Food Biotechnology & Agricultural Sciences

Received: 2 December 2024 | Revised: 20 December 2024 | Accepted: 30 December 2024

DOI: 10.70734/fbas/202855

REVIEW ARTICLE

The Dry Aging of Beef and its Effect on Selected Quality Aspects

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Abstract

The review aimed to provide an overview of the current knowledge about changes occurring in dry aged beef and the influence of this process on meat quality parameters, such as aroma and flavour. The review also focuses on the formation of taste- and aroma-active compounds and the role of microbes during beef dry aging. The improvement in the flavour of beef during dry aging may be attributed to the release of reducing sugars from the transition of glycogen and ATP; the formation of free amino acids (FAAs) and peptides through proteolysis, and IMP, GMP, inosine and hypoxanthine, which are breakdown products produced by the degradation of nucleotides. Moreover, the volatile aroma-active components, produced by the thermal oxidation/degradation of fatty acids and the Maillard reaction between amino acids and reducing sugars, are responsible for the improvement of the aroma of dry aged beef after thermal treatment. A crucial and beneficial role in developing a unique flavour and aroma profile of dry aged beef and its tenderness is that it also has microbes. Especially observed on the crust, formed during the dry aging process, is a rich source of beneficial microbes that contribute to dry-aged beef's unique flavour and aroma profile.

The basic and undeniable advantage of dry aging beef is obtaining a specific aroma and taste of the meat, described as nutty, umami, buttery, and meaty. It is also important to improve tenderness, which improves with the extension of aging. The disadvantage of dry aging is that it is a costly process due to the resulting losses of raw materials. Although extended dry ageing contributes to flavour development, it also affects colour and lipid stability. Those relationships are of significant importance in understanding the complex process of dry aging and its impact on beef quality. Thus, further research is required on the proteome and metabolome profiles as well as the safety of eating dry aged beef.

KEYWORDS
beef, meat ageing, meat quality

Introduction

One of the critical processes shaping the quality of culinary beef is how it is aged [Smith et al. 2008; DeGreer et al. 2009; Perry, 2012; Terjung et al. 2021; Álvarez et al. 2025]. Ageing is a complex process involving numerous biochemical transformations and physicochemical changes occurring in proteins, fat and pigments [Dikeman et al. 2013; Li et al. 2014; Stenström et al. 2014]. As a result of these changes, the most important characteristics of the sensory quality of beef, such as tenderness and palatability, develop. It is, therefore, debatable not whether beef should be aged but how long this process should be carried out and by what method [Hanagasaki, Asato, 2018].

Meat aging methods can be classified into wet and dry [Kim et al. 2016; Šulcerová et al. 2017; Ryu et al. 2018]. Both methods have their advantages and disadvantages. Even though the wet-aging (or vacuum-packaged storage) of beef is currently the most widely utilised aging practice, as indicated in the literature, dry aged beef has a more favourable flavour-aroma profile and texture than wet-aged meat [Li et al. 2013 and 2014; Stenström et al. 2014; Kim et al. 2016; Setyabrata et al. 2023]. For example, dry aged beef had higher scores on some typical attributes, e.g. umami, butter-fried meat, and nutty aroma, compared to wet aged [Koutsidis et al. 2008a].

There is a growing consumer interest in dry aged beef in the USA, Australia, Japan, and European Countries [Dashdroj et al. 2016; Ryu et al. 2020; Savini et al. 2024]. Dry aged beef is not always visually acceptable to consumers due to the visible mould growth on the surface and the unusually dark and low-intensity red colour of the muscle tissue. However, consumers familiar with its unusual flavour and aroma profile are willing to spend more on it. Dry aged beef is often considered a niche and exclusive product [Ribeiro et al. 2021]. Increased interest led slaughterhouses, retailers, meat shops, and restaurants to produce and sell dry aged beef, also for special orders. Some of them use commercially available small, ageing chambers. The use of such devices, especially among non-professional food business operators, poses a rising problem of the microbiological safety of dry aged beef, which has recently been addressed by the EFSA [EFSA Panel on Biological Hazards (BIOHAZ), 2023].

