Comprehensive Reviews in Food Science and Food Safety

COMPREHENSIVE REVIEW

Protein-Flavor Interactions in Plant Protein Food Matrix: Molecular Binding Mechanisms, Influencing Factors, and Modulation Strategies

Xinran Dai[1,3] | Jiaping Zhang[1] | Zhaoshi Chen[1] | Muhammad Awais[4] | Bei Fan[1,2] | Marie-Laure Fauconnier[3] | Liya Liu[1,2] | Fengzhong Wang[1,2]

[1]Institute of Food Science and Technology, Chinese Academy of Agricultural Sciences, Key Laboratory of Agro-Products Processing, Ministry of Agriculture and Rural Affairs, Beijing, China | [2]Institute of Western Agriculture, the Chinese Academy of Agricultural sciences, Changji, China | [3]Gembloux Agro-Bio Tech, University of Liège, Gembloux, Belgium | [4]School of Food and Biological Engineering, Jiangsu University, Zhenjiang, China

Correspondence: Liya Liu (liuliya1218@163.com) | Fengzhong Wang (wangfengzhong@caas.cn)

Received: 11 June 2025 | **Revised:** 20 September 2025 | **Accepted:** 7 October 2025

Keywords: Plant-based protein food | protein-flavor interactions | molecular binding | analytical models | influencing factors | flavor modulation

ABSTRACT

As plant-based diets gain momentum for health, environmental, and ethical reasons, the demand for plant-based protein foods is accelerating. However, a critical barrier to consumer acceptance lies in their flavor profiles, which are often perceived as off-putting due to complex interactions between plant proteins and flavor compounds. While individual interactions have been explored, an integrated understanding of their mechanisms and modulation remains limited. This review synthesizes current knowledge on plant protein–flavor interactions across molecular, physicochemical, and sensory levels. We examine the structural and functional diversity of plant proteins (legumes, cereals, nuts, seeds, and novel sources), categorize their interaction modes (non-covalent and covalent), and assess the impact of intrinsic (e.g. protein conformation, hydrophobicity) and extrinsic factors (e.g. pH, ionic strength, processing). Analytical models such as Scatchard and Hill equations, alongside QSAR and molecular docking approaches, are discussed. We further explore emerging strategies-physical, chemical, biological, and hybrid-for targeted flavor modulation. It is noted that plant protein-flavor interactions play a dual role: enabling flavor retention and protection, but also triggering off-flavors through irreversible binding or volatile entrapment. These interactions vary across protein types, flavors properties and processing conditions, requiring tailored strategies for optimization. For instance, enzymatic hydrolysis, micro-encapsulation, and data-driven protein engineering (leveraging computational tools to design proteins) offer promising solutions. Future progress hinges on combining sensory physiology with computational modeling and structural bioengineering to develop plant-based foods with improved flavor authenticity, stability, and consumer appeal.

Abbreviations: ENaC, epithelial sodium channel; GC, gas chromatography; GC-MS, gas chromatography-mass spectrometry; GC-O, Gas chromatography-olfactometry; HMMA, Hybrid meat-mimicking analog; HPLC, high-performance liquid chromatography; HPLC-DAD, high-performance liquid chromatography with diode array detection; HPLC-MS, high-performance liquid chromatography-mass spectrometry; HPLC-UV, high-performance liquid chromatography with UV detection; HS-SPME, headspace solid-phase microextraction; LC-MS/MS, liquid chromatography–tandem mass spectrometry; LOX, lipoxygenase; OSN, olfactory sensory neuron; PBMA, plant-based meat analog; PBPF, plant-based protein food; PDS, pH differential spectrophotometry; PMb, porcine myoglobin; PPI, pea protein isolate; QSAR, quantitative structure-activity relationship; SPI, soy protein isolate; TBARS, thiobarbituric acid reactive substances; TGase, transglutaminase; TRC, taste receptor cell; UV–Vis, ultraviolet–visible spectroscopy..

1 | Introduction

The rapid global shift toward plant-based diets is driven by environmental sustainability, animal welfare, and health-conscious lifestyles. Consequently, plant proteins from legumes, cereals, nuts, and other emerging sources are increasingly used in food manufacturing (Kadam et al. 2025). Plant protein-flavor interactions are pivotal in determining the sensory quality and consumer acceptance of food based on plant protein matrix (Yin et al. 2024). More than 300 flavor compounds have been identified in plant-based protein foods, and new compounds continue to emerge with more advanced analytical techniques (Liu et al. 2023). Among them, 130 compounds, listed in Table 1, were established as the key compounds responsible for the unique flavor characteristics, with the aid of gas chromatography–olfactometry (GC-O), high-performance liquid chromatography (HPLC) and quantitative measurements. However, the underlying mechanisms of plant protein-flavor interactions has not been reviewed in detail, and the knowledge of flavor modulation analysis is lacking.

Flavor perception in plant-based protein foods is governed by both physiological and physicochemical mechanisms. During ingestion, olfactory pathways, salivary activity and taste perception modulates the release and perception of flavor compounds (Wang et al. 2024). These sensations rely not only on the sensory buds of the nose/tongue but also on those of the trigeminal nerve (Li et al. 2025). At molecular levels, interactions between plant proteins and flavor compounds involve a combination of non-covalent forces and irreversible covalent bonds, which affect both the volatility and availability of flavor-active molecules (Reineccius 2022). For instance, legume proteins (e.g. soy, pea, faba bean) are known to form strong hydrophobic and covalent interactions with aldehydes and sulfur-containing compounds, which are key contributors to aroma and taste (Zeng et al. 2024). Several analytical and computational models have been developed to characterize the types of forces, site compatibility, free energy and structural compatibility in the protein-flavor interactions. Classical approaches such as the Scatchard equation and Hill model quantify binding affinity and cooperativity between plant proteins and flavor ligands (Zhang et al. 2021). Recently, quantitative structure-activity relationship (QSAR) and molecular docking simulations have been employed to predict binding behaviors based on protein structure and flavor compound polarity (Barallat-Pérez et al. 2024). Despite these developments, little information about model frameworks is available that may highlight the need for more advanced physiologically and physicochemically modeling systems.

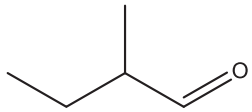
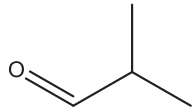
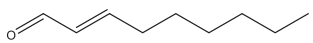
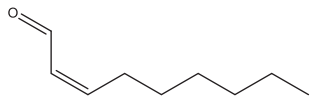
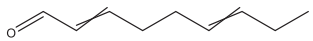
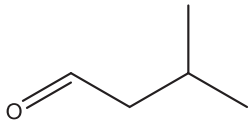
Plant protein-flavor interactions are influenced by both intrinsic and extrinsic factors, which jointly determine flavor release in protein matrix. Intrinsic factors mainly include protein conformation and flavor compound properties. Extrinsic factors such as pH, ionic strength, processing conditions can also significantly alter interactions. These interactions yield dual outcomes, as controlled binding could stabilize desirable volatiles and prolong the shelf life. Conversely, strong or irreversible binding can remove flavor-active molecules from the volatile pool, leading to flavor suppression or even new off-flavors in processed or stored products. For instance, reactive aldehyde flavor compounds can form Schiff-base adducts with lysine residues in proteins, immobilizing the aldehydes and eliminating their aroma. Similarly, vanillin has been shown to covalently bind to plant proteins, causing notable flavor loss (flavor "fade"). These mechanisms explain how protein interactions may degrade key flavor compounds and thereby dull the sensory profile (Xu et al. 2024). However, the undesirable flavor profiles in plant-based protein foods significantly limits consumer acceptance (Xu et al. 2025). To address these challenges, an array of modulation strategies has been developed, including physical approaches (e.g. encapsulation, spray-drying, emulsification), chemical modifications (e.g. protein denaturation, additive masking, solvent-assisted extraction) and biological techniques (e.g. enzymatic hydrolysis, targeted fermentation) (Nagassa et al. 2024). Moreover, hybrid strategies combining structural engineering with computational tools are emerging as promising methods to modulate flavor retention and release kinetics in protein food matrices, such as machine learning-guided protein design or pH-triggered delivery systems (Wang et al. 2024). Due to the complexity and functionality of plant protein-flavor interactions, the flavor modulation of plant-based protein foods remains challenges and should be further explored.

