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Bacterial populations and the volatilome associated to meat spoilage

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ABSTRACT

Microbial spoilage of meat is a complex event to which many different bacterial populations can contribute depending on the temperature of storage and packaging conditions. The spoilage can derive from microbial development and consumption of meat nutrients by bacteria with a consequent release of undesired metabolites. The volatile organic compounds (VOCs) that are generated during meat storage can have an olfactory impact and can lead to rejection of the product when their concentration increase significantly as a result of microbial development. The VOCs most commonly identified in meat during storage include alcohols, aldehydes, ketones, fatty acids, esters and sulfur compounds. In this review, the VOCs found in fresh meat during storage in specific conditions are described together with the possible bacterial populations responsible of their production. In addition, on the basis of the data available in the literature, the sensory impact of the VOCs and their dynamics during storage is discussed to highlight their possible contribution to the spoilage of meat.

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1. Introduction

Meat spoilage is a complex event, in which a combination of biological and chemical activities may interact and render the product unacceptable for human consumption (Gram et al., 2002). Besides lipid oxidation and autolytic enzymatic reactions, spoilage of meat can be considered the result of microbial activity of a wide variety of microorganisms because meat nutrient composition, pH (5.5–6.5) and high moisture content allow the growth and survival of a large range of microorganisms (Nychas et al., 2007, 2008; Doulgeraki et al., 2012). Microbial quality of raw meat results from the physiological status of the animal at slaughter, processing, transportation, preservation and storage conditions (Nychas et al., 2008). On the basis of knowledge of a few chemical and physical parameters it is possible to predict which microorganisms will grow and dominate during the storage of the meat. Temperatures and packaging atmospheres are the most important factors affecting microbial growth and selection during storage of fresh meat, therefore the spoilage is caused only by a fraction of species and strains of the initial microbial association (Dainty et al., 1983; Gill and Molin, 1991; Borch et al., 1996; Nissen et al., 1996; Nychas and Skandamis, 2005; Nychas et al., 2007). The refrigeration selects psychrotrophic species while further selection is introduced by the type of packaging. In particular, the availability of oxygen affects microbial growth and metabolism (Nychas et al., 2007, 2008; Doulgeraki et al., 2012). Therefore, depending on the affinity of each species to oxygen, bacteria differ in their competitive growth potential under aerobic or anaerobic conditions. Their spoilage potential depends on which groups or microorganisms will dominate the meat matrix, and on their ability to produce spoilage-associated compounds such as esters, ketones, aldehydes, sulfur compounds, amines and volatile fatty acids (Dainty et al., 1985; Lambert et al., 1991; Kakouri and Nychas, 1994). When microbial spoilage occurs as slime and/or off-odors and flavors, the so-called specific spoilage organisms (SSO) (Dalgaard et al., 1993; Dalgaard, 1995; Huis in't Veld, 1996) include the microorganisms that have contributed to the spoilage and others that have grown but not necessarily caused unpleasant changes. The term SSO was originally coined to describe the single species being responsible for spoilage. Afterwards, Jørgensen et al. (2000) introduced the term "metabiotic spoilage association" to describe situations where two or more microbial species contribute to spoilage through exchange of metabolites or nutrients, so the "SSO" concept should be used to specify a set of organisms that interact to spoil the product

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(Gram et al., 2002). Several types of interactions have been studied in food ecosystems including both antagonistic and coordinated behavior and interactions where growth or a particular metabolism of one organism is favored by the growth of another organism (Gram et al., 2002). The spoilage potential of a microorganism is determined by its ability to produce the metabolites that are associated with the spoilage. However, it is also important to consider the interaction between microbial growth and enzyme activities (Nychas et al., 2008). The microbial ecology associated to the spoilage of meat in different storage conditions has been recently reviewed (Doulgeraki et al., 2012). The microbial populations associated with the meat environment are known as belonging to the groups of *Enterobacteriaceae*, lactic acid bacteria (LAB), *Brochothrix thermosphacta*, pseudomonads and some clostridia (Borch et al., 1996; Labadie, 1999; Doulgeraki et al., 2012). In addition, several pathogens can develop in meat, potentially affecting meat safety. The rate and the type of spoilage seem to depend on the concentration of glucose, lactic acid, nitrogenous compounds and free amino acids present in meat, resulting the principal precursors of those microbial metabolites responsible for spoilage (Nychas et al., 1998; Tsigarida and Nychas, 2001; Skandamis and Nychas, 2002; Nychas et al., 2008). These compounds are attacked in various order to produce different catabolic by-products depending on the microbial species and their oxygen affinity. The volatile fraction of the microbial catabolites includes: organic acids, volatile fatty acids, ethyl esters, sulfur compounds, ketones, aldehydes, alcohols, ammonia and other molecules. All these molecules will affect the sensory quality of both fresh and cooked meat. Depending on their olfactory thresholds and on the masking and synergic effects within volatiles or between volatiles and non-volatile compounds, they can cause off-odors that will render meat spoiled.

In this article, the volatile organic compounds (VOCs) potentially produced by spoilage-associated microorganisms will be described and their possible impact on meat quality will be discussed.

