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Dry-Aged Beef: A Global Review of Meat Quality Traits, Microbiome Dynamics, Safety, and Sustainable Strategies

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ABSTRACT

Dry-aged beef is valued for its tenderness, complex aroma, and concentrated flavor. However, variability in aging protocols and limited understanding of underlying biological and technological processes can compromise consistent quality and safety. This review examines factors influencing meat characteristics, including genetics, breed, sex, age, diet, intramuscular fat deposition, antioxidant reserves, and endogenous enzyme pools. Postmortem biochemical pathways, such as proteolysis, lipid oxidation, and nucleotide degradation, are discussed in relation to flavor and texture development. The dynamics of surface microbiota are analyzed, highlighting the succession from psychrotrophic spoilage bacteria to molds and yeasts, which collectively form an enzymatic crust that contributes umami and nutty notes while providing antimicrobial barriers. Regulatory frameworks in major markets are reviewed, alongside valorization strategies that convert crust trimmings into umami-rich powders, bioactive peptides, starter cultures, or industrial enzymes. Despite advances, critical knowledge gaps remain, including the functional roles of minor crust taxa, the efficacy of defined starter cultures or bacteriophage blends, and standardized methods for texture and flavor measurement. By focusing on these biochemical and microbiological mechanisms and their applications, this review provides a roadmap for transforming dry aging into a reproducible, safe, and high-quality process in modern meat science.

1 | Introduction

Dry aging, storing unpackaged carcasses or cuts at low temperature, moderate humidity, and steady airflow for several weeks, has re-emerged as a premium maturation method that yields a distinctive roasted–nutty flavor profile and enhanced tenderness (Dashdorj et al. 2016; Liu et al. 2024; Savini, Indio, Panseri, et al. 2024). Interest has grown across fine dining and industry, but outcomes remain sensitive to environmental control and hygiene. Current risk assessments and regulatory updates indicate that,

when time–temperature parameters are respected, dry-aged beef need not pose greater microbiological risk than fresh meat (Koutsoumanis et al. 2023; Savini, Indio, Giacometti, et al. 2024; Savini, Indio, Panseri, et al., 2024).

Understanding of the surface “crust” ecosystem has advanced from descriptive surveys to function-oriented studies. Culture-dependent and metagenomic work consistently highlights aerobic psychrotrophs (e.g., *Pseudomonas*, *Brochothrix*, and *Psychrobacter species*) in commercial settings, with emerging

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evidence that community shifts correlate with key volatiles and texture traits in real processing environments (Cheng et al. 2024; Coton et al. 2024). Building on this ecology, targeted bio-interventions are being explored to improve reproducibility.

Sustainability considerations are increasingly shaping practice, complementing yield-optimization strategies and hybrid/in-bag approaches (Setyabrata et al. 2024). In parallel, controlled trials using defined starter cultures show reproducible shifts in volatile profiles, tenderness, and surface uniformity—offering practical routes to standardize sensory outcomes without compromising safety (Park and Choi 2025; Przybylski et al. 2023; Yoo et al. 2023).

This review synthesizes the determinants of quality and safety in modern dry-aged beef, spanning pre-harvest factors, postmortem biochemistry, and the functional crust microbiome; evaluates process controls and emerging biotechnologies; summarizes regulatory expectations and risk considerations; and examines sustainability and valorization opportunities, while identifying outstanding knowledge gaps and outlining a practical research and implementation roadmap for scientists and industry.

2 | Overview

Dry aging is one of the oldest methods of beef maturation, dating back centuries to when butchers simply hung whole sides or primals in cool, humidified rooms to tenderize meat and develop deeper flavors. With the rise of industrial-scale slaughter and global distribution in the latter half of the twentieth century, vacuum-packaged wet aging became the norm, offering faster turnover and minimal weight loss, whereas dry aging retreated into the realm of artisanal butchers (Dashdorj et al. 2016; Henrique Rezende-de-Souza et al. 2021). However, discerning diners and luxury steak purveyors have reignited interest in dry-aged beef, particularly in Asia and North America, creating a revived premium niche that commands a significant price premium (Dashdorj et al. 2016; DeGeer et al. 2009).

Dry aging is among the oldest techniques for beef maturation, historically involving carcasses or primals hung in cool, humid rooms to enhance tenderness and deepen flavor. Its modern resurgence reflects premium dining trends and improved chamber technology, but outcomes still hinge on strict control of temperature, relative humidity (RH), airflow, and hygiene (Koutsoumanis et al. 2023; Savini, Indio, Panseri, et al. 2024; Terjung et al. 2021).

In practice, two postmortem aging techniques dominate modern production. Wet aging involves vacuum-sealing cuts and refrigerating them for 1 to several weeks, during which endogenous enzymes tenderize the muscle, but few new flavor compounds accumulate prior to cooking (Khazzar et al. 2023; Terjung et al. 2021). Dry aging, by contrast, exposes unpackaged meat to strictly controlled conditions of temperature, RH, and air flow for 2–8 weeks, during which surface dehydration forms a protective crust, proteolytic and lipolytic reactions release amino acids, peptides, and fatty acids, and molds and yeasts generate distinctive volatile profiles, collectively concentrating umami, nutty, and beefy notes (Lee et al. 2021; Mikami et al. 2021; Ribeiro et al. 2024). Figure 1 summarizes the main processing

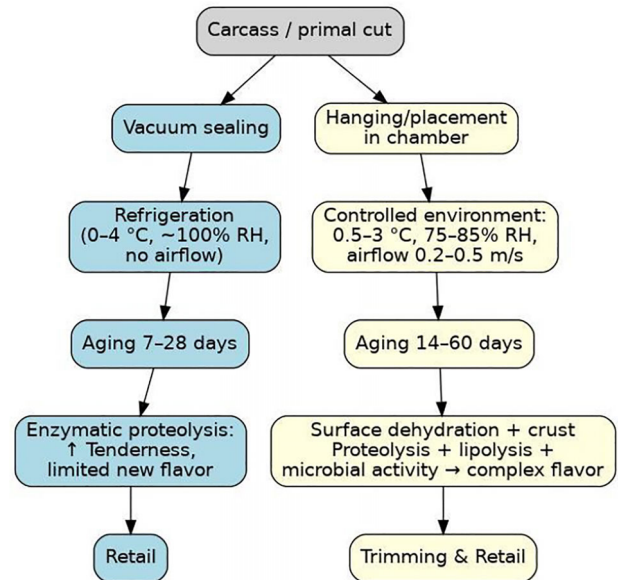


FIGURE 1 | Process flowchart of wet aging (blue squares) and dry aging (yellow squares) of beef (Lee et al. 2021; Mikami et al. 2021; Ribeiro et al. 2023, 2024; Savini, Indio, Panseri, et al. 2024; Terjung et al. 2021).

steps and environmental conditions for wet- and dry-aged beef, providing a concise visual comparison of the two approaches. Dry aging protocols vary according to cut type, facility design, and flavor objectives (Henrique Rezende-de-Souza et al. 2021). Some producers hang whole carcass sides for 3 weeks before dividing them into primals for further aging, whereas others age individual cuts for 2–6 weeks depending on marbling level and desired taste intensity (Dashdorj et al. 2016; Mikami et al. 2021). Evaporative losses, often 10%–20% of initial weight, concentrate flavor but reduce saleable yield, necessitating a balance between sensory gains and economic viability. High-marbled carcasses are most commonly aged to capitalize on both yield and palatability (Dashdorj et al. 2016; Kim et al. 2016). Today, dry aging signals premium quality in steakhouses and specialty butcher shops. Achieving consistent results demands rigorous hygiene, precise environmental control, and scientific insight into the microbial and biochemical transformations underlying flavor and tenderness (Gowda et al. 2022; Ribeiro et al. 2023; Savini, Indio, Panseri, et al. 2024). As consumer demand for provenance and sensory excellence grows, integrating traditional craftsmanship with data-driven process optimization will be essential to sustaining and expanding the dry-aged beef market.

The global market for aged beef, of which dry-aged product represents a specialized, high-value segment, is overwhelmingly concentrated in a handful of regions. North America commands over 40% of the world's dry-aged beef consumption, with the United States alone accounting for the lion's share (Figure 2; Gowda et al. 2022; Ortez et al. 2022; Smith et al. 2018). Europe follows with roughly 30% of global volume, driven by fine-dining cultures and a burgeoning interest in specialty butchers across Spain, Italy, Germany, the United Kingdom, and France (Farmer and Farrell 2018; Gowda et al. 2022; Hocquette et al. 2018). Asia, the fastest growing region at roughly 40%, sees rapid demand increases in China, Korea, and Japan, where aged Wagyu

