



## Review

## Interaction of microorganisms within leafy green phyllospheres: Where do human noroviruses fit in?



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## ABSTRACT

Human noroviruses (hNoV) are one of the major causes of foodborne disease outbreaks linked to leafy greens. However, the interactions—including attachment and persistence—of hNoV with leafy greens are not well characterized. In the present review, three mechanisms are hypothesized for the interaction of hNoV with leafy green phyllospheres: 1) specific binding to histo-blood group antigen (HBGA)-like carbohydrates exposed on leaf surfaces and present on bacterial microbiota; 2) non-specific binding through electrostatic forces; and 3) internalization of hNoV through contaminated water (e.g. hydroponic feed water). To add more complexity, there is a rich diversity of microbial communities (i.e., bacteria, fungi, protozoa) residing in leafy green phyllospheres, and the attachment and persistence of hNoV could be largely impacted by these microorganisms through direct and indirect interactions. For instance, enzymes produced by bacteria and fungi could potentially compromise the structure of HBGA-like carbohydrate binding sites on leaves, leading to a reduction in hNoV binding. On the other hand, some bacteria also possess HBGA-like binding sites on their cell surface, which may provide extra binding locations for hNoV. There are also numerous metabolic compounds that can be produced by leafy greens and its microbial inhabitants and be subsequently distributed within leafy green phyllospheres. These compounds could theoretically play roles in enhancement or reduction in the attachment of hNoV. Overall, increasing the understanding of the various types of hNoV attachment and interactions with leafy green phyllospheres will be crucial for elucidating hNoV transmission via leafy greens as well as for the development of effective control measures.

## 1. Introduction

## 1.1. Public health burden of human noroviruses

Human noroviruses (hNoV) are non-enveloped, single-strand RNA viruses that are a causative agent of acute gastroenteritis. Norovirus genus belongs to the family *Caliciviridae*. The genus is classified into at least 6 genogroups and further divided into at least 38 genotypes (Vinjé, 2015). Human noroviruses from genogroups I, II, and IV are infectious to humans (de Graaf et al., 2016; Verhoef et al., 2015). This group of viruses is transmitted through multiple routes: food, water (drinking and recreational contact), environmental surfaces, and person-to-person, among which person-to-person transmission is predominant. Specifically, 24% of hNoV outbreaks in the United States (U.S.) are foodborne, and in the European Union (EU) the percentage is estimated to be lower at 10% (Belliot et al., 2014). Globally, 14% of hNoV caused diarrheal diseases are due to food contaminations (Lopman et al., 2015). Among all of the hNoV genogroups and genotypes, GII.4 are more related to person-to-person transmission while non-GII.4

genotypes are frequently related to foodborne transmission (de Graaf et al., 2016).

Infections caused by hNoV are usually self-limiting among healthy populations, while more severe in elderly, young children, and immunocompromised populations. As reported by the U.S. Centers for Disease Control and Prevention (CDC), hNoV causes 56,000–71,000 hospitalization and 570–800 deaths annually, which are 15–20% and 2–10% of the total food-caused hospitalizations and deaths, respectively (CDC, 2016). The total cost of hNoV illness in the U.S. every year is \$2 billion with 5000 quality-adjusted life-years for illnesses and deaths (Belliot et al., 2014). Worldwide, hNoV results in a median number of 699 million illnesses (95% uncertainty interval [UI]: 489–1086 million) and 219,000 deaths (95% UI: 171,000–277,000) annually (Bartsch et al., 2016). These illnesses and deaths result in \$4.2 billion in costs directly to health care and \$56.2 billion related to loss in productivity.

Nevertheless, the disease burden due to hNoV is nearly always underestimated due to the underreporting of outbreaks. For instance, during an epidemiological investigation in the U.S., Hall et al. (2013)

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**Table 1**  
The bacterial community identified on leafy greens.

