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COMPREHENSIVE REVIEWS IN FOOD SCIENCE AND FOOD SAFETY

Flavor challenges in extruded plant-based meat alternatives: A review

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Abstract

Demand for plant-based meat alternatives has increased in recent years due to concerns about health, ethics, the environment, and animal welfare. Nevertheless, the market share of plant-based meat alternatives must increase significantly if they are to support sustainable food production and consumption. Flavor is an important limiting factor of the acceptability and marketability of plant-based meat alternatives. Undesirable chemosensory perceptions, such as a beany flavor, bitter taste, and astringency, are often associated with plant proteins and products that use them. This study reviewed 276 articles to answer the following five research questions: (1) What are the volatile and nonvolatile compounds responsible for off-flavors? (2) What are the mechanisms by which these flavor compounds are generated? (3) What is the influence of thermal extrusion cooking (the primary structuring technique to transform plant proteins into fibrous products that resemble meat in texture) on the flavor characteristics of plant proteins? (4) What techniques are used in measuring the flavor properties of plant-based proteins and products? (5) What strategies can be used to reduce off-flavors and improve the sensory appeal of plant-based meat alternatives? This article comprehensively discusses, for the first time, the flavor issues of plant-based meat alternatives and the technologies available to improve flavor and, ultimately, acceptability.

KEYWORDS

Extrusion, flavor, legumes, meat alternatives, plant-based, proteins

Abbreviations: ADH, Alcohol dehydrogenase; AEDA, aroma extraction dilution analysis; βCD, β-cyclodextrin; EOX, Epoxygenase; HPD, Hydroperoxide dehydrase; HPL, Hydroperoxide lyase; HS-SPME-GC-MS, Headspace solid-phase microextraction coupled with gas chromatography and mass spectrometry; LAB, Lactic acid bacteria; LDL, Low-density lipoprotein; LOX, Lipoxygenase; POX, Peroxygenase; ROOHs, Hydroperoxides.

1 | INTRODUCTION

By 2050, demand for animal-source products is projected to be 70% higher than it is now, as a result of the growing world population, increasing income, and urbanization (Yitbarek, 2019). Meat production has a variety of impacts on the environment such as significant greenhouse gas emissions (it accounts for 54% of the total emissions from agriculture) that cause global warming, sea level rise, extreme weather events, drought, and other catastrophic impacts; pollution from fossil fuel usage; freshwater depletion; and biodiversity loss (Henning, 2011; OECD-FAO Agricultural Outlook, 2021–2030). To reduce global meat consumption, the replacement of meat with alternative protein products is being promoted. Meat alternatives are classified into three major types: plant-based; in vitro meat, which is meat cultured in laboratories using tissue-engineering technology; and edible insects (Lee et al., 2020). Plant-based alternatives are currently the most popular type of meat alternative in industrialized countries (Gómez-Luciano et al., 2019; Lundén et al., 2020).

Plant-based meat alternatives are texturized food products made from plant-derived proteins that mimic or replace meat (Lee et al., 2020). The global plant-based protein market is estimated to grow at a compound annual growth rate of 7.2% to reach $15.6 billion in 2026 (MarketsandMarkets, 2021). This growth will likely be driven by rising venture investments in alternative protein companies, technological innovation, the potential health benefits of plant-based diets, the environmental sustainability associated with the production and consumption of plant proteins, and the increasing shift to a flexitarian diet. The transition to a more plant-based diet would help to mitigate climate change because such a diet requires less energy, water, and land resources than an animal-based diet (Pimentel & Pimentel, 2003). Soy, pea, and wheat, in the forms of isolate, concentrate, or textured protein, are the most commonly used ingredients (MarketsandMarkets, 2021). On the other hand, the soy-free and gluten-free trends have encouraged the use of other protein sources, specifically legumes such as faba beans, lupins, and chickpea. Legume crops are sustainable and contribute to nitrogen fixation, biological diversity, and soil quality (Toomsan et al., 2012). Additionally, the consumption of legumes has demonstrated a number of health benefits, such as a reduced risk of developing type 2 diabetes, lower total and LDL (low-density lipoprotein) cholesterol levels, and a positive impact on weight and blood pressure management (Polak et al., 2015).

Despite many benefits of plant-based meat alternatives, however, their absolute market share is still low, at only around 1% of the total meat market (Choudhury et al., 2020). The main barriers to the transition to a less meat-based diet include the unfamiliarity of meat-alternative products and their low sensory appeal (Hoek et al., 2011; Onwezen et al., 2021). Meat and meat products are highly appreciated by consumers due to their sensory properties and nutritional composition, which include high-quality proteins, minerals (e.g., iron, zinc, and selenium), and vitamins (e.g., A, B6, and B12; Ahmad et al., 2018). A reduction in meat consumption is expected to occur when the alternative products can assume not only the health, nutritional, and physiological functions of meat but also the associated food experience (preference and flavor). Flavor is a multisensory perceptual integration of taste, retronasal smell, and chemical irritation (chemesthesis) that is perceived during eating (Fondberg et al., 2018). The flavor of plant-based meat alternatives is a crucial factor of their acceptance and regular consumption, whereas other food-choice drivers, such as animal welfare, environmental ethics, and health benefits, appear to be less influential (Szejda et al., 2020). Plant-based meat alternatives are targeted especially for omnivores and flexitarians, who consider the similarity of these products (in texture and flavor) to meat to be important (Michel et al., 2021). However, Hoek et al. (2011) found that the more often consumers ate meat alternatives, the less they required the meat alternatives to be similar to meat. Thus, it may be more important for the sensory properties of plant-based meat alternatives to be desirable than to closely resemble those of meat.

A meat-like fibrous texture has been developed via multiple techniques such as extrusion cooking, shear, spinning, and 3D printing (Dekkers et al., 2018; Sha & Xiong, 2020). High-moisture (or wet) extrusion is the predominant technique used to texturize plant proteins, which is done under high-moisture (>50%) and high-temperature (140–180°C) conditions. The intensive processing leads to the unfolding, aligning, and cross-linking of the plant proteins, which results in the formation of layer and fiber structures. Nevertheless, the fibrous network formed by denatured plant proteins does not entirely resemble the structure of muscle fibers in their hierarchical architecture and interstitial matrix, which are essential for water binding (Sha & Xiong, 2020). Plant-based meat-alternative products are often perceived as having a dry mouthfeel or low juiciness. Another challenge is simulating the taste and aroma of meat products due to the extreme complexity of the compounds associated with the flavor of meat (He et al., 2020; Li & Li, 2020). Furthermore, off-flavors, such as a beany flavor, a bitter taste, an aftertaste, and astringency, are often detected in plant-based alternatives (Mittermeier-Kleßinger et al., 2021; Sha & Xiong, 2020). "Off-flavors" refer to objectionable flavors, including perceived undesirable tastes, odors, and other sensations such as astringency. Off-flavors in plant-based products can be either inherent to the plant ingredients (e.g., intrinsic

off-taste constituents) or can arise from processing and storage (e.g., from the oxidative deterioration of unsaturated fatty acids in protein-bound lipids; Rackis et al., 1979). These off-flavors hinder consumer preference and acceptability. Efforts have been made to reduce or eliminate the off-flavors in plant-based alternatives; however, progress is limited compared to that for textural improvement. Furthermore, the structuring process of plant-based meat alternatives induces modifications to flavor due to the high heat and pressure applied (He et al., 2020).

The scientific literature on the factors that influence the flavor characteristics of plant-based protein ingredients and meat alternatives is limited. In this study, we focus on flavor-active compounds (both volatiles and nonvolatiles) and precursors in various plant protein sources, with an emphasis on legumes (particularly nonsoy sources), as well as the principal formation pathways of off-flavors. The flavor changes in plant materials during extrusion cooking are also discussed. In addition, this review considers flavor in a holistic way including both chemical compounds and human sensory perceptions. Finally, this review discusses approaches to removing or masking off-flavors and generating the desired flavors in plant-based meat alternatives.

2 | FLAVOR CHARACTERISTICS OF PLANT-BASED INGREDIENTS (FLOURS, PROTEIN CONCENTRATES, AND ISOLATES)

2.1 | Components or precursors related to flavor

Plants and plant-based products are well known for having distinctive flavors because they can synthesize, accumulate, and release a wide array of flavor-active compounds (Schwab et al., 2008). Plant-derived flavor molecules are synthesized as such by plants as a defense response mechanism or generated from flavor precursors in plants (e.g., amino acids, fatty acids, and carbohydrates) during harvesting, processing, and storage (Roland et al., 2017). Understanding the chemical composition of plant-based ingredients can provide indicative and useful insights into the volatiles and nonvolatiles that can be produced under certain conditions. However, it must be considered that variations in composition are found within and between plant species and that factors, such as cultivars, growing conditions, and post-harvest storage and processing conditions, affect such composition both qualitatively and quantitatively (Singh, 2017). Furthermore, the chemical and sensory profiles of protein concentrates and isolates are different from those of the original flours and depend largely on the protein isolation methods used. Flavor precursors present in the plant's raw materials are transmitted to the isolated proteins either in a protein-associated form or as processing residues (Damodaran & Arora, 2013). The resulting protein concentrates or isolates usually exhibit significantly lower levels of starch, fat, ash, and fiber than do the flours (Cruz et al., 2020).

2.1.1 | Proteins

The role of proteins in defining the flavor of plant-based foods is multifaceted because they can act as flavor precursors, especially if hydrolyzed to amino acids (e.g., in Maillard reactions, which are nonenzymatic browning reactions), retain flavor molecules in the food matrix, and be hydrolyzed to produce peptides with flavor properties. Legume seeds (e.g., soy, faba bean, pea, chickpea, lupin, common bean, lentil, and cowpea) contain proteins in the range of 21 to 37 g/100 g seed dry weight, which is about double of that found in cereals (Sánchez-Chino et al., 2015; Singh, 2017). The main fraction of legume proteins consists of globulins (35 to 72%), albumins (15 to 25%), and a minor amount of glutelins (10 to 20%) (Sánchez-Chino et al., 2015). Legumes exhibit relatively low levels of sulphur-containing amino acids (methionine and cysteine) and tryptophan but much higher lysine levels than in cereals such as wheat and rice.

Legume protein ingredients vary in their protein content depending on the isolation techniques used, which are generally divided into two types: (1) dry fractionation processes (milling and air classification), which fractionate legume seeds into starch and protein concentrates (protein content, 60 to 75%), and (2) wet fractionation processes, such as alkaline (pH 8 to 10) or acid (pH < 4) extraction, followed by precipitation at a pH close to the isoelectric points (pH 4 to 5) of the proteins, which yields a protein isolate of 90 to 95% purity (Klupšaitė & Juodeikienė, 2015). The amino acid profiles of legume protein isolates generally showed higher concentrations of both essential and nonessential amino acids than did their respective seeds (Fernández-Quintela et al., 1997). The amino acid compositions were slightly different between protein concentrates (e.g., soy, faba bean, and chickpea) and their isolates (Ma, 2016; Vogelsang-O'Dwyer et al., 2020b) and were not altered when the protein isolates were prepared via different techniques such as micellization or isoelectric precipitation (Paredes-López et al., 1991).

Proteins are well known to bind to several volatile and nonvolatile compounds and to act as flavor carriers (Guichard, 2002). For instance, oleosin proteins can act as carriers of phospholipids (important substrates of lipid oxidation) by forming a monolayer membrane that surrounds the oil bodies (Damodaran & Arora, 2013). The

undesirable flavors or flavor precursors are bound to proteins and, thereby, transmitted to protein-rich fractions and products (Zhang et al., 2021a). The focus of research has been on soy and pea proteins and their interactions with flavor molecules. Proteins provide complex chemical sites of interaction with flavor molecules through noncovalent and covalent forces. Most protein-flavor interactions are reversible such as hydrophobic interactions, hydrogen bonding, van der Waals interactions, and ionic bonding (Zhang et al., 2021a). Hydrophobic interactions often occur at the interior hydrophobic areas (binding sites) of the proteins. The typical volatiles involved are aldehydes, ketones, alcohols, and esters (Wang & Arntfield, 2017). Hydrogen bonds bind flavor components (e.g., aliphatic alcohols, lactone, and volatile acids) to the hydroxyl (-OH), carboxyl (-COOH), and sulfhydryl (-SH) groups of the proteins. Volatile acids can form ionic bonds and electrostatic linkages at the hydroxyl (-OH) and amino ($-NH_2$) groups of proteins. Some flavor compounds may form irreversible covalent bonds with proteins and result in a loss of flavor. The covalent linkages usually occur between hydrocarbons, aldehydes, sulfur-containing compounds, and the functional groups (-SS-, -SH, and $-NH_2$) of proteins.