Although numerous studies have examined protein–flavor interactions in plant-based foods, past reviews have seldom integrated findings across diverse protein sources, flavor types, and matrix formats, often focusing on a single protein category, limited flavor classes, or only reversible interactions. As a result, irreversible covalent binding, matrix-dependent flavor release, and the translation from molecular mechanisms to sensory perception remain underexplored. This review addresses these gaps by systematically analyzing legume, cereal/pseudocereal, nut, seed, and novel protein matrices, considering both aroma and taste-active compounds, and linking binding thermodynamics to sensory outcomes such as flavor intensity, stability, and off-odor development. Physical, chemical, biological and hybrid strategies for flavor modulation are further evaluated, with attention to their limitations in retention, nutritional impact, and scalability. By integrating molecular insights, structural engineering, sustainable processing, and "flavoromics," emerging approaches-such as computational modeling, digital oral processing, targeted protein editing, and advanced encapsulation-are outlined to guide the design of plant-based foods with improved flavor authenticity, controlled release, and consumer acceptance.

2 | Plant-Based Protein Food (PBPF)

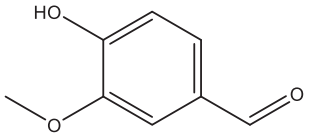
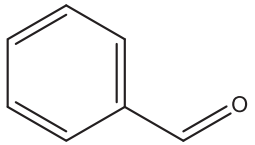
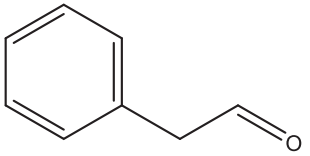
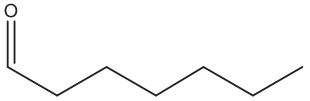
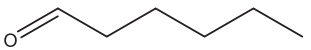
Consumer demand for low-fat, high-fiber, and nutrient-dense options has accelerated market growth, particularly in Asia and Europe, where plant-based analogs (e.g. tofu, tempeh) have long been staples of vegetarian cuisine (Pérez et al. 2023). Products with protein content of ≥12 g/100 g (solid) or ≥6 g/100 mL (liquid) can be classified as high-protein products, with advanced formulations, such as plant-based meat analogues (PBMAs), protein bars and non-dairy beverages, achieving protein concentrations of 20–50% (Codex Alimentarius Commission 1985; National Health Commission of the People's Republic of China 2011). The International Organization for Standardization defines vegetarian and vegan foods and sets requirements for ingredients, processing, and labeling (International Organization for Standardization 2021); while the China Institute of Food Science and Technology defines plant-based foods as products

TABLE 1 | Flavor compounds from different plant protein materials for which sensory attributes have been described.

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Aldehydes						
2-methylbutanal	Pea (yellow, gray, green), faba bean		Malty	0.83	HS-SPME; GC-MS; GC-O; Sensory evaluation	(Ferawati et al. 2020)
2-methylpropanal	Faba bean		Malty	0.86	HS-SPME; GC-MS	(Akkad et al. 2019)
2-nonenal, (*E*)	Pea (yellow, gray), flaxseed, hemp, lupin, black bean, pinto bean, faba bean		Grass, fruity, cardboard, fatty, green	2.71	HS-SPME; GC-MS; GC-O	(Lan et al. 2020)
2-nonenal, (*Z*)	Lupin		Cardboard	2.70	GC-MS; GC-O	(Bader et al. 2009)
2,4-nonadienal	Soybean		Cucumber, green, fatty	2.62	HS-SPME; GC-MS	(Xu et al. 2019)
2,4,6-nonatrienal	Lupin		Nutty, oat flake	2.50	GC-MS; GC-O	(Bader et al. 2009)
2,6-nonadienal	Hemp, lupin		Cucumber, green	2.80	HS-SPME; GC-MS; GC-O	(Shen, Gao et al. 2020)
3-methylbutanal	Pea (yellow, gray), faba bean		Malty	1.00	HS-SPME; GC-MS; GC-O	(Ferawati et al. 2020)

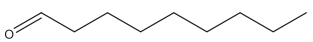
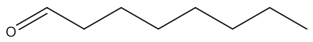
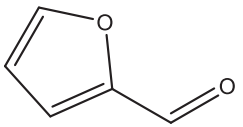
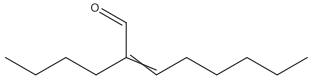
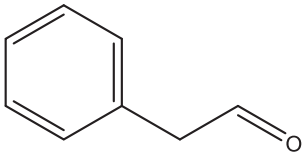
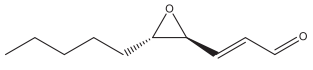
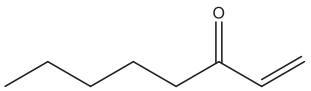
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
4-hydroxy-3-methoxy benzaldehyde	Pea		Sweet, vanilla	1.20	GC-MS	(Murat et al. 2013)
Benzaldehyde	Pea (yellow, gray), hemp, black bean, pinto bean, faba bean, green bean		Bitter almond, sweet, woody	1.69	Solvent extraction (Simultaneous distillation–extraction); GC-MS	(Shen, Gao et al. 2020)
Benzeneacetaldehyde	Lentil (green, red)		Harsh, green, honey, cocoa, floral, sweet	1.78	HS-SPME; GC-MS	(Xu et al. 2019)
Heptaldehyde	Soy		Citrus, fat, green, nut	2.20	HS-SPME; GC-MS	(Yang, Zhang et al. 2023)
Decanal	Pea (yellow, gray, green), hemp, black bean, pinto bean, kidney bean, faba bean, green bean		Fatty	3.97	HS-SPME; GC-MS	(Shen, Gao et al. 2020)
Hexanal	Pea (yellow, gray, green), hemp, black bean, pinto bean, kidney bean, faba bean, green bean, lentil (green)		Green, strong, grassy, floral, fruity, pea	1.65	HS-SPME; GC-MS; GC-O	(Shen, Gao et al. 2020)

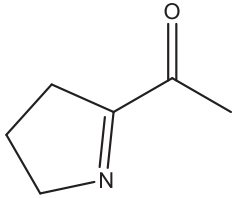
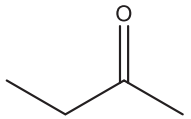
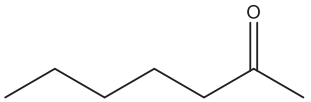
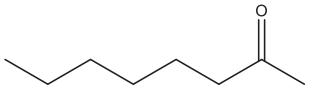
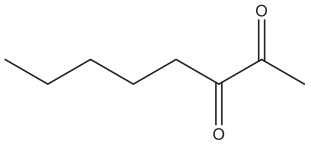
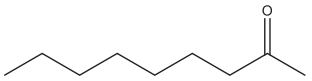
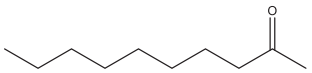
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
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	2.99	HS-SPME; GC-MS	(Lan et al. 2020)
Octanal	Pea (yellow, gray, green), hemp, black bean, kidney bean, faba bean		Orange, sweet, fruity, fatty	2.54	HS-SPME; GC-MS	(Shen, Gao et al. 2020)
Furfural	Soybean		Sweet, woody, almond, fragrant, and baked bread	0.41	GC-MS	(Yang, Ying et al. 2023)
2-butyl-octenal	Soy		Fruity, fatty	4.00	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
Phenyl acetaldehyde	Faba bean		Flowery	1.38	HS-SPME; GC-MS	(Akkad et al. 2019)
Trans-4,5-epoxy-dec-2-enal, (*E*)	Lupin		Metallic	3.00	GC-MS; GC-O	(Bader et al. 2009)
Ketones						
1-octen-3-one	Pea (green), soybean, lupin		Mushroom	2.20	HS-SPME; GC-MS; GC-O	(Xu et al. 2019)