Many microorganisms can participate in the meat aging process conducted by the dry method; among them, fungi of the genus *Thamnidium* sp., *Penicillium* sp., *Aspergillus* sp. and/or *Mucor* sp. are present. For example, *Thamnidium elegans*, *Penicillium camemberti*, *Aspergillus oryzae* and *Mucor flavus* may play a unique role in the development of a specific flavour and aroma profile of dry aged beef and its tenderness, which is possible due to the activity of enzymes. These act mainly on the protein and lipid components of the product [Dashdorj et al. 2016; Ryu et al. 2018; Lee et al. 2019b; Jaworska et al. 2025]. For example, short peptides and free amino acids, as products of proteolysis, may undergo various metabolic reactions, such as transamination, decarboxylation, and oxidative deamination, and the derived products develop the flavour profile of meat [Chávez et al. 2011; Lee et al. 2019a and 2019b]. Since microbes metabolise nutrients in the meat and produce different metabolites that affect not only the flavour and tenderness but also the rancidity of dry aged beef, the continuous control of aging conditions is an important strategy in reducing the risk of meat spoilage, especially for extended aging periods.

Papers included in the review were researched and in those review papers that focused on the dry aging of beef, specific attention was paid to papers that included flavour profiling. Eligible papers to be included in the review were those published in peer-reviewed scientific journals up to September 2024 and written in English. The literature search was performed in Scopus using keywords such as 'dry aging' or 'beef aging' or 'meat aging methods' or 'flavour compounds dry aged beef.' All papers identified through the database search were screened based on information in titles and abstracts. Papers that met the criteria were reviewed in full text. To capture any additional relevant papers, the reference lists of all papers reviewed in full text were examined, as were the reference lists of review papers. The additional papers identified by the reference lists were screened based on information available in titles and abstracts, and selected studies were reviewed in full text. In total, 72 papers were included in the review.

Post-mortem changes occurring in meat

Generally, in the process of post-slaughter changes occurring in meat, three stages are distinguished: (1) post-slaughter contraction and its subsidence, (2) meat aging, and (3) autolytic decomposition of meat (meat spoilage). Post-slaughter changes in meat result from the susceptibility of its components to biochemical changes. Both the meat's own proteolytic enzymes (endogenous changes) and enzymes from microorganisms with which the meat was contaminated during slaughter, post-slaughter processing and cutting (exogenous changes) participate in those changes. The climatic conditions of meat storage significantly influence the type and direction of these changes [Huff-Lonergan et al. 2010; Khan et al. 2016].

After slaughter, due to the bleeding of the animal, the blood stops delivering oxygen to the muscles. The process of breaking down muscle glycogen into lactic acid then begins. From the glycogen level and the rate of its decomposition in the process of the so-called anaerobic glycogenolysis, later changes and the development of meat quality characteristics are dependent. This component content significantly determines the meat's final pH and the degree of proteolysis. It substantially impacts many of its characteristics, i.e. water absorption, tenderness, juiciness, taste and aroma [Ramanathan et al. 2020; Kaur et al. 2021]. Lactic acid formed during anaerobic glycogenolysis acidifies the environment, and this process continues until glycolytic enzymes are inactivated under the influence of low pH or because most of the glycogen stores are depleted. During these changes, the pH of the meat decreases from the vital level of 7.0 to 5.6-5.8 [Geesink, Veiseth, 2008; Laville et al. 2009; De Oliveira et al. 2019]. At the same time, with the breakdown of glycogen, the reserves of phosphocreatine and ATP (constant and progressive enzymatic degradation) are depleted, and the amount of the remaining products of ATP breakdown (ADP, AMP, and IMP) gradually increases, which are important in developing the meat's palatability. Without ATP, myosin interacts with actin to form an actomyosin, a complex protein compound. The sarcomere shortens, and the muscle becomes contracted (rigor mortis occurs). In the contraction process, increased calcium ions Ca^{2+} secreted from the sarcoplasmic reticulum also play an important role. Post-slaughter contraction occurs in beef about 7 h after slaughter. During the contraction, the muscles harden and become stiff and dull. Muscle contraction may occur with varying intensity, and the greater the shortening of the sarcomeres (and therefore the entire muscle), the less tender the meat is [Cramer et al. 2018; De Oliveira et al. 2019; Ramanathan et al. 2020; Kaur et al. 2021]. The post-slaughter contraction also has a negative effect on the water-holding capacity of meat, as the pH of the meat in contraction is close to the isoelectric point (pI) of myofibrillar proteins, which under such conditions shows a minimum water capacity. The phenomenon of post-slaughter contraction disappears 24-48 h after slaughter, and as it subsides, the water-holding capacity of the meat increases. The activation of enzymes that break down proteins (initiation of proteolysis) starts the meat ageing process [Laville et al. 2009; De Oliveira et al. 2019; Álvarez et al. 2023].