The protein-flavor binding behavior is affected by several factors, including the reactivity and chemical structure of the flavor compounds and proteins; the composition of the food matrix, such as the moisture content; and the processing conditions such as the pH and temperature (Zhang et al., 2021a). The hydrophobicity of flavor molecules and proteins is positively correlated with flavor-protein interactions (Guichard, 2002). Processing that leads to the unfolding or denaturation of proteins may change the number and distribution of their binding sites and, thereby, affect their flavor-binding capacity. The amino acid sequence is also an important determinant of the binding ability of proteins. Proteins with higher levels of cysteine, lysine, and arginine residues show higher flavor-binding capacities, likely due to the formation of covalent linkages. More fundamental knowledge of the mechanisms of flavor-protein interactions and the factors that influence the binding behavior would contribute to the control of flavor release and retention and the removal of off-flavors from plant-based protein foods.

2.1.2 | Lipids

Lipids constitute one of the major groups responsible for the formation of volatile and non-volatile flavor compounds because they participate in oxidation and other reactions (Jeleń & Wąsowicz, 2012). The total fat content of legume seeds is 2–20 g/100 g (Khrisanapant et al., 2019). Soy and chickpea seeds have the highest lipid contents (19–20 and 6–8 g/100 g, respectively), whereas lower levels (2–6 g/100 g) are observed in faba bean, pea, lentil, cowpea, mung bean, navy bean, kidney bean, white bean, and black bean seeds (Caprioli et al., 2016; Khrisanapant et al., 2019). The fatty acid profiles of legume seeds consist of mainly palmitic (16:0), stearic (18:0), oleic (18:1), linoleic (18:2), and α-linolenic (18:3) acids. Regarding the percentage of their total saturated fatty acids (SFAs), it varies from 12 to 37%, with higher palmitic acid levels than stearic acid levels (Caprioli et al., 2016; Khrisanapant et al., 2019). Legumes have a high level of unsaturated fatty acids, of which monounsaturated fatty acids (MUFAs) account for 6–40% and polyunsaturated fatty acids (PUFAs) account for 40 to 70%. Linoleic acid is the most abundant PUFA in majority of legume seeds, especially in soy, faba bean, and chickpea (Khrisanapant et al., 2019). The exceptions are navy bean, black bean, and kidney bean, in which the most abundant PUFA is α-linolenic acid.

Lipid content in protein concentrates and isolates is heterogeneous according to the legume type, affected greatly by the method of protein isolation, and commonly between 0 and 6 g/100 g (EI-Adawy et al., 2001; Fernández-Quintela et al., 1997; Paredes-López et al., 1991; Vioque et al., 2012; Zar Oo et al., 2017). Research on the fatty-acid composition of protein concentrates and isolates is limited. Vogelsang-O'Dwyer et al. (2020a, b) showed that the SFAs, MUFAs, and PUFAs in lupin protein isolates (total fat content, 1 g/100 g) were 52 to 61%, 27 to 40%, and < 22%, respectively, whereas in faba bean concentrates (2.4 g/100 g) and isolates (4.4 g/100 g), these percentages were 16 to 18%, 23 to 24%, and 55%, respectively. The proportions of fatty acids in lupin protein isolates could be influenced by defatting, which is done during the processing of the isolates. Commercially available (e.g., MYPROTEIN) soy protein isolates (fat, 1.5 g/100 g) and pea protein isolates (5.5 g/100 g) contain 33 and 18% SFAs, respectively.

2.1.3 | Carbohydrates

The importance of carbohydrates in flavor compound formation is linked to the presence of amino acids and/or the application of heating (e.g., Maillard reaction and caramelization; Majcher, 2011). Most legume seeds are high in carbohydrates (50 to 68 g/100 g), such as pea, faba bean, chickpea, lentil, cowpea, pigeon pea, kidney bean, green gram, and black gram, but lupin, soy, and groundnut contain less carbohydrates (19 to 37 g/100 g; Maphosa & Jideani, 2017; Tripathi et al., 2021). Starch is the dominant carbohydrate in legumes. It may influence flavor retention and release during extrusion cooking through the formation of inclusion complexes with flavor molecules (Escher et al., 2000). The seed starch content of pea, faba bean,

chickpea, and lentil is approximately 40 to 50 g/100 g, and of soy and lupin, less than 10 g/100 g (Tayade et al., 2019). The sugars in legumes are composed of monosaccharides (glucose, fructose, galactose, and ribose) and disaccharides (sucrose and maltose); and in addition, there are oligosaccharides belonging to the α-galactosides group (raffinose, stachyose, and verbascose) with a mildly sweet taste (Buttriss, 2017). Legume seeds are rich in α-galactosides, with their content thereof ranging from 30 to 66 mg/g, and with the highest level commonly found in pea seeds (Maphosa & Jideani, 2017; Pedrosa et al., 2021). The sucrose content of legume seeds reported in the literature is usually 0.3 to 4% (dry weight; Tripathi et al., 2021). Glucose, fructose, ribose, and maltose are often present at low levels, below 0.5% (Berrios et al., 2010). The dietary fiber content of most legume seeds is 8 to 28 g/100 g, and of soluble fiber specifically, 3 to 14 g/100 g (Guillon & Champ, 2002). Lupin seeds are uniquely rich in dietary fiber (25 to 40 g/100 g).

The total carbohydrate, starch, and dietary fiber contents of legume protein concentrates are generally higher than those of isolates (Bhatty & Christison, 1984; Ferawati et al., 2021; Fernández-Quintela et al., 1997; Ma, 2016; Macarulla et al., 2001; Reilly et al., 2020; Vioque et al., 2012; Vogelsang-O'Dwyer et al., 2020a, b). Likewise, the sucrose (1 to 3%) and α-galactosides (4.9 to 8.7%) in legume protein concentrates are more abundant than in isolates (below 0.6%) (Bhatty & Christison, 1984; Joehnke et al., 2021; Vogelsang-O'Dwyer et al., 2020a, b).

2.2 | Flavor-active compounds

Plant raw materials contain a vast diversity of flavor-active compounds, which are commonly produced as secondary metabolites. The profiles of these compounds are specific to each material, though they can be modified by genetic factors and environmental conditions, as well as agricultural practices. The number of such compounds is very large, and their concentrations range from parts per billion to several percentage points. It is extremely difficult to cover all the compounds that contribute to flavor because their flavor thresholds vary dramatically, and even minor differences may have a huge impact. Moreover, the way in which flavors are perceived is also affected by the chemical and physical properties of the matrix, as well as by the presence of other components. In this section, we will cover the most important volatile and nonvolatile compounds found in protein-rich plant materials.

2.2.1 | Volatile compounds

The volatile profiles of several plant ingredients (soy, pea, faba bean, chickpea, cowpea, lentil, lupin, adzuki bean, black bean, green bean, flaxseed, hemp, kidney bean, mung bean, navy bean, and pinto bean) and their corresponding flavor descriptions are presented in Table 1. The following classes of compounds were identified: carboxylic acids, aldehydes, alkanes, alkenes, alkynes, alcohols, furans, ketones, esters, lactones, acetates, aromatic compounds, terpenes, sulfuric, and amino compounds. Aldehydes and alcohols are the most abundant compounds. Among them, hexanal, octanal, nonanal, 1-hexanol, 1-octen-3-ol, and octanol have been detected in numerous different protein-rich materials. It is worth noting that not all individual volatile compounds contribute to the flavor experience in the same way. For instance, hexanal, 1-octen-3-ol, 1-hexanol, and 2-pentylfuran are products of lipid oxidation that are associated with unpleasant odors (Frankel, 1985). On the other hand, limonene, which was found in several plant ingredients, is usually linked to pleasant citrus odors. Moreover, it must be considered that volatile compounds have different odor thresholds, meaning that the extent to which they are perceived depends on their concentration. Also, their retention may vary significantly based on the food matrix they are in. However, little research has been conducted on this topic (Roland, 2017).

2.2.2 | Nonvolatile compounds

The nonvolatile taste-active compounds identified in plant ingredients, especially legume-based ingredients include saponins, tannins, flavonoids, phenolic acids, and alkaloids (Campos-Vega et al., 2010). These compounds have been found to contribute to bitter taste, acrid (or pungent) flavor, and astringency (Drewnowski & Gomez-Carneros, 2000). Literature data on the role of such compounds in the perception of the flavor of legume-based ingredients are very limited and mostly focus on compounds detected in low-protein plant foods (e.g., tea, coffee, wine, and fruits). Notably, some of these compounds are present in protein-bound form and retained during the preparation of protein concentrates or isolates.

Saponins

Saponins are secondary plant metabolites that are widely found in legume seeds. In the past, they had been identified as antinutrients; but recently, they have been studied for their beneficial effects such as their antioxidant, hypocholesterolemic, and anticancer properties in humans (Shi et al., 2004). Structurally, saponins are made up of a triterpene or a steroid aglycone that is linked to sugar (monosaccharide or oligosaccharide) moieties through ester and ether linkages (Shi et al., 2004). The structures of saponins vary among plant species and are generally classified into three groups by type (Supporting information Figures S1-2): (1) group A, which includes the acetylated (Aa, Ab, Ac, Ad, Ae, Af, Ag, and

TABLE 1 Volatile compounds from different protein-rich plant materials for which sensory attributes have been described[1]

Compound names	Plant sources	Sensory descriptors	References[2]
Acids			
2-Methylbutanoic acid	Pea, Lupin, Faba bean	Sweaty, Fruity, Cheese	[12], [2], [1]
3-Methylbutanoic acid	Faba bean, Pea, Flaxseed, Lupin	Sweaty, Acid, Rancid, Fruity, Cheese, Animal	[5], [12], [6], [2], [1], [7]
Acetic acid	Lupin, Faba bean	Vinegar	[2], [1]
Hexanoic acid	Chickpea, Flaxseed, Hemp, Faba bean, Pea	Sickening, Sweaty, Rancid, Sour, Sharp, Pungent	[5], [6], [11], [7], [13]
Octanoic acid	Hemp, Pea	Sweaty	[11], [7], [13]
Pentanoic acid	Lupin, Pea	Cheese, Sweaty, Fruity	[2], [7]
Phenylacetic acid	Lupin	Beeswax, Honey	[2]
Aldehydes			
2-Methylbutanal	Pea (Yellow, Gray, Green), Faba bean	Malty	[3], [4],[12], [1]
2-Methylpropanal	Faba bean	Malty	[1]
2-Nonenal, (E)	Pea (Yellow, Gray), Flaxseed, Hemp, Lupin, Black bean, Pinto bean, Faba bean	Grass, Fruity, Cardboard, Fatty, Green	[3], [6], [11], [2], [8], [1]
2-Nonenal, (Z)	Lupin	Cardboard	[2]
2,4-Nonadienal	Soybean	Cucumber, Green, Fatty	[5], [13]
2,4,6-Nonatrienal	Lupin	Nutty, Oat flake	[2]
2,6-Nonadienal	Hemp, Lupin	Cucumber, Green	[11], [2]
3-Methylbutanal	Pea (Yellow, Gray), Faba bean	Malty	[3], [12], [1]
4-Hydroxy-3-methoxy-benzaldehyde	Pea	Sweet, Vanilla	[7]
Benzaldehyde	Pea (Yellow, Gray), Hemp, Black bean, Pinto bean, Faba bean, Green bean	Bitter almond, Sweet, Woody	[3], [11], [8], [1], [10], [13]
Benzene acetaldehyde	Lentil (Green, Red)	Harsh, Green, Honey, Cocoa, Floral, Sweet	[9], [13]
Decanal	Pea (Yellow, Gray, Green), Hemp, Black bean, Pinto bean, Kidney bean, Faba bean, Green bean	Fatty	[3], [12], [11], [8], [1], [10], [7]
Ethyl Vanillin	Lupin	Vanilla	[2]
Hexanal	Pea (Yellow, Gray, Green), Hemp, Black bean, Pinto bean, Kidney bean, Faba bean, Green bean, Lentil (Green)	Green, Strong, Grassy, Floral, Fruity, Pea	[3], [4], [12], [11], [8], [1], [10], [9], [7], [13]
Nonanal	Pea (Yellow, Gray, Green), Chickpea, Flaxseed, Hemp, Black bean, Pinto bean, Kidney bean, Faba bean, Green bean, Lentil (Green, Red)	Milky off-flavor, Fat, Citrus, Green, Beany, Solvent, Plastic	[3], [4], [5], [12], [6], [11], [8], [1], [10], [9], [7], [13]
Octanal	Pea (Yellow, Gray, Green), Hemp, Black bean, Kidney bean, Faba bean	Orange, Sweet, Fruity, Fatty	[3], [4], [12], [11], [8], [1]
Phenyl acetaldehyde	Faba bean	Flowery	[1]
Trans-4,5-Epoxy-dec-2-enal, (E)	Lupin	Metallic	[2]