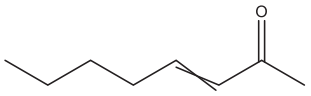
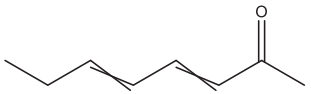
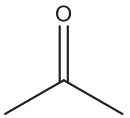
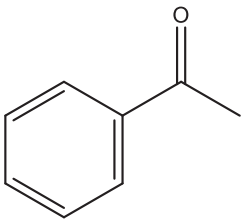
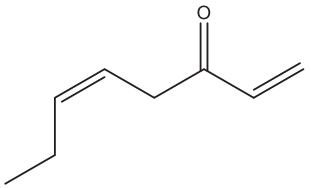
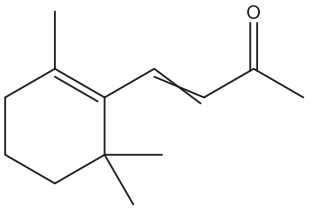
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
2-acetyl-1-pyrroline	Lupin		Popcorn	0.30	GC-MS; GC-O	(Bader et al. 2009)
2-butanone	Soybean, pea, black bean, pinto bean, faba bean		Fishy	0.29	HS-SPME; GC-MS	(Khrisanapant et al. 2019)
2-heptanone	Pea (yellow, gray, green), faba bean and soy		Cheese, fruity, coconut, waxy, and green	1.98	HS-SPME; GC-MS; GC-O	(Ferawati et al. 2020)
2-octanone	Flaxseed, faba bean, pea		Soap, gasoline, earthy, weedy, natural, woody, and herbal	2.37	HS-SPME; GC-MS	(Akkad et al. 2019)
2,3-octanedione	Hemp		Mushroom, vegetable	1.50	HS-SPME; GC-MS	(Shen, Gao et al. 2020)
2-nonanone	Soy		Fresh, sweet, green, weedy, earthy, and herbal	3.14	GC-MS	(Yang, Ying et al. 2023)
2-decanone	Soy		Fermented and cheesy	3.70	HS-SPME; GC-MS	(Yang, Ying et al. 2023)

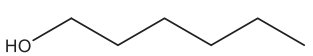
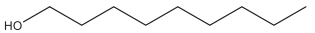
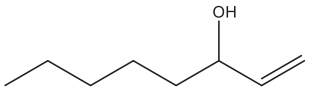
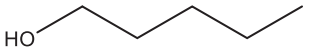
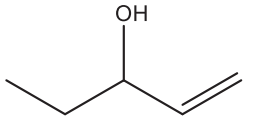
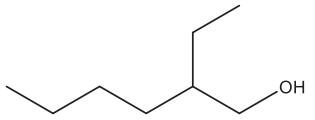
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
3-octen-2-one	Pea (yellow, gray), flaxseed and soybean		Beany, earthy, oily, spicy, ketonic, fermented, blue cheese, waxy, fatty, and woody	2.10	HS-SPME; GC-MS; GC-O	(Lan et al. 2020)
3,5-octadien-2-one	Pea (yellow, gray), flaxseed, hemp, faba bean		Beany, spicy, earthy, green pepper	1.90	HS-SPME; GC-MS; GC-O	(Shen, Gao et al. 2020)
Acetone	Black bean, pinto bean, kidney bean, faba bean		Fishy	−0.24	HS-SPME; GC-MS	(Shen, Gao et al. 2020)
Acetophenone	Black bean, pinto bean, kidney bean, faba bean, lentil (green, red)		Sweet, flower, almond	1.58	HS-SPME; GC-MS	(Shen, Gao et al. 2020)
Octa-1,5-dien-3-one, (*Z*)	Lupin		Geranium, metallic	1.70	GC-MS; GC-O	(Bader et al. 2009)
β-ionone	Lupin, faba bean		Violet, flower	3.50	HS-SPME; GC-MS; GC-O	(Akkad et al. 2019)

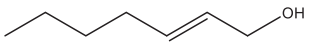
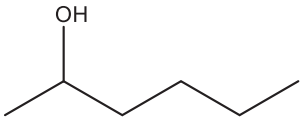
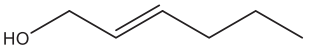
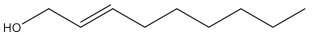
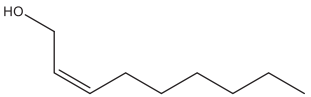
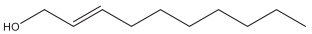
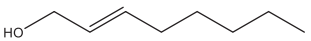
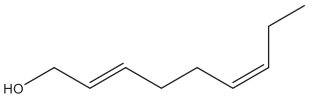
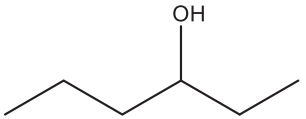
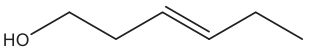
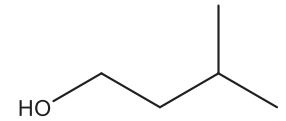
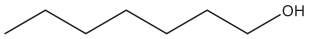
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
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	2.03	HS-SPME; GC-MS; GC-O	(Shen, Gao et al. 2020)
1-nonanol	Pea (yellow, gray), flaxseed, hemp, black bean, pinto bean, kidney bean, faba bean		Soapy, pea, vegetable, silt, earth, rose-orange	3.77	HS-SPME; GC-MS	(Shen, Gao et al. 2020)
1-octen-3-ol	Pea (yellow, gray, green), soybean, flaxseed, black bean, pinto bean, kidney bean, faba bean, green bean		Beany, mushroom, vegetable	2.50	HS-SPME; GC-MS	(Xu et al. 2019)
1-pentanol	Pea (yellow, gray, green), soybean, flaxseed, hemp, black bean, pinto bean, faba bean		Balsamic, grilled, dust	1.50	HS-SPME; GC-MS	(Lan et al. 2020)
1-penten-3-ol	Pea (green), black bean, pinto bean, kidney bean		Beany, green	1.05	HS-SPME; GC-MS; GC-O	(Khrisanapant et al. 2019)
2-ethylhexanol	Soy		Citrus, fresh, floral, oily, and sweet	2.80	HS-SPME; GC-MS	(Yang, Ying et al. 2023)

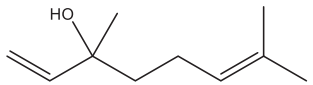
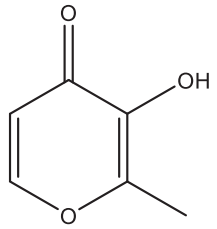
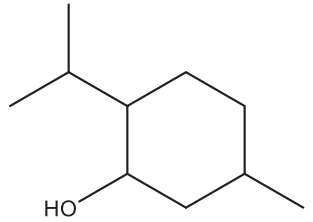
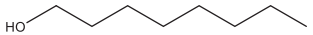
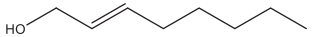
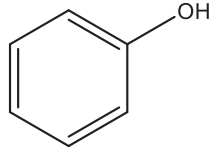
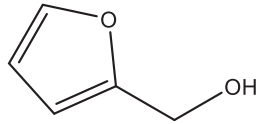
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
2-hepten-1-ol, (*E*)	Flaxseed		Floral	2.30	HS-SPME; GC-MS	(Lan et al. 2020)
2-hexanol	Flaxseed		Herbaceous	1.80	HS-SPME; GC-MS	(Lan et al. 2020)
2-hexen-1-ol, (*E*)	Pea (green), flaxseed		Grass, green, fruity	1.60	HS-SPME; GC-MS; GC-O	(Lan et al. 2020)
2-nonen-1-ol, (*E*)	Flaxseed		Melon, mint, grass	3.30	HS-SPME; GC-MS	(Lan et al. 2020)
2-nonen-1-ol, (*Z*)	Soy		Slightly waxy, melon, and sweet	3.30	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
2-decen-1-ol, (*E*)	Soy		Waxy, fresh air, citrus, rose, and rue	4.30	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
2-octen-1-ol, (*E/Z*)	Hemp		Cucumber, grass, green	2.70	HS-SPME; GC-MS	(Shen, Gao et al. 2020)
2,6-nonadien-1-ol, (*E/Z*)	Flaxseed		Melon, cucumber	3.00	HS-SPME; GC-MS	(Lan et al. 2020)
3-hexanol	Flaxseed		Woody, green	1.80	HS-SPME; GC-MS	(Lan et al. 2020)
3-hexen-1-ol, (*E/Z*)	Pea (green), flaxseed, green bean		Grass, herbal	1.60	HS-SPME; GC-MS; GC-O	(Lan et al. 2020)
3-metyhl-1-butanol	Pea (green), navy bean, black bean, kidney bean, pinto bean, faba bean		Flower intense, whiskey, fruity, banana	1.00	HS-SPME; GC-MS; GC-O	(Wang, Guldiken et al. 2020)
Heptanol	Pea (yellow, gray, green), flaxseed, faba bean		Skunky, rancidity	2.50	HS-SPME; GC-MS; GC-O	(Lan et al. 2020)