Proteolysis, lipolysis, and oxidation are some biochemical reactions that occur during post-mortem meat aging. It is a complex and long-lasting process and is one of the methods of improving the palatability and flavour of meat, especially beef [Dikeman et al. 2013; Li et al. 2013; Kim et al. 2014; Álvarez et al. 2023; Bischof et al. 2023]. The most important enzymes involved in the proteolysis of meat proteins are calpains, cathepsins, and a multi-catalytic protease. As a result of this process, the relaxation of protein chains and the breakdown of muscle proteins into simple peptides and free amino acids takes place. Those act as water-soluble flavouring precursors responsible for meaty taste and flavour characteristics [Koutsidis et al. 2008a and 2008b; Khan et al. 2016]. These products react with reducing sugars and contribute to the flavour of meat. Further, the release of free fatty acids occurs due to the degradation of lipids. This process is followed by the production of peroxides, which react with peptides to form aroma compounds [Zhou, Zhao, 2007]. Moreover, myofibrillar proteins are broken down by the weakening and fragmentation of the Z-disk and the degradation of cytoskeletal proteins such as desmin and titin. These changes result in the fragmentation of myofibrils, which is closely related to an increase in meat tenderness [Ramanathan et al. 2020; Ryu et al. 2020; Kaur et al. 2021]. Myofibrillar and sarcoplasmic proteins are most susceptible to proteolytic transformations. Post-slaughter proteolysis during meat aging is a function of pH and temperature. The degree of acidification of meat mainly affects the extent of the proteolysis when the temperature of the environment affects the rate of proteolysis. During aging, the meat’s natural enzymes break down not only proteins but also connective tissue, leading to increased tenderness [Terjung et al. 2021]. The meat aging process depends not only on endogenous enzymes in animal muscle [Ouali et al. 2006; Huff-Lonergan et al. 2010] but also and/or on enzymes derived from microorganisms [Flores, Toldra, 2011]. For example, the enzyme isolated from *Aspergillus oryzae* can degrade myofibrillar proteins effectively [Bekhit et al. 2014a and 2014b].

Excessive aging, accompanied by an intensive multiplication of putrid microbiota, leads to the autolytic decomposition of meat. It is manifested by the appearance of stickiness and mucus on the surface of the meat, noticeable organoleptic changes in the aroma (with the aroma of hydrogen sulphide and ammonia), a visible change of colour to dark red with a greenish and/or yellow tinge. The structure of the meat becomes less cohesive and pasty, and its pH exceeds 6.5 [Huff-Lonergan et al. 2010; Dashdroj et al. 2016].

Dry aging of beef

The dry aging method involves suspending the entire beef half-carcass/quarter-carcass and its primal cuts (usually with bones) or culinary elements in climatic chambers or special aging cabinets. Beef should be aged under controlled environmental conditions: in a cooling room (0-4°C) and with an air relative humidity of 75-85% and air-flow 0.2 to 2.5 m/s, to improve its quality characteristics such as tenderness and flavour. Usually, the meat ages without packaging/protection or is packed in bags permeable to water vapour [Li et al. 2014; Dashdorj et al. 2016]. Typically, dry aging is performed for at least 21 days, but numerous researchers have reported that the most frequent range is between 14 and 60 days [DeGreer et al. 2009; Kim et al. 2020, Xu et al. 2023]. Sometimes beef dry aging could be prolonged, even up to 8 months [Perry, 2012], however longer storage is associated with the possibility of unfavourable changes in the colour, taste and aroma of the meat caused by the development of undesirable groups of microorganisms and the oxidation of fat and pigments. During aging, the dried and discoloured surface layer of the meat and fat tissue is removed, which also causes higher mass losses compared to wet aging [Park et al. 2018].