(Continues)

TABLE 1 (Continued)

Compound names	Plant sources	Sensory descriptors	References[2]
Vanillin	Lupin	Vanilla, Sweet	[2]
Alkanes			
Octane	Pea (Yellow, Gray), Black bean, Pinto bean, Kidney bean, Faba bean, Lentil (Red, Green)	Green grass, Fat, Citrus, Soap	[3], [8], [1], [9]
Alcohols			
1-Hexanol	Pea (Yellow, Gray, Green), Flaxseed, Hemp, Black bean, Pinto bean, Kidney bean, Faba bean, Lentil (Red, Green)	Fruity, Green, Grass, Fat, Lemon	[3], [4], [12], [6], [11], [8], [1], [9], [7], [13]
1-Nonanol	Pea (Yellow, Gray), Flaxseed, Hemp, Black bean, Pinto bean, Kidney bean, Faba bean	Soapy, Pea, Vegetable, Silt, Earth, Rose-orange	[3], [12], [6], [11], [8], [1], [7], [13]
1-Octen-3-ol	Pea (Yellow, Gray, Green), Soybean, Flaxseed, Black bean, Pinto bean, Kidney bean, Faba bean, Green bean	Beany, Mushroom, Vegetable	[3], [4], [5], [12], [6], [8], [1], [10], [7], [13]
1-Pentanol	Pea (Yellow, Gray, Green), Soybean, Flaxseed, Hemp, Black bean, Pinto bean, Faba bean	Balsamic, Grilled, Dust	[3], [4], [5], [12], [6], [11], [8], [1], [7]
1-Penten-3-ol	Pea (Green), Black bean, Pinto bean, Kidney bean	Beany, Green	[4], [5], [12], [8], [7], [13]
2-Hepten-1-ol, (E)	Flaxseed	Floral	[6]
2-Hexanol	Flaxseed	Herbaceous	[6]
2-Hexen-1-ol, (E)	Pea (Green), Flaxseed	Grass, Green, Fruity	[4], [6]
2-Nonen-1-ol, (E)	Flaxseed	Melon, Mint, Grass	[6], [13]
2-Octen-1-ol, (E/Z)	Hemp	Cucumber, Grass, Green	[11], [13]
2,6-Nonadien-1-ol, (E/Z)	Flaxseed	Melon, Cucumber	[6]
3-Hexanol	Flaxseed	Woody, Green	[6]
3-Hexen-1-ol, (E/Z)	Pea (Green), Flaxseed, Green bean	Grass, Herbal	[4], [6], [10], [7]
3-Metyhl-1-butanol	Pea (Green), Navy bean, Black bean, Kidney bean, Pinto bean, Faba bean	Flower intense, Whiskey, Fruity, Banana	[4], [5], [12], [8], [1], [7], [13]
Heptanol	Pea (Yellow, Gray, Green), Flaxseed, Faba bean	Skunky, Rancidity	[3], [4], [12], [6], [1], [7], [13]
Maltol	Lupin	Caramel	[2], [
Menthol	Lentil (Orange), Faba bean	Mint	[5], [1]
Octanol	Pea (Yellow, Gray, Green), Chickpea, Flaxseed, Black bean, Pinto bean, Kidney bean, Faba bean	Mushroom, Vegetable, Oily, Aldehydic	[3], [4], [5], [12], [6], [8], [1], [7], [13]
Phenol	Black bean, Pinto bean	Peppery, Woody	[8], [13]
Furans			
2-Pentylfuran	Pea (Yellow, Gray, Green), Faba bean, Lentil (Green, Red)	Beany, Fatty, Oily, Green beans, Butter	[3], [4], [12], [1], [9], [13]

(Continues)

TABLE 1 (Continued)

Compound names	Plant sources	Sensory descriptors	References[2]
3-Hydroxy-4,5-dimethyl-2(5H)-furanone	Lupin	Spicy, Savory	[2]
5-Pentyl-5(H)-furan-2-one	Pea	Mint, Strawberry	[7]
5-Pentyldihydro-2(3H)-furanone	Pea	Sweet, Coconut, Candies, Peach	[7], [13]
Ketones			
1-Octen-3-one	Pea (Green), Soybean, Lupin	Mushroom, Strong	[4], [5], [2], [13]
2-Acetyl-1-pyrroline	Lupin	Popcorn	[2]
2-Butanone	Soybean, Pea, Black bean, Pinto bean, Faba bean	Fishy	[5], [12], [8], [1]
2-Heptanone	Pea (Yellow, Gray, Green), Faba bean	Fruity pear	[3], [12], [1], [7]
2-Octanone	Flaxseed, Faba bean, Pea	Soap, Gasoline, Earthy	[6], [1], [7]
2,3-Octanedione	Hemp	Mushroom, Vegetable	[11], [7]
3-octen-2-one	Pea (Yellow, Gray), Flaxseed	Beany, Earthy	[3], [12], [6], [13]
3,5-Octadien-2-one	Pea (Yellow, Gray), Flaxseed, Hemp, Faba bean	Beany, Spicy, Earthy, Green Pepper	[3], [6], [11], [1], [13]
Acetone	Black bean, Pinto bean, Kidney bean, Faba bean	Fishy	[8], [1]
Acetophenone	Black bean, Pinto bean, Kidney bean, Faba bean, Lentil (Green, Red)	Sweet, Flower, Almond	[8], [9]
Octa-1,5-dien-3-one, (Z)	Lupin	Geranium, Metallic	[2]
β-ionone	Lupin, Faba bean	Violet, Flower	[2], [1]
Esters, Lactones, and Acetates			
2-Ethylhexyl acetate	Faba bean	Fruity	[1]
Hexyl acetate	Pea (Green), Green bean	Sweet, Perfume	[4], [10]
Methyl 3-methylbutyrate	Faba bean	Fruity	[1]
γ-Decalactone	Lupin	Peach, Fruity	[2]
γ-Nonalactone	Lupin	Coconut, Sweet	[2]
γ-Octalactone	Lupin	Coconut, Sweet	[2]
Aromatic compounds			
3-isobutyl-2-methoxypyrazine	Pea (Green), Lupin	Green, Peas, Bell/Green pepper, Earthy	[4], [2]
3-isopropyl-2-methoxypyrazine	Pea (Green), Lupin	Pea, Pea pod, Bell/Green pepper, Blanched peas, Earthy	[4], [2], [13]
3-sec-butyl-2-methoxypyrazine	Pea (Green)	Green	[4]
5- or 6-methyl-3-isopropyl-2-methoxypyrazine	Pea (Green)	Dry grass, Spruce	[4], [7]
Benzothiazole	Pea	Grilled meat	[7]
Toluene	Pea (Yellow, Gray), Mung bean, Black bean, Pinto bean, Kidney bean, Faba bean, Lentil (Green, Red)	Pungent, Caramel, Fruity, Solvent	[3], [5], [8], [1], [9]

(Continues)

TABLE 1 (Continued)

Compound names	Plant sources	Sensory descriptors	References[2]
Terpenes			
Limonene	Pea (Green), Lentil (Orange, Red, Green), Hemp, Navy bean, Black bean, Kidney bean, Faba bean, Green bean	Citrus, mint	[4], [5], [11], [8], [1], [10], [9], [7]
Sulfuric compound			
Dipropyl disulfide	Pea (Green)	Sulfurous, Sour	[4]

[1]The table does not contain volatile compounds that have not been described for their flavor properties.
[2][1] Akkad et al. (2019); [2] Bader et al. (2009); [3] Ferawati et al. (2020); [4] Jakobsen et al. (1998); [5] Khrisanapant et al. (2019); [6] Lan et al. (2020); [7] Murat et al. (2013); [8] Oomah et al. (2007); [9] Pauceat et al. (2018); [10] Rodriguez-Bernaldo De Quirós et al. (2000); [11] Shen et al. (2020); [12] Wang et al. (2020a); [13] Xu et al. (2019).

Ah) and deacetylated (A1, A2, A3, A4, A5, and A6) types; (2) group B, which encompasses DDMP (2,3-dihydro-2,5-dihydroxy-6-methyl-4H-pyran-4-one)-conjugated (αg, βa, βg, γa, and γg) and non-DDMP-conjugated [I (Bb), II (Bc), III (Bb′), IV (Bc′), and V (Ba)] saponins; and (3) group E, which includes Bd and Be (Kang et al., 2010; Yoshiki et al., 1998). Saponin content is also species-dependent and affected by environmental conditions and processing methods (Singh et al., 2017b). Soy, chickpea, faba bean, and pea seeds are some of the richest sources of saponins among legumes, with their saponin content accounting for 2.5 to 5.6 g/100 g dry weight (Shi et al., 2004). Plant-based diets that are rich in saponins are described by consumers as having a bitter taste and astringent notes (Liener, 1994; Okubo et al., 1992; Prince et al., 1985). The intensity of the bitter taste of saponins is associated with their chemical structure and appears to be concentration-dependent. For instance, DDMP-conjugated saponin from pea seeds has exhibited a significantly higher bitterness level and a lower odor threshold than saponin B (perceived at <2 and 8 mg/mL, respectively; Heng et al., 2006a). When the concentration of pea saponin extracts was increased from 2 to 12 mg/L, its perceived bitterness gradually increased (Heng et al., 2006a).

Saponins have a high affinity to the protein bodies of legumes, which results in their enrichment during protein isolation (Heng et al., 2004). For example, Elkowicz and Sosulski (2006) studied 11 legume flours and found that the use of air classification was effective in concentrating saponins in the protein concentrates, whereas the starch fractions were almost free of legume saponins. A similar phenomenon was observed during the preparation of soy protein isolates (Lin et al., 2006). The authors also reported the partial conversion of DDMP saponins to non-DDMP saponins during the protein isolation process. The accumulation of saponins in protein concentrates and isolates not only imparts bitterness and astringency but also affects the overall flavor properties by impeding the binding of other flavor components due to competition for the available binding sites on proteins (Heng et al., 2004).

Phenolic compounds

Phenolic compounds are almost ubiquitous in plants including legumes (Cheynier, 2012). They consist of a very broad spectrum of molecules that contain at least one aromatic ring bearing one or more hydroxyl substituents. They range from simple phenolic acids to complex families tannins and flavonoids. Phenolic compounds may deliver characteristic flavors—examples of those that do are lower molecular-weight (*Mw*) aromatic phenolics (e.g., vanillin, eugenol, and vinylphenol) and astringent and bitter-tasting tannins (Cheynier, 2012). They can exist in soluble free, soluble esterified or conjugated (to sugars and low-*Mw* compounds), and insoluble-bound forms in plants. Free and esterified phenolics are water soluble and are more flavor active (e.g., bind to taste receptor cells) than insoluble-bound phenolics that are covalently bound to cell wall structural components (Heiniö et al., 2016).

Tannins are water-soluble polyphenolic compounds that bind to and precipitate proteins. They principally include hydrolysable tannins (esters of gallic acid) with *Mw* values of 0.5 to 3 kDa, and condensed tannins (or proanthocyanidins), which are polymers of polyhydroxyflavan-3-ol monomers with *Mw* values of up to 20 kDa (Balasundram et al., 2006; Cheynier, 2012). Condensed tannins are the most common tannins in plants and plant-based foods. The astringency elicited from tannins is a result of tannin-salivary proline-rich protein interactions and adsorption on oral mucosa cells (Cheynier, 2012). Astringency is a tactile sensation described as "dryness, puckering, and roughness" (Cheynier, 2012). In general, the astringency of tannins increases and their bitter taste decreases with the degree of their polymerization (DP), expressed in *Mw*. Tannins are naturally present in the testa (seed coat) of various beans and peas, such as soy, faba bean, chickpea, pea, kidney bean, and cowpea, at concentrations of 0.03 to 2.4 g catechin equivalent/100 g (Reddy et al., 1985; Sarwar Gilani et al., 2012). In the study of

Fernández-Quintela et al. (1997), condensed tannins were reduced by 69 to 95% during protein isolation in soy, faba bean, and pea. The drop in the tannin content was likely due to the removal of the testa prior to the protein isolation and/or due to the remaining of tannins in the water-soluble phase (Olivera-Castillo et al., 2007).

