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Lactic acid bacteria and their controversial role in fresh meat spoilage

Vasileios Pothakos [a], Frank Devlieghere [a], Francesco Villani [b], Johanna Björkroth [c], Danilo Ercolini [b],*

[a] Laboratory of Food Microbiology and Food Preservation, Department of Food Safety and Food Quality, Member of Food2Know, Faculty of Bioscience Engineering, Ghent University, Ghent, Belgium
[b] Department of Agricultural Sciences, Division of Microbiology, University of Naples Federico II, Portici, Italy
[c] Department of Food Hygiene and Environmental Health, University of Helsinki, Helsinki, Finland

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ABSTRACT

Lactic acid bacteria (LAB) constitute a heterogeneous group that has been widely associated with fresh meat and cooked meat products. They represent a controversial cohort of microbial species that either contribute to spoilage through generation of offensive metabolites and the subsequent organoleptic downgrading of meat or serve as bioprotective agents with strains of certain species causing unperceivable or no alterations. Therefore, significant distinction among biotypes is substantiated by studies determining spoilage potential as a strain-specific trait corroborating the need to revisit the concept of spoilage.

1. Introduction

Food is a susceptible commodity bound to decompose in time (Gram et al., 2002). In general, apart from the physicochemical alterations (e.g., respiration, macromolecule breakdown, lipid oxidation, or other autolytic reactions catalyzed by the endogenous enzymes), food is prone to microbial growth since the composition of nutrients facilitates cell proliferation. Hence, microbial activity leads inevitably to undesirable deterioration accelerating the decay of foodstuffs. Fresh raw meat constitutes a highly perishable ecological niche (Borch, Kant-Muermans, & Blixt, 1996), due to intrinsic parameters and the direct exposure of the carcass to the environment once the natural anatomical barrier of the skin/hide is removed. More in detail, the high water content ($a_w > 0.99$), the pH that corresponds to the optimal range for microbial growth (5.5–6.5), the availability of energy-yielding nutrients (e.g., glucose, ribose, amino acids, and nucleosides) as well as vitamins and minerals, account for meat being a foodstuff with a short shelf-life (Buncic et al., 2014).

Meat is contaminated with microbiota originating initially from the animal and/or the abattoir facilities. Additionally, microorganisms can also derive from the processing environment, whereat carcasses are handled, during transportation and distribution (Nychas, Skandamis, Tassou, & Koutsoumanis, 2008). Therefore, the initial, diverse microbial community colonizing retail meat encompasses biota with heterogeneous traits that require different environmental conditions to thrive and eventually cause spoilage manifestations (Gram et al., 2002). Meat spoilage is usually caused by Gram negative bacteria (pseudomonads, *Enterobacteriaceae*, *Shewanella putrefaciens*) and several Gram positive (lactic acid bacteria (LAB), *Brochothrix thermosphacta*, clostridia) that dominate under different conditions (Casaburi, Piombino, Nychas, Villani, & Ercolini, 2015; Doulgeraki, Ercolini, Villani, & Nychas, 2012; Nychas et al., 2008).

Currently, the microbial spoilage is defined as the perceivable biochemical alteration occurring on food by the microbiota reaching the highest cell density among the microbial community and thus the alterations are generally attributed to the dominant microbial consortium (Huis in' t Veld, 1996). LAB constitute a group that has been greatly associated with fresh meat and cooked meat products but represents a controversial cohort of microbial species that either contribute to generation of offensive metabolites and the subsequent organoleptic downgrading of meat (Huis in' t Veld, 1996; Labadie, 1999) or serve as bioprotective agents with strains of certain species demonstrating reduced spoilage capacities and inhibitory activity against spoiling microbiota (Chaillou et al., 2014b; Fall et al., 2012; Vasilopoulos et al., 2010). Consequently, this suggests that the presence of high LAB communities does not necessarily result in quality defects. In addition, the intra-species variation in the capability of LAB strains to cause spoilage has been recognized (Björkroth, Vandamme, & Korkeala, 1998; Pothakos, Snauwaert, De Vos, Huys, & Devlieghere, 2014b). Currently, significant distinction among biotypes is substantiated by studies monitoring spoilage potential at strain level corroborating the need to revisit the concept of spoilage, at least in the case of LAB.