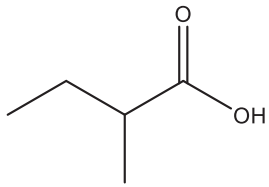
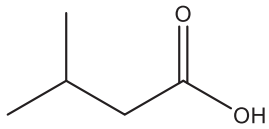
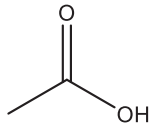
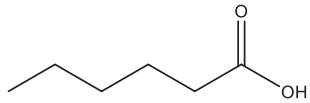
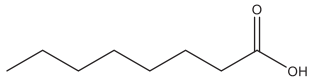
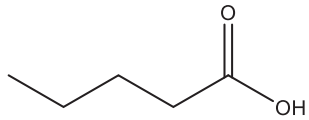
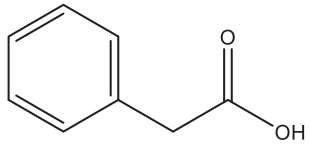
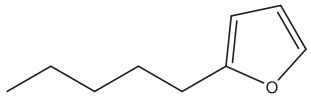
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Linalool	Soy		Citrus, orange, lemon, floral, waxy, aldehydic, and woody	2.80	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
Maltol	Lupin		Caramel	0.08	GC-MS	(Bader et al. 2009)
Menthol	Lentil (orange), faba bean		Mint	3.20	HS-SPME; GC-MS	(Khrisanapant et al. 2019)
Octanol	Pea (yellow, gray, green), chick pea, flaxseed, black bean, pinto bean, kidney bean, faba bean		Mushroom, vegetable, oily, aldehydic	2.90	HS-SPME; GC-MS; GC-O	(Ferawati et al. 2020)
2-octen-1-ol, (*E*)	Soy		Fatty, oily, sweet, and fruity	2.70	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
Phenol	Black bean, pinto bean		Peppery, woody	1.48	Solvent extraction; GC-MS	(Xu et al. 2019)
Furfuryl alcohol	Soy		Alcoholic, chemical, musty, sweet, caramel, bread, and coffee	0.28	GC-MS	(Yang, Ying et al. 2023)

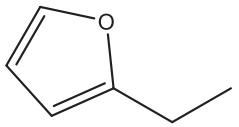
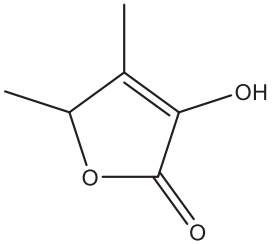
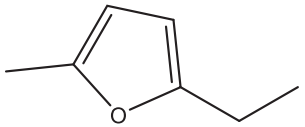
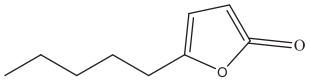
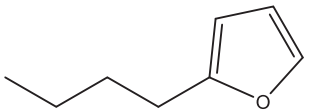
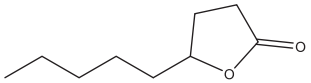
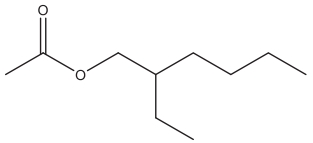
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Acids						
2-methylbutanoicacid	Pea, lupin, faba bean		Sweaty, fruity, cheese	1.18	HS-SPME; GC-MS; GC-O	(Wang, Guldiken et al. 2020)
3-methylbutanoicacid	Faba bean, pea, flaxseed, lupin		Sweaty, acid, rancid, fruity, cheese, animal	1.30	HS-SPME; GC-MS; GC-O	(Khrisanapant et al. 2019)
Acetic acid	Lupin, faba bean		Vinegar	−0.17	HS-SPME; GC-MS; GC-O	(Akkad et al. 2019)
Hexanoic acid	Chickpea, flaxseed, hemp, faba bean, pea		Sickening, sweaty, rancid, sour, sharp, pungent	1.90	HS-SPME; GC-MS	(Lan et al. 2020)
Octanoic acid	Hemp, pea		Sweaty	3.05	HS-SPME; GC-MS	(Shen, Gao et al. 2020)
Pentanoic acid	Lupin, pea		Cheese, sweaty, fruity	1.39	HS-SPME; GC-MS; GC-O	(Murat et al. 2013)
Phenylacetic acid	Lupin		Beeswax, honey	1.41	GC-MS; GC-O	(Bader et al. 2009)
Furans						
2-pentylfuran	Pea (yellow, gray, green), faba bean, lentil (green, red)		Beany, fatty, oily, green beans, butter	3.00	HS-SPME; GC-MS	(Ferawati et al. 2020)

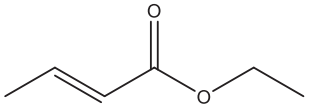
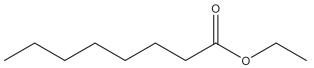
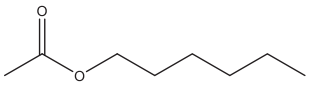
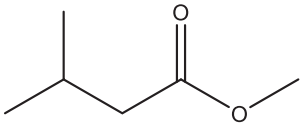
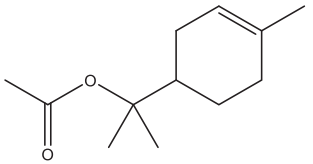
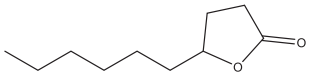
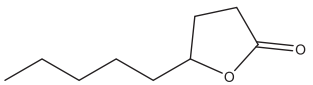
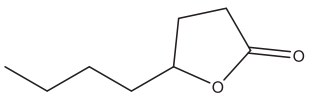
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
2-ethylfuran	Soy		Sweet, burnt, earthy, and malty	1.50	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
3-hydroxy-4,5-dimethyl-2(5 h)-furanone	Lupin		Spicy, savory	−0.50	GC-MS; GC-O	(Bader et al. 2009)
2-ethyl-5-methyl furan	Soy		Fresh, gassy, and burnt	2.00	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
5-pentyl-5(h)-furan-2-one	Pea		Mint, strawberry	2.00	HS-SPME; GC-MS	(Murat et al. 2013)
2-n-butyl furan	Soy		Mild, fruity, wine, sweet, and spicy	2.50	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
5-pentyldihydro-2(3 h)-furanone	Pea		Sweet, coconut, candies, peach	1.94	HS-SPME; GC-MS	(Xu et al. 2019)
Esters, lactones, and acetates						
2-ethylhexyl acetate	Faba bean		Fruity	4.20	HS-SPME; GC-MS	(Akkad et al. 2019)