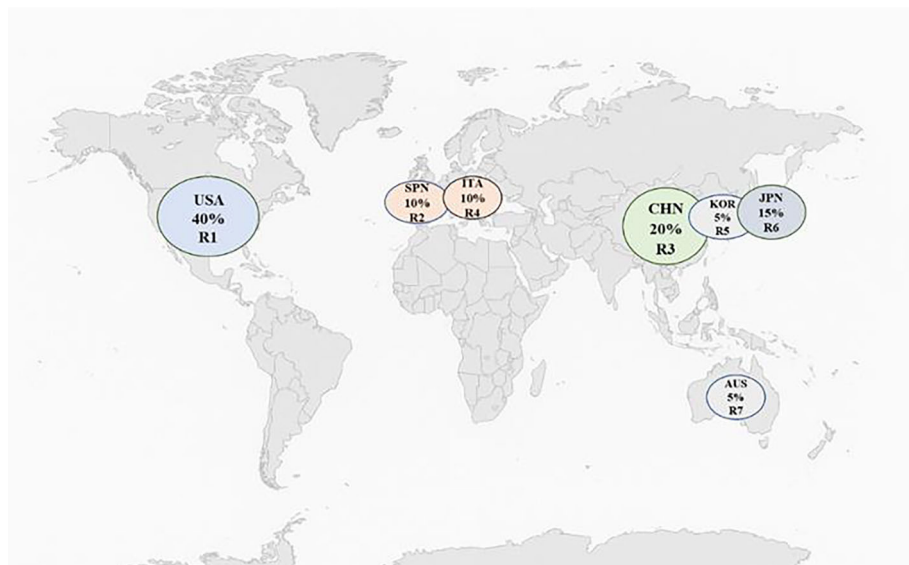


FIGURE 2 | World map of the global dry-aged beef market. Bubble diameters indicate bibliometric research rank (R1 USA; R2 SPN; R3 CHN; R4 ITA; R5 KOR; R6 JPN; R7 AUS) and are scaled to each country's market share of dry-aged beef (USA 40%, CHN 20%, JPN 15%, SPN 10%, ITA 10%, KOR 5%, AUS 5%) (Farmer and Farrell 2018; Gotoh et al. 2018; Hocquette et al. 2018; Lee, Jang et al. 2019; Mikami et al. 2021; Moreira et al. 2022; Setyabrata et al. 2019).

commands top prices (Gotoh et al. 2018; Lee, Jang et al. 2019; Mikami et al. 2021). Australia, despite its smaller share, boasts among the highest per capita beef consumption and a strong metropolitan niche for dry-aged cuts. Urban consumers there prize the nuanced flavors and textures of dry-aged cuts, leading to sustained growth in both on- and off-premise channels (Dashdorj et al. 2016). Although no bibliometric study focuses exclusively on “dry-aged beef,” broader analyses of meat-aging research, including wet aging, microbial ecology, and quality traits, show that six countries produce roughly three-quarters of the scientific output (Figure 2). The United States leads in publication count and citation impact, and it is followed by Spain, China, Italy, South Korea, and Japan (Moreira et al. 2022). This geographic concentration of research mirrors these regions' market leadership and underscores the synergy between scientific innovation and commercial development in the dry-aged beef sector.

3 | Intrinsic Animal Factors

3.1 | Animal Characteristics

Optimizing dry aging starts with cattle, the biology of which supports marbling, controlled proteolysis, and manageable moisture loss. Sex class is a first-order lever: Across contemporary datasets, steers and heifers generally show higher marbling and more favorable eating quality than entire males under comparable management, although the magnitude varies with age, diet, and end point (Wood et al. 2008). A large 2020 production study found only minor sensory differences overall but still detected higher tenderness and more desirable flavor in heifers than steers or bulls; a recent study likewise reports greater marbling in steers/heifers than bulls, whereas other work at 15 months shows that intensive finishing can narrow steer–bull gaps for striploin/ribeye palatability (Blanco et al. 2020; Hossain et al. 2024).

Breed strongly modulates intramuscular fat (IMF) potential, fiber phenotype, and lipid chemistry relevant to dry aging outcomes. Japanese Black Wagyu exhibits exceptional marbling capacity and oxidative muscle traits; contemporary syntheses report very high IMF potential in the longissimus and distinct lipid profiles (e.g., elevated oleic acid), and Japanese production commonly harvests around 28–30 months, supporting extended postmortem tenderization and flavor development (Campbell et al. 2001; Kerth and Miller 2015; Khatri and Huff-Lonergan 2023). Crossbred (F1) Wagyu programs also demonstrate practical routes to higher marbling in commercial chains (Gotoh et al. 2018; Tan and Jiang 2024; Velazco et al. 2024; Yoshinaga et al. 2021). Conversely, mainstream British/Continental breeds (e.g., Angus, Charolais, Limousin) present moderate marbling and a more glycolytic muscle phenotype, typically benefiting from conventional 21- to 35-day aging to reach target tenderness. Large multi-breed sensory work also shows breed clustering for tenderness/flavor, emphasizing that programs should be tailored by genotype × muscle rather than a single “days-on-aging” rule (Conanec et al. 2021; Valenzuela et al. 2020; Vázquez-Mosquera et al. 2023; Yoshinaga et al. 2021).

Beyond marbling, connective tissue architecture influences time-to-tenderness. New data tracking collagen type I/III content and μ -calpain autolysis across aging show muscle-specific changes consistent with the known role of cross-link density in background toughness—useful when deciding longer versus shorter dry aging for tougher cuts or categories (Song and Hwang 2025). Genomic tools can refine selection for predictable tenderization. Recent reviews highlight CAPN1/CALPAIN and CAST/CALPASTATIN along with lipogenesis genes (e.g., SCD, FASN, LEP) as the most informative panels for tenderness/marbling, though individual marker effects vary by population; breed-specific validations remain important (Kostusiak et al. 2023; Romero et al. 2024; Saucedo-Uriarte et al. 2024). Iberian breeds, including Spain's Rubia Gallega,

Retinta, and Avileña-Negra Ibérica and Portugal's Iberian native breeds—Spain's Rubia Gallega, Retinta, Avileña-Negra Ibérica and Portugal's Mirandesa, Barrosã, Maronesa—combine fine marbling with pasture-influenced fatty acid signatures and meaningful α -tocopherol status that can support color/oxidative stability during longer maturation if hygiene and drying are well controlled. Comparative studies show: (i) Rubia Gallega finishing system (pasture vs. concentrate) shifts IMF composition and sensory notes; (ii) Avileña-Negra Ibérica tends to lower IMF under extensive systems, with packaging/finishing affecting acceptability; and (iii) PDO Portuguese meats (Mirandesa/Barrosã) retain favorable *n*-3 and antioxidant profiles linked to grass feeding. Sensory work on Iberian beef aged beyond standard wet-aging also reports “beefy” and occasionally “sweet/nutty” notes consistent with crust-driven volatile development (Barahona et al. 2020; López-Pedrouso et al. 2020; Pestana et al. 2012; Rodríguez-Vázquez et al. 2020).

3.2 | Nutrition and Physiological Status

Feeding regimen, in particular, exerts a profound influence on IMF deposition and oxidative stability. Grass-fed cattle accumulate higher levels of long-chain omega-3 fatty acids and endogenous antioxidants such as α -tocopherol and β -carotene, which improve color/lipid stability during extended aging and help prevent off-flavors (Evans et al. 2024; Revilla et al. 2021; Salim et al. 2022). By contrast, energy-dense grain finishing tends to increase IMF and marbling, enhancing juiciness and providing a larger reservoir of lipid-derived flavor precursors like free fatty acids and lipid-derived volatiles that intensify the characteristic nutty and buttery notes of dry-aged beef (O'Quinn et al. 2024; Tan and Jiang 2024).

Preslaughter handling and welfare directly affect the biochemical starting point for aging. Rough handling, prolonged transport, or inadequate lairage deplete muscle glycogen, raise ultimate pH, and predispose to dark, firm, dry (DFD) beef that ages unevenly and is more spoilage-prone. Conversely, low-stress handling protocols preserve glycogen reserves, ensuring a normal pH decline to 5.4–5.8, which optimizes protease activity, water-holding capacity (WHC), and color stability during aging (Colle et al. 2015; Faustman et al. 2010; Hultgren et al. 2022; Poveda-Arteaga et al. 2023). Animal husbandry factors, including growth rate, health status, and welfare, also modulate the structural characteristics of muscle. Breeds selected for rapid growth may exhibit larger fiber diameter and increased connective-tissue cross-linking, which can resist enzymatic tenderization; in contrast, heritage or slow-maturing breeds often display a finer fiber structure and lower collagen density, yielding more predictable tenderness gains during aging (Hocquette et al. 2010; Roy and Bruce 2024; Warner et al. 2022). Similarly, systemic health challenges (e.g., subclinical infections) can alter muscle pH and protease activity, underscoring the importance of robust biosecurity and veterinary care for consistent dry-aging performance (Huff-Lonergan and Lonergan 2005).

3.3 | Postmortem pH and WHC

After slaughter, muscle pH falls sharply as residual glycogen is converted to lactic acid, dropping from near neutral (\sim 7.0) to an

ultimate pH of 5.4–5.8 within 24 h (Huff-Lonergan and Lonergan 2005; Khatri and Huff-Lonergan 2023). This pH decline is pivotal for dry aging, as it modulates enzyme activity, microbial growth, color stability, and the meat's ability to retain water. Within the 5.5–5.8 pH window, endogenous proteases, particularly μ - and m-calpains and cathepsins, exhibit peak activity, cleaving myofibrillar and connective proteins to enhance tenderness during early aging (Cadavez et al. 2019; Kaur et al. 2021; Stafford et al. 2024). When ultimate pH is elevated (DFD; typically >6.0 – 6.2), beef appears dark and firm and exhibits higher WHC (low purge) but shortened shelf life because high pH favors spoilage growth and color instability (Colle et al. 2015; Khatri and Huff-Lonergan 2023). WHC, the muscle's ability to retain its intrinsic water under external forces, is closely tied to pH. As pH approaches the isoelectric point of myofibrillar proteins (\sim pH 5.2), WHC decreases, leading to increased purge and drip loss (Ha et al. 2019; Zhu et al. 2025). Conversely, a higher ultimate pH (>6.0) can increase WHC but often yields a dry, crumbly texture and fosters spoilage organisms (Colle et al. 2015; Koutsoumanis et al. 2023). Optimally, dry-aged beef maintains a pH that balances minimal purge with sufficient free water to support juiciness and texture without compromising microbial safety. The rate and extent of pH decline depend on factors such as muscle glycogen reserves (influenced by breed and diet), muscle fiber type, pre-slaughter handling (stress), and carcass chilling rate. Rapid chilling before significant pH drop can induce cold shortening, whereas slow chilling increases the risk of microbial proliferation and uneven drying (Ha et al. 2019).

