyl hydrolases; (f) secondary metabolites, viz., phenolic derivatives, steroids, terpenoids. As a result, the microbial communities in the soil are believed to be attracted toward the spermosphere because of the chemotaxis toward the exudates.

Enteric pathogens as earlier discussed (in Section 15.1) are known to be associated with food-associated disease outbreaks, which are especially similar to contaminated seeds. Harris et al. (2003) reported that sprouted-seed-related disease outbreaks were linked to seeds contaminated with *S. enterica*. Much recently in 2013, sprouted fenugreek seeds were contaminated with *E. coli* (EHEC) strain of serotype O104:H4 (European Food Safety Association, 2013). Their consumption resulted in an outbreak of HUS and HC. Reports on epidemiological investigation suggested that the seed contamination with STEC O104:H4 occurred more than a year before the seeds were used for sprout production. Recently, Knödler et al. (2016) carried out long-term survival studies and observed that in none of the strains tested cultivable cells were found without enrichment on contaminated seeds after more than 24 weeks of storage, thereby suggesting that contamination previous to the distribution of fenugreek seeds from the importer was less likely.

Much recently, researchers have been attempting to understand the changes that occur in the composition of seed and early root exudates once the seeds are contaminated with *S. enterica.* Kwan et al. (2015) in this context carried out studies using *S. enterica*-contaminated alfalfa

seeds as a model system. The authors concluded that individual amino acids are important, but not essential, for *S. enterica* growth in the spermosphere. The protein surveys carried out by the researchers revealed that central carbon metabolites serve as essential intermediates for cellular biosynthesis and therefore to achieve dramatic reductions in bacterial growth in spermospheres, central metabolic networks need to be targeted in future studies.

15.3.2 Survival and Growth of Enteric Bacterial Pathogens on Fresh Produce

For enteric pathogenic bacteria to survive on fresh produce, it must possess certain characteristic features that allow them (a) to form synergistic/antagonistic relation with the existing microbiota, (b) to separate themselves from the existing microbiota in space, (c) to evade plant defense, just like certain phytopathogens, and (d) formation of specialized biological networks, that is, biofilm formation.

15.3.2.1 Synergistic/antagonistic relation of enteric bacteria with the existing microbiota

The existing microbiota on the plant may be plant beneficial or pathogenic to the host plant. Therefore, the enteric pathogenic bacteria must be in synergism/antagonistic relation with either of them or both. Recent research in this regard indicates that the presence of plant pathogenic bacteria would idly favor the colonization by enteric bacteria; therefore the two groups of bacterium are believed to act in synergism. The two probable reasons are (a) because of the injury to the plants, the entry for the enteric pathogenic bacteria into the plant is facilitated and (b) because of the damaged plant tissue, the wide variety of nutrients are easily accessible to the enteric pathogens (Campbell et al., 2001, Wu et al., 2000). Enteric pathogens synergism or antagonism with the host plants microbiota is also believed to be dependent on the iron acquisition systems with enteric pathogens in the plant habitat (Brandl, 2006). This mechanism of iron acquisition is believed to be carried out by siderophores (low-molecular-weight molecules that bind ferric iron with an extremely high affinity). In the case of enteric bacterial pathogens, it is hypothesized that the siderophores act in a similar manner as that observed in the case of plant pathogens. The iron-acquiring ability of siderophore assists the pathogenic microbe to chelate iron and thereby increase its possibilities to colonize the host plant.

15.3.2.2 Ability of enteric bacteria to colonize internal plant tissue

Enteric bacteria causing food-borne diseases have the ability to colonize the internal plant tissues, in a manner similar to the one adopted by beneficial or pathogenic microbes residing in the phyllosphere/rhizosphere. In an attempt to avoid the harsh environmental conditions, enteric bacterial pathogens are known to gain entry within the plant tissue. Similar to phytopathogens, enteric pathogenic bacteria can preferentially attach to the cut surfaces and natural openings such as the stomata that provides not only a protective niche, but also a source of nutrients into the apoplastic fluid. Documented literature is testament to the

endophytic colonization of pathogens such as *Salmonella* and *E. coli* O157:H7 into the cracks of the developing lateral roots of seedlings, which is especially relevant for sprouted seeds such as alfalfa, mung bean sprouts, and spinach (Klerks et al., 2007; Warriner et al., 2003; Dong et al., 2003; Cooley et al., 2003; Erickson et al., 2014). Many researchers have reported internal colonization by *E. coli* O157:H7 into tissues. Warriner and Namvar (2010) based on their review of the documented literature suggested that under preharvest conditions and natural environmental conditions there is significantly low frequency of internal colonization by enteric pathogens. The possible reason being the fact that tissue injury is very frequent. However, with the modernization of agricultural systems and the use of modern machinery in farms, the green leafy vegetables and other crops can sustain injury which can facilitate the entry of enteric pathogens and thus can cause food-borne disease outbreaks.

15.3.2.3 The ability of enteric bacterial pathogens to evade plant defense mechanisms

Plant defense system has been studied in great deal over the last decade, in an attempt to understand the response of plants against phytopathogens (Esposito et al., 2008; Mahajan and Shirkot 2014). Upon infection plants respond by a hypersensitive response, coupled with secretion of plant hormones (salicylic acid, jasmonic acid, and ethylene). This activates the PR genes that trigger the systemic acquired resistance (SAR) defense. With the continuous evolution of phytopathogens, certain strategies have been developed to avoid detection by plant defenses. Enteric pathogenic bacteria such as *Salmonella* have devised similar methods as that of phytopathogens to avoid detection. They are known to avoid detection by alteration of their LPS and their lack of outer structures, such as the ability of *Salmonella* to shed flagella, facilitates its unnoticed entry into the plant system.