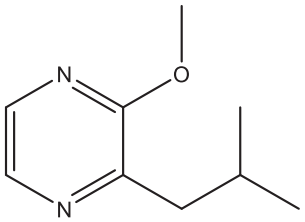
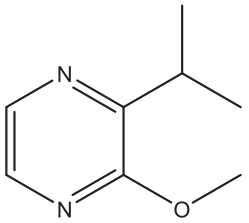
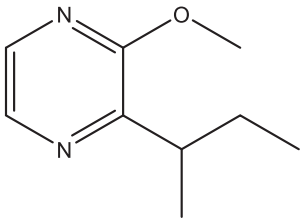
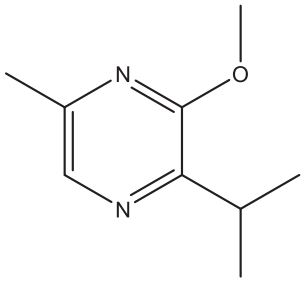
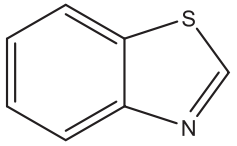
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Ethyl crotonate	Soy		Musty, onion and garlic, caramelly, and brown notes	1.85	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
Ethyl caprylate	Soy		Sweet, waxy, fruity and pineapple with creamy, fatty, mushroom, and cognac notes	3.84	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
Hexyl acetate	Pea (green), green bean, soy		Sweet, perfume	3.00	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
Methyl-3-methylbutyrate	Faba bean		Fruity	1.70	HS-SPME; GC-MS	(Akkad et al. 2019)
Terpinyl acetate	Soy		Herb, wax	3.30	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
γ-decalactone	Lupin		Peach, fruity	4.00	GC-MS; GC-O	(Bader et al. 2009)
γ-nonalactone	Lupin		Coconut, sweet	2.50	GC-MS; GC-O	(Bader et al. 2009)
γ-octalactone	Lupin		Coconut, sweet	2.00	GC-MS; GC-O	(Bader et al. 2009)

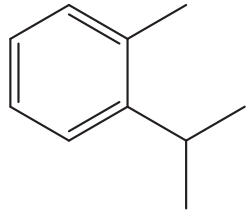
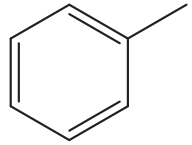
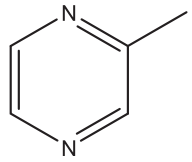
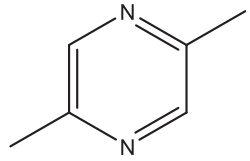
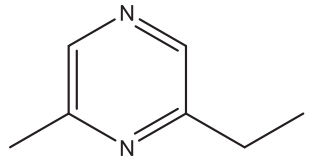
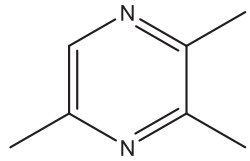
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Aromatic compounds						
3-isobutyl-2-methoxypyrazine	Pea (green), lupin		Green, peas, bell/green pepper, earthy	1.60	HS-SPME; GC-MS; GC-O	(Bader et al. 2009)
3-isopropyl-2-methoxypyrazine	Pea (green), lupin		Pea, peapod, bell/green pepper, blanched peas, earthy	1.40	HS-SPME; GC-MS; GC-O	(Xu et al. 2019)
3-sec-butyl-2-methoxypyrazine	Pea (green)		Green	1.60	HS-SPME; GC-MS; GC-O	(Xu et al. 2019)
6-methyl-3-isopropyl-2-methoxypyrazine	Pea (green)		Dry grass, spruce	1.50	HS-SPME; GC-MS; GC-O	(Murat et al. 2013)
Benzothiazole	Pea		Grilled meat	2.00	Solvent extraction; GC-MS	(Murat et al. 2013)

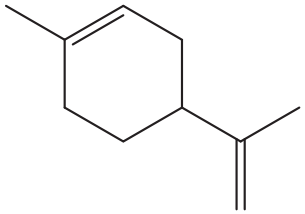
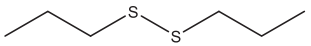
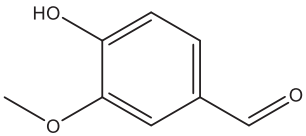
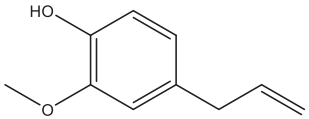
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
2-isopropyltoluene	Soy		Dry grass	3.70	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
Toluene	Pea (yellow, gray), mung bean, black bean, pinto bean, kidney bean, faba bean, lentil (green, red)		Pungent, caramel, fruity, solvent	2.70	HS-SPME; GC-MS	(Ferawati et al. 2020)
Pyrazines						
2-methylpyrazine	Soy		Nutty, brown, roasted, musty, and astringent	0.18	Microtrap; GC-MS	(Yang, Ying et al. 2023)
2,5-dimethyl pyrazine	Soy		Cocoa, roasted nuts, roast beef, woody, grassy, and medicinal	0.50	Microtrap; GC-MS	(Yang, Ying et al. 2023)
2-ethyl-6-methylpyrazine	Soy		Roasted potato	1.00	Microtrap; GC-MS	(Yang, Ying et al. 2023)
Trimethyl-pyrazine	Soy		Raw nut skin, vegetable, cocoa toasted, earthy, chocolate, and coffee	0.80	Microtrap; GC-MS	(Yang, Ying et al. 2023)

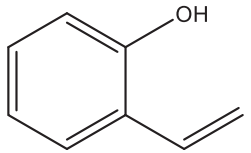
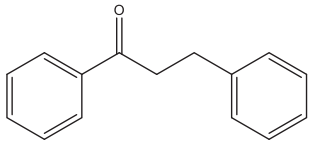
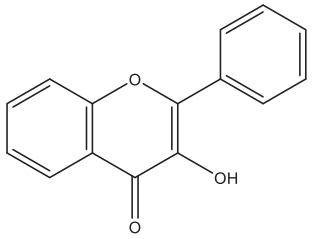
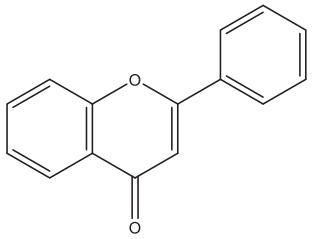
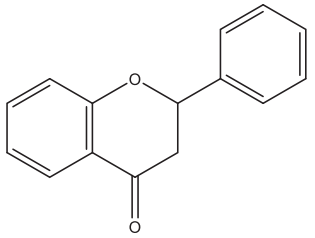
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Terpenes						
Limonene	Pea (green), lentil (orange, red, green), hemp, navy bean, black bean, kidney bean, faba bean, green bean		Citrus, mint	4.57	HS-SPME; GC-MS	(Khrisanapant et al. 2019)
Sulfuric compound						
Dipropyl disulfide	Pea (green)		Sulfurous, sour	3.00	HS-SPME; GC-MS	(Khrisanapant et al. 2019)
Saponins						
Acetylated saponins (aa, ab, ac, ad, ae, af, ag)	Soy, chickpea, faba bean, and pea	/	Bitter, astringent	1.00	HPLC-MS; Sensory evaluation	(Wang et al. 2022)
Deacetylated saponins (a1, a2, a3, a4, a5, and a6)	Soy, chickpea, faba bean, and pea	/	Bitter, astringent	0.80	HPLC-MS; Sensory evaluation	(Wang et al. 2022)
Ddmp-conjugated saponin (αg, βa, βg, γa, and γg)	Soy, chickpea, faba bean, and pea	/	Bitter, astringent	0.70	HPLC-MS; Sensory evaluation	(Wang et al. 2022)
Non-ddmp-conjugated saponins [i (bb), ii (bc), iii (bb′), iv (bc′), and v (ba)]	Soy, chickpea, faba bean, and pea	/	Bitter, astringent	0.80	HPLC-MS; Sensory evaluation	(Wang et al. 2022)
Phenolic compounds						
Vanillin	Lupin, pea		Vanilla	1.21	HPLC-MS; Sensory evaluation	(Wang et al. 2022)
Eugenol	Soy bean, pinto beans		Burnt, clove, spice	2.49	HPLC; GC-MS; UV–Vis	(Wang et al. 2022)

