



Review

Horizontal gene transfer among microorganisms in food: Current knowledge and future perspectives



Franca Rossi¹, Lucia Rizzotti, Giovanna E. Felis, Sandra Torriani*

Dipartimento di Biotecnologie, Università degli Studi di Verona, Strada le Grazie 15, 37134 Verona, Italy

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ABSTRACT

The possibility of horizontal gene transfer (HGT) among microorganisms in food matrices has been specifically targeted in a few investigations, though most current knowledge has been obtained indirectly or derived from genome sequence analyses.

In this review, we have assembled reported examples of the HGT events that probably occurred in food matrices since the bacterial partners involved are commonly found in association in a food matrix or are specifically adapted to it. Exchanged genes include those encoding for substrate utilization, bacteriocin, exopolysaccharide and biogenic amine (BA) production, immunity to bacteriophages and antibiotic resistance (AR). While the acquisition of new traits involved in substrate utilization led to the natural genetic improvement of the microbial cultures for food production, the acquisition of hazardous traits, e.g., AR, virulence or BA production genes, can give rise to health concerns in otherwise innocuous species.

Available evidence suggests that it would be opportune to determine what conditions favour HGT among bacteria in food ecosystems in order to naturally obtain improved starter or adjunct cultures, and also to prevent the propagation of hazardous traits.

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1. Introduction

Horizontal gene transfer (HGT) was defined as “the non-genealogical transmission of genetic material from one organism to another” (Goldenfeld and Woese, 2007), and implies that new genes, thus new functions, are transferred from a donor to a recipient even when these are not taxonomically related. HGT has a primary role in bacterial evolution since it causes genome rearrangements by the integration and/or deletion of genetic regions.

A computational study carried out on 116 prokaryotic complete genomes suggested that 14% of open reading frames derived from recent HGT events (Nakamura et al., 2004). The genes predicted to be horizontally transferred belonged mainly to cell surface, DNA binding and pathogenicity related functional categories. Thus, it was concluded that the transferability of genes depends on their functions. Genes acquired by HGT might be deleterious, neutral, or beneficial to the recipient so that the type of acquired genes affects

the consequences of gene acquisition. Deleterious genes should be eliminated by selection; neutral genes may be maintained, while beneficial genes can be selected for.

HGT in food-associated microbial communities can have direct implications for human health via the acquisition of new metabolic traits – to what extent, however, has not yet been well established. HGT in bacteria in food can, theoretically, contribute to the distribution of acquired traits to intestinal bacteria. Contaminating intestinal bacteria may be transformed in food or in the gastrointestinal (GI) tract after ingestion. HGT can also alter the safety status of strains belonging to those microbial species Generally Recognized as Safe (GRAS) or those with a Qualified Presumption of Safety (QPS), as defined respectively by the Food and Drug Administration (FDA) and the European Food Safety Authority (EFSA), through the acquisition of virulence traits or anti-microbial resistance (AR) genes.

HGT may occur in all matrices, but it is reasonable to assume that it is more probable in those containing high numbers of microbial cells. Some categories of foods, such as fermented and minimally processed foods, like fresh vegetables and raw salads, supply numerous living microorganisms of diverse species and genera that come into direct contact with the GI tract and other districts of the human body. Specifically adapted microorganisms

* Corresponding author. Tel.: +39 045 802 7930; fax: +39 045 802 7051.

E-mail address: sandra.torriani@univr.it (S. Torriani).

¹ Present address: Università degli Studi del Molise, Dipartimento Agricoltura Ambiente Alimenti, via De Sanctis, 86100 Campobasso, Italy. Tel.: +39 0874 404607.

can reach cell densities ranging from 10^7 to 10^9 CFU/g in food matrices. These are mostly lactic acid bacteria (LAB), acetobacteria, yeasts and, for dairy products, dairy propionibacteria.

Some reported data suggest that new bacterial biotypes can arise in food post-HGT. Here we review the known, presumed and artificially induced cases of HGT among microorganisms in food. The most relevant examples gathered are summarized in Tables 1 and 2. The aim of this work is to demonstrate the need for improved understanding of the conditions that favour HGT in the complex microbial populations of varying numerical and qualitative composition in fermented and minimally processed food matrices. Better insight into HGT probability in food could lead to the development of methods favouring the acquisition of useful traits in industrially exploited and probiotic microorganisms and to ways of resisting the transfer of undesirable traits.

2. Principal HGT mechanisms

Three independent gene transfer mechanisms, conjugation, transduction, and transformation, are associated with HGT.

Conjugative transfer requires direct contact between the donor and the recipient bacterial cells, and it has been most often studied under laboratory conditions. While reproducibility and repeatability have been demonstrated in a stable laboratory environment, little is known about how these bacteria behave in their natural habitats. Some reports have shown that conjugative transfer in food could have relevant safety consequences due to the mobilization of AR and toxin genes (Coconcelli et al., 2003; Van der Auwera et al., 2007; Gazzola et al., 2012). Therefore, this mechanism needs further investigation in foodstuffs.

In transduction, a major class of bacteriophages, the transducing phages, can package bacterial-host DNA and transfer it to new hosts. The ability of a bacterial species to acquire the phage-carried genetic information of foreign species and genera represents a source of interesting biological functions. Given the number of extant bacteria and phages, intergeneric phage-mediated genetic exchange is a possibility in food. However, phages generally have narrow host ranges, and phage-mediated genetic exchange is considered to be restricted (Brabban et al., 2005). A type of transduction is mediated by the virus-like Gene Transfer Agents (GTAs): these are small, tailed bacteriophage-like particles encapsidating their own viral genome and random pieces of the host DNA –

approximate size 4 kb. GTAs are active in natural environments and have the potential to catalyse very high levels of gene transfer (McDaniel et al., 2010). GTAs occur in intestinal bacterial parasites like the *Brachyspira* spp. spirochetes (Motro et al., 2009) but their presence in food associated bacteria remains uninvestigated.