* Corresponding author at: Department of Agricultural and Food Sciences, Division of Microbiology, University of Naples Federico II, Via Università 100, 80055 Portici, Italy. Tel.: +39 0812539449; fax: +39 0812539407.
E-mail address: ercolini@unina.it (D. Ercolini).

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2. Occurrence of LAB in relation to storage conditions

Packaging food under impermeable (plastic) polymer wrapping is a hurdle frequently applied to protect food products from the environment (Cutter, 2002). It can enhance product quality and freshness, while extending the shelf-life of portioned meat (i.e., beef, poultry, pork, lamb etc.) providing convenience (Singh, Wani, Saengerlaub, & Langowski, 2011). Especially modified atmosphere (MA) and vacuum packaging (VP) have become widely implemented food preservation techniques with minimal effect on fresh meat characteristics, and therefore fit well with the recent consumer's preference for additive-free foods (Gould, 1996, 2000). High O_2 levels are required to ensure red meat color by keeping the heme pigment in the oxymyoglobin form and avoid brown discolorations that render the products uninviting for consumption (Lorenzo & Gómez, 2012; McMillin, 2008). Although, high O_2 MAP is widely employed by meat industries, certain LAB species have demonstrated adaptation to oxidative stress and ability to proliferate competitively under a large range of gas combinations (Fig. 1) (Argyri, Doulgeraki, Blana, Panagou, & Nychas, 2011; Faucitano et al., 2010; Jääskeläinen et al., 2013; Kiermeier et al., 2013). Moreover, packaging is very often coupled with low-temperature storage (<7 °C) since it successfully retards microbial growth (Kreyenschmidt et al., 2010; Welch & Mitchell, 2000). Cold-chain maintenance, avoidance of fluctuations or temperature abuse during handling and transportation are crucial for the quality of meat (Nychas et al., 2008; Säde, 2011). The inhibition of deterioration is also more effective at low temperature, since CO_2 solubility to the aqueous phase of the product increases (Kiermeier et al., 2013).

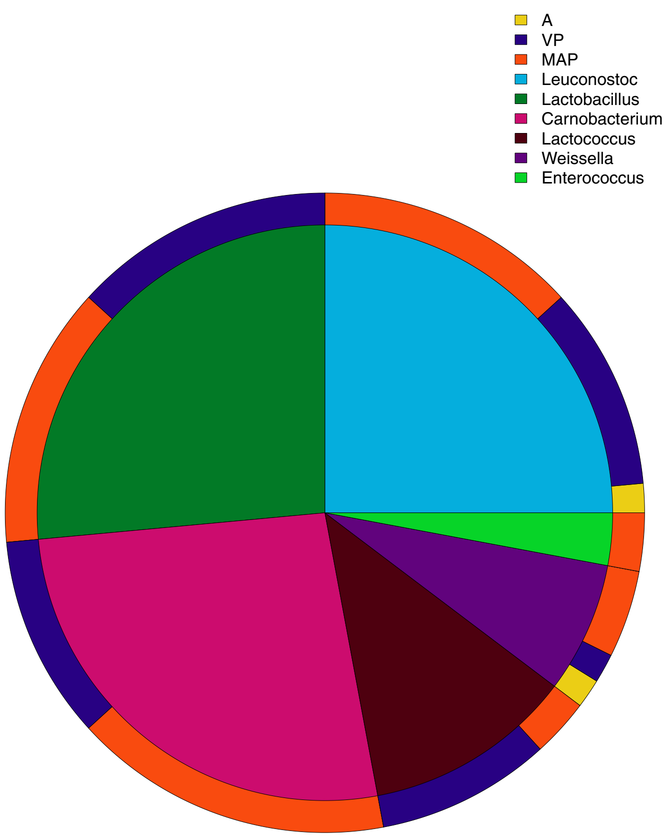

Fig. 1. Occurrence of different LAB genera as dominant members of the microbial community of spoiled meat (inner pie). Packaging technology implemented in every spoilage case (outer ring), A, air; VP, vacuum packaging; MAP, modified atmosphere packaging. Reports used for the construction of the present combination chart range from 1996 to 2014. The species of the major genera are sorted based on number of cases wherein their involvement was documented: *Leuconostoc* (*L. gelidum*, *L. mesenteroides*, *L. carnosum*), *Lactobacillus* (*Lb. sakei*, *Lb. algidus*, *Lb. curvatus*, *Lb. fuchuensis*), *Carnobacterium* (*C. divergens*, *C. maltaromaticum*), *Lactococcus* (*Lc. piscium*, *Lc. lactis*).