Dry aging should be completed at the lowest possible temperature that will not result in freezing the meat [Smith et al. 2008; Khan et al. 2016; Ramanathan et al. 2020]. Even though a higher temperature would increase the enzymatic processes, it can stimulate rapid bacterial growth that could produce off-odours. Moreover, spoilage bacteria (especially on the meat surface) will develop if the relative humidity is too high, producing off-flavours. On the other hand, if the humidity is too low, bacteria growth will be limited, but weight loss will increase, causing the meat to dry out too quickly and decrease juiciness. Sufficient airflow in the cooling room is also crucial. The meat will not be able to release the required amount of moisture for the drying process without adequate air circulation. However, if there is too much circulation, the meat could dry out too quickly, causing an increase in trimming losses. That is why the airflow and velocity should be consistent throughout the dry aging process [Lee et al. 2019b; Ramanathan et al. 2020]. A summary of basic information on the beef dry aging parameters is presented in Table 1.

The dry aging process of beef is not only time-consuming but also expensive process due to the resulting raw material losses. A crust is formed on the surface of dry aged meat, on which mould growth is mainly observed. It is considered as waste by producers due to its hardness and dryness and the visible loss of colour caused by significant weight losses [Xue et al. 2021; Park, Kim, 2023]. This crust is usually trimmed away during meat aging, and losses may reach over 30% [Park et al. 2018; Xu et al. 2023]. However, other studies have shown that a more intense taste characterises the crust compared to the internal layers of the entire element [Ryu et al. 2020; Xue et al. 2021]. Some authors [Xue et al. 2021] propose its management, and it could be added (e.g. after grinding) to all kinds of meat products as a flavour enhancer. This would, therefore, be an added value, thanks to which the financial losses related to the process of removing the crust from the surface of the dry aged meat would be reduced.

Table 1. Summary of basic information on the dry aging of beef parameters, along with the most important observations from selected research papers from 2020-2025

Dry aging parameters					Most important findings	Reference
Cut	Aging time [days]	Tempera-ture [°C]	Relative humidity [%]	Air flow velocity [m/s]		
Striploin	0, 7, 14, 21, and 28	4	75	2.5	The crust showed more unique metabolic changes that accelerated proteolysis (total free amino acids and biogenic amines) and inosine 5'-monophosphate depletion than dry-aged beef and generated specific microbial catabolites (3-indoxyl sulphate) and γ-aminobutyric acid (GABA), while asparagine, glutamine, tryptophan, and glucose in the crust were maintained or decreased. Compared to the crust, dry-aged beef showed similar patterns of biogenic amines, bioactive compounds, and GABA without a decrease in free amino acids and glucose.	Kim et al. (2020)
Sirloin	0, 12, 30, 70, and 160	1-4	80-90	not specified	16S rRNA sequencing revealed that dry aging led to increased bacterial diversity, and Actinobacteria and Firmicutes, mostly lactic acid bacteria, were dominant on dry aged beef. Prolonged dry aging reduced the diversity of lactic acid bacteria. Sequencing of the internal transcribed spacer (ITS) region showed that fungal diversity was reduced by aging and that Helicostylum sp. was the most common species.	Ryu et al. (2020)
Striploin *(M. longissimus thoracis et lumborum)*	0, 20, 24, 40, and 50	2.0	85	2	No further tenderization effect was found after 20 days of aging, but aging for 50 days significantly increased lipid oxidation. The generation of aroma volatiles in the roast steak from aged samples was higher ($p<0.05$) than that of non-aged samples.	Utama et al. (2020)
Striploin *(M. longissimus thoracis et lumborum, cut from the 10th rib)*	0, 21, and 28	2.0	75	0.5-2.0	As dry aging progressed, the meat proteome and related biological processes changed differently between sampling locations; proteins related to cell-cell adhesion and ATP metabolic processes pathways were revealed in the external location at 21 and 28 days, respectively. The impact of aging on the proteome of the interior meat samples evidenced that muscle contraction and structure, together with energy metabolism, were the major pathways driving dry aging. Aging impacted other pathways in the interior tissues, such as the regulation of calcium import, neutrophil activation, and regeneration.	Álvarez et al. 2023
Loin	0, 30, 45, 60, and 90	1.0	78	1.8	Meat pH, colour and fatty acids were stable during the process. The concentration of the main volatile compounds increased over time. Any oxidation of protein residues was detected, and the main proteins undergoing proteolytic degradation early in the process were myoglobin, myofibrillar constituents and sarcoplasmic enzymes. The total bacteria count increased without signs of spoilage, Enterobacteriaceae were not enumerated, and few reads of foodborne pathogens were detected by shotgun metagenomic.	Savini et al. 2023
Striploin *(M. longissimus thoracis et lumborum, cut from the 10th rib)*	0, 21, and 28	2.0	75	0.5-2.0	UV pre-treatment may have caused oxidation and structural changes in proteins. UV pre-treatment and proteolysis, microbial activity and drying during dry aging may have contributed to the differences in the proteome between external and internal locations after 21 and 28 days of dry aging. Proteins related to skeletal muscle, energy, and fatty acids metabolisms were identified at 21 days of dry aging, evidencing that these proteins and the associated pathways may play a role in the production of dry-aged beef and the factors underlying its determination.	Álvarez et al. (2025) [1]