Leafy green type	Location	Microorganism	Method	Proportion	Reference
Romaine lettuce	Leaf surface	<i>Pseudomonas</i> (17%), <i>Bacillus</i> (7%), <i>Massilia</i> (5%), <i>Xanthomonas</i> (4%), <i>Arthrobacter</i> (1%), <i>Pantoea</i> (6%)	Washing of leaf samples (n = 106)	Percentage of microorganisms in all tested samples.	(Rastogi et al., 2012)
Romaine lettuce, baby spinach, green leaf lettuce, iceberg lettuce, red leaf lettuce	Leaf surface	<i>Pseudomonas</i> , <i>Pantoea</i> , <i>Chryseobacterium</i> , and <i>Flavobacterium</i>	Sterile or unsterile samples were placed in bottle and shake at 200 rpm; culture isolate	Exist in > 20% of samples	(Jackson et al., 2013)
Lettuce ( <i>Lactuca sativa</i> )	Leaf surface	<i>Xanthomonas</i> sp., <i>Pantoea</i> sp. (Enterobacteriaceae), <i>Pectobacterium</i> sp., <i>Leuconostoc</i> sp., <i>Janthinobacterium</i> sp.	Swabbing conventional and organic lettuce	Large proportions (> 5% of bacterial community on lettuce).	(Leff and Fierer, 2013)
Spinach	Leaf surface	<i>Pantoea</i> sp. (Enterobacteriaceae), <i>Klebsiella/Raoultella</i> sp.	Sterile water rinse of conventional and organic spinach	Large proportions (> 5% of bacterial community on spinach).	(Leff and Fierer, 2013)
Lettuce	Leaf tissue	<i>Acinetobacter</i> (53%)	5 g lettuce leaf tissue were broken down and re-suspended in 10 ml of 0.85% NaCl.	Percentage of microorganisms in all tested samples.	(Erlacher et al., 2014)
Lettuce ( <i>L. sativa</i> )	Leaf surface	<i>Acinetobacter</i> (10%), <i>Alkanindiges</i> (5%), <i>Pantoea</i> (4%), <i>Pseudomonas</i> (30%), <i>Arthrobacter</i> (12%), <i>Pantoea</i> (10%), <i>Acinetobacter</i> (8%)	Shaking at 100 rpm in 0.15 M NaCl, 0.1% Tween 20 solution at room temperature for 15 min.	Percentage of microorganisms in all tested samples.	(Dees et al., 2015)

observed a 25-fold difference between the highest and lowest states reporting hNoV outbreaks on a population-based rate. These discrepancies are partly due to incidence variations among states, but more likely, this is an indication of outbreak reporting and investigation resources at the state level. Also, hNoV outbreaks on a global scale are underestimated as the epidemiological investigations are normally performed within each individual country with varying resources (de Graaf et al., 2016).

## 1.2. hNoV and leafy greens

A majority of confirmed hNoV outbreaks in Belgium from 2002 to 2007 were caused by food handlers (42.5%) followed by contaminated water (27.5%), bivalve shellfish (17.5%), and fresh produce (12.5%) (Baert et al., 2009). While the reporting on hNoV outbreaks in water and shellfish has been intensive, reporting of outbreaks associated with fresh produce is less frequent (Baert et al., 2011). According to the outbreak summary for leafy greens and fresh fruits in the U.S. and EU, hNoV is the primary causative agent followed by *Salmonella* (Callejón et al., 2015). In the U.S., hNoV outbreaks are more often related to consumption of salad, and in the EU, reported outbreaks are mainly due to contaminated berries (Callejón et al., 2015).

Between 1973 and 2012 in the U.S., there were a total of 606 outbreaks associated with leafy greens, leading to 20,003 illness, 1030 hospitalization and 19 deaths. Among all outbreaks, most of them were caused by hNoV (55%), followed by Shiga toxin-producing *Escherichia coli* (18%), and *Salmonella* (11%) (Herman et al., 2015). Leafy green contamination with hNoV is more often related to GI hNoVs with positive GI results found in 100% (2/2), 72.5% (133/181), and 66.7% (2/3) of tested samples collected from food companies or supermarkets in Belgium, Canada, and France (Baert et al., 2011). This is potentially due to the fact that GI genotypes are more often associated with contaminated environmental sources such as water and have been shown to persist longer in the environment when compared to GII hNoVs (Bitler et al., 2013; Escudero et al., 2012; Matthews et al., 2012). In addition, the risk of hNoV contamination of leafy greens is conceivably greater due to the globalization of the food supply chain, especially when products are imported from countries with poor sanitation practices (Callejón et al., 2015; Nyachuba, 2010). With respect to fresh vegetables including leafy greens, 25% of those on the U.S. market are imported each year (Johnson, 2015). Meanwhile, this globalization provides increased opportunities for viral strains to come along and possibly increase the chance for viral recombination—one of the primary ways for viruses to evolve—leading to more challenges related to prevention and control through vaccine and anti-viral compound development (de Graaf et al., 2016).

## 2. Overview: interactions of microorganisms with leafy greens

In recent decades, outbreaks related to consumption of leafy greens are becoming more frequent and recognized. Unexpected pathogens have been associated with fresh produce including *E. coli* O157:H7 in baby spinach, *Yersinia pseudotuberculosis* in lettuce, and *Listeria monocytogenes* in bagged salads, etc. (Lynch et al., 2009). To control and reduce these undesired pathogens as well as to hypothesize the less well-understood interactions of human enteric viruses with leafy greens, it is crucial to understand how microorganisms colonize and interact with leafy greens.

### 2.1. Bacteria

#### 2.1.1. General bacterial habitants on leafy greens

Fresh produce harbors a diverse population of residential bacterial communities, which are determined by many factors. The microbial diversity is large across different fruits and vegetables, but often the same type of fresh produce (i.e., lettuce, spinach, tomato etc.) share

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