However, the combination of these preservation techniques exerts a selection pressure towards psychrotrophic and strictly or facultative anaerobic microbes, like LAB (Fig. 1) since most respiring microbes are inhibited by CO_2 used in the gas composition or accumulating due to microbial activity (Labadie, 1999; Nychas et al., 2008; Pothakos, Snauwaert, De Vos, Huys, & Devlieghere, 2014a). This ecological selection towards cold-acclimatized, CO_2-resistant and aerotolerant LAB has underpinned few species of the spoilage-related core microbiota of meat, which dominate at the end of shelf-life of packaged and chilled-stored foodstuffs (Chaillou et al., 2014a,b). Thus LAB are optimal candidates to develop regardless the packaging system, while their occurrence is dependent on the competitive microbes and the influence of the storage conditions upon the latter.

Apart from the preservation conditions, specific technological practices and types of products, such as marinated, value-added, moisture-enhanced and nonintact meat are more prone to contaminations due to sugar enriched preparations supplemented in/on the meat tissue in order to tenderize or spice it (Sofos & Geornaras, 2010; Vihavainen & Björkroth, 2007). In several cases spoilage of these type of products have been associated with LAB activity (Björkroth, 2005; Schirmer, Heir, & Langsrud, 2009).

2.1. Possible contamination sources of LAB

Numerous LAB taxa, related to food spoilage are ubiquitous in soil and plants (Axelsson, 2004; Chen, Yanagida, & Shinohara, 2005), animal skin and epithelia (Lundström & Björkroth, 2011; Rieder et al., 2012), abiotic surfaces and food processing plants (Bokulich, Bamforth, & Mills, 2012). Nowadays, due to the economical globalization, packaged meat portions are manufactured in processing facilities characterized by significant degree of automation and computerization (Welch & Mitchell, 2000). This systematic food production has corroborated the role of industrial meat-processing environments and technology upon the microbial consortium of the end-product (Audenaert et al., 2010). A reciprocal relation between the carcasses handled in the plant and the actual production environment has been developed. The indigenous microbiota of unprocessed raw meat are introduced in the production facilities and can become resident microbes contaminating meat handling tools and surfaces in the plant wherefrom they are normally transferred to fresh meat, intermediates or final products (De Filippis, La Storia, Villani, & Ercolini, 2013). Few studies have been dealing with the investigation of the environmental origin of LAB found in meat. Cross-contamination of the final retail products by LAB species deriving from the raw materials is speculated on the basis of air- and surface-mediated spreading (Björkroth & Korkeala, 1996, 1997b; Vihavainen & Björkroth, 2009; Vihavainen et al., 2007). Additionally, the conditions characterizing the meat manufacturing installations are favoring the adaptation of psychrotolerant LAB species populations that colonize the plant, thrive under low temperatures and subsequently contaminate the following production batches (Björkroth, 2005; Björkroth & Korkeala, 1997b; Vihavainen & Björkroth, 2009; Vihavainen et al., 2007). This theory of adaptation and survival as house-microbiota has been suggested for other types of foodstuffs highlighting the occurrence of LAB on equipment parts and sites of the premise (Koo et al., 2013; Pothakos et al., 2014c). Therefore, the processing environment can be an important source of LAB contamination for meat, provided that suitable growth conditions and substrate availability are established in processing microclimates that can favor LAB enriched niches that will spread on meat.

2.2. Diversity of LAB in spoiled meat

A large number of LAB genera and species have been found in spoiled meat products constituting a significant diversity (Fig. 1). Species belonging to the genus *Lactobacillus* (e.g., *Lactobacillus sakei*,