4 | Biochemical Transformations During Aging

4.1 | Proteolysis and Biogenic Amines

Proteolytic breakdown begins immediately post-slaughter as endogenous μ - and m-calpains, together with lysosomal cathepsins, cleave myofibrillar proteins (titin, nebulin, and desmin) into peptides and free amino acids (FAAs) (Cui et al. 2022; Joo et al. 2023). In the lean interior, total FAAs increase by 25%–40% over the first 7–14 days (Fu et al. 2017; Kim et al. 2016), whereas crust FAAs rise by about 60% in the same interval (Lee and Shin 2019). Metabolomics and targeted assays consistently show time-dependent increases in total FAAs (including Glu, Ala, and Gly) in dry-aged beef, with faster and more pronounced changes in the crust because of surface dehydration and microbial proteases. Table 1 shows the proteolysis changes and biogenic amine formation during aging. Individual FAAs follow distinct patterns: Glutamine declines by over 50% within 2 weeks via mold and lactic acid bacteria-mediated deamidation (Vermeulen et al. 2007); glycine and alanine accumulate steadily, imparting sweet and briny notes (Jayasena et al. 2015); glutamate rises 30%–45% over 21 days, enhancing umami (Jayasena et al. 2015); and tryptophan peaks around Day 21 (\approx 0.8 mg/g) before conversion into indolic compounds like 3-indoxyl sulfate, which contribute subtle bitter and earthy aromas (Lee, Jang et al. 2019; Kim et al. 2020). These FAAs not only drive sweetness, umami, and mild bitterness in the raw meat but also act as precursors for Maillard and Strecker reactions during cooking, generating key aroma volatiles such as 3-methylbutanal and phenylacetaldehyde (Kerth and Miller 2015; Zhang et al. 2025). However, extensive FAA availability and microbial activity also fuel biogenic amine for-

TABLE 1 | Meat biochemical transformations over dry aging process.

Biochemical transformations	Aging (days)	Changes	Mechanism	Impact	References
<i>Proteolysis and BAs</i>					
Total FAAs	7–14	Inner meat: +25%–40%; external surface (crust): +60%	Calpains, cathepsins; microbial proteases	↑ Sweetness, umami; Maillard precursors	Cui et al. (2022), Joo et al. (2023), Lee, Jang et al. (2019)
Glutamine	14	>50%	Mold/LAB deamidation	↓ Bitter/Sweet precursor pools	Vermeulen et al. (2007)
Glutamate	0–21	30%–45%	Proteolysis	↑ Umami	Jayasena et al. (2015)
Tryptophan	21–>21	Peak (≈0.8 mg/g) → ↓	Proteolysis → indolics	Bitter/Earthy aroma precursors	Kim et al. (2020)
Putrescine/Cadaverine	7–28	<5 to 15–25 mg/kg	Decarboxylases	Flavor complexity vs. off-odors	Schirone et al. (2022), Kim et al. (2020)
Histamine	28	8–12 mg/kg	Histidine decarboxylase	Scombroid risk if excessive	Kim et al. (2020), Daniel Collins et al. (2011)
<i>Lipid oxidation and VOCs</i>					
TBARS (MDA/kg)	<21; >21	0 → 1.0 mg MDA/kg; plateau	ROS + heme iron peroxidation	Optimal flavor vs. rancidity risk	Lee and Shin (2019), Li et al. (2013)
Hexanal		0.3–0.6 µg/g optimal; >1.2 µg/g off-notes	Hydroperoxide breakdown	Fresh/Nutty (low) vs. green notes (high)	Liu et al. (2024), Lee, Jo et al. (2025)
2,3-Octanedione		<0.1 µg/g buttery; ↑ → metallic	Secondary lipid oxidation	Buttery vs. metallic off-note	Domínguez et al. (2019)
<i>Nucleotide degradation</i>					
IMP	3–7	0 → 150–200 µmol/100 g	Phosphatases, nucleotidases	Peak umami	Joo et al. (2023), Kim et al. (2019)
Inosine	>7	↑ following IMP peak	IMP dephosphorylation	Mild flavor transition	Bischof et al. (2021)
Hypoxanthine	28–35	0 → 80–120 µmol/100 g	Nucleoside phosphorylase	Bitter-savory complexity	Bischof et al. (2021), Khan et al. (2016)
<i>Maillard & Strecker precursors</i>					
Reducing sugars		+15%–20% crust	Moisture loss; proteolysis	↑ Maillard substrates; deeper roast flavors	Lee, Jang et al. (2019; Lee et al. 2025), Setyabrata et al. (2021)
FAAs		+30% by Day 21	Proteolysis	Enhanced Strecker aldehyde formation	Fu et al. (2017), Jayasena et al. (2015)
Strecker aldehydes		High on searing (200–250°C)	Dicarbonyl + α-AA reactions	3-Methylbutanal, 2-methylpropanal, and so forth	Bischof et al. (2021), Liu et al. (2022)
Pyrazines and furans		Form above 120°C	Thermal breakdown of Amadori products	Caramel, nutty, floral notes	Shakoor et al. (2022), Kerth et al. (2023)

Abbreviations: FAAs: free amino acids; IMP: inosine 5'-monophosphate; LAB: lacto-acid bacteria.

mation via amino acid decarboxylases. Putrescine and cadaverine levels in high-marble ribeyes typically rise from <5 mg/kg after 1 week to 15–25 mg/kg by 28 days, whereas histamine reaches 8–12 mg/kg (Kim et al. 2022; Schirone et al. 2022). Although moderate amine concentrations can add flavor complexity, excessive

histamine poses safety risks, off-odors, and potential scombroid-type reactions, and regulatory guidance recommends keeping total biogenic amines below 100–200 mg/kg (Daniel Collins et al. 2011; Ruiz-Capillas and Jiménez-Colmenero 2005; Schirone et al. 2022). Optimal decarboxylase activity occurs at pH 5.5–

6.0 and 2–8°C, underscoring the need for precise control of aging parameters and surface microbiota, which helps to manage undesirable amine accumulation by promoting beneficial molds while suppressing spoilage bacteria (Kim et al. 2021; Liu, Gao, et al. 2025).

4.2 | Lipid Oxidation and Volatile Compound Formation

Controlled oxidation of intramuscular lipids is essential for the hallmark nutty, roasted, and buttery aromas of dry-aged beef, yet excessive oxidation leads to rancidity. Initiation occurs as reactive oxygen species, catalyzed by heme iron in myoglobin and trace metal ions, abstract hydrogen from unsaturated fatty acids (oleic, linoleic), forming lipid hydroperoxides. These intermediate peroxides decompose into secondary volatiles: aldehydes (hexanal, *trans*-2-heptenal), ketones (2,3-octanedione), alcohols (1-hexanol), and short-chain hydrocarbons, which at low concentrations contribute fresh, nutty, and toasted notes (Faustman et al. 2010; Lee, Jo, et al. 2025; Liu et al. 2024). Typically, thiobarbituric acid–reactive substances (TBARS) values rise over the first 21 days of aging, peaking around 0.5–1.0 mg MDA/kg, before plateauing, reflecting a balance between flavor-enhancing oxidation and rancidity risk (Lee and Shin 2019; Li et al. 2013). TBARS above 1.5 mg MDA/kg generally signal perceptible off-odors and reduced acceptability (Campo et al. 2006; Ribeiro, Lau, Pflanzler, et al. 2021). Dietary and endogenous antioxidant strategies help manage this trade-off. Feeding cattle 500–1000 IU/day of vitamin E (α -tocopherol) elevates muscle antioxidant stores, delaying hydroperoxide formation by up to 30% and lowering TBARS after 35 days of aging, with corresponding improvements in sensory scores (Herrera et al. 2022). Proteolysis-derived peptides in the crust also contribute radical-scavenging activity, further stabilizing subcrust lipids (Fu et al. 2017). Volatile profiling by GC–MS reveals that hexanal levels above 1.2 μ g/g strongly correlate with green off-notes, whereas moderate levels (0.3–0.6 μ g/g) enhance perception of freshness and nuttiness (Lee, Jo, et al. 2025; Liu et al. 2024). Likewise, 2,3-octanedione imparts buttery aromas at concentrations <0.1 μ g/g but develops metallic notes when over-accumulated (Dom nguez et al. 2019; Lee, Jo, et al. 2025). For a concise overview of these kinetics, mechanisms, and sensory impacts, see Table 1.