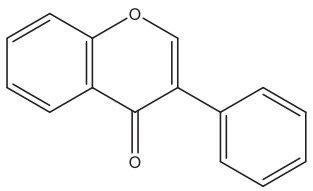
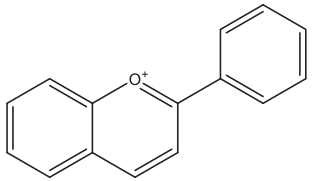
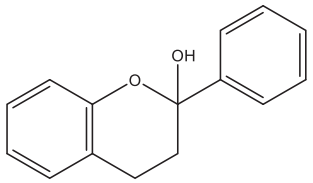
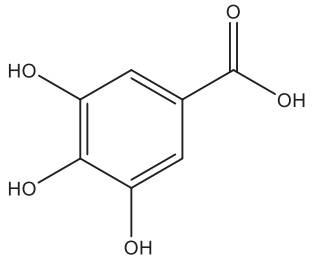
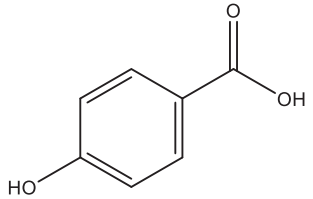
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Vinylphenol	Soy bean, pinto beans		Sweet, meat	2.34	HPLC; GC-MS	(Wang et al. 2022)
Dihydrochalcone	Soy, faba bean, lentil, common bean, and kidney bean, green pea, black soy seeds and yellow pea		Sweet	2.00–3.00	HPLC; LC-MS/MS	(Soto-Vaca et al. 2012)
Flavonol	Soy, faba bean, lentil, common bean, and kidney bean, green pea, black soy seeds and yellow pea		Bitter, astringent	1.50–3.50	HPLC-DAD; LC-MS/MS	(Soto-Vaca et al. 2012)
Flavone	Soy, faba bean, lentil, common bean, and kidney bean, green pea, black soy seeds and yellow pea		Bitter, astringent	1.80–3.00	HPLC-DAD; LC-MS/MS	(Soto-Vaca et al. 2012)
Flavanone	Soy, faba bean, lentil, common bean, and kidney bean, green pea, black soy seeds and yellow pea		Bitter, astringent	2.20–3.00	HPLC-DAD; LC-MS/MS	(Soto-Vaca et al. 2012)

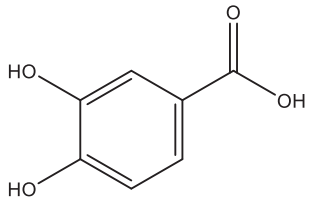
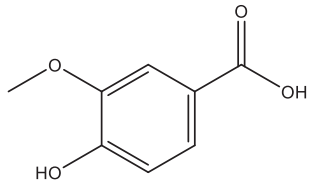
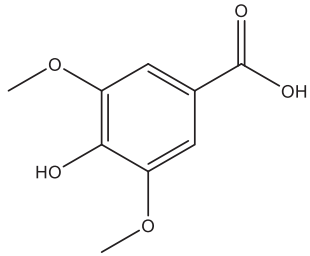
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Isoflavone	Soy, faba bean, lentil, common bean, and kidney bean, green pea, black soy seeds and yellow pea		Bitter, astringent	2.20–3.00	HPLC-DAD; LC-MS/MS	(Soto-Vaca et al. 2012)
Anthocyanidin	Soy, faba bean, lentil, common bean, and kidney bean, green pea, black soy seeds and yellow pea		Bitter, astringent	1.00–2.00	HPLC-DAD; PDS	(Soto-Vaca et al. 2012)
Flavanol	Soy, faba bean, lentil, common bean, and kidney bean, green pea, black soy seeds and yellow pea		Bitter, astringent	1.50–3.00	HPLC-DAD; LC-MS/MS	(Soto-Vaca et al. 2012)
Gallic	Beans, peas, and lentils		Sourness, astringency, and bitter ness	0.70	HPLC-DAD; UV–Vis; LC-MS	(Singh et al. 2017)
p-hydroxybenzoic	Beans, peas, and lentils		Sourness, astringency, and bitter ness	1.58	HPLC-DAD; LC-MS/MS	(Singh et al. 2017)

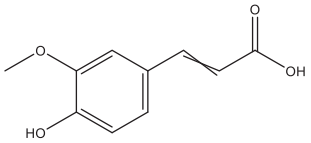
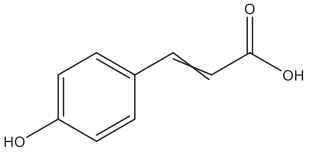
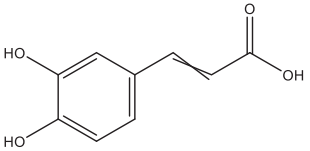
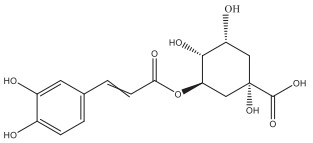
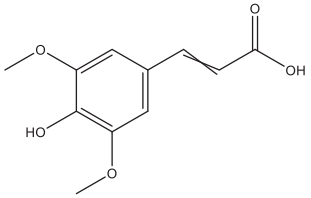
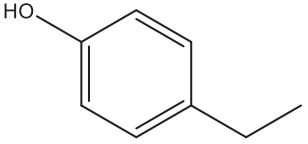
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Protocatechuic	Beans, peas, and lentils		Sourness, astringency, and bitterness	1.12	HPLC-DAD; UV–Vis; LC-MS	(Singh et al. 2017)
Vanillic	Beans, peas, and lentils		Sourness, astringency, and bitterness	1.34	HPLC-DAD; LC-MS/MS	(Singh et al. 2017)
Syringic acid	Beans, peas, and lentils		Sourness, astringency, and bitterness	1.11	HPLC-DAD; LC-MS/MS	(Singh et al. 2017)

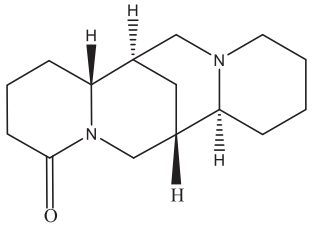
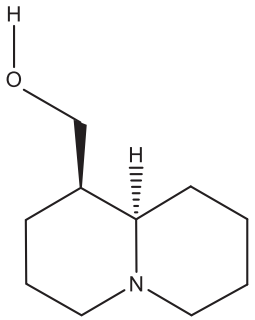
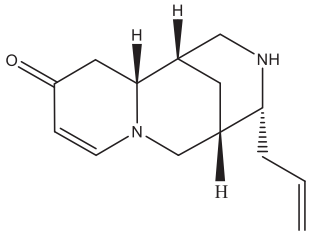
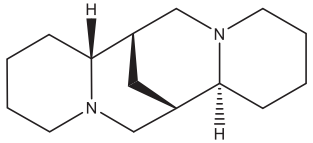
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Ferulic	Beans, peas, and lentils		Sourness, astringency, and bitterness	1.42	HPLC-DAD; LC-MS/MS	(Singh et al. 2017)
p-coumaric	Beans, peas, and lentils		Sourness, astringency, and bitterness	1.79	HPLC-DAD; LC-MS/MS	(Singh et al. 2017)
Caffeic	Beans, peas, and lentils		Sourness, astringency, and bitterness	1.06	HPLC-DAD; LC-MS/MS	(Singh et al. 2017)
Chlorogenic	Beans, peas, and lentils		Sourness, astringency, and bitterness	−0.58	HPLC-DAD; LC-MS/MS	(Singh et al. 2017)
Sinapic acid	Beans, peas, and lentils		Sourness, astringency, and bitterness	1.52	HPLC-DAD; LC-MS/MS	(Singh et al. 2017)
4-ethyl-phenol	Soy		Phenolic, smoke, bacon, and ham	2.76	HS-SPME; GC-MS	(Yang, Ying et al. 2023)