15.3.2.4 Specialized abilities of enteric bacteria to form biofilms

The bacterial cells that colonize the phyllosphere are subjected to adverse environmental conditions (as discussed previously). The bacteria can secrete exopolysaccharides, which can contribute to the formation of a specialized matrix-like structure referred to as biofilm. Researchers since the advent of 21st century have been carrying out studies on the ability of enteric pathogenic bacteria to form biofilm on agricultural fresh produce. Fett (2000) studied biofilm formation by *Salmonella* and *E. coli* O157:H7 on different plant parts of broccoli, cloves, and afalfa. Several well-documented reports of biofilm formation on leaf surfaces of Chinese cabbage, spinach, lettuce, and other green leafy vegetables are available (Méric et al., 2013). Recent studies carried out by Méric et al. (2013) show that plant-associated *E. coli* when compared with strains from other sources had a greater ability to form biofilms. Moreover, significant differences were also observed in the utilization of common carbon sources between strains of *E. coli* isolated from spinach and rocket salad in comparison to *E. coli* strains isolated from the mammalian counterpart. Recent work being carried out in our laboratory on *Cronobacter* spp. shows the biofilm-forming ability on different biotic and abiotic surfaces (Singh et al., 2017).

Quorum sensing (QS) mechanism is a well-known mechanism for bacterial cell-to-cell communication and several documented reports suggest that QS is essential for biofilm formation, which is often used as a strategy by phytopathogens to colonize the plant hosts. A review of the documented literature shows that Hughes and Sperandio (2008) reviewed the presence of the mechanism as part of plants' defense system, in which the plants secrete hormones that mimic bacterial QS signals and as a result causing confusion in the signaling pathogenic bacterium. It would be of interest to investigate that whether on similar lines food-borne pathogenic enteric bacteria could be prevented to form biofilms on fresh produce by plant hosts using a similar mechanism.

15.3.3 Molecular Capabilities of Enteric Pathogens That Allow Them to Use Plants as Vehicles for the Transmission

As discussed in the above sections, the survival and growth of enteric pathogenic bacteria relies essentially on its ability to colonize plant host. A recent review on enteric pathogen-plant interactions, Martínez-Vaz et al. (2014) highlight the importance of genes involved in the cell surface structures, virulence, motility, and biofilm formation.

Previous reports highlight the presence and role of virulence genes such as *intimin* and *stx* in *E. coli* O157:H7. Kyle et al. (2010) tracked the expression of these genes on lettuce leaves. Molecular interaction of enteric bacteria with green leafy vegetables is mediated by a number of diverse genes. In *E. coli*, genes involved in Curli formation (*csgA*) and flagella biosynthesis (*fliN*) have been reported. Similarly regulator of biofilm formation through the production of colanic acid (*ybiM*) has also been reported by researchers to play an important role in biofilm formation (Fink et al., 2012; Hou et al., 2012). In *S. enteric* genes involved in stress response regulator and biofilm modulation (*ycfR*), cellulose biosynthesis (*bcsA*), adhesin expressed from pathogenicity island-3 (*misL),* and response regulator involved in biofilm formation *(sirA)* are few of the important documented genes involved in attachment and biofilm formation (Fink et al., 2012; Hou et al., 2012; Kroupitski et al., 2013; Salazar et al., 2013).

Transcriptomic analysis of enteric bacterial association with agricultural fresh produce has been recently carried out by researchers in an attempt to understand transcriptional responses triggered by the association of these organisms with plant tissues. Transcriptional responses of the *E. coli* strains K-12 and O157:H7 associated with intact lettuce leaves has been recently studied in detail by Fink et al. (2012). The authors reported that genes involved in the formation of biofilms and curli fibers were expressed at high levels. A time-dependent experiment studying the transcriptional responses of phyllosphere-associated K-12 and O157:H7 over 3 days showed that adaptation to the leaf environment was characterized by an overall decrease in the expression of genes mediating cellular energy and metabolism, especially those involved in the synthesis of ribosomal RNA and iron homeostasis. The findings thus supported the hypothesis that enteric pathogens survive and propagate in leafy

greens by inducing physiological responses that allowed them to cope with the scarcity of food sources encountered on vegetable surfaces. Studies on the molecular events triggered by the association of enteric pathogens with green leafy vegetables have improved our understanding of the mechanisms by which these organisms survive outside their normal host (Martínez-Vaz et al., 2014).

15.4 Future Research Prospects and Conclusion

In today's scenario, where global population is on an all time high, there is an ever-increasing pressure on the food industry to deliver. In order to feed the growing population, it is essential to have ready-to-eat food available, with the prerequisite being that the quality of food is not compromised. Contamination of fresh vegetables with enteric pathogens has reached concerning proportions in recent years. The slogan of "farm to fork" can be truly realized if appropriate diagnostic tests are available to keep a check on the enteric pathogenic contaminants. As researchers make new discoveries it is essential that the implications of the basic and fundamental research reach the consumer. Recent technological advancements allow us to track the course of contamination; however, it is worthwhile to mention that these technological advancements are put to use before there is any disease outbreak.

Today the scientific community has advanced understanding of food-borne enteric bacterial contaminations in fresh produce. However, the presence of cross-domain pathogens continues to challenge human health. Bacterial evolution poses a challenge in managing food-borne diseases because of the horizontal gene transfer. Another challenge being faced by researchers is the viable but nonculturable state, which the enteric pathogens enter while they interact with the foods at different stages of the food production chain. The use of highly sensitive and rapid diagnostic methodologies, backed by molecular biology tools for analysis of the global transcriptional changes that occur in enteric food-borne pathogens while they interact with agricultural fresh produce is the need of the hour.

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