4.3 | Nucleotide Degradation

The breakdown of muscle adenine nucleotides during dry aging follows the pathway ATP \rightarrow ADP \rightarrow AMP \rightarrow inosine 5'-monophosphate (IMP) \rightarrow inosine \rightarrow hypoxanthine, driven by endogenous phosphatases and nucleotidases (Bischof et al. 2023; Khan et al. 2016; Li et al. 2024). IMP is a key umami nucleotide that synergizes with free glutamate to amplify savory taste; as IMP wanes and hypoxanthine rises (\approx 3–5 weeks), sensory character shifts from “clean umami” toward a more bitter-savory complexity. These relationships, long established, are now supported by updated receptor-level work on umami potentiation and by contemporary reviews linking nucleotide trajectories to flavor (Joo et al. 2023; Kim et al. 2019; Yamamoto and Inui-Yamamoto 2023). Table 1 summarizes the changes during time. As aging

progresses beyond 2 weeks, IMP is dephosphorylated to inosine and further degraded to hypoxanthine, which accumulates to 80–120 μ mol/100 g by Days 28–35 (Bischof et al. 2021; Zhang et al. 2019). Hypoxanthine imparts a mild bitterness and adds savory complexity, tempering the pure umami of IMP. Temperature and pH modulate the kinetics of these processes: Lower aging temperatures (0.5–2°C) slow enzyme-mediated conversion, extending the IMP-rich window, whereas higher temperatures (\sim 4°C) accelerate hypoxanthine buildup (Khan et al. 2016). A pH between 5.5 and 6.0 optimizes the activity of IMPase and nucleoside phosphorylase; deviations can lead to uneven or stalled nucleotide turnover (Colle et al. 2015; Zuo et al. 2022). Surface microbiota also play a role: Molds and yeasts in the crust may catabolize ribose moieties or utilize free nucleotides, subtly altering local IMP/inosine/hypoxanthine ratios in subcrust layers (Bischof et al. 2023; Ryu et al. 2018). Sensory evaluations mirror these chemical trends: steaks aged 7–14 days, when IMP predominates, score highest for umami, whereas 21- to 35-day-aged steaks, enriched in hypoxanthine, are described as more bitter-savory and complex, demonstrating how precise control of nucleotide degradation shapes the dynamic flavor progression of dry-aged beef (Campbell et al. 2001; Joo et al. 2023).

4.4 | Maillard and Strecker Reactions (Cooking Phase)

When dry-aged steaks are seared at high temperatures (\approx 200–250°C), the aged-in precursor pools, reducing sugars (ribose, glucose), and FAAs liberated by proteolysis and mild dehydration feed Maillard chemistry. In dry-aged versus wet-aged beef, both FAAs and reducing sugars are consistently higher (and inversely related to moisture), providing more substrate for browning pathways during cooking (Table 1) (Lee et al. 2021; Lee et al. 2025; Setyabrata et al. 2021). Initial condensation between carbonyl groups and amino moieties forms Amadori and Heyns products, which rearrange into reactive dicarbonyls such as glyoxal and methylglyoxal. These intermediates drive Strecker degradation of α -amino acids, yielding characteristic aldehydes: 3-methylbutanal (from leucine), 2-methylpropanal (from valine), and phenylacetaldehyde (from phenylalanine), which impart malty, roasted, and floral notes to cooked beef (Bischof et al. 2021; Liu et al. 2022). Dry aging concentrates Maillard precursors by 10%–20% moisture evaporation and extensive proteolysis. Lee, Choe et al. (2019) observed a 15%–20% increase in reducing sugars in the crust of 21-day-aged ribeye compared to its lean core, amplifying the substrate pool for Maillard pathways during searing (Lee, Choe, et al. 2019). Above 120°C, the thermal degradation of Amadori compounds accelerates, forming heterocyclic volatiles such as pyrazines and furans that deepen caramel and nutty aromas (El Hosry et al. 2025; Kerth et al. 2023; Shakoor et al. 2022). Moreover, elevated FAAs in 21-day aged beef, up to 30% higher than in fresh meat, drive enhanced Strecker aldehyde formation, enriching the cooked profile with intense savory and sweet notes (Fu et al. 2017; Jayasena et al. 2015; Zhang et al. 2025). Interactions between lipid oxidation products and Maillard intermediates yield alkyl-pyrazines and thiophenes when sulfur-containing amino acids (methionine, cysteine) participate, adding complex roasted and meaty aromas (Liu et al. 2024; Park and Choi 2025).

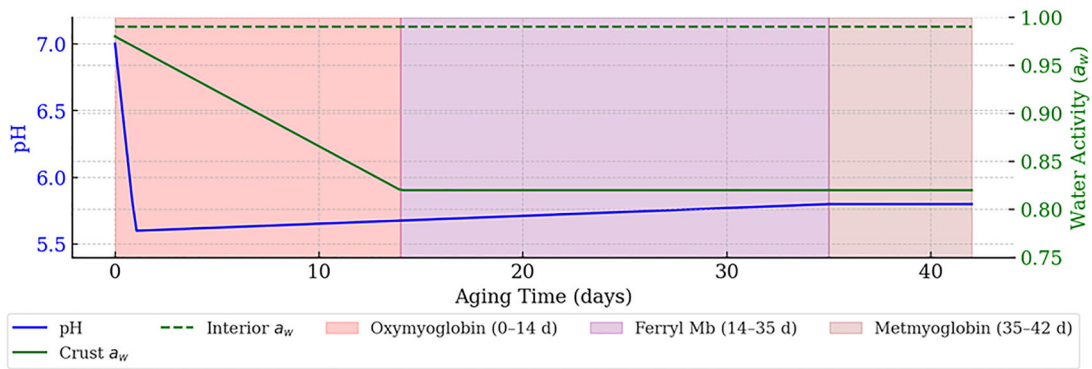


FIGURE 3 | Timeline of physicochemical changes during 0–42 days of dry aging. Solid blue line shows meat pH. Solid green line shows crust a_w and dashed green line shows inner meat a_w . Colored bands indicate dominant myoglobin forms (Colle et al. 2015; Ribeiro et al. 2025; Ribeiro, Lau, Furbeck, et al. 2021; Ribeiro, Lau, Pflanzler, et al. 2021; Tomasevic et al. 2021).

4.5 | Myoglobin Derivatives and Color Stability

The rich red–purple hue of dry-aged beef reflects a delicate interplay between myoglobin oxidation–reduction cycles, lipid oxidation products, and antioxidant defenses. Immediately post-mortem, oxymyoglobin predominates, imparting a bright red color. During 14–35 days of low-oxygen aging (0.5–2°C; 75%–85% RH), oxymyoglobin slowly autoxidizes to metmyoglobin, yet residual metmyoglobin-reductase activity, driven by NADH, regenerates deoxy- and oxymyoglobin, sustaining lean muscle redness (Denzer et al. 2025; Ramanathan et al. 2023). Meanwhile, controlled lipid oxidation generates hydroperoxides and secondary radicals that convert myoglobin into ferryl ($\text{Fe}^{4+} = \text{O}$) and protein-bound hydroxyl forms. These high-valence species exhibit stable deep red and purple tones, resisting further oxidation under the process's low pH (5.4–5.8) and limited oxygen availability (Colle et al. 2015; Faustman et al. 2010; Ribeiro et al. 2025). Evaporative moisture loss concentrates pigments in the crust, reducing L^* (lightness) and producing a gray–brown surface (Tomasevic et al. 2021). Beneath this layer, lean muscle a^* (redness) often transiently increases during Days 7–21 as low-oxygen niches stabilize oxymyoglobin before declining past 35 days due to metmyoglobin accumulation (Han, Wang, et al. 2024; Ribeiro, Lau, Pflanzler, et al. 2021). Chroma (C^*) typically rises early, signaling vivid color, then wanes with prolonged aging as pigment oxidation and crust opacity obscure lean redness (Colle et al. 2015; Ribeiro, Lau, Pflanzler, et al. 2021). Maintaining airflow (0.2–0.5 m/s) and RH (60%–85%) controls surface desiccation and oxygen exposure to limit metmyoglobin buildup (Ramanathan et al. 2023; Ribeiro et al. 2024; Ribeiro, Lau, Pflanzler, et al. 2021). Figure 3 illustrates these physicochemical trajectories over a 0- to 42-day dry aging period, overlaying pH, crust and inner meat water activity, and the dominant myoglobin redox forms. Intramuscular antioxidants, dietary α -tocopherol, and proteolysis-derived peptides scavenge lipid radicals, further preserving pigment stability (Herrera et al. 2022).

4.6 | Water Activity and pH Influence

A defining feature of dry aging is surface dehydration, which creates a desiccated crust with low water activity (a_w) that suppresses spoilage bacteria while fostering beneficial xerotolerant

molds. Under controlled chamber conditions, evaporative loss during the first 7–14 days drives crust a_w from near 0.98 down to 0.80–0.85, whereas the underlying muscle remains hydrated (a_w 0.98–0.99), preserving moisture necessary for proteolytic tenderization and juiciness (Figure 2) (Gowda et al. 2022; Ribeiro et al. 2023; Savini, Indio, Panseri, et al. 2024). The a_w gradient effectively inhibits Gram-negative spoilers (e.g., *Pseudomonas* and *Shewanella* require $a_w \geq 0.95$) and selects for molds such as *Thamnidium* spp., *Mucor* spp., and *Penicillium* spp., which can grow at a_w as low as 0.71–0.77 (Capouya et al. 2020; Mikami et al. 2021). Concurrently, postmortem pH decline, described in Section 3.3, interacts with this a_w gradient to influence dry aging outcomes. Maintaining a muscle pH between 5.4 and 5.8 maximizes endogenous protease activity, preserves color stability, and limits growth of pathogens such as *Listeria monocytogenes* and *Salmonella* spp. (Gowda et al. 2022; Ribeiro, Lau, Furbeck, et al. 2021; Ribeiro et al. 2023). Slight pH increases over 14–35 days (0.1–0.3 units) result from proteolytic release of basic amino groups and surface mold metabolism (Ha et al. 2019; Kim et al. 2022). Controlled pH in combination with low surface a_w ensures uniform proteolysis, juiciness, and microbial safety. Notably, when pH is properly managed, WHC shows no significant difference between dry- and wet-aged beef, highlighting pH's dominant role across aging methods (Ramanathan et al. 2019).