Dry aged meat flavour development

The mechanism of beef dry aging is not well understood. Many complex processes, such as biochemical transformations and physicochemical and microbiological changes, occur in the meat during dry aging, influencing its quality, including the appropriate tenderness and flavour profile. In general, the palatability of the meat is assumed to increase as the aging time is extended until it reaches the optimum [Dashdroj et al. 2016; Khan et al. 2016; Kaur et al. 2021]. One common theory of how the unique flavour of dry aged beef is developed is that during this process, moisture evaporates, and flavour components are concentrated [Dashdorj et al. 2016; Kim et al. 2016]. Also, the juices are absorbed into deeper layers of the meat, and the chemical breakdown of protein and fat constituents occurs. It results in a more intense 'nutty' and 'beefy' flavour of dry aged beef [Dashdroj et al. 2016]. Moreover, dry aging improved the flavour of meat, described as 'sweet', 'beefy', 'buttery', 'brothy', 'roasted-nut', and 'brown-roasted' [Xue et al. 2023]. According to Jayasena (2013a and 2013b) and Lee et al. (2019a and 2019b), the development of meat flavour during aging (but also thermal treatment) is attributable to the reaction between flavour compounds (taste-related compounds and aroma volatiles). The main taste-related compounds are inosine 5'-monophosphate (IMP), reducing sugars, and free amino acids (FAAs), whereas several hundred aroma volatiles are derived from the oxidation of lipids, such as triglycerides, phospholipids, and free fatty acids (FFAs) and/or the Maillard reaction between reducing sugar and FAAs (after the thermal treatment of meat). Gorraiz et al. (2002), Koutsidis et al. (2008a and 2008b), and Dashdroj et al. (2015) reported that during meat aging, the accumulation of inosine nucleotides - IMP, IDP, and ITP, as well as inosine and hypoxanthine, derived from the breakdown of adenine nucleotides - AMP, ADP, and ATP occurs. Together with their decomposition products and ribose, these compounds are characterised by a specific flavour profile. Additionally, they form complex flavour-aroma complexes in subsequent chemical reactions with other substances. During aging the meat, the share of high molecular weight hydrocarbons, peptides, benzene compounds, pyrazines, aliphatic hydrocarbons (especially branched alkanes, including 2-octene, 3-octene, 2,2,5-trimethylhexane, derived from lipid oxidation) and free fatty acids, especially oleic acid also increases. According to Dashdroj et al. (2016), carbohydrates are broken down into sugars that give meat a sweet taste, while fats and fat-like membrane molecules degrade to aromatic fatty acids. All of these breakdown products contribute to an intensely meaty, nutty, and savoury flavour. Khan et al. (2016) observed that a more 'aged beef' aroma is attributed to the presence of the derivatives of 2-methyl-3-furanthiol. Lee et al. (2019a) suggested that moisture evaporation affects the concentration of FAAs, reducing sugars and the final flavour of dry aged beef. Nevertheless, it was also reported that another factor might affect the dry aged flavour over the concentration of flavour compounds. It should be emphasised that the whole sensory quality of aged beef is obtained during thermal processing, most often grilling and frying. During thermal treatment, flavour precursors also react with each other to form new molecules or volatile compounds that enrich the aroma further. The taste of meat after such treatment is closely related to the properties and quantity of precursors present in raw muscle tissue [Dashdroj et al. 2015 and 2016; Watanabe et al. 2015]. According to Zhang et al. [2022] the volatile profile of dry aged meat has not been studied properly until recently. In more recent studies on beef dry aging, a greater proportion of volatile compounds, including aldehydes, ketones and N-containing compounds was observed, which may improve the buttery, beefy, roasted and nutty flavours of such beef [Ha et al. 2019; Setyabrata et al. 2020; Lee et al. 2021]. Some volatiles have been associated with the lipid oxidation (e.g. propanal, 2-heptanone, 3-heptanone, 2,3-butanedione and 2,3-pentanedione) and enzymatic activities of microorganisms (e.g. 2-methylbutanal, 3-methylbutanal, 2-methylpropanal, 1-butanamine, trimethylamine, 2-methyl-2-propanethiol and ethyl propanoate) [Setyabrata et al. 2020; Lee et al. 2021]. Moreover, in the studies of Xue et al. (2021) a unique volatile, decane, derived from lipid degradation was detected, and this may serve as a potential signature for a dry aged flavour.