Flavonoids are the major phenolic compounds in grain legumes. They are concentrated in the testa. Chemically, flavonoids are based on a C_6-C_3-C_6 skeleton comprising two phenyl rings linked by a heterocyclic pyrane ring. They are structurally subclassified as flavonols, flavones, flavanones, isoflavones, anthocyanidins, and flavanols. Flavonoids can taste sweet (dihydrochalcones), astringent (flavanols), and/or bitter (most subclasses; Soto-Vaca et al., 2012). The intensity of the bitterness and astringency of flavonoids depends on their DP and the type of their interlinkage. Flavanol monomers (e.g., catechins) tend to be less bitter and more astringent than dimers and trimers (Peleg et al., 1999). Flavonoid content varies across and within legume species (Wang et al., 2008). The total flavonoid content of soy, faba bean, lentil, common bean, and kidney bean is 1.0 to 6.9 mg catechin equivalent per grams, whereas that of green and yellow peas is less than 0.2 mg/g (Ren et al., 2012; Singh et al., 2017a). Black soy seeds contain three times as many flavonoids as the yellow and green varieties (Ren et al., 2012). The flavonoid profiles in legume protein concentrates have been less studied. In the study of Bolanho and Beleia (2011), the total flavonoid content decreased during processing of soy protein isolate compared to soy flour, and in the study of Lin et al. (2006), about 40% of the total isoflavones was retained in the protein isolate. The flavonoids were partially lost during the protein extraction (with NaOH) and precipitation steps and, to a lesser extent, upon washing with water.

Phenolic acids are mainly present in the cotyledons of legume seeds. They are divided into hydroxybenzoic acid derivatives, with a C6–C1 structure (e.g., gallic, *p*-hydroxybenzoic, protocatechuic, vanillic, and syringic acids), and hydroxycinnamic acid derivatives, with a C6–C3 structure (e.g., ferulic, *p*-coumaric, caffeic, chlorogenic, and sinapic acids; Singh et al., 2017a). Protocatechuic, *p*-hydroxybenzoic, gallic, ferulic, and *p*-coumaric acids are the primary free and/or esterified phenolic acids that have been identified in beans, peas, and lentils. The levels of these compounds in legume seeds differ significantly, ranging from 0 to 180 μg/g (Singh et al., 2017a). Most phenolic acids are retained in the protein concentrates and isolates but in reduced concentrations compared to those of legume flours (How & Morr, 1982). Phenolic acids elicit complex sensations of sourness, astringency, and bitterness, the intensity of which depends on the structure and concentration of the acids. For instance, in the study of Langfried (2013), vanillic acid was perceived as more sour than ferulic acid, and ferulic acid was described as more bitter than vanillic acid, but their astringency levels were similar.

Alkaloids

Alkaloids comprise a large and diverse group of heterocyclic compounds that contain one or more nitrogen atoms. They are comprehensively classified based on their biogenesis or ring structure (Dey et al., 2020). The majority of alkaloids, such as cocaine, morphine, quinine, and caffeine, taste bitter. Lupin seeds are known to contain considerable amounts of quinolizidine alkaloids (Mohan et al., 2016). Lupin varieties with high levels of alkaloids (up to 4 mg/g) have a strong bitter taste, and are thus, called "bitter lupins." Among them is *Lupinus albus L.* (white lupin), which must be debittered before it is consumed (Erbas, 2010). The low-alkaloid varieties (<0.3 mg/g) are referred to as "sweet lupins." Among them are *L. angustifolius L.* (blue lupin) and *L. luteus L.* (yellow lupin). Lupin seeds contain predominantly the alkaloids lupanine, lupinine, albine, and sparteine (Mohan et al., 2016). These quinolizidine alkaloids are toxic when consumed at high doses, affecting the nervous, circulatory, and digestive systems of humans. In the study of Resta et al. (2008), the protein isolation process effectively removed quinolizidine alkaloids from both sweet and bitter lupin seeds, as they remained at very low levels, much lower than the 0.2 mg/g limit set by the health authorities of Australia, the UK, and France.

3 | LIPID-DERIVED OFF-FLAVORS IN PLANT PROTEIN-BASED INGREDIENTS

Lipids are the main cause of off-flavor formation in plant protein ingredients. The oxidation of unsaturated fatty acids, together with the hydrolysis of lipids, is an important reaction in the development of volatile and nonvolatile off-flavor compounds, which may or may not require enzymes (Shahidi & Abad, 2018). Oxidation mechanisms generally fall into three categories: auto-oxidation, photo-oxidation, and enzymatic oxidation. Auto-oxidation and enzymatic oxidation are the most important mechanisms in terms of the storage stability of raw materials and the production and stability of ingredients. As such, they are discussed in this article. Toward the end of this article, methods of retarding or preventing the formation of off-flavor compounds are discussed.

3.1 | Auto-oxidation as producer of off-flavor compounds

Auto-oxidation is a free-radical chain reaction that involves oxygen and unsaturated lipids. It is propagated mainly by the reactions of lipid radicals and oxygen, hydrogen abstractions, and β-scissions. Allylic hydrogens,

TABLE 2 Volatile and nonvolatile compounds formed from homolytic β-scission of oleic and linoleic hydroperoxides[1]

Fatty acids	Hydroperoxides	Route A[2]	Route B		
		Volatile Compounds			
				+ •OH	+ •H
Oleic acid	8-ROOH	2-Undecenal		Decanal	1-Decene
	9-ROOH	2-Decenal		Nonanal	1-Nonene
	10-ROOH	Nonanal		Octanol	Octane
	11-ROOH	Octanal		Heptanol	Heptane
Linoleic acid	9-ROOH	2,4-Decadienal		3-Nonenal	1,3-Nonadiene
	13-ROOH	Hexanal		Pentanol	Pentane
		Nonvolatile compounds			
		+ •OH	+ •H		
Oleic acid	8-ROOH	7-Hydroxyheptanoic acid	Heptanoic acid	8-Octanoic acid	
	9-ROOH	8-Hydroxyoctanoic acid	Octanoic acid	9-Nonanoic acid	
	10-ROOH	9-Oxononanoic acid	8-Nonenoic acid	10-Oxo-8-decenoic acid	
	11-ROOH	10-Oxodecanoic acid	9-Decenoic acid	11-Oxo-9-undecenoic acid	
Linoleic acid	9-ROOH	8-Hydroxyoctanoic acid	Octanoic acid	9-Oxo-nonanoic acid	
	13-ROOH	12-Oxo-9-dodecenoic acid	9,11-Dodecadienoic acid	13-Oxo-9,11-tridecadienoic acid	

[1][1] Damerau (2015); [2] Dobarganes (2021).
[2]Route A: Scission on the bond closer to the carboxylate function of allylic hydroperoxides; Route B: Scission on the bond closer to the methyl group of allylic hydroperoxides.

especially at the bis-allylic methylene positions, are easily abstracted from a lipid, yielding relative reaction rates for oleate, linoleate, and α-linolenate in the order of 1:12:25 (Frankel, 1985; Min, 1998). The classical auto-oxidation mechanism has been complemented with alternative reactions of radicals that compete with hydrogen abstraction to build an integrated lipid oxidation scheme, which further enlarges the diversity of products (Schaich, 2017; Schaich et al., 2013). Especially in protein-rich materials, co-oxidation with proteins should be considered. Once the chain reaction is started, it is very difficult to stop. Thus, preventing the initiation of the chain reaction is the most efficient means of controlling auto-oxidation.

The formation of off-flavor compounds begins when the primary lipid oxidation products hydroperoxides (ROOHs) react further and form a wide range of volatile and nonvolatile secondary products (Gunstone & Norris, 1983). Depending on the structures of the ROOHs, the secondary oxidation products are different. The major volatile and nonvolatile decomposition products of oleic and linoleic acid hydroperoxides are summarized in Table 2 (Frankel, 2005; Jeleń & Wąsowicz, 2012; Schaich et al., 2013). The off-flavor characteristics, such as the perceived specific flavors and the threshold values of the synthesized compounds, significantly differ. The hydrocarbons have the highest threshold values (90 to 2150 ppm) and are, therefore, the least likely to be responsible for oxidized flavors (Frankel, 1985). In contrast, compounds such as *(E,E)*−2,4-decadienal, *n*-hexanal, 1-octen-3-ol, pentanol, and 2-pentylfuran have very low threshold values and are, thus, important contributors to flavor (Frankel, 1985; Mistry, 1992).

3.2 | Enzyme-catalyzed oxidation reactions that produce off-flavor compounds

The activity of lipid-modifying enzymes in legumes has been suggested as directly linked to key off-flavor compounds, mostly volatile ones. It should be emphasized that high levels of off-flavor compounds can develop even with a very low lipid content (Roland et al., 2017; Zhang et al., 2020). Enzymatic oxidation begins with the action of lipoxygenase (linoleate: oxygen oxidoreductase, EC 1.13.11.12, Lipoxygenases (LOXs)), which catalyzes the

deoxygenation of PUFAs containing *cis*,*cis*-1,4-pentadiene units to produce conjugated hydroperoxides (Eskin et al., 1977; Gardner, 1991; Newcomer & Brash, 2015; Shi et al., 2020). In fact, LOXs are widely distributed in nature, and are especially abundant in leguminous plants (Hayward et al., 2017). High LOX activity has been seen in soy, lentil, and cowpea, and moderate activity, in faba bean, field pea, and chickpea (Chang & McCurdy, 1985). Also, LOXs being complex lipoxygenase pathways that produce numerous oxylipids with, for example, signaling and plant-defense properties (Feussner et al., 2001).

Plants contain multiple LOX isoenzymes that differ in optimal pH, substrate preference, product specificity, and stability (Gardner, 1991; Hayward et al., 2017; Robinson et al., 1995). Among plant LOXs, soy LOX is the best characterized enzyme. Plant LOXs can be classified into two groups: type I LOXs, which have optimal activity in the alkaline pH region, and type II LOXs, which are most active at a neutral pH (Robinson et al., 1995). Because oxidation commonly occurs regiospecifically, with oxygen incorporated at either C9 or C13 (Gardner, 1991; Robinson et al., 1995), LOXs can also be classified as 9- or 13-LOXs. For example, soy LOX-1 is a 13-LOX, LOX-2 is a 9-/13-LOX, and soy LOX-3 is a 9-LOX or 9/13-LOX (Baysal & Demirdöven, 2007; Robinson et al., 1995; Shibata, 1987, 1988). Furthermore, soy LOX-1 prefers free fatty acids as substrates, as do most type I LOXs, whereas LOX-2 and -3 also oxygenate esterified fatty acids, as do most type II LOXs (Baysal & Demirdöven, 2007; Eskin et al., 1977; Zhang et al., 2020). Type II LOXs in legumes (e.g., soy, pea, and chickpea) also exhibit high co-oxidation activity toward carotenoids and chlorophyll via a free-radical mechanism that is used in, for example, the baking industry (Sanz et al., 1994; Shi et al., 2020; Wu et al., 1999).

In addition to ROOHs, some LOXs also produce ketodienoic fatty acids. In faba beans, there are two LOX isoenzymes with similar pH optima of approximately 5.8 (Clemente et al., 2000). One of them yields hydroperoxide and ketodiene products, and the other forms solely hydroperoxides. Additionally, in chickpeas, there are two isoenzymes that display peak activity at pH 6.0 and 5.5 (Sanz et al., 1992). One of them forms 13-ROOHs, and the other produces equal amounts of 9- and 13-ROOHs and 9- and 13-ketodienes. Thus, the properties of LOXs in plant-based materials vary remarkably, which is important in terms of the formation of off-flavors in foods.

Because most LOX isoenzymes prefer free fatty acids over esters as substrates, it is important to include lipid-hydrolyzing enzymes in the discussion of the LOX pathway. Lipases (triacylglycerol hydrolases EC 3.3.3.3) and other acyl hydrolases catalyze the hydrolysis of triacylglycerols and/or phospholipids into free fatty acids, making them more susceptible to LOX (MacLeod et al., 1988). High lipase activity has been reported in legumes such as faba beans, peas, and soy (Yang et al., 2017; Zhang et al., 2020). Furthermore, free fatty acids, such as linoleic and alpha-linolenic acids, have been shown to be key contributors to bitterness in oats and pea protein isolates (Gläser et al., 2021; Günther-Jordanland et al., 2016, 2020; Moltenberg et al., 1996), making lipid hydrolysis a potential source of off-flavors.

The further reactions of ROOHs may proceed via autoxidation, as presented above, or via enzymes. Enzymes, such as hydroperoxide lyase (HPL), alcohol dehydrogenase (ADH), and peroxygenase (POX) catalyze ROOHs, modifying reactions to produce numerous oxylipids (Fauconnier & Marlier, 1997; Zhuang et al., 1998). The HPL pathway produces mainly volatile degradation products, and the POX pathway produces nonvolatile lipid oxidation products.