5 | Microbial Dynamics and Safety

5.1 | Indigenous Succession

From the moment beef leaves the slaughter floor, its surface microbiota shifts in response to drying, cooling, and nutrient availability. Initially, residual blood and tissue fluids support high loads (10^5 – 10^6 CFU/cm²) of Enterobacteriaceae and *Pseudomonas* spp. (Figure 4; Ryu et al. 2020). As the meat enters the dry aging chamber, the first week fosters rapid proliferation of psychrotrophic spoilers, such as *Pseudomonas* spp. and *Shewanella*, in the moist subcrust, reaching 10^5 – 10^7 CFU/cm² and releasing off-flavor precursors like sulfur volatiles and trimethylamine (Gowda et al. 2022; Koutsoumanis et al. 2023). As evaporation lowers surface a_w below 0.90 within 7–14 days, these Gram-negative bacteria decline, yielding to lactic acid bacteria (*Lactobacillus* spp., *Leuconostoc* spp., and *Enterococcus* spp.) to

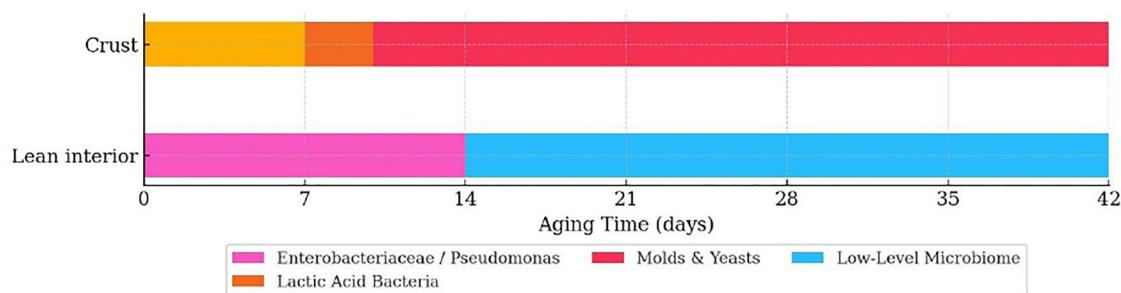


FIGURE 4 | Microbial succession profiles in crust versus inner meat during dry aging (Gowda et al. 2022; Ha et al. 2019; Koutsoumanis et al. 2023; Li et al. 2013; Ribeiro et al. 2023; Ryu et al. 2018; Savini, Indio, Giacometti, et al. 2024).

dominate at 10^3 – 10^5 CFU/cm². Lactic acid bacteria produce mild acidification (~0.1 pH units over 14–35 days), which suppresses pathogens but may impart lactic notes if unchecked (Colle et al. 2015; Ha et al. 2019; Ribeiro, Lau, Furbeck, et al. 2021). High-throughput sequencing shows surface community α -diversity rising over the first 2 weeks as bacterial decline and fungal emergence overlap, then stabilizing as the crust ecosystem matures; β -diversity analyses reveal clear separation between crust and lean interior microbiomes, reflecting steep gradients in a_w and oxygen that select for aerobic, xerophilic fungi versus facultative anaerobes deeper in the tissue (Capouya et al. 2020; Oh et al. 2019). Together, these sequential shifts, from spoilage bacteria to acidifying lactic acid bacteria to mold and yeast-rich crust, create multiple hurdles (low a_w , mild acidity, and competitive colonization) that extend shelf life beyond wet aging, provided psychrotrophs remain under 10^6 CFU/cm² and LAB below 10^5 CFU/cm² to avoid off-odors and ensure premium quality (Li et al. 2013; Ribeiro et al. 2023; Ryu et al. 2018).

5.2 | Crust Microbiome Function

The crust of dry-aged beef hosts a specialized community of xerotolerant molds, notably *Thamnidium*, *Mucor*, and *Penicillium* species, and osmophilic yeasts such as *Debaryomyces hansenii* that thrive under low a_w (0.80–0.85) and cool temperatures (0.5–3°C) (Ahnström et al. 2006; Capouya et al. 2020; Mikami et al. 2021). These fungi colonize the surface early (within 7–10 days), forming a dense mycelial network that both protects the underlying muscle from unwanted bacterial invasion and produces a suite of extracellular proteases and lipases critical for flavor and texture development (Oh et al. 2019; Ryu et al. 2018). *Thamnidium* spp. are often the dominant mold, secreting collagenolytic enzymes that weaken perimysial connective tissues, thereby enhancing tenderness beyond the effects of endogenous calpains (Capouya et al. 2020). *Mucor* species contribute robust protease activity that liberates peptides and FAAs, key Maillard and Strecker precursors, whereas lipases from both *Mucor* and *Penicillium* spp. generate free fatty acids that oxidize into desirable aldehydes and ketones (Liu, Gao, et al. 2025; Mikami et al. 2021). Yeasts such as *D. hansenii* colonize microcracks in the crust, tolerating salt residues and low moisture. They produce glutaminase and arginase activities that deamidate glutamine and arginine, modulating pH and contributing to complex umami and nutty flavors (Oh et al. 2019; Ryu et al. 2018). Together, molds and yeasts establish a synergistic enzyme consortium:

Proteolysis by molds increases substrate availability for yeast deaminases, whereas yeast acid-neutralizing activities create a favorable microenvironment for continued mold growth and enzyme function (Capouya et al. 2020). Critically, fungal colonization must be controlled to avoid species capable of mycotoxin production. However, under typical dry-aging conditions (–0.5°C to 3.0°C; RH 75%–85%; airflow 0.2–0.5 m/s), *Penicillium* spp. and *Aspergillus* spp. rarely synthesize toxins, as confirmed by Mycotoxin Risk Assessments (Meat & Livestock Australia 2018; Koutsoumanis et al. 2023; Savini, Indio, Giacometti, et al. 2024). Concurrent with mold growth, osmophilic and psychrotolerant yeasts colonize microscopic fissures in the crust. *D. hansenii*, often isolated alongside dominant molds, tolerates residual salt and low moisture, producing glutaminase and arginase activities that deamidate glutamine and arginine, subtly raising pH and contributing umami and nutty flavor nuances (Oh et al. 2019; Ryu et al. 2018). More recently, *Candida sake* has emerged as a ubiquitous crust inhabitant, detected in over 80% of commercial samples (Coton et al. 2024; Gao et al. 2025). Preliminary in vitro assays demonstrate that *C. sake* exhibits strong proteolytic and lipolytic activity against beef proteins and fats, and controlled inoculation trials reveal its capacity to shift flavor profiles toward fermented or “cheesy” notes, modulate bacterial communities (increasing *Lactobacillus* spp., suppressing *Pseudomonas* spp.), and boost production of hydroxy fatty acids and vitamin B₃ (Gao et al. 2025). Together, molds and yeasts form a synergistic enzyme consortium: Mold-derived proteolysis exposes substrates for yeast deaminases, whereas yeast-mediated pH modulation supports continued fungal growth and enzyme activity (Capouya et al. 2020). Targeted starter-culture inoculation, using spores of *Thamnidium* spp., *Mucor flavus*, or even *C. sake*, can standardize crust composition, ensuring consistent texture, flavor intensity, and safety across batches (Przybylski et al. 2023; Ryu et al. 2020).

5.3 | Pathogen Behavior and Control Strategies

As described previously, dry aging inherently imposes a series of antimicrobial hurdles (storage conditions and pH) that together suppress common meatborne pathogens. Inoculation studies on beef surfaces show net declines of *L. monocytogenes* at 2°C (≈ 10 – 10^2 CFU/cm²/day), multi-week reductions of *Salmonella* spp. (≈ 2 – 4 log over 6 weeks at 2–6°C; 75%–85% RH), and similar downward trends for *Escherichia coli* O157:H7 and *Listeria innocua*, driven mainly by surface desiccation and microbial competition (da Silva et al. 2019; Koutsoumanis et al. 2023; Savini, Indio,

TABLE 2 | Quality attributes of dry-aged beef and their relationship to biochemical and microbial changes during aging.

Attribute	Driver (variable)	Aging window (days)	Effect	References
Marbling	IMF (%)	21–45	↑ Juiciness; compensates 10%–20% weight loss	Khazzar et al. (2023), Zhang et al. (2025)
Tenderness	WBSF ↓ (25%–45%)	14–35	Calpains + mold proteases	Feng et al. (2020), Han et al. (2024)
Flavor	FAAs, IMP, VOCs	21–35	Beefy, nutty, buttery, earthy notes	Fu et al. (2017), Lee, Yu et al. (2025)
Color	CIE <i>a</i> *, <i>L</i> *, MetMb	7–35	Vivid red → purple → brown (crust)	Ribeiro, Lau, Pflanzner et al. (2021)
Juiciness	WHC, fat melt	28–35	Peak succulence, mouthfeel	Bulgaru et al. (2022), Martinez et al. (2023), Benli and Yildiz (2023)

Abbreviations: FAAs: free amino acids; IMF: intramuscular fat; IMP: inosine 5'-monophosphate; MetMb: metmyoglobin; VOCs: volatile odor compounds; WBSF: Warner–Bratzler shear force; WHC: water-holding capacity.

Giacometti, et al. 2024; Tittor et al. 2011). As noted previously, dry aging combines low temperature, reduced surface water activity, mild acidity, and continuous airflow into a hurdle system that suppresses many meatborne pathogens. Recent syntheses and challenge tests agree that *Salmonella* spp. and *E. coli* (O157:H7) generally decline during dry aging, often by a few log units over multi-week programs, whereas *L. monocytogenes* may persist under certain parameter combinations; a new cabinet study up to 60 days at 1°C reported no significant change in *L. monocytogenes* but transient growth of *Yersinia enterocolitica*, underscoring the need for verified settings and hygiene (Koutsoumanis et al. 2023; Savini et al. 2025; Van Damme et al. 2022).