Natural transformation, i.e. the acquisition of exogenous DNA from the medium, is known to occur in more than 60 bacterial species, but this number is probably an underestimate since the favourable conditions for its occurrence are still unknown. Competence is often activated as a quorum sensing response and, unlike other mechanisms such as transduction and conjugation, it does not depend on extra-chromosomal elements for the uptake and integration of exogenous DNA into the recipient genome. More than one hundred genes have been described to be involved in competence in different species (Claverys et al., 2006; Kovács et al., 2009; Skippington and Ragan, 2011). HGT in some species (e.g. *Escherichia coli*, *Salmonella enterica*, *Staphylococcus aureus* and the oenological bacterium *Oenococcus oeni*) is more likely because of a defective Mismatch Repair (MMR) system (Marcobal et al., 2008).

3. Biofilm formation and HGT

An important feature in food production plants is the formation of bacterial biofilms in pipes, rubber seals and working surfaces. Bacterial biofilms can cause hygienic problems and economic losses due to food spoilage, though it has also been reported that gene transfer can be facilitated in biofilms through a better donor–recipient interaction (Ghigo, 2001; Madsen et al., 2012). Furthermore, biofilms promote plasmid stability and may enhance the host range of horizontally transferred mobile genetic elements (MGEs).

A study of the transfer of the *Lactococcus lactis* cell-surface component CluA, which favours cell aggregation and biofilm development and is encoded by the sex factor, found that enhanced expression of CluA and the subsequent facilitation of biofilm formation are the consequences of a conjugation event. This enhanced biofilm-forming trait helps the mobilization of other genetic elements. Indeed, the broad-host-range plasmid pAMβ1 carrying erythromycin resistance was efficiently transferred in lactococci carrying the intrinsic high-frequency conjugation mechanism and the acquired clumping mechanism (Luo et al., 2005). As a consequence, those lactococci have the potential to effectively disseminate AR genes. Cell aggregation-associated high-frequency

Table 1
Genes possibly exchanged in food and bacterial species involved: niche adaptation and substrate utilization genes.

Gene/gene cluster	HGT partners	Food matrix	Reference
Bacteriocin genes			
Macedovicin	<i>S. macedonicus</i> / <i>S. thermophilus</i>	Milk, dairy products	Georgalaki et al., 2013
Nisin U	<i>S. uberis</i> / <i>L. lactis</i>	Raw milk	Wirawan et al., 2006
Pediocin PA-1	<i>P. acidilactici</i> / <i>Lactobacillus</i> spp./ <i>B. coagulans</i> / <i>Enterococcus</i> spp.	Plant material, fermented food	Van Reenen et al., 2006; Devi and Halami, 2013
Plantaricin	<i>L. plantarum</i> / <i>L. pentosus</i>	Fermented olives	Hurtado et al., 2011
Genes for substrate utilization			
Alpha-amylase gene, plasmid encoded	<i>R. pikettii</i> / <i>R. solanacearum</i> / <i>L. lactis</i>	Plants for food production	Wasko et al., 2010
<i>cbs-cblB</i> (<i>cglB</i>)- <i>cysE</i> cluster	<i>L. helveticus</i> / <i>L. delbrueckii</i> subsp. <i>bulgaricus</i> / <i>S. thermophilus</i>	Dairy products	Liu et al., 2009b
<i>gal-lac</i> operon	<i>S. infantarius</i> subsp. <i>infantarius</i> / <i>S. thermophilus</i>	Dairy products	Jans et al., 2012
<i>metC</i>	<i>L. delbrueckii</i> subsp. <i>bulgaricus</i> / <i>S. thermophilus</i>	Dairy products	Bolotin et al., 2004a
<i>prtS</i>	<i>S. thermophilus</i> / <i>S. thermophilus</i>	Dairy products	Delorme et al., 2010
Genes conferring selective advantages			
<i>cadA</i> , <i>cadC</i>	<i>L. innocua</i> / <i>L. lactis</i> / <i>S. thermophilus</i>	Dairy products	Schirawski et al., 2002
<i>gadB</i>	<i>S. thermophilus</i> / <i>L. lactis</i> subsp. <i>lactis</i> / <i>Lactobacillus</i> spp.	Cheese	Somkuti et al., 2012
<i>gtf</i>	<i>S. mutans</i> / <i>Lactobacillus</i> and <i>Leuconostoc</i> spp.; wine bacteria	Unspecified fermented foods	Hoshino et al., 2012; Dols-Lafargue et al., 2008
Phage resistance protein STER_1698	<i>S. thermophilus</i> / <i>Lactococcus</i> spp.	Dairy products	Liu et al., 2009b
Other genes			
<i>epsIM</i> and <i>epsII</i>	<i>S. thermophilus</i> / <i>L. bulgaricus</i>	Yogurt	Liu et al., 2009b
<i>gsiB</i>	<i>Bacillus</i> / <i>Paenibacillus</i> / <i>Pediococcus acidilactici</i> / <i>P. pentosaceus</i> / <i>L. sakei</i>	Plant or dairy niches	Asteri et al., 2011

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