The HPL (E.C. 4.2.1.92) pathway produces ω-oxo-acids and short-chain saturated or unsaturated aldehydes (Fauconnier & Marlier, 1997). Plant HPLs can be divided according to their substrate specificity. For example, 13-HPL catalyzes the decomposition of 13-ROOHs to produce C6-volatile aldehydes, and 9-HPL catalyzes the decomposition of 9-ROOHs to produce C9-volatile aldehydes (Zhuang et al., 1998). These HPL products may further isomerize. Peas exhibit high 9- and 13-HPL isoenzyme activities with a pH optimum of approximately 6.5 (Hornosta & Robinson, 2000). However, in soy, the 13-HPL pathway is predominant and shows peak activity at a pH range of 7 to 7.5 (Gardner et al., 1991). Many HPL products have low flavor thresholds and, thus, cause flavor problems. Plant ADHs (E.C. 1.1.1.1) catalyze interconversion between aldehydes, alcohols, and acids (Hatanaka, 1993). For example, hexanal can be converted to hexanol and further converted to hexanoic acid. Alcohol dehydrogenase activity has been observed in legumes, such as faba beans, soy, and chickpeas, with an optimum pH at 8.7–8.8 (Gomes et al., 1982; Leblova, 1974; Leblová & Perglerova, 1976). Peroxygenase (EC 1.11.2.1) is another enzyme in legumes such as in faba beans, peas, and soy. It is a hydroperoxide-dependent oxygenase that catalyzes the transfer of one oxygen atom from an ROOH to a fatty-acid substrate (BIée, 1993; Hamberg & Hamberg, 1996; Yang et al., 2017). The POX pathway leads to the formation of, for example, hydroxy and epoxy fatty acids, which have been suggested as contributing to a bitter taste (Hamberg & Hamberg, 1996). The optimum activity of plant POX occurs at a neutral pH (Piazza et al., 2001).

3.3 | Control of lipid oxidation

The reduction of ROOH formation is necessary to prevent further reactions that concomitantly form off-flavors. Strategies commonly used to minimize chemical lipid

oxidation reactions in food materials include reducing the oxygen level, avoiding exposure to ultraviolet light, storing the materials at a low temperature, and adding antioxidants (Frankel, 2005). Both plant-endogenous and added antioxidants help to control lipid oxidation via numerous mechanisms (Choe & Min, 2009; Decker, 1998).

Because undesirable flavors of plant-based foods are mostly of enzymatic origin, the inactivation of LOXs and other lipid-modifying enzymes provides an effective means of controlling lipid oxidation during the storage and production of protein-rich ingredients. Thermal treatment is the most common and most cost-effective method of eliminating the formation of undesirable flavors. However, the treatment should not be so severe as to reduce the functional properties of the ingredients or initiate autoxidation. For instance, Henderson et al. (1991) and Kubo et al. (2021) completely inactivated pea and soy LOXs via heat treatment at 65 to 90°C, and Chong et al. (2019) inactivated soy LOX by steaming it at 119°C. Alternative techniques include infrared radiation (Li et al., 2016), radio frequency heating (Jiang et al., 2018), and microwave heating (Jiang et al., 2016). Several nonthermal methods have also been developed to replace conventional heat treatment such as ultrasonic cavitation, high-pressure processing, and pulsed electric light (Alhendi et al., 2017; Indrawati et al., 2001; Thakur & Nelson, 1997). Additionally, in vitro studies using antioxidants, such as polyphenols, to inhibit LOX activity have been reported (Ratnasari et al., 2017; Xanthopoulou et al., 2009). The inhibition of LOX activity has also been described in cases of competitive inhibition, Fe^{2+} chelation, or Fe^{3+} reduction to the inactive Fe^{2+} state (Decker, 1998; Shi et al., 2020). Lowering pH values to <4 has also been shown to be effective in the inactivation of LOXs (Cheman et al., 1989; Kon et al., 1970).

4 | FLAVOR FORMATION AND RETENTION DURING EXTRUSION PROCESSING

Extrusion cooking is the technique which is mostly studied and extensively utilized to produce meat alternatives. It is currently used in the industrial manufacture of meat-alternative products (Sha & Xiong, 2020). Thus far, most research has focused on the development of a meat-like fibrous texture with plant proteins using extrusion processing (Sha & Xiong, 2020). However, flavor formation or modification during extrusion has not been well studied, particularly regarding the various types of extrusion (i.e., low- and high-moisture extrusion, also known as dry and wet extrusion). Meat-alternative products were first produced via low-moisture extrusion (<40% water content) in the 1970s, primarily using soy (Aguilera & Kosikowski, 1976; Cumming et al., 1972). The products of low-moisture extrusion have a characteristic expanded or porous structure due to the pressure drop as the hot materials (>100°C) exit the die of the extruder. The evaporation of water is usually accompanied by the volatilization of aroma compounds, leading to a significant loss of the overall flavor intensity in the extrudates (Riha III & Ho, 1996). More recently, high-moisture (>50%) extrusion has been used to prepare meat alternatives with protein isolates or concentrates from a wider range of plant sources such as soy, pea, wheat gluten, lupin, faba bean, peanut, hemp, and microalgae (do Carmo et al., 2021; Grahl et al., 2018; Osen et al., 2014; Wittek et al., 2021; Zahari et al., 2020; Zhang et al., 2021b). This had led to significant achievements in creating anisotropic fibrous meat-like structures. The extruder typically used in high-moisture extrusion is a heated extruder barrel equipped with corotating twin screws and a long cooling die (Osen & Schweiggert-Weisz, 2016). The twin screws mix and convey forward the protein-rich ingredients. The fibrous protein structures of the final product with high-moisture content are formed in the long cooling die that is used to prevent expansion and water evaporation.

4.1 | Flavor generation pathways of extrusion cooking

Flavor generation during dry extrusion cooking has been extensively studied. During the dry extrusion, rich-in-protein plant ingredients are subjected to high pressures, temperatures, and shear forces, leading to a number of flavor-related chemical reactions, that is, the Maillard reaction, the deamidation of glutamine and asparagine, lipid oxidation, and the breakdown of carotenoids (Riha III & Ho, 1996). The Maillard reaction plays an important role in flavor formation for extrudates, but this role depends on the extrusion conditions such as the reaction temperature, residence time in the barrel, pH, and water activity of the system (Riha III & Ho, 1996). The Maillard reaction, which occurs between the reducing sugars and the free amino groups of amino acids, peptides, or proteins, is often divided into three basic stages according to the model of Hodge (1953): the initial, intermediate, and final stages. The initial condensation reaction between the amino group and the carbonyl group of the reducing sugar results in the formation of *N*-glycosylamine and water. This *N*-glycosylamine undergoes Amadori or Heyns rearrangement, generating ketosamines or aldosamines, respectively (van Boekel, 2006). In the intermediate stage, the Amadori or Heyns products are further degraded via different pathways (e.g., sugar dehydration and fragmentation, and amino acid degradation) that lead to the

formation of Schiff's base of hydroxymethylfurfural or furfural, reductones, dehydroreductones, and short-chain hydrolytic fission products (Yaylayan, 2003). The produced dicarbonyl compounds are highly active and react with amino acids to form flavor-significant Strecker aldehydes, a process that is well recognized as *Strecker degradation* (Yaylayan, 2003). In the final stage, aldol condensation takes place, and the heterocyclic compounds (brown pigments, e.g., melanoidins; and volatile compounds, e.g., pyrazines, pyrroles, furans, oxazoles, thiazoles, and thiophenes) are produced. The representative Maillard-derived flavor compounds formed during the heat processing and storage of plant protein-based ingredients include pyrazines (roasted), alkylpyridines (bitter and astringent), furans (burnt and pungent), furanones (burnt and pungent), and pyranones (burnt; van Boekel, 2006). A high extruder barrel temperature and a low water content and availability generally promote the generation of Maillard reaction products (Leonard et al., 2020). An analysis of the volatile flavor compounds of the extrudates indicated that dry extrusion eliminated the volatiles that originated from the native plant protein ingredients but introduced new flavors, that is, Maillard reaction products such as pyrazines, thiophenes, furans, and 1-pentanethiol (Kaleda et al., 2020).

Lipid degradation during extrusion may include both thermolytic pathways and oxygen-attacking reactions (Choe & Min, 2007). Free fatty acids could be formed via lipid hydrolysis due to moisture, lipases, heat, and the mechanical mixing of the ingredients (increased contact between lipase and substrate; Camire et al., 1990). The oxidative or thermal degradation of unsaturated fatty acids is promoted by a longer residence time, higher water content (>20%), and lower extrusion temperature (<150 °C) because Maillard reaction products could act as free-radical scavengers and inhibit lipid oxidation (Bredie et al., 1998).

Deamidation is a nonenzymatic hydrolytic reaction, in which an amide functional group is removed from asparagine or glutamine, leading to their conversion into aspartic acid and glutamic acid, respectively (Riha III & Ho, 1996). The released ammonia reacts more readily with dicarbonyl compounds to produce pyrazines, compared to the α-amino groups. Carotenoids are vulnerable to heat due to the presence of conjugated double bonds (polyene chain), which generate low-*Mw* volatiles during the thermal process of extrusion (Ames & Macleod, 1984; Bonnie & Choo, 1999; Bredie et al., 1998). Furthermore, phenolic acids (e.g., ferulic acid and caffeic acid) and thiamine (vitamin B1) may also be thermally degraded to generate aroma and taste-active compounds, such as 4-vinylphenol (cooked off-flavor), 4-vinylguaiacol (cooked off-flavor), vanillin, 4-ethylcatechol (pungent), 2-methylfuran (ethereal), and 2-methylthiophen (sulfury; Ames & Macleod, 1984; Arnold et al., 1969; Bredie et al., 1998; Rackis et al., 1979).

It is worth noting that the flavor formation and retention mechanisms during the high-moisture extrusion cooking of meat-alternative products must still be clarified, particularly in comparison with dry extrusion cooking. In high-moisture extrusion, the long cooling die attached to the end of the extruder barrel is crucial to fibrous texture formation and the product's sensory properties. This cooling die channel decreases the temperature, increases the viscosity, and inhibits the expansion of the hot extrudates before exiting, which may affect the flavor release and perception of the final product differently from the effects of dry extrusion.

4.2 | The effect of extrusion parameters on the sensory flavor properties of plant-based meat alternatives

The types, yields, and retention levels of flavor compounds depend on the composition of the raw materials (e.g., free amino acids, sugars, and fatty acids) and the extruder operating conditions (i.e., feed moisture content, mass temperature, screw speed, and residence time; Bhandari et al., 2001). The moisture content has been shown to be the parameter that predominantly affects the flavor properties of the extrudate in both low- and high-moisture extrusion cooking of plant proteins. In dry extrusion cooking, a lower moisture content is often associated with less aroma intensity and better sensory acceptability of the extrudates. For instance, in the study of Milani et al. (2014), the extrusion of soy protein isolate at 30% moisture resulted in lower overall aroma intensity and a higher preference score for the products than in the case of extrusion at 40% moisture. Meat alternatives prepared at a higher moisture content exhibited a denser structure (or a lower degree of expansion), which was accompanied by a change in the protein conformation (Guo et al., 2020; Milani et al., 2014). The change in the protein's secondary structure may affect the binding capacity of aroma compounds and, consequently, alter the volatilization and release of aroma.

In high-moisture extrusion cooking, for example, meat alternatives prepared with faba bean protein concentrate, which increased the moisture content from 46 to 61%, seemed to have reduced the overall intensity of the odor and the beany flavor but did not significantly affect the sweet taste, bitter taste, and after taste (do Carmo et al., 2021). The extrudates produced at a higher moisture content were associated with less fracturability and gumminess in texture, which might have been related to the decrease in the perceived aroma intensity. Moreover,

the retention rate (the ratio of the volatile substances in the meat alternatives to those in the raw materials) of the added volatile compounds or flavor enhancers in extrudates during high-moisture extrusion decreased with increasing moisture content. For instance, the meat-alternative products made from soy using high-moisture extrusion showed a reduced retention rate of both the total and individual volatile flavor compounds when the moisture content increased from 40 to 80%, besides which a sharp decline in the total volatile retention was observed at above 60% moisture (Guo et al., 2020; Xun et al., 2019). This might have been due to the greater release of volatiles, along with the increased water evaporation. Furthermore, there may be greater hydrophobic interactions or hydrogen bonds between flavor molecules and food components, such as proteins and starch, under low-moisture conditions.