An evenly distributed intramuscular fat content (marbling) in meat is necessary to achieve the proper quality of dry aged beef. Therefore, only beef with necessary marbling should be dry aged, according to Dashdroj et al. (2016), and most of the data on the development of beef quality during the aging process concerns beef with high marbling or meat from sirloin - which does not require a long time aging as it is tender by default [e.g. Ryu et al. 2018; King et al. 2021]. Only a few studies show that the sensory quality of low-marbled beef can be improved by dry aging [Lee et al. 2015 and 2017a].

The phenomenon of the relationship between the high marbling of aged beef and its high sensory rating Dashdorj et al. (2016) can be explained by the dissolution and migration of fatty components during the thermal processing of meat, most often by grilling and frying. This ensures proper juiciness, delicacy, and the characteristic buttery aftertaste of the product. In addition, the adipose tissue between the bundles and muscle fibres contributes to the relaxation of connective tissue structures, positively affecting the meat's tenderness. The characteristic honeycomb structure in the endomysium is partially disturbed, while thinner collagen fibres are formed in the perimysium [Perry, 2012]. Dikeman et al. (2013) and King et al. (2021) indicated that marbling directly affects meat tenderness. Therefore, low-marbled beef intended for aging may not develop the sensory characteristics of the raw material desired by consumers. Meat with high marbling, on the other hand, will be more susceptible to fat oxidation processes. Many compounds responsible for forming a rancid, undesirable taste and aroma are fat oxidation products. These include low-molecular volatile substances, mainly short-chain aldehydes, and the acids originating from their oxidation [Dashdroj et al. 2015; Watanabe et al. 2015]. Ribeiro et al. (2021) observed a significant interaction between the aging method and aging time for lipid oxidation. Dry aging induced more lipid oxidation than wet aging at day 56. Also, Utama et al. (2020) reported the longer the aging period, the higher the amount of malondialdehyde.

The role of microorganisms in the dry aging of beef

Moisture evaporation during dry aging often causes a hardened 'crust' formation on the outer surface of the beef, which is usually trimmed away and discarded during fabrication and processing [Dashdroj et al. 2016; Lee et al. 2019b]. The crust is microbe-laden and has visual microbial growth in the form of patches of mycelia. Various microorganisms, especially beneficial mould and yeast, can grow on the surface of beef during dry aging [Capouya et al. 2020; Ramanathan et al. 2020; Ryu et al. 2020]. However, only a few of them have been characterised in detail. Microorganisms likely to be present during this process are, among others: Thamnidium sp., Penicillium sp., Aspergillus sp., Cladosporium sp., Rhizopus sp., Mucor sp. and Aureobasidium sp. [Hanagasaki, Asato, 2018; Ryu et al. 2018; Oh et al. 2019]. Some studies suggest that a major surface coloniser, which is also the most desirable in dry aged beef, is a fungus or group of fungi in the genus Thamnidium within the phylum Zygomycota [Capouya et al. 2020]. The growth of Thamnidium mould can start within three weeks after the aging process has begun. This mould is known to be adapted to cooling conditions. It has the appearance of pale grey patches, called whiskers, on the fatty parts of the carcass or cut [Ramanathan et al. 2020]. It is also notable for its ability to produce collagenolytic enzymes that help break down the connective tissue in the meat and create a more tender texture [Dashdorj et al. 2016]. In the studies of Jaworska et al. (2025) it was demonstrated that a 28-day dry ageing process enhanced meat quality attributes and using Mucor flavus improved meat quality attributes such as aroma, flavour and the overall liking of beef. Also, Hanagasaki and Asato (2023) found that several aldehydes detected only in dry aged beef with the Mucor flavus were related to the savoury flavours of meat, such as being nutty. On the other hand, the main benefits of Penicillium sp. mould on aged meat include the antagonistic effect against undesirable microbiota [Chávez et al. 2011]. Some yeast, such as Pichia, Saccharomyces, and Debaryomyces, commonly occur in dry aged meat [Oh et al. 2019; Capouya et al. 2020].