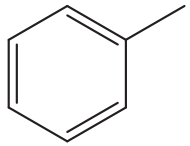
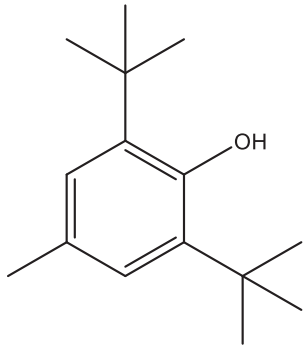
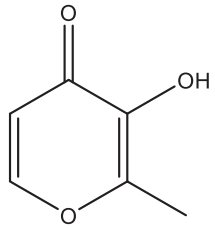
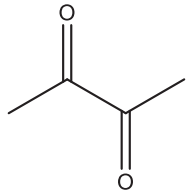
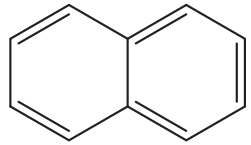
(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Alkaloids						
Lupanine	Lupin seeds		Bitterness	2.35	HPLC-UV; GC-MS; LC-MS/MS	(Mohan et al. 2016)
Lupinine	Lupin seeds		Bitterness	0.36	HPLC-UV; GC-MS	(Mohan et al. 2016)
Albine	Lupin seeds		Bitterness	1.80	HPLC; LC-MS/MS	(Mohan et al. 2016)
Sparteine	Lupin seed		Bitterness	2.66	HPLC-UV; GC-MS; Thin-layer chromatography	(Mohan et al. 2016)

(Continues)

TABLE 1 | (Continued)

Flavor compounds	Plant sources	Chemical structure	Odor description	Hydrophobicity (log P)	Study technology	Reference
Other						
Toluene	Soy		Sweet	2.73	HS-SPME; GC-MS	(Yang, Ying et al. 2023)
Butylated hydroxytoluene	Soy		Mild, phenolic, and camphor	5.30	Solvent extraction; GC-MS; HPLC	(Yang, Ying et al. 2023)
Maltol	Soy		Sweet, caramel, cotton candy, jam, fruity, and baked bread	−0.36	SPME; GC-MS; HPLC	(Yang, Ying et al. 2023)
Diacetyl	Soy		Butter, pastry, yeast	−1.34	GC; Sensory analysis; Static headspace analysis	(Yang, Ying et al. 2023)
Naphthalene	Soy		Pungent, dry, and tarry	3.30	HS-SPME; GC-MS	(Yang, Ying et al. 2023)

primarily derived from plant proteins that replicate or replace animal-derived counterparts (China Institute of Food Science and Technology 2021). This category spans five major classes under standards: plant-based meat, dairy, egg substitutes, frozen products, and hybrid derivatives. And the plant proteins mainly sourced from legumes, cereals, nuts, and novel sources like algae etc. (Klost et al. 2020; Wang, Pei et al. 2025). Legumes (e.g. soybean, pea) primarily contain globulins (e.g. β-conglycinin) and storage proteins (e.g. glycinin), rich in lysine but deficient in sulfur-containing amino acids; cereals (e.g. wheat, oat) are dominated by prolamins (e.g. gluten) and glutelins while lacking lysine, except oat and quinoa which contain complete amino acids; nuts and seeds (e.g. almond, walnut, chia seed) are rich in albumins and globulins, with ample sulfur-containing amino acids; and algae (e.g. spirulina) contain high quality complete proteins such as phycocyanin (Yin, Li et al. 2024). While these plant proteins have diverse nutritional profiles, their inherent functional limitations still pose certain challenges in the formation of high-quality plant protein products.

In particular, a key challenge lies in replicating the texture and techno-functional characteristics of animal-based products, which in practice requires targeted protein processing methods (Xie and Grossmann 2025). For example, plant-based meat analogues commonly use extruded soy or pea protein isolates to create fibrous, meat-like structures, plant-based egg substitutes utilize modified legume proteins (via controlled denaturation and cross-linking) to emulate egg's gelation and emulsifying properties (Khalifa et al. 2025; Yin et al. 2024). In addition, flavor attributes are pivotal determinants of consumer acceptance and commercial success in high plant-protein products, as flavor perception directly governs product preference and repurchase intent. In protein-enriched systems, the intensification of hydrophobic interactions and covalent binding significantly contributes to the entrapment of key flavor compounds, such as aldehydes and pyrazines (Qian et al. 2025). Therefore, the other critical challenge lies in understanding plant protein-flavor compound interactions, which directly influence flavor retention and release in the high content protein system. The following sections will provide a detailed summary of plant protein-flavor interactions.

3 | The Interactions of Different Plant Proteins and Flavor Compounds

The sensory attributes of plant-based protein foods are profoundly influenced by the interactions between proteins and flavor compounds, which present significant differences across plant protein sources (Figure 1). This following section categorizes these interactions by the protein sources, focusing on their specificity to flavor classes and role in modulating flavor retention or release.

3.1 | The Interactions Between Legume Proteins and Flavor Compounds

The interactions between legume proteins and flavor compounds are central to the sensory quality of plant-based protein foods, yet it also presents unique challenges due to the inherent complexity of legume-derived ingredients. Structurally, legumes are rich in globulins and storage proteins, such as β-conglycinin and glycinin (Yu et al. 2025). For instance, soybeans contain abundant storage proteins, primarily composed of 7S (vicilin) and 11S (legumin) fractions. Similarly, pea protein has a comparable composition, with its 11S legumin divided into α and β subunits. Legumes proteins have strong binding affinities for aldehydes (e.g. hexanal, nonanal) and alcohols (e.g. 1-hexanol, 1-octen-3-ol) driven by interactions with hydrophobic pockets in their structures (Wu et al. 2011). However, this binding often traps off-flavors such as beany and grassy odors, as well as an astringent mouthfeel, particularly in minimally processed ingredients (Wang et al. 2018).

Plant species-specific differences further complicate flavor binding and release. Soy proteins are associated with bitterness mainly contributed by aldehydes (e.g. n-hexanal) and non-volatile compounds (such as saponins and phenolic glycosides). Pea proteins tend to accumulate (Z)-2-penten-1-ol and hexanal, amplifying green odors (Bi et al. 2020). Faba bean ingredients, on the other hand, contend with lipid-oxidation byproducts like 2-pentylfuran and certain non-volatile polyphenols (e.g. tannins) that bind to bitter taste receptors and create a drying, astringent mouthfeel (Wang et al. 2022). Nevertheless, comparative analyses of emerging legumes (e.g. chickpea, lentil) versus conventional sources in regulating species-specific flavors are scarce, which may not only limits mechanistic understanding but also hinders the development of targeted flavor management strategies in plant-based foods. Thus, precise regulation of flavor binding and release across different legume proteins is critical for improving product quality.

3.2 | The Interactions Between Cereal/Pseudocereal Proteins and Flavor Compounds

Proteins in cereals are typically categorized into albumin, globulin, gliadin, and glutenin. Pseudocereals (e.g. quinoa, buckwheat) exhibit high 11S globulin content and balanced amino acid profiles (e.g. lysine-rich subunits). They can form thermally stable oligomers to enhance gelation and water-binding capacity, while hydrophobic residues drive structural integrity and interfacial stabilization in gluten-free matrices (Shahbaz et al. 2023). Cereals and pseudocereals generate various volatile flavor molecules during processing, including alcohols, aldehydes, esters, and heterocyclic compounds (e.g. 1-hexanol, nonanal, methyl palmitate, 2-acetyl-1-pyrroline) (Bailliere et al. 2022; Zhang et al. 2025). These compounds originate from lipid oxidation, enzymatic activity, or thermal reactions (Ying et al. 2011).