The extrusion temperature seems to have a significant influence on lipid oxidation. Various studies have been performed to evaluate the effect of the extrusion temperature (100 to 175°C) on the lipid peroxidation and storage stability of plant materials using dry extrusion cooking (10 to 30% moisture; Imran et al., 2015; Rao & Artz, 1989). Extrusion temperatures above 120°C have been reported to effectively inactivate lipase, lipoxygenase, and other lipid-modifying enzymes in legumes and cereals, such as soy, wheat, and oat, thereby preventing undesirable flavor-forming reactions (Berghofer, 1992; Hayakawa et al., 1992; Meister et al., 1994). A higher extrusion temperature has been linked to a lower peroxide value, which was explained by the faster decomposition of peroxides at a high temperature (Alvarez et al., 1990). Extrusion may also foster lipid complexation with starch (amylose) and thus, reduce the susceptibility of lipids to oxidation. Nevertheless, controversial results have been reported in other studies, which suggested that increasing the extrusion temperature resulted in higher peroxide formation due to the increased iron content and, thereby, the iron-catalyzed auto-oxidation of lipids at an elevated temperature (Rao & Artz, 1989). A high extrusion temperature promoted the formation of volatiles such as hexanal, 2-pentylfuran, and nonanal (Sjövall et al., 1997). This was likely related to a higher degree of extrudate expansion and surface area exposure. Additionally, a higher temperature may also lead to the degradation of antioxidants and, thus, to less inhibition of oxidation rancidity (Martin et al., 1993).

It can be concluded that moisture content and extrusion temperature play a role in the flavor generation, volatile release, and sensory perception of meat alternatives, but more studies are needed to understand the fundamental mechanisms, particularly in high-moisture extrusion cooking.

5 | MEASUREMENT OF FLAVOR QUALITY IN PROTEIN-RICH INGREDIENTS AND PRODUCTS

There are several scopes of the analysis of flavor compounds. In protein-rich foods, the scope is usually either to identify all or certain key compounds or to compare the changes in the flavor profiles caused by, for example, varietal differences, storage, or processing. Modern instrumental methods can provide a great deal of information on chemical compounds, but the data become valuable only when combined with knowledge about sensory attributes and/or sensory analyses.

The analysis of flavor compounds is challenging due to the huge diversity of chemical compounds (Table 1), their low content levels and interactions with other food components, and their instability. Moreover, the sensitivity of instrumental techniques may be limited compared to consumers' sensory perceptions and assessments. Considering instrumental methods, it is practical to divide the flavor compounds into volatile and nonvolatile compounds.

5.1 | Instrumental analysis of flavor compounds

Volatiles

Volatile flavor compounds are commonly analyzed using GC, with a variety of techniques used to isolate the volatiles. The isolation of volatile compounds was comprehensively discussed in two recent review articles on flavor compounds—in one article, in oats (McCorrin, 2019), and in the other article, in soy proteins (Wang et al., 2021b). The authors pointed out that the differences in the profiles of volatile compounds could help in, for example, selecting ingredients and processing methods or controlling reaction pathways that lead to off-flavor formation. When studying volatile compounds, it is also important to consider the interactions of flavor compounds with proteins and other matrix compounds. Techniques intended to isolate volatile compounds include vacuum distillation, solvent and supercritical fluid extractions, and headspace methods such as headspace solid-phase microextraction (HS-SPME) GC-MS.

Over the past 20 years, HS-SPME-GC-MS has been the most commonly used technique for analyzing volatile compounds from protein-rich plant materials. Volatile compounds are released from the sample matrix in controlled conditions and adsorbed by the SPME fiber, from which they are released to the GC injector to be analyzed. Several SPME coatings with different specificities and efficacies are available (Xu et al., 2016). Divinylbenzene/

carboxen/polydimethylsiloxane (DVB/CAR/PDMS) and CAR/PDMS are considered most suitable for off-flavor analysis in legumes (Wang et al., 2021b). Specifically, HS-SPME-GC-MS using a DVB/CAR/PDMS fiber has been used to characterize the volatile compound profiles of legume seeds (Khrisanapant et al., 2019), legume protein isolates (Xu et al., 2020), low- and high-tannin faba beans (Akkad et al., 2019; Oomah et al., 2014), and yellow and gray peas (Ferawati et al., 2020). Similar methods have also been used in studies on the effects of processing on the sensory, functional, and/or nutritional properties of protein-rich plant products. These studies included the effect of lipid oxidation during the germination of legumes (Xu et al., 2020), the alcohol washing of pea protein-enriched flour (Wang et al., 2020a), the effect of pH on the extraction yield of yellow pea protein isolate (Gao et al., 2020), and the fermentation of pea-oat protein blends in the production of meat analogs (Kaleda et al., 2020).

With GC-MS, it is possible to separate, identify, and, to some extent, quantify individual compounds. However, GC-MS does not reveal the impact of the compounds on sensory attributes. In fact, GC, together with olfactometry (O), in which trained panelists evaluate separated compounds using the powerful sense of smell, can be used to recognize flavor-active compounds and estimate their contributions. Combining GC-O with GC-MS would be useful in the analysis of flavor compounds. To analyze the overall aroma profile of a material, GC-O with aroma extraction dilution analysis (AEDA) can be used. With AEDA, it is possible to detect threshold levels of compounds and compare the contributions of different compounds to the flavor (McGorrin, 2019). Solvent-assisted flavor evaporation extraction was found to be the most suitable method of isolating volatiles from pea flour in terms of sensory representativeness (Murat et al., 2012).

Nonvolatiles

Analyzing major nonvolatile flavor compounds is challenging because each raw material has its own profile of compounds that require specific analytical methods. The extraction step plays a crucial role in the quantitative analyses of nonvolatile compounds in protein-rich ingredients. The solubility of compounds is dependent on the solvent used, and the resulting extract is always a mixture (of compounds). Phenolic compounds and saponins have been extracted from plant materials with methanol, ethanol, acetone, water, ethyl acetate, and their combinations (Cheok et al., 2014; Naczk & Shahidi, 2006). Ha et al. (2014) extracted saponins from various legume seeds, and Vernoud et al. (2021) extracted them from pea seeds using 80% methanol in water. Valente et al. (2019) used 70% methanol in water to extract free phenolic compounds from faba bean seeds (*Vicia faba* L.).

Various colorimetric methods are routinely used to analyze phenolic compounds and saponins in plant extracts. However, these methods only estimate the total content of such compounds and may lead to under- or overestimations. HPLC or ultra-high-performance liquid chromatography (UHPLC) with various detection techniques are the most widely used methods of qualitatively and/or quantitatively determining phenolic compounds (Naczk & Shahidi, 2006) and saponins (Cheok et al., 2014). Liquid chromatography combined with mass spectrometry offers tools for identifying compounds based on their *Mw* and structure. Not all compounds are available as pure analytical-standard compounds in the market, which complicates their identification and quantitative analysis. Heng et al. (2006) analyzed bitter saponins B and DDMP from dry peas with the HPLC method coupled with evaporative light-scattering detection (ELSD), whereas Vernoud et al. (2021) used HPLC connected to a UV detector to quantify saponins in pea seeds and HPLC-MS to identify them. HPLC-UV methods have also been used to analyze the phenolic profile of faba bean seeds (Johnson et al., 2021; Valente et al., 2019) and several legume seeds (Magalhaes et al., 2017).

Colorimetric assays, such as the so-called vanillin, dimethylaminocinnamaldehyde, and acid-buthanol assays, are commonly used methods of estimating the total condensed tannin content. Low-molecular mass subunits of condensed tannins, flavan-3-ols, can be separated and identified with RP-HPLC methods (Hümmer & Schreier, 2008). However, the thiolytic degradation of polymeric tannin molecules allows for the collection of structural information and the quantification of, flava-3-ol monomeric subunits with LC methods or with LC methods combined with mass spectrometry (Zeller, 2019). The thiolytic degradation method has been used in studies to characterize and quantify flava-3-ol subunits in pea and faba bean seeds (Jin et al., 2012) and in other protein-rich plant products (Mattila et al., 2018).

Nonvolatile lipid degradation products, such as free fatty acids and oxidized fatty acids, are commonly extracted with organic solvents, fractionated via preparative chromatography, and finally analyzed via HPLC/UHPLC with ELSD or MS detection (Gläser et al., 2020; Yang et al., 2019). It is possible to identify the key contributors to taste using sequential solvent extraction and fractionation, followed by HPLC/UHPLC separation, and finally, sensory evaluation of the fractions, in combination with taste dilution analysis, which was introduced by Schieberle and Hofmann (2011). Taste dilution analysis has been used to identify bitter-tasting lipids in oats (Günther-Jordanland et al., 2020) and pea-protein isolates (Gläser et al., 2020, 2021).

5.2 | Sensory analysis

The human senses are necessary to measure the perceived flavor of meat alternatives and their ingredients. The flavor of a sample cannot be predicted based on chemical characteristics alone, especially if that relationship has not been previously defined using information from both chemical and sensory analyses. The complexity of the flavor perception of foods like meat alternatives arises not only from interactions between flavor-active molecules but also from interactions between the senses (multisensory integration). A sensory profile is usually a mixture of different sensory properties. Focusing only on a single characteristic (e.g., bitterness) is not sufficient, due to the interaction between taste and smell properties. Applying various statistical multivariate methods to integrated data obtained from the instrumental analysis of flavor compounds and a sensory analysis of flavor can provide important insights into the development of meat alternatives.

The two main categories of sensory analysis techniques are analytical sensory evaluation and hedonic tests (affective tests). The former uses trained panelists to evaluate, as objectively as possible, the quality and intensity of the sensory properties of samples to create sensory profiles. The latter measures consumers' hedonic responses, such as liking, to the samples to reveal acceptance. Scientific sensory studies are often conducted under sensory laboratory conditions (ISO 8589), using quantitative methodology. For more information on the sensory techniques used with meat alternatives, see Fiorentini et al. (2020) and McClements et al. (2021).

Analytical sensory evaluation has been applied to both meat alternatives and their ingredients (protein concentrates and isolates), focusing on the intensities of different sensory properties using various scales. Instead, consumer acceptance is often studied only with meat-alternative products or prototypes. Plant protein concentrates and isolates have typically been analyzed for the intensity of their key sensory attributes (such as bitterness and astringency) in water solutions (2 to 4%; Cosson et al., 2020; El Youssef et al., 2020; García Arteaga et al., 2021; Schlegel et al., 2019a). Recently, Chigwedere et al. (2022) reviewed literature to investigate the sensory descriptors used for pulses and pulse-derived ingredients, observed the inconsistency in the use of descriptive terms among the studies, and highlighted the need for a standardized sensory lexicon for this food category.

The analytical sensory evaluation of meat alternatives has often been but a part of a larger study that also includes instrumental measurements and is focused on soy-based meat-alternative products. Lin et al. (2002) used descriptive sensory analysis to study the texture of meat alternatives made of soy protein isolate. Katayama and Wilson (2008) studied the sensory properties of soy-based meat alternatives but focused on aroma and flavor. Bakhsh et al. (2021) studied the effects of methylcellulose on the sensory profile and overall acceptability of soy-based meat alternatives. The first analytical sensory studies of non-soy-based meat alternatives have been published only recently. De Angelis et al. (2020) conducted sensory profiling of meat alternatives made of oats and pea or soy protein. Wi et al. (2020) reported on sensory profiling of meat alternatives made of soy protein isolate and wheat gluten. All the aforementioned studies also included an analysis of the physicochemical properties of the meat alternatives such as their basic chemical composition (e.g., moisture, protein, fat, and ash content), color (as Hunter Lab values), rheological properties (e.g., through Texture Profile Analysis using a texture analyzer), or volatile compounds. However, none of the studies analyzed data from sensory and physicochemical analyses jointly, using multivariate statistical methods to find associations between the variables.

Sensory studies of consumer acceptance of plant-based meat alternatives were recently reviewed by Fiorentini et al. (2020). Of the 10 studies that they reviewed, only four used an adequate number of participants (60 to 125), whereas the rest included only 24 to 56 participants. As in studies of analytical sensory evaluation, most of the meat alternatives (8/10) in consumer sensory studies included soy as the major protein ingredient.

In sum, sensory studies of plant-based meat alternatives are still rare, especially those concerning non-soy-based products. There is a need for sensory studies on meat alternatives that use both analytical and hedonic sensory techniques and, ideally, also chemical analysis of flavor-active compounds and analysis of the combined data to identify underlying associations.

6 | APPROACHES TO IMPROVE THE FLAVOR OF PROTEIN-RICH INGREDIENTS AND MEAT ALTERNATIVES

To increase the sensory acceptability of plant protein ingredients and their corresponding meat-alternative products, it is imperative to prevent the formation of, reduce, or mask the associated off-flavors, such as beany, green, pea odors (volatiles), as well as the bitter taste, astringency, and metallic taste (nonvolatiles), which ideally entails eliminating both the precursors and compounds responsible for off-flavor while minimizing the alteration of the functional properties of the protein isolate or concentrate. Nevertheless, to date, there is still scant information on the removal of off-flavors in plant proteins. It can be envisaged that one of the simplest approaches is to use cultivars that are low in

off-flavor components or precursors, or enzymes that support off-flavor development, because the sensory attributes of plant proteins are largely dependent on the cultivar used (Roland et al., 2017). Several treatments that have shown potential in large-scale operations aimed at the removal or reduction of off-flavor compounds are discussed below. It should be noted that no technique is perfect, and each method has its own intrinsic benefits and shortcomings. Compounds that contribute to off-flavors are diverse and show different binding affinities to plant proteins; thus, it is difficult to completely remove all off-flavors and their precursors using the current techniques. Additionally, pretreatment methods are tailored to the optimization of the flavor characteristics of plant protein ingredients, and only a few studies have examined their effects and suitability on extruded meat alternatives.