Various microorganisms, including yeasts and moulds, are well-known in food flavour and texture development (also based on multiple studies conducted on fermented meat products). It is associated with their proteolytic and/or lipolytic and/or collagenase activities as well as their metabolic products [Bolumar et al. 2006; Perrone et al. 2015; Lee et al. 2019a and 2019b; Ryu et al. 2020]. Some reports [Capouya et al. 2020; Kim et al. 2020] state that the mould/yeast growth on the dried surface of beef (crusts) during aging should not be considered as contamination but rather a key aid in enhancing the dry aging process which has a unique flavour and is associated with dry aged beef as well. Lee et al. (2019a) suggested the role of microorganisms on the crust in dry aged beef flavour development based on its higher trimethylamine content. The typical resultants of microbial growth, including increased trimethylamine content and pH, were observed in dry aged beef without additional microbial growth inside the meat. These indicated that microbial growth on the crust may affect the sensory properties of dry aged beef [Lee et al. 2019]. Oh et al. (2019) suggested that yeasts Pilaira anomala and Debaryomyces hansenii can improve the quality of beef (including tenderness) by releasing proteases, breaking down myofibrils with collagenolytic enzymes, and producing flavour compounds. Both microorganisms used as starter cultures decreased the dry aging time compared to the non-inoculated beef. Recently, Ryu et al. (2018 and 2020) reported that lactic acid bacteria were present during the dry aging of meat. It has been shown that the microbiota composition (mould/yeast/bacteria) changes during aging [Ryu et al. 2018 and 2020, Oh et al. 2019]. According to Ryu et al. (2018), those variations influence the quality of dry aged beef and fungi, which may play an important role in the palatability and flavour development of such meat. For example, authors observed an increase in Penicillium camemberti and Debaryomyces hansenii (moulds used in cheese manufacturing) after 40 to 60 days of dry aging.

Safety of dry aged beef

The safety of dry aged beef is not well-known. It has been shown that spoilage and pathogenic taxa may develop in addition to the beneficial microbiota (from the point of view of meat quality after the aging process) [Ercolini et al. 2011; Lee et al. 2017b]. These microorganisms can limit the shelf-life of the raw material, but they can also produce toxic metabolites that are important from the point of view of food safety. These can be toxins, products of amino acid decarboxylation, or toxic secondary fungal metabolites [Capouya et al. 2020; Gowda et al. 2022]. Considered beneficial, mould growths can develop the flavour and texture of meat [Ryu et al. 2018; Oh et al. 2019], but at the same time, limited information relates that it could also create a concern to consumer health as allergens (i.e. Penicillium) or these fungi can be a potential source of toxic secondary fungal metabolites (i.e. Aspergillus). These metabolites, in turn, may inhibit the development of other microorganisms. Because the beef is dry aged without packaging, there is a risk of microbiological contamination with Candida sp., Cladosporium sp. and Rhodotorula sp. moulds, the growth of which can cause meat spoilage [Lee et al. 2019b; Capouya et al. 2020]. However, the development of different bacteria was also observed during beef dry aging, in particular lactic acid bacteria, e.g. Bifidobacteriaceae, Lactobacillaceae, Leuconostocaceae and Streptococcaceae. Their presence inhibits the development of pathogenic microorganisms [Ryu et al. 2020].