Accordingly, control in practice emphasizes verification rather than repeating the hurdles: maintain a validated time-temperature–RH–airflow program consistent with regulatory guidance (e.g., EU 2024/1141 baseline conditions) and EFSA’s risk conclusions; map and verify airflow/RH uniformity to eliminate “wet pockets” where pathogens can persist; run routine environmental swabbing (e.g., *L. monocytogenes* and indicators) with trend analysis and periodic challenge testing where feasible; and apply robust sanitation standard operating procedure (SOPs) for chambers, racks, and drains. Where permitted and defined, non-toxigenic surface cultures may help stabilize the competitive crust microbiota without compromising safety.

6 | Quality Attributes

6.1 | Fat Content and Beef Grade/Marbling

IMF, or marbling, is essential for high-quality dry-aged beef: During aging and cooking, marbling melts to distribute lipophilic flavor compounds, lubricate muscle fibers, and enhance mouthfeel, while also compensating for the 10%–20% moisture loss typical of dry aging by sustaining juiciness (Table 2) (Khazzar et al. 2023; Zhang et al. 2025).

Mechanically, the infiltrated fat disrupts connective-tissue networks, amplifying enzymatic tenderization mediated by calpains

and cathepsins (Hocquette et al. 2010; Kim et al. 2016). Chemically, marbling rich in monounsaturated fatty acids, especially oleic acid, has a lower melting point, improving mouthfeel and enhancing flavor liking. Recent reviews and sensory studies in highly marbled beef (e.g., Hanwoo/Wagyu) reinforce the positive contribution of oleic acid to overall palatability (Hoa et al. 2024; Utama et al. 2022).

Global beef-grading systems reflect marbling’s pivotal role in selecting carcasses for dry aging. In the United States, USDA Prime and the top two-thirds of USDA Choice (“Top Choice”), all bearing “Modest” or greater marbling, are preferred, as these grades justify the trim losses and weight shrinkage inherent to aging; USDA Select (“Slight” marbling) rarely achieves sufficient flavor intensity or succulence to offset economic costs (Dashdorj et al. 2016). Canada’s AAA grade, comparable to USDA Choice, delivers robust flavor after 28–42 days of dry aging without excessive yield loss (Carcass Grading—Canada 2024). In Europe, the EUROPE U+ and R classes, often certified under labels such as France’s Label Rouge or Spain’s Certificado de Gu a, target carcasses with ample external and IMF; PDO (protected designation of origin) designations (e.g., Rubia Gallega, Mirandesa) further guarantee high marbling and regional character, with typical aging durations of 21–45 days showcasing terroir-driven flavor nuances (Dashdorj et al. 2016; Hocquette et al. 2010, 2018; Liu et al. 2020, 2021).

Japanese Wagyu grades A4–A5 (BMS 6–12) are dry-aged for 30–100 days to develop the hallmark buttery, umami-rich profile of Kuroge Washu (Mikami et al. 2021), whereas Korea’s 1+ and 1++ Hanwoo grades, valued for high oleic acid fat that melts at lower temperatures, undergo 21–35 days of aging to maximize tenderness and flavor (Lee, Jang et al. 2019; Mikami et al. 2021). In Australia, Meat Standards Australia (MSA) index scores ≥ 65 , often from Angus and Wagyu crosses, predict superior eating quality after 28–42 days of dry aging (Smith et al. 2018). Breed-specific fat chemistry further informs protocol design: Wagyu and Angus marbling is rich in monounsaturated fatty acids, producing softer fat that enhances mouthfeel and flavor release (Wood et al. 2008), whereas Iberian breeds (Rubia Gallega, Mirandesa, and Barros ) offer moderate marbling but elevated

pasture-derived omega-3 and antioxidants, which stabilize lipids and prevent rancidity during 21–35 days of aging (Hocquette et al. 2018; López-Pedrouso et al. 2020; Rodríguez-Vázquez et al. 2020).

6.2 | Tenderness and Texture

Dry-aging transforms beef's texture through a phased interplay of endogenous and microbial proteolysis that dismantles both myofibrillar structures and connective tissues. In the early aging stage (0–14 days), endogenous calpains (μ - and m-calpain) and cathepsins cleave key structural proteins, titin, nebulin, and desmin, loosening the myofibril lattice and reducing Warner–Bratzler shear force (WBSF) by up to 25%–30% after 14–21 days (Table 2) (Feng et al. 2020; Kim et al. 2016). This proteolytic burst is maximized at pH 5.5–6.0 and in the presence of millimolar Ca^{2+} , facilitating enzyme activation within the slightly acidic postmortem milieu (Feng et al. 2020; Han et al. 2024; Khatri and Huff-Lonergan 2023). From Day 14 onward, the dehydrated crust nurtures xerotolerant molds (e.g., *Thamnidium* and *Mucor* species) and yeasts (*Debaryomyces* spp.), which release collagenolytic proteases and lipases. These microbial enzymes diffuse into the subcrust region, further degrading perimysial and endomysial collagen and extending WBSF reductions by an additional 10%–15% between Days 21 and 35 (Capouya et al. 2020; Przybylski et al. 2023, 2024). Concomitant structural alterations, Z-line fragmentation, myofibril dissociation, and loss of heat-stable collagen cross-links further enhance tenderness by decreasing fiber rigidity and increasing collagen solubility during cooking (Liu et al. 2024). Microscopically, aged muscle exhibits reduced mean fiber diameter and greater interfibrillar spacing, producing a softer, more cohesive bite (Feng et al. 2020; Soji 2021). Sensory panel evaluations consistently score dry-aged ribeye and striploin as more tender than wet-aged equivalents, particularly after 28–42 days of aging, highlighting the cumulative impact of sequential enzymatic and microbial tenderization phases (Kim et al. 2022; Soji 2021). Producers calibrate aging duration against cut type, marbling level, and breed genetics: Highly marbled Wagyu may reach optimal tenderness in 21–28 days, whereas leaner continental breeds often require 35–60 days to achieve comparable softness, but at the expense of greater weight loss (Dashdorj et al. 2016; Kim et al. 2022; Ha et al. 2019).

6.3 | Flavor and Aroma

Dry-aged beef's signature bouquet, often characterized as beefy, nutty, buttery, and earthy, emerges from a multilayered convergence of biochemical and microbial processes. Early in aging, muscle calpains and cathepsins liberate FAAs such as glutamate and leucine, which impart sweetness and umami and serve as critical precursors for Maillard and Strecker reactions during cooking (Table 2) (Fu et al. 2017; Hoa et al. 2024; Kim et al. 2019; Lee, Yu, et al. 2025). Concurrently, nucleotide degradation yields IMP and guanosine monophosphate (GMP), amplifying savory depth; as aging progresses, their breakdown to inosine and hypoxanthine introduces mild bitterness and complexity (Kerth and Miller 2015; Kim et al. 2019).

Within IMF, controlled lipid oxidation generates key aroma volatiles: aldehydes like hexanal (green-nutty), heptanal

(fruity), and benzaldehyde (almond-like); ketones such as 2,3-octanedione (buttery); and alcohols including 1-hexanol (floral), each at sub-threshold concentrations that enrich rather than overwhelm the sensory profile (Liu et al. 2024; Li et al. 2021). Endogenous and microbial antioxidant peptides, released during proteolysis, help moderate rancidity by scavenging radical intermediates (Zhang et al. 2013, 2025). Although dry aging itself occurs at refrigeration temperatures that preclude significant Maillard browning, the concentration of reducing sugars and FAAs through evaporative loss enhances Strecker chemistry during high-heat cooking, producing aldehydes such as 3-methylbutanal (malty), 2-methylpropanal (nutty), and phenylacetaldehyde (floral) that deepen roasted and caramel notes (Passetti et al. 2020; Zhang et al. 2019, 2025). Crust-resident molds and yeasts, particularly *Thamnidium*, *Penicillium*, and *Debaryomyces* species, secrete proteases and lipases that generate unique volatile metabolites (e.g., 1-octen-3-one mushroom note and methyl sulfides spicy note) that diffuse into underlying tissue, imparting earthy and spicy nuances absent in wet-aged beef (Capouya et al. 2020; Ryu et al. 2018). Finally, moisture evaporation concentrates these precursors, enhancing both the intensity and clarity of aroma, solidifying dry-aged beef's status as the pinnacle of flavor craftsmanship.

6.4 | Juiciness and Visual Appearance

Juiciness in dry-aged beef reflects a balance between managed moisture loss, proteolysis-driven water retention, and melted IMF during cooking. Typical programs incur ~15%–30% weight loss by 21–28 days, concentrating tastants but risking dryness if proteolysis and fat coverage do not compensate. Time-course studies also show rising dry matter with modest pH drift as aging progresses (Table 2) (Marie-Pierre et al. 2022; Ribeiro et al. 2024). Endogenous enzymes (μ - and m-calpain, cathepsins) degrade myofibrils and connective tissue, increasing the muscle's ability to retain bound water, which sustains internal succulence even as the surface dehydrates (Berger et al. 2018). Upon cooking, marbled fat melts and coats the mouth, enhancing lubrication and the perception of juiciness, whereas lipid-derived volatiles stimulate salivation and deepen flavor release (Bulgaru et al. 2022; Martinez et al. 2023; Miller et al. 2023). Sensory panels typically find optimal juiciness at 28–35 days of aging for heavily marbled cuts, beyond which additional drying yields diminishing benefits (Campbell et al. 2001; Martinez et al. 2023). Genetic factors and antioxidant status (e.g., vitamin E supplementation) further modulate juiciness by preserving lipid integrity and water retention during prolonged aging (Herrera et al. 2022). Visually, dry-aged beef's appeal is defined by its desiccated crust and vivid internal color. After ~35 days, a 20%–25% trimming loss exposes a bright cherry-red lean (high CIE a^*), underpinned by stable oxymyoglobin at pH 5.4–5.8 (Colle et al. 2015). The crust, a gray–brown layer with white and green mold patches, signals authenticity and must be removed prior to sale (Mikami et al. 2021; Ribeiro et al. 2023). Extended aging beyond 42 days can lead to slight browning from metmyoglobin accumulation if airflow or humidity is suboptimal (Ribeiro, Lau, Pflanzler, et al. 2021; Savini, Indio, Panseri, et al. 2024). Concurrently, moisture evaporation accentuates marbling contrast, enhancing visual richness; appearance scores for marbling correlate strongly with overall quality perceptions (Benli and Yildiz 2023).