6.1 | Use of flavoring additives

Flavoring additives are widely used in plant-based meat alternatives to mask off-notes from plant ingredients and/or create a meat-like flavor, thus, improving the sensory quality and consumer acceptance of the final products (Li & Li, 2020). A wide array of flavoring agents has been used in plant-based meat products. Their functions are summarized below.

I. Natural spices and herbs, such as garlic, onion, pepper, fennel, basil, and thyme, can be added to meat-alternative products to impart specific flavors (Bohrer, 2019; Li & Li, 2020). These spices may also mask undesirable flavors originating from plant protein sources and prevent lipid oxidation due to their antioxidant components (Yashin et al., 2017).
II. Maillard reaction precursors, such as reducing sugars (xylose, ribose, and glucose), amino acids (methionine, cysteine, serine, threonine, glycine, and alanine), flavor nucleotides (5′-guanosine monophosphate and 5′-inosine monophosphate), and thiamine, have been added to produce meaty or roasty volatiles in plant-based alternatives (Li & Li, 2020).
III. Hydrolyzed vegetable proteins that are produced via hydrochloric acid or enzymatic hydrolysis of protein-rich ingredients (e.g., soy, corn, and wheat gluten) have been used to impart a meat-like flavor (Wu et al., 2003). The resulting products are amino acids (e.g., glutamic acid with an umami flavor), short peptides, and various volatile aroma compounds (Aaslyng et al., 1998).
IV. Yeast extract (YE) is a natural flavoring agent that is produced from food-grade yeast. It has a roasted, meaty, and sweet aroma due to the presence of thiophene and pyrazine (Lin et al., 2014). It may also deliver umami and kokumi flavors due to glutamic acid, 5′-nucleotides, and other constituents (Liu et al., 2015). Furthermore, YE is considered a flavor enhancer that provides nonvolatile flavor precursors such as amino acids, peptides, and thiamine (Alim et al., 2018).
V. Vegetable oils, such as coconut oil, canola (rapeseed) oil, and sunflower oil, are often used in commercial meat-alternative products to simulate the role of animal fats in flavor formation and to contribute to the tenderness, juiciness, and mouthfeel of the final plant-based products (Bohrer, 2019).

However, the use of flavorings and other additives, such as preservatives and texturing agents, together with high saturated fat content, raises concerns about nutrition and health, the clean label, food safety, prices, and consumer confidence. This has incentivized the development of clean-label (generally meaning free from artificial or synthetic ingredients, uses natural production methods, and has no pesticides, chemicals, and toxins) alternatives to flavoring additives.

6.2 | Solvent extraction

Organic solvents (e.g., ethanol and isopropanol) have long been used to extract polar lipids (e.g., PUFA-rich phospholipids that act as off-flavor precursors) and volatile compounds from plant protein concentrates or isolates (Damodaran & Arora, 2013). The use of solvent extraction to remove undesirable flavor compounds has the advantages of low cost, easy operation, and good controllability. Moreover, the bitter-tasting nonvolatile components, such as bitter peptides, phenolics, and saponins, tend to accumulate in the solvent phase and can be extracted subsequently (Saha & Hayashi, 2001). Legume-like flavor and total volatiles, in particular, hexanal and (*E*,*E*)−3,5-octadien-2-one, were significantly reduced after legume proteins (e.g., lupin, lentil, and pea proteins) were treated with ethanol, 2-propanol, or isopropanol, which led to higher acceptance of the protein isolates (Bader et al., 2011; Chang et al., 2019; Wang et al., 2020a). Moreover, increasing the solvent concentration, for example, from 20 to 80%, resulted in a gradually increased removal effect on the volatile compounds of legume proteins, likely due to the decrease in the polarity of the solvent and, thereby, the greater affinity to flavor compounds. High concentrations of alcohols (>50%) also have a strong inhibitory effect on lipoxygenase and peroxidase enzymes, retarding lipid oxidation and beany flavor development (Bader et al., 2011; Sessa & Rackis, 1977). A new trend has emerged—that of

using supercritical carbon dioxide extraction (SC−CO_2) in combination with ethanol to remove volatile compounds and reduce the bitterness of pea flour, which has shown benefits in the form of shorter processing time and lower ethanol requirements (22%) compared to conventional solvent extraction methods (Vatansever et al., 2021; Vatansever & Hall, 2020). Taken together, although these solvent treatments have proven useful in reducing off-flavor molecules and, concomitantly, in improving the flavor properties, protein denaturation and the loss of protein functionality are among the detrimental collateral consequences that mandate extensive optimization. Solvent extraction is also complicated by a reduced level of essential amino acids, vitamins, and minerals (Lokuruka, 2011; Wang et al., 2020a). Thus, the best extraction solvent is not necessarily the best method of maintaining protein functionality and nutrition value.

6.3 | Soaking and heat treatment

The soaking of legume seeds is a process often used prior to other treatments, such as germination and cooking or heating. The seeds are hydrated in water for a few hours to allow water absorption and leaching of unwanted compounds (e.g., antinutrients and off-flavor compounds) into the soaking water. For instance, the soaking of lupin seeds has been shown to reduce bitterness due to the leached alkaloids (Yadesa & Biadge, 2017). Soaking in water also decreased free phenolic compounds in faba beans, peas, chickpeas, and kidney beans (El-Hady & Habiba, 2003). However, the soaking of legumes may result in a partial loss of nutritional components such as water-soluble proteins and vitamins (Prodanov et al., 2004; Roland et al., 2017). The influence of the soaking process on the volatile compounds of legumes likely depends on the pH of the soaking water. The soaking of soy led to increased LOX activity due to the presence of water, whereas soaking under alkaline conditions (0.25% $NaHCO_3$, pH 8.3) inhibited LOX activity and resulted in a less beany flavor (Bollegala and Rajapakse, 2015).

Heat treatment has shown success in eliminating the beany flavor from faba beans (Jiang et al., 2016) and soy (Cai et al., 2021), as described in section 3.1.3. However, the effect of heating on nonvolatile compounds that cause bitterness of plant proteins depends on the nature of the specific compounds. Specifically, DDMP-conjugated saponin, the predominant form of saponin in legumes, became unstable and lost its DDPM group at temperatures above 30°C (in water solutions), forming saponin B, with significantly less bitterness (Barakat et al., 2015; Heng et al., 2006a, b). Heat treatment was effective in cleaving both noncovalent and covalent bonds between phenolic compounds and proteins and liberating free phenolic compounds (Nyembwe et al., 2015). For instance, the roasting of marama beans (at 150 °C for 20 min) increased the level of water-soluble phenolic acids and, consequently, increased the bitter taste (Nyembwe et al., 2015). Similarly, the heating of lentils increased the tannin content due to a decline in the degree of polymerization and thus, less protein-binding affinity (Vidal-Valverde et al., 1994). However, the extrusion cooking (at 150 to 180°C) and/or autoclaving of presoaked faba beans, peas, and chickpeas substantially reduced tannins and total free phenolic content (Alonso et al., 2000; El-Hady & Habiba, 2003; Khalil & Mansour, 1995). Thus, a specific thermal treatment may need to be carefully selected based on the characteristics (i.e., the type of bitter-tasting compounds) of the plant protein ingredients or performed in conjunction with other debittering treatments.

6.4 | Molecular inclusion, interaction, and physical entrapment

Off-flavors can be masked by exploiting the binding interactions between flavor precursors or compounds in plant proteins (guest molecules) and certain chemical compounds (host molecules that can form a cavity) to form inclusion complexes (Zhu et al., 2019). For example, the structure of β-cyclodextrin (βCD), specifically, the hydrophobic inner cavity formed by the seven-membered glucopyranoside ring molecule, allows the formation of stable inclusion complexes with off-flavor compounds and precursors such as carbonyl compounds, fatty acids, phospholipids, and bitter-tasting compounds like small-*Mw* phytochemicals (Damodaran & Arora, 2013; Zhu & Damodaran, 2018). A model study showed that approximately 94% of soy protein isolate-bound 2-nonanone could be removed using 6-mM βCD (Arora & Damodaran, 2010). Because βCD must be labeled as a food additive (E 459), other studies have explored the use of alternative inclusion compounds with helical structures, such as pea dextrin, to mask off-flavors related to lipid oxidation products (e.g., propanal, 1-penten-3-one, 1-penten-3-ol, and hexanal) and had promising results (Böttcher et al., 2015). Furthermore, gum Arabic has been used to form conjugates with plant proteins through Maillard reactions, and it effectively eliminated the beany flavor and improved the functionalities of plant proteins (Zha et al., 2019). Nevertheless, the economics of such processes at a commercial scale remain to be evaluated.

Polysaccharides are known to affect flavor release and perception through direct binding with flavor molecules and/or the entrapment of these molecules within a food matrix (i.e., modification of the textural properties and

TABLE 3 Flavor properties (bitterness and other off-flavors) of protein isolates treated by proteolytic enzymes under various hydrolysis conditions

Proteolytic enzymes	Activity	Protein isolates	Hydrolysis conditions	Degree of hydrolysis (%)	Flavor properties compared to control	References[1]
Flavourzyme	Exo- and endopeptidase	Lupin	120 min, 50°C, pH 6	6.9	Lower bitterness	[4]
		Soy	10 to 120 min, 5 °C, pH 6	8.5	Lower bitterness	[3]
		Pea	4 h, 50°C, pH 7	55	Higher bitterness	[2]
Papain	Cysteine exo- and endopeptidase	Lupin	120 min, 80°C, pH 7	2.6	Lower bitterness	[4]
		Soy	10 to 120 min, 80°C, pH 7	4.6	Similar bitterness, but less beany flavor and astringency	[3]
		Pea	4 h, 40°C, pH 6.5	19	Lower bitterness	[2]
		Pea	15 min, 65°C, pH 7	5.0	Lower bitterness	[1]
Protamex	Serine endopeptidase	Lupin	120 min, 60°C, pH 8	6.5	Higher bitterness, astringency, and grassy	[4]
		Soy	0 to 30 min, 45°C, pH 6	60	Lower bitterness and beany flavor (less *n*-hexanal volatiles)	[5]
		Soy	10 to 120 min, 60°C, pH 8	5.4	Higher bitterness	[3]
		Pea	15/120 min, 65°C, pH 7	4.2	Lower bitterness	[1]
Chymotrypsi	Serine endoprotease	Pea	4 h, 37°C, pH 8	17	Lower bitterness	[2]
		Pea	120 min, 50°C, pH 8	1.8	Lower bitterness	[1]
Pepsin	Aspartic endopeptidase	Lupin	120 min, 50°C, pH 2	3.4	Higher bitterness and astringency	[4]
		Soy	10 to 120 min, 50°C, pH 2	10.6	Higher bitterness	[3]
Corolase	Endopeptidase	Lupin	120 min, 55°C, pH 7	5.1	Lower bitterness	[4]
		Soy	10 to 120 min, 55°C, pH 7	7.8	Higher bitterness	[3]
		Pea	120 min, 50°C, pH 7	4.7	Lower bitterness	[1]
Trypsin	Serine endopeptidase	Soy	10 to 120 min, 50°C, pH 9	2.8	Higher bitterness	[3]
		Pea	4 h, 37°C, pH 8	18	Higher bitterness	[2]
		Pea	15 min, 50°C, pH 8	7.6	Lower bitterness	[1]
Alcalase	Serine endopeptidase	Lupin	120 min, 50°C, pH 8	9.1	Higher bitterness, astringency, and grassy	[4]
		Pea	4 h, 50 °C, pH 8.5	28	Higher bitterness	[2]
		Soy	10 to 120 min, 50°C, pH 8	13	Higher bitterness	[3]
		Pea	15 min, 65°C, pH 8	9.2	Higher bitterness	[1]
Protease	Serine endopeptidase	Lupin	120 min, 55°C, pH 7.2	2.4	Higher bitterness and grassy	[4]

(Continues)

TABLE 3 (Continued)

Proteolytic enzymes	Activity	Protein isolates	Hydrolysis conditions	Degree of hydrolysis (%)	Flavor properties compared to control	References[1]
		Soy	10 to 120 min, 55°C, pH 7.2	4.8	Higher bitterness	[3]
Neutrase	Metalloendopeptidase	Lupin	120 min, 50°C, pH 6.5	4.7	Similar bitterness	[4]
		Soy	10 to 120 min, 50°C, pH 6.5	6.3	Higher bitterness	[3]
		Pea	120 min, 50°C, pH 7	5.2	Lower bitterness	[1]

[1][1] Arteaga et al. (2020); [2] Humiski and Aluko (2007); [3] Meinlschmidt et al. (2016b); [4] Schlegel et al. (2019b); [5] Yoo and Chang (2016).

thereby, the diffusion coefficients of flavor compounds) (Tournier et al., 2007). An increase in the polysaccharide concentration generally decreases the aroma and taste perception in solutions (characterized by increased viscosity) and solid systems (characterized by increased cohesiveness) (Tournier et al., 2007; Wang et al., 2020b). For instance, dextrans produced by lactic acid bacteria (LAB) showed great potential for use in masking a beany flavor, bitter taste, and aftertaste in soy-enriched or wholegrain baked products (Wang et al., 2020b, 2021a). The incorporation of polysaccharides into meat-alternative products may be one way to reduce the undesirable smells and tastes associated with plant proteins. However, further research is necessary to confirm the feasibility of such a method.