In contrast to fungal composition and identification, most of the bacterial analyses presented in the literature have focused only on the reduction of pathogenic bacteria, such as Escherichia coli, E. coli O157:H7, coliforms, Listeria monocytogenes, and Salmonella sp. during the dry aging of beef [Knudsen et al. 2011; Tittor et al. 2011; Gowda et al. 2016; da Silva et al. 2019; Ryu et al. 2020]. Ryu et al. (2018) examined dry aged beef over 60 days stored at 1-4°C and 80-90% RH. The authors found that total aerobic bacteria (TPC), lactic acid bacteria (LAB), and total yeast and mould (YAM) counts increased within the first 25 days of dry aging each reaching ~4 log cfu/g, and then slowly increasing by an additional 2 log cfu/g up to day 60. Also, Li et al. (2014) assessed TPC, LAB, and YAM counts of surface fat and meat from dry aged beef at approximately 2.9°C for 8 and 19 days (but unknown RH). The counts of these bacteria were higher on the meat surfaces than on the fat surfaces, and all counts increased with time. Gowda et al. (2016) surveyed dry aged beef in Belgium (conditions unspecified) and found high numbers of Pseudomonas (>4.7 log cfu/cm2), LAB (>3.7 log cfu/cm2) and yeasts (>4.0 log cfu/cm2) on lean and adipose surface tissues of meat. Moulds were detected (>1 log cfu/cm2), but their identities were not determined. On the other hand, Ryu et al. (2018) observed that potentially harmful yeasts and moulds (Candida sp., Cladosporium sp., Rhodotorula glutinis and Rhodotorula mucilaginosa) were present after 25 days of the dry aging of beef, and these strains disappeared after extending the dry aging to 60 days, where however Penicillium camemberti was detected. Extending the dry aging time of meat also creates conditions for developing aerobic and psychrotrophic strains capable of multiplying at cooling temperatures [Gowda et al. 2022]. Ryu et al. (2020) reported that Pseudomonas sp., especially Pseudomonas psychrophila, was present at high levels at day 30 and day 160 and is considered a spoilage bacterium causing the deterioration of beef and as the consequence of a failure of dry aging. Some works have reported that undesirable flavours and aromas can also be developed during aging due mainly to the effects of microbial growth, but also the rancidity of the fat and adsorption of off-odors if present in the cooling room [Garlough, Campbell, 2012]. On dry aged meat, species that may potentially produce mycotoxins have been found, and low levels of aflatoxin [Capouya et al. 2020]. According to Ramanathan et al. (2020), proper handling practices, aging time, temperature, relative humidity, and airflow are required to grow beneficial moulds and limit other microbial contamination. Therefore, the risk related to the development of unfavourable microorganisms is generally minimised by following the principles of good production practice, as well as selecting appropriate aging parameters. However, none of these activities completely eliminates this risk. This issue is significant as dry aged meat is unprotected, so there is a high risk of microbial contamination [Stenström et al. 2014]. Moreover, different rates of microbial growth during the meat aging process may result in the appearance of different metabolites at various times, resulting from the use of substrate/meat components by the microbes. These metabolites, in turn, can provide nutrients for other co-existing microorganisms. That may influence the broadly understood quality and safety of dry aged beef.

One of the innovative directions of research in the field of the dry aging of beef may be determination of the effect of selected strains of fungi on the transformations occurring in beef during its dry aging, in a comprehensive approach using metabolomic studies. Moreover, the potential food safety risks, associated with fungi ability to produce toxic secondary metabolites within the environmental conditions of the process must be considered.

Conclusions

The main advantages of dry aged beef are its specific aroma and taste, which are described as nutty, umami, buttery, beefy, and improved tenderness. Biochemical reactions arising from endogenous and exogenous pathways contribute to the unique flavour profile of dry aged beef. It is developed due to the interplay of microbial activity (mostly microbiome of the surface), lipid oxidation and dehydration (crust formation). Moreover, the changes in the content of nucleotides, sugars, amino acids and fatty acids affect the taste and flavour of beef and, consequently, the quality of the beef. The distinct metabolites derived from oxidation and microorganism activity including some unique (small) peptides, amino acids, aldehydes, and other fermentation- related compounds may be suitable biomarkers for dry aged meat. Since there are growing meat plants and consumer interest, further research is required on the proteome and metabolome profiles and the safety of dry-aged beef.

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