2. Meat spoilage microorganisms

The microorganisms that can colonize the fresh meat depend highly on the characteristics of meat and way it is processed and stored (Huis in't Veld, 1996). The factors affecting the development of microorganisms in fresh meat can be categorized into five groups: intrinsic, processing, extrinsic, implicit and the emergent; the factors and their combination will influence the development of SSO (Nychas et al., 2008). Bacteria developing in meat at chill temperatures are regarded as psychrotrophic and they include Acinetobacter, Pseudomonas, Brochothrix, Flavobacterium, Psychrobacter, Moraxella, Staphylococcus, Micrococcus, *Clostridium*, LAB and different genera of the family of *Enterobacteriaceae* (Dainty et al., 1983; Dainty and Mackey, 1992; Labadie, 1999; Doulgeraki et al., 2012). A list of bacterial genera commonly found in fresh meat during storage in different conditions is reported in Table 1. Despite the high number of microorganisms, only few species dominate to cause spoilage because temperature, time of storage and packaging atmosphere can affect both microbial growth and species selection during storage of fresh meat (Ercolini et al., 2006, 2009, 2010b, 2011; Doulgeraki et al., 2010, 2011; Pennacchia et al., 2011). In aerobic storage at low temperatures several *Pseudomonas* species are often isolated from spoiled meat (Stanbridge and Davies, 1998; Labadie, 1999; Liao, 2006; Ercolini et al., 2007, 2010a) and *Pseudomonas fragi* results the most frequently found species followed by the *Pseudomonas lundensis* and *Pseudomonas fluorescens* (Erichsen and Molin, 1981; Molin and Ternstrom, 1982; Shaw and Latty, 1982, 1984; Banks and Board, 1983; Molin et al., 1986; Dainty and Mackey, 1992; Stanbridge and Davies, 1998). Although at lower extent, *P. fragi* can also occur in meat stored in vacuum packaging (VP) and modified atmosphere packaging (MAP) (Ercolini et al., 2007, 2010b, 2011; Pennacchia et al., 2011) and its spoilage activity is due to the production of many VOCs (Edwards et al., 1987; Dainty et al., 1989; Ercolini et al., 2009, 2010a) recognized as odor active molecules possibly responsible for off-odor release during meat storage at chill temperature. Also other Gram-negative bacteria such as *Enterobacteriacae* and *Aeromonas* can also contribute to meat spoilage (Dainty et al., 1983; Dainty and Mackey, 1992; Borch et al., 1996; Nychas et al., 1998). Particularly, *Serratia* (S.) *liquefaciens* is the most common member of the *Enterobacteriaceae* in meat stored in different atmospheres (Lee et al., 1985; Stanbridge and Davies, 1998; Doulgeraki et al., 2011), *Hafnia (H.) alvei* is very frequently found in beef stored in MAP or VP (Lee et al., 1985; Drosinos and Board, 1995; Borch et al., 1996; Nychas et al., 1998; Stanbridge and Davies, 1998; Ercolini et al., 2006, 2009; Doulgeraki et al., 2011), *Enterobacter agglomerans* is found in meat stored aerobically and in MAP (Samelis, 2006) whereas *Rahnella* spp. has been found during beef storage in MAP and VP (Ercolini et al., 2006; Pennacchia et al., 2011). *Shewanella (Sh.) putrefaciens* is recognized as one of the major spoilage agents in meat due to its ability to produce H_2S (McMeekin, 1982; Molin and Ternstrom, 1982; Dainty et al., 1983; Gram and Daglaard, 2002; Nychas et al., 2007). LAB such as *Lactobacillus* spp., *Carnobacterium* spp. and *Leuconostoc* spp. are involved in meat spoilage stored in MAP or VP (Tsigarida et al., 2000; Castellano et al., 2004; Nychas and Skandamis, 2005) and sometimes also in aerobic conditions (Labadie, 1999). The species mainly found are *Lactobacillus curvatus*, *Leuconostoc* spp. and *Lactobacillus sakei* (Yost and Nattress, 2002; Fontana et al., 2006; Pennacchia et al., 2011). In addition, *Leuconostoc* spp. has been identified as predominant organisms in beef stored aerobically (Doulgeraki et al., 2010) and in VP/MAP (Stanbridge and Davies, 1998; Yost and Nattress, 2002). Within the LAB group, *Carnobacterium maltaromaticum* and *Carnobacterium divergens* are the carnobacteria mainly found in meat (Stanbridge and Davies, 1998; Sakala et al., 2002; Jones, 2004; Laursen et al., 2005; Axelsson, 2008; Ercolini et al., 2010b, 2011; Pennacchia et al., 2011). *Br. thermosphacta* is another important spoilage bacterium found in meat stored in air,

Table 1
Genera of bacteria commonly found in raw meat stored in different conditions.

Gram-positive	Storage conditions			Gram-negative	Storage conditions		
	Air	MAP	VP		Air	MAP	VP
Bacillus	+		+	*Achromobacter*	+		
Brochothrix	+	+	+	*Acinetobacter*	+	+	+
Carnobacterium	+	+	+	*Aeromonas*	+		+
Corynebactenum	+			*Alcaligenes*	+	+	+
Clostridium			+	*Alteromonas*	+	+	+
Enterococcus	+	+		*Campylobacter*	+		
Kocuria	+			*Chromobacterium*	+		
Kurthia	+			*Citrobacter*	+	+	
Lactobacillus	+	+	+	*Enterobacter*	+	+	
Lactococcus	+			*Escherichia*	+		
Leuconostoc	+	+	+	*Flavobacterium*	+		
Listeria	+	+		*Hafnia*	+	+	+
Microbacterium	+	+	+	*Klebsiella*	+		
Micrococcus	+	+		*Kluyvera*	+		
Paenibacillus	+			*Moraxella*	+		
Staphylococcus	+	+	+	*Pantoea*	+		+
Streptococcus	+	+		*Proteus*	+	+	
Weissella	+	+	+	*Providencia*	+	+	+
				Pseudomonas	+	+	+
				Serratia	+	+	+
				Shewanella	+		
				Vibrio	+		
				Yersinia	+		+
				Moraxella	+		

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