6.5 | Enzymatic hydrolysis

Enzymatic hydrolysis of plant proteins has been used to improve functional properties (e.g., gelation, emulsification, foaming, and water absorption capacity) and decrease allergenicity (Sun, 2011) as well as to produce meat flavor precursors to enhance the umami taste of meat alternatives (see Section 6.1). However, the use of this technique to mitigate or eliminate the off-flavors of plant proteins and products that contain them has been less studied. Research has focused on the modification of protein technofunctionality and the optimization of the hydrolysis process to avoid compromising the sensory quality (i.e., without increasing and perhaps even reducing bitterness and/or other off-flavors).

The effect of proteolytic hydrolysis on the flavor properties of plant proteins depends on the proteases used and the hydrolysis conditions, as summarized in Table 3. Bitterness is related to the average hydrophobicity of the peptide and, specifically, the chain length or number of the hydrophobic amino acid residues such as isoleucine, proline, leucine, tyrosine, phenylalanine, and tryptophan (Damodaran & Arora, 2013; Saha & Hayashi, 2001). Specific enzymatic debittering strategies have, therefore, focused on the application of exopeptidases and endopeptidases that hydrolyze bitter peptide bonds by selectively releasing or removing the *N*-terminal hydrophobic amino acid residues from proteins and peptides. Focus has been given to soy, pea, and lupin protein isolates, and decreased bitterness was obtained using flavourzyme, papain, protamex, chymotrypsin, corolase, trypsin, and neutrase (Arteaga et al., 2020; Humiski & Aluko, 2007; Meinlschmidt et al., 2016b; Schlegel et al., 2019b; Yoo & Chang, 2016). However, the use of these enzymes led to increased bitterness when a longer hydrolysis time was applied, which was likely associated with a higher degree of hydrolysis. This suggests that the duration of enzymatic hydrolysis is a key factor in optimizing enzymatic debittering in different plant proteins. In addition, enzymatic treatment may affect the perceived intensity of other off-flavors such as a beany flavor, astringency, and a grassy taste (Schlegel et al., 2019b; Song et al., 2009).

6.6 | Fermentation

Fermentation with LAB or mixed cultures of LAB and yeasts has been the most common approach to improve the aroma profile and reducing off-flavor formation in plant protein ingredients. Studies have focused on masking or reducing bitter and beany off-notes in isolated soy, pea, and lupin proteins and related products. The flavor properties of the fermented legume proteins depend mainly on the starters used, their metabolic activities (e.g., the synthesis of flavor compounds and/or precursors), and the release or activation of specific enzymes that degrade targeted off-flavor compounds (e.g., proteases that cleave bitter peptides, enzymes that catabolize bitter alkaloids, and enzymes that hydrolyze bitter saponins). In fact, LAB strains belonging to the (former) genus *Lactobacillus*, which are important sources of exopeptidases, have been frequently used as debittering starters in plant protein fermentation (Saha & Hayashi, 2001). The fermentation of soy protein with LAB alone (e.g., *Lactobacillus helveticus* or *Schleiferilactobacillus perolens*) or in combination with yeasts (e.g., *Saccharomyces*) led

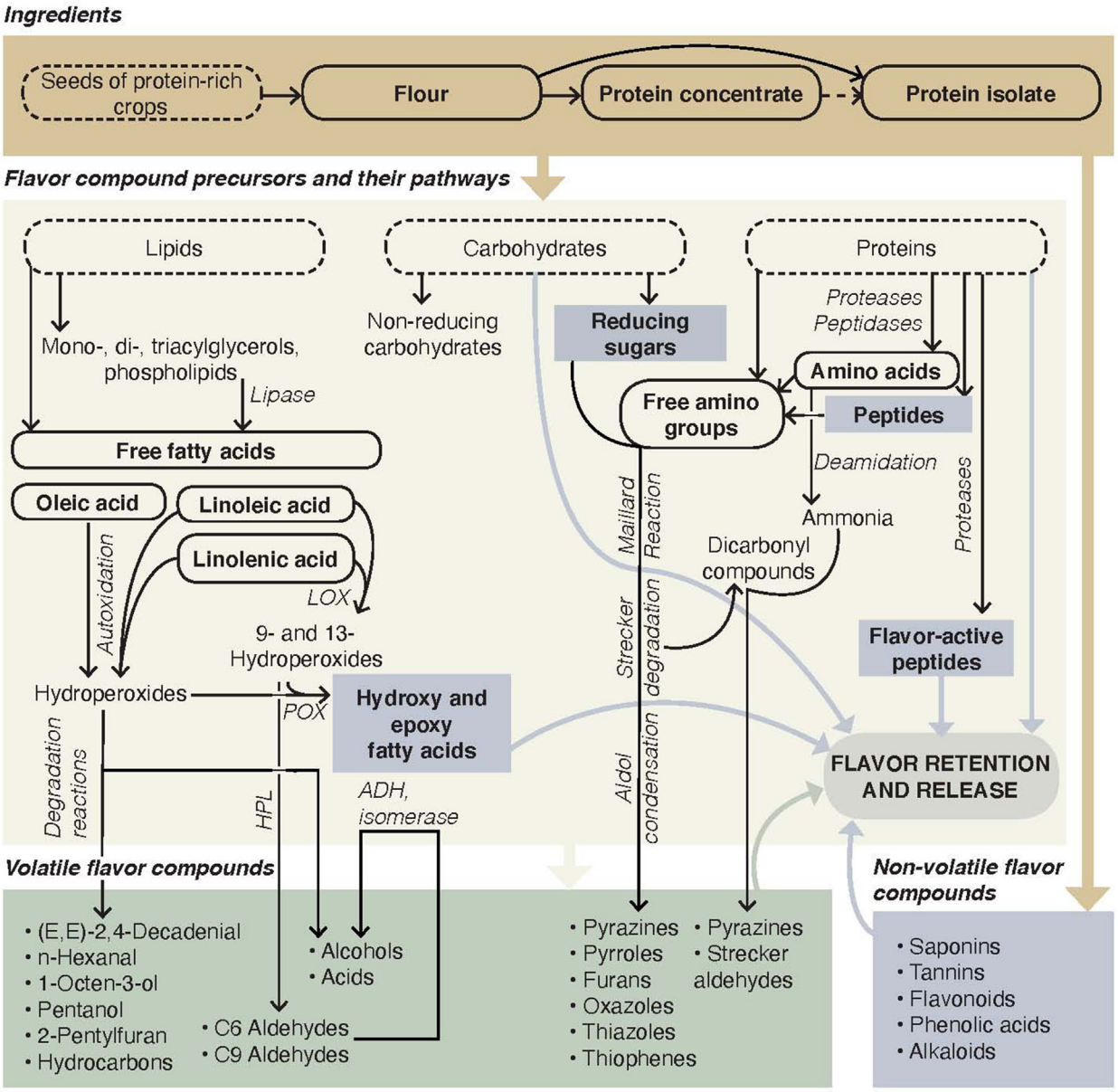

FIGURE 1 Principal pathways for the formation of flavor compounds in plant-based meat alternatives

to a significantly reduced bitter taste and a beany aroma or taste, in addition to the formation of a pleasant buttery or fruity flavor (Meinlschmidt et al., 2016a, c; Tangyu et al., 2019). The decrease in the beany off-flavor was likely related to the conversion of aldehydes and alcohols into the corresponding acids (e.g., *n*-hexanal to *n*-hexanoic acid) via enzyme activity (aldehyde dehydrogenase and alcohol dehydrogenase), and the inhibited activity of lipid oxidation enzymes at a low pH (Cai et al., 2020; Chiba et al., 1979; Nedele et al., 2021).

Regarding pea protein isolates, previous studies have shown that fermentation by LAB (e.g., *Lactiplantibacillus plantarum*, *Pediococcus pentosaceus*, *Lacticaseibacillus casei*, or *Leuconostoc mesenteroides subsp. cremoris*) or in combination with yeasts (*Kluyveromyces lactis*, *K. marxianus*, or *Torulaspora delbrueckii*) decreased the bitter taste and pea off-note (decreased hexanal and 2-pentylfuran), resulting in a more pleasant smell (e.g., a milky, apple cider, or beer note) compared to the unfermented counterpart (Arteaga et al., 2021; Schindler et al., 2012; Youssef et al., 2020). Nevertheless, extrudates prepared from pea-oat protein blends fermented with commercial LAB starters and *Weissella* species had higher scores for the intensity of the bitter taste, the overall off-taste, and the aftertaste than the control (Kaleda et al., 2020). The optimization of fermentation conditions is, thus, required to avoid the formation of unpleasant flavor-associated compounds.

Fermentation of lupin protein isolates with the former genus *Lactobacillus* and *Staphylococcus* resulted in lower intensities of pea-like aroma and bitter taste than in the unfermented isolates due to the masking effect of the aromas generated by fermentation such as popcorn-like, roasty, and cheesy aromas (Schlegel et al., 2019a). However, the fermentation of lupin with commercial yogurt culture (*Lactobacillus delbrueckii subsp. bulgaricus* and *Streptococcus thermophillus*) led to a higher intensity of the beany odor (increased hexanal and (*E*)−2-nonenal) than in the unfermented control (Kaczmarska et al., 2019). The different results obtained in the above studies can be attributed to the different LAB strains used, considering their variable genomic features and metabolic capabilities (Klaenhammer et al., 2005). This highlights the importance of the characterization of starters and their metabolic activities in correlation with a specific fermentation substrate.

7 | CONCLUSIONS

The perceived main barrier to the widespread use of plant-based meat alternatives is their inferior sensory quality compared to meat. Currently, various plant-derived proteins are used to manufacture meat alternatives. The choice of protein sources has a significant influence on the perceived flavor attributes of the final product. Understanding how flavors and off-flavors are formed in plant-based products will help to promote the development of effective methods of reducing their unwanted flavors and enhancing their desired flavors.

This review concludes that flavor compounds in plant-based meat alternatives are synthesized through multiple mechanisms, including, but not limited to, lipid oxidation, the Maillard reaction, deamidation, and thermal degradation of phenolic acids, carotenoids, and vitamins (Figure 1). In general, volatile off-flavor compounds, such as aldehydes, ketones, alcohols, and lactones (representative compounds: *n*-hexanal, 3-*cis*-hexenal, 2-pentylfuran, 1-octen-3-ol, and ethyl vinyl ketone), originate mainly from the oxidation of unsaturated fatty acids. The oxidative products depend on the fatty-acid substrate of the plant materials, the type and amount of their lipid-modifying enzymes, and the environmental and extrusion conditions. Off-taste is strongly correlated to the presence of free fatty acids, phenolic compounds, saponins, alkaloids, and bitter peptides or amino acid content. These off-taste components were found to be species-specific. The analysis of volatile and nonvolatile flavor compounds and their flavor characteristics requires a multidisciplinary approach that combines sensory and instrumental techniques.

Developing blander (or milder-tasting and -smelling) plant protein ingredients with fewer off-flavors is challenging. Removal or masking strategies should be selected based on the problematic flavor compounds present and must ensure minimal loss of the protein functionalities and the nutritional quality of the protein ingredients. Clean-label approaches, that is, enzyme treatment and fermentation, are promising because the perceived naturalness is a crucial factor that affects consumer acceptance of plant-based meat alternatives. Altogether, the flavor-related sensory properties of plant-based meat alternatives should be a primary target of future product development and applied research. We require more systematic studies to further investigate the origin and identity of off-flavor compounds from different plant protein sources, particularly considering the fate of these compounds and the newly formed flavor volatiles during high-moisture extrusion cooking.

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CONFLICTS OF INTEREST

None.

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