7 | Dry Aging Process

Dry aging transforms beef through a precise interplay of time, temperature, RH, airflow, and even controlled UV exposure to orchestrate biochemical tenderization, flavor concentration, and microbial control, while minimizing economic losses. Aging days: reported aging periods span from 7 to over 60 days for subprimal cuts, but most producers settle on 14–40 days; 21 days is widely considered the optimal compromise among tenderness, flavor intensity, and yield (Dashdorj et al. 2016). During the initial 7–14 days, endogenous calpains and cathepsins cleave myofibrillar proteins, reducing shear force by up to 30% (Perry 2012). As aging progresses past 3 weeks, enzymes secreted by crust fungi further accelerate proteolysis, liberating FAAs that deepen umami and nutty flavor notes, though sensory improvements plateau around 35 days even as evaporative weight loss climbs (10%–15% by Day 21; 20%–30% by Day 40) and trimming losses escalate (Mikami et al. 2021). Metabolomic profiling confirms that the length of aging is the predominant driver of meat composition changes: by 28 days, abundant small peptides (notably di- and tripeptides), FAAs, and their derivatives accumulate to levels far exceeding those in shorter-aged samples (Liu, Yu, et al. 2025). On balance, a 21- to 28-day window, adjusted by ± 7 days according to breed and marbling, is the industry standard. Extended dry aging (45–60 days) is typically reserved for highly marbled breeds such as Wagyu, where IMF both shields against excessive moisture loss and yields distinctive flavor nuances during prolonged aging (Dashdorj et al. 2016). Temperature control: Aging temperature dictates both enzyme kinetics and microbial dynamics. Calpain activity at 2–4°C yields significant proteolysis within 14–21 days, whereas –0.5°C to 0°C slows tenderization by 20%–30% but further suppresses psychrotrophic spoilage (Dashdorj et al. 2016). Psychrotrophs like *Pseudomonas* spp. halve growth rates with every 5°C drop, so maintaining 1–2°C minimizes spoilage while allowing tenderization (Pennacchia et al. 2011). Below 2°C, pathogens such as *L. monocytogenes* and *Salmonella* spp. cannot grow, reinforcing safety (Koutsoumanis et al. 2023; Savini et al. 2025). Modern facilities therefore stabilize chambers at 0.5–3°C ($\pm 0.5^\circ\text{C}$), often with stepwise profiles, warmer early on for faster tenderization and colder later for safety and flavor concentration (Meat & Livestock Australia 2016; Mikami et al. 2021). RH governs both surface a_w and moisture loss. An RH of 75%–85% creates a crust a_w of 0.80–0.85, low enough to inhibit *Pseudomonas* spp., yet permitting molds (e.g., *Thamnidium* spp.) to develop flavor-enhancing enzymes (Dashdorj et al. 2016; Koutsoumanis et al. 2023). RH >85% risks high a_w (>0.90), encouraging spoilage organisms, whereas RH <70% accelerates evaporation and excessive yield losses (Ribeiro et al. 2024). Some operations employ dynamic RH, starting at 85% to form the crust, then reducing to 75% to control dehydration, for consistent quality and economics (Meat & Livestock Australia 2016). Airflow: Uniform airflow (0.2–0.5 m/s) ensures even drying and prevents moisture pockets that harbor spoilage bacteria (Lancaster et al. 2022). Computational fluid dynamics studies highlight the risk of stagnant zones with elevated microbial counts, whereas excessive airflow (>1 m/s) can produce overly thick crusts and oxidative off-flavors (Mikami et al. 2021). Variable-speed systems, gentle early on and then increased as the crust matures, optimize both safety and yield (Dashdorj et al. 2016). UV-C irradiation: Some premium facilities integrate low-dose UV-C (254 nm) pulses (1–2 kJ/m² for 30 s daily) to reduce surface *Pseudomonas* spp.,

Listeria spp., and coliforms by 1–2 Log₁₀ without impairing proteolysis or color (Kim et al. 2018; Monteiro et al. 2023). Limited to the outer 1–2 mm, UV-C complements low a_w and pH hurdles. However, doses must remain <5 kJ/m²/day to avoid increased lipid oxidation and crust darkening (Monteiro et al. 2023).

8 | Food Safety Regulatory Context

Regulatory oversight of dry-aged beef is built on three pillars: clear process definitions, enforceable environmental criteria, and stringent microbial standards, whose specifics vary by jurisdiction but share the goal of ensuring product safety without compromising sensory quality (Table 3). In the European Union, Commission Delegated Regulation (EU) 2024/1141 formally defines “dry aging” as the aerobic storage of unpackaged carcasses or cuts (or in water-vapor-permeable packaging) for ≥ 14 days in certified chambers maintained at –0.5°C to 3°C, $\leq 85\%$ RH, and 0.2–0.5 m/s airflow. This is enforced alongside Regulation (EC) No 853/2004, which governs meat hygiene, and Regulation 2073/2005, which sets mandatory microbiological criteria for ready-to-eat meats (e.g., absence of *L. monocytogenes* in 25 g) to ensure uniform safety across all Member States. In the United States, although no federal statute explicitly codifies dry-aging parameters, the USDA Food Safety and Inspection Service (FSIS) controls labeling under 9 CFR Part 412 and general sanitation under 9 CFR Part 416. Beef may be labeled “Aged” or “Dry Aged” only if held fresh, unfrozen, and aerobic for ≥ 14 days. Although industry guidance suggests 0–4°C, up to 90% RH, and controlled airflow, these remain advisory; FSIS enforces microbial safety via performance standards (e.g., *Salmonella* spp. <5% positive in raw beef trim) and requires that aging claims be truthful and non-misleading. In Australia & New Zealand, AS 4696:2007 (“Hygienic Production and Transportation of Meat and Meat Products”), harmonized with the Australia New Zealand Food Standards Code, mandates HACCP-based controls, facility design requirements, traceability, and microbial limits (e.g., *E. coli* ≤ 100 CFU/g; absence of *Salmonella* spp. in 25 g). Meat & Livestock Australia’s guidelines recommend 0.5–3°C, 75%–85% RH, and 0.2–0.5 m/s airflow for ≥ 14 days of dry aging. In Canada, the Safe Food for Canadians Regulations (SFCR) and Meat Inspection Act, administered by the Canadian Food Inspection Agency (CFIA), govern all interprovincial and export meat. Although SFCR does not explicitly define dry aging, federally registered establishments must implement preventive (HACCP) controls, maintain cold-chain integrity, and meet microbial standards (e.g., absence of *L. monocytogenes* in ready-to-eat products). Any novel dry-aging claim or nonstandard storage declaration requires CFIA pre-approval with full process validation. In China, processors of dry-aged meat fall under the Food Safety Law and national standards GB 7718-2011 (labeling) and GB 28050-2011 (nutrition), but no dedicated standard for dry aging exists. Consequently, products must comply with general meat hygiene, additive, and labeling rules established by the National Health Commission. In Japan, the Food Sanitation Act and Food Labeling Standards (Consumer Affairs Agency) require that any “dry-aged” designation be factually substantiated. Although no statutory temperature, RH, or airflow thresholds are specified, operators must demonstrate, via facility design, sanitation plans, and record-keeping, that their processes prevent contamination

TABLE 3 | Regulatory frameworks and standards for dry-aged beef.

Region	Legislation/Standard	Microbiological criteria	Labeling requirements	Process parameters/guidelines	References
European Union	Commission Delegated Regulation (EU) 2024/1141 (amending EC 853/2004)	EU Regulation 2073/2005: mandatory pathogen limits for RTE meat (e.g., <i>Listeria monocytogenes</i> , <i>Salmonella</i> spp.)	Must state “dry aged,” aging duration, and method; deviations from defined parameters require reclassification as fresh meat	Certified chambers with continuous monitoring of Temp, RH, airflow; proof of equipment calibration and maintenance	EU 2024/1141 EU 2073/2005 E 853/2004
The United States	USDA FSIS 9 CFR Part 412 and FSIS Labeling Policy Book: regulates “Aged”/“Dry Aged”	FSIS performance standards for pathogens (under general inspection); no separate dry-age criteria	Label must be accurate and non-misleading; “Dry Aged” claims require FSIS approval for special statements	Industry guidance (advisory): 0–4°C; RH ≤ 85%–90%; airflow control; sanitation under 9 CFR Part 416 (HACCP, GMP)	eCFR: 9 CFR Part 412 (2023) Food Standards and Labeling Policy Book (2005) eCFR: 9 CFR Part 416 (1996)
Australia & New Zealand	AS 4696:2023 “Hygienic Production and Transportation of Meat...” (HACCP, traceability, facility design) Meat & Livestock Australia: Guidelines for Dry Aging	FSANZ and/or state food authority microbiological limits under the Australia New Zealand Food Standards Code	Must comply with general labeling rules (product name, aging method, storage conditions) under Food Standards Code	Recommended: 0.5–3°C; RH 75%–85%; airflow 0.2–0.5 m/s; minimum 14 days in purpose-built chambers; HACCP oversight	Australian Government AS4696:2023 (2023)
	Export Control (Meat & Meat Products)				Meat and Livestock Australia. Guidelines for the Safe Production of Dry Aged Meat (2019) Australian Government (2025). Export Control—Rules 2021

(Continues)

TABLE 3 | (Continued)

Region	Legislation/Standard	Microbiological criteria	Labeling requirements	Process parameters/guidelines	References
Canada	Canadian Food Inspection Agency (CFIA) framework under Safe Food for Canadians Regulations (SFCR): licensing, preventive controls (HACCP), traceability	CFIA's general meat inspection and RTE microbiological standards; no bespoke dry-aged limits	Labels must be truthful and clear; special dry-age or non-standard storage claims require CFIA pre-approval	Operators follow SFCR: maintain cold chain, implement HACCP, and validate processes via documented environmental and product testing	Safe Food for Canadians Regulations (2023) Government of Canada Regulations Amending the Meat Inspection Regulations, 1990 (2014)
China	Consumer Packaging and Labelling Act for label accuracy Food Safety Law of the PRC GB 7718-2011 "General Rules for Labeling of Prepackaged Foods" GB 28050-2011 "Nutritional Labeling of Prepackaged Foods"	General hygiene and pathogen criteria under national food safety standards; no dry-age-specific limits	Must meet GB 7718/GB 28050 label requirements (product name, origin, date, storage)	No dedicated dry aging standard—processors apply general chilled meat hygiene: maintain low temp, monitor hygiene, and control additives	Consumer Packaging and Labelling Act (1999) Food Safety Law of the PRC (2015) Meador and Bugang (2014) CIRS: GB 28050-2011 (2014)
Japan	Food Sanitation Act (FSA) and enforcing ordinances Consumer Affairs Agency Food Labeling Standards	RTE food microbiological criteria under FSA; no specific dry-age thresholds	"Dry aged" claims must be factually substantiated; labels require product name, ingredients, dates, storage	Processors must document facility sanitation, hazard controls, and environmental monitoring; no numeric dry-age parameters—rely on validated in-house procedures	Food Sanitation Act (2018) Food Labeling Act (2018)

and meet general pathogen limits (e.g., absence of *Salmonella* spp. in 25 g; *Staphylococcus aureus* ≤ 100 CFU/g).

9 | Sustainability and New Perspectives

9.1 | Yield Losses and Crust Valorization

Dry-aged beef's signature sensory enhancements—pronounced umami, tender texture, and complex aroma—come at a tangible cost: Moisture evaporation and crust trimming typically reduce yield by 15%–30% over a 35-day aging period, inflating refrigeration, handling, and waste-disposal expenses (Berger et al. 2018; Dashdorj et al. 2016).

Transforming crust trimmings into value-added co-products mitigates these losses. Dehydrated crust, rich in FAAs and volatile flavor precursors, can be milled into umami-intense powders; overall, 1%–3% inclusion in broths or snacks yields savory depth rivaling monosodium glutamate, with high consumer acceptance (Liu et al. 2024).

Upcycling the crust offers a direct route to recapture value. Multiple studies show that crust powders (lyophilized trimmings) elevate savory intensity and consumer liking when incorporated into patties, sauces, or other foods, and they contribute useful techno-functional properties (emulsifying capacity, water/oil binding). Recent work characterizing lyophilized fresh, wet-, and dry-aged powders confirms the crust's favorable composition for use as a food additive (Park et al. 2018, 2020; Park and Kim 2023).

Ultrafiltration of crust hydrolysates isolates bioactive peptides exhibiting antioxidant and ACE-inhibitory activity suitable for nutraceuticals (Choe et al. 2020; Fu et al. 2017). However, conventional dry aging requires precise environmental control, accelerates weight and trim losses, and heightens contamination risks (Cho et al. 2018; Smith et al. 2008). To overcome these drawbacks, “bag” dry aging systems, using water-permeable films like Tublin or Dry Aging Bags, have been introduced. Research demonstrates that bag-aged beef matches traditional dry-aged meat in tenderness, flavor intensity, and overall sensory appeal, while significantly curbing trim waste and reducing microbial counts (Berger et al. 2018; Correa et al. 2025; Setyabrata et al. 2024). Further economic returns arise from microbial valorization: dominant crust fungi and yeasts such as *Thamnidium elegans*, *D. hansenii*, and lactic acid bacteria can be isolated and redeployed as starter cultures. Inoculation of fresh beef cuts with these cultures reduces required aging time by up to 20%, thereby cutting energy consumption and storage space needs, while delivering consistent flavor profiles (Laranjo et al. 2017; Oh et al. 2019; Ryu et al. 2018). Beyond whole-cell applications, psychrotolerant proteases and collagenases extracted from crust biomass have proven effective across industries, from meat tenderization to leather processing, thereby converting what was once waste into a valuable enzyme source (Capouya et al. 2020). Building on these advances, an *M. flavus*-based fungal biostarter has recently been shown to standardize and enhance the dry aging process by raising meat pH by approximately 0.25 units, accelerating light-myosin-chain proteolysis by around 16%, boosting sensory acceptability by one point on a nine-point scale, and maintaining a stable, non-pathogenic bacterial community dominated by

Pseudomonas spp., outcomes that not only improve product quality but also ensure consistent flavor (Capouya et al. 2020; Jaworska et al. 2025; Przybylski et al. 2023, 2024). Psychrotolerant fungal proteases and collagenases extracted from crusts also have industrial applications in tenderization and leather processing, unlocking additional revenue streams (Capouya et al. 2020).

9.2 | Technological Innovations

Advancing dry-aged beef production will rely on synergistic integration of microbiome science, intelligent automation, valorization strategies, and supportive regulatory frameworks to create a scalable, sustainable industry. High-resolution multi-omics mapping, combining metagenomics, metatranscriptomics, and metabolomics in commercial aging chambers, offers unprecedented insight into the functional roles of native and inoculated microbial consortia in flavor precursor synthesis, proteolysis, and safety enhancement, enabling deliberate microbiome engineering for tailored taste profiles and spoilage control (Barcenilla et al. 2024; Oh et al. 2019; Ryu et al. 2020; Setyabrata et al. 2021).

On the engineering side, AI-assisted sensing and control can move aging from static set-points to predictive, lot-specific programs. Recent studies and reviews demonstrate non-destructive prediction of beef quality using hyperspectral and NIR imaging, sometimes attaining lab-scale correlations for tenderness/freshness near $r \approx 0.95$ – 0.98 , whereas emerging VOC/e-nose platforms provide rapid spoilage/volatilome fingerprints suitable for online monitoring. In practice, fusing HSI/NIR, cabinet telemetry (T/RH/airflow), and VOC streams can train models that recommend dynamic adjustments (e.g., stepwise cooler set-points, RH ramps, and fan speeds) and forecast optimal endpoints for flavor, tenderness, and risk—reducing variability between cabinets and loads (Alvarez-García et al. 2024; Lee, Yu, et al. 2025; Wang and Li 2024).

Hybrid aging modalities represent a promising avenue to balance sensory quality, yield, and energy use: An initial dry-aging phase concentrates FAAs and peptides, followed by modified-atmosphere or active-film packaging to seal moisture and volatile compounds, achieving comparable organoleptic outcomes with up to 50% less weight loss and 20%–30% lower energy consumption, as demonstrated by life-cycle assessments (Ahmed et al. 2022; Correa et al. 2025; Leighton et al. 2023).

To further decarbonize operations, facilities can incorporate diverse renewable energy sources, such as biomass-fired boilers and geothermal heat exchange loops, to meet simultaneous refrigeration and heating demands, striving for net-zero carbon footprints without compromising environmental stability (Liang et al. 2017; Singh Tomar and Pradhan 2024). Finally, the widespread adoption of novel microbial and phage-based interventions, including defined starter cultures and clustered regularly interspaced short palindromic repeats (CRISPR)-edited consortia, will depend on clear regulatory pathways that balance innovation with consumer protection; establishing science-based guidelines for safety testing, labeling, and environmental monitoring will be essential to scale these biotechnologies in commercial dry-aging contexts (Abuladze et al. 2008; Chang 2020; Dhulipalla et al. 2025; Koutsoumanis et al. 2023; Rivera-Lopez et al. 2025).

10 | Conclusion

Dry-aged beef can be produced reliably and sustainably when biology, engineering, and verification are treated as one system. Success starts with suitable raw material (fine marbling, normal ultimate pH) and validated set-points for time, temperature, RH, and airflow, which together enable early endogenous tenderization and later surface-driven flavor development while controlling risk. Managing the crust microbiome—via sanitation, cabinet uniformity, and defined starters, with phage aids where permitted—improves reproducibility without sacrificing safety. Sustainability hinges on process optimization (dynamic RH/airflow, hybrid or in-bag formats, energy-efficient cabinets) and crust valorization (umami powders, peptide/enzyme fractions) to offset shrink/trim and reduce the footprint. A practical roadmap prioritizes common quality metrics (WBSF/MFI, TBARS/hexanal, key FAAs/IMP-hypoxanthine, surface a_w /pH, and indicators), multi-site trials of starter/phage strategies, and sensor-driven, AI-assisted control. Executed together, these steps move dry aging from artisanal variability to quality-by-design, consistently delicious, safe, and economically and environmentally sound.

Author Contributions

Ana J. Ribeiro: writing—original draft, conceptualization, writing—review and editing, investigation, methodology. **Filipe Silva:** supervision, validation. **Paula Teixeira:** supervision, validation. **Cristina M. Saraiva:** supervision, validation.

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Conflicts of Interest

The authors declare no conflicts of interest.

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