Different cereal and pseudocereal species exhibit distinct flavor-protein interaction patterns driven by their structural dynamics and conformational changes. During thermal processing, these proteins exhibit unfolding, aggregation, and disulfide bond rearrangement. For example, rice proteins can undergo unfolding and aggregation during cooking, leading to increased surface hydrophobicity and exposure of hydrophobic domains (Zhang et al. 2025). This facilitates the selective binding of hydrophobic aldehydes, stabilizing desirable aroma molecules like 2-acetyl-1-pyrroline and 2-methoxy-4-vinylphenol, while sequestering off-flavor (2-pentylfuran) in hydrophobic pockets (Zhang et al. 2025;

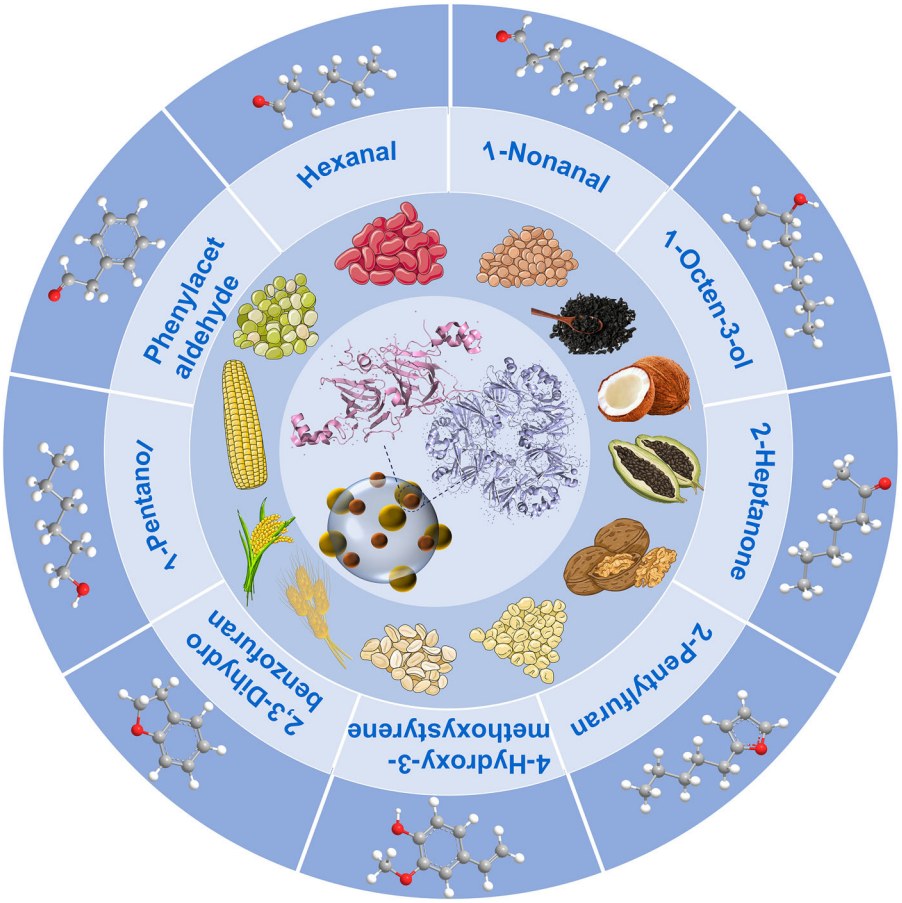


FIGURE 1 | The molecular interactions between different plant-based proteins and flavor compounds.

Zhou et al. 2023). In contrast, oat globulins bind hexanal and 1-hexanol via native hydrophobic regions, which amplifies green odors due to limited structural unfolding (Harper et al. 2022). Brown rice proteins in mixed systems selectively bind terpenes to mask berry odors while enhancing citrus notes (Kelemen et al. 2022). This interplay extends to glutinous rice, where aldehyde-protein interactions stabilize fruity-sweet flavors, underscoring how protein conformation modulates flavor equilibrium (Zhou et al. 2023). Consequently, the sensory profile of cereal and pseudocereal products is shaped not only by the formation of volatile compounds but also by the selective binding and stabilization of these molecules through protein conformational dynamics during processing.

3.3 | The Interactions Between Nut, Seed Proteins, and Flavor Compounds

The sensory profiles of nuts and seeds are shaped by dynamic interactions between proteins and flavor compounds, where proteins act as precursors, carriers, and binding platforms. Nuts and seeds are rich in albumins and globulins, which provide abundant sulfur-containing amino acids. In almonds, pyrazines, critical for roasted nutty aromas, arise from thermal degradation of amino acids (e.g. asparagine) during protein-sugar Maillard reactions (do Livramento et al. 2017). Additionally, lipid-binding proteins in almond trap hydrophobic volatiles (e.g. almond esters), modulating their release during mastication (Chen et al. 2023). In sunflower seeds, their proteins stabilize lipid-derived volatiles enhancing roasted depth while also exhibiting affinity for terpene derivatives to suppress competing aromas (Tangyu et al. 2023; Wang et al. 2020). The flavor compounds in pecan, such as hexanal (grassy) and D-limonene (citrus), are primarily formed through pathways such as lipid oxidation, carbohydrate fermentation, lipolysis, amino acid catabolism, proteolysis, and microbial metabolism (Luo 2024). Phenolic compounds in walnuts, such as juglone and ellagic acid, bind tightly to salivary proteins, intensifying their inherent bitterness and astringency (Zuo et al. 2024). Overall, the interactions between nut and seed proteins and flavor compounds contribute to a multifaceted sensory profile, wherein volatile formation, binding affinities, and complexation collectively determine the balance between desirable flavor notes and undesirable attributes.

3.4 | The Interactions Between Other Proteins and Flavor Compounds

Beyond legume, cereal, nut, and seed proteins, diverse novel plant protein sources can also bind, stabilize, or generate flavor-active compounds. Hemp protein in plant-based yogurts enhances fruity, floral, and creamy notes by elevating alcohols and ketones while suppressing rancid aldehydes, with its hydrophobic domains trapping hemp-specific terpenes (caryophyllene) to enrich flavor (Xu et al. 2022). Coconut protein binds vanillin via Schiff-base formation and van der Waals forces, causing flavor

fade; however, enzymatic deamidation reduces this binding affinity, freeing vanillin to intensify sweetness perception (Temthawee et al. 2020). Cassava leaf protein concentrate modulates cassava flour flavor at low concentrations (2.5%) by balancing characteristic "manioc" odors and suppressing bitterness, likely through selective adsorption of polar flavor compounds (Lima et al. 2013). Alfalfa proteins with abundant hydrophobic pockets are more prone to adsorb terpenoid compounds than chlorophyll-binding proteins, and alfalfa polyphenols can synergistically bind flavors through hydrophobic interactions with proteins, while excessive amounts may mask desirable flavors or impart astringency (Müller et al. 2025). Microalgal proteins, such as those in *Chlorella pyrenoidosa*, interact with lipid-derived aldehydes (hexanal) and alcohols (1-octen-3-ol) via enzymatic oxidation of linoleic acid, amplifying grassy and fishy flavors; while *Haematococcus pluvialis* addition in PBMAs enhances plant-like aromas (pyrroline for rice-like odors) and reduces fishy triethylamine by altering gel network adsorption capacities (Liu 2024). Kelp protein primarily binds to aldehydes ((E,Z)-2,6-nonadienal, (E,E)-2,4-decadienal, hexanal), ketones, and unsaturated carbonyls, which impart fishy and bitter flavors. And it can be converted into umami and salty peptides through fermentation or enzymatic hydrolysis (Zhu et al. 2021). These studies highlight the diverse ways in which novel plant proteins interact with flavor-active compounds, thereby modulating the sensory profiles of plant-based foods.

These aforementioned findings collectively emphasize the structural and functional diversity of plant proteins in modulating flavor compound binding, retention and release, driven by species-specific protein conformations and molecular affinities. Legume proteins primarily associate with sulfur volatiles and lipid-derived compounds, while cereal/pseudocereal proteins interact with phenolic acids and carbohydrate-based flavors. Nut/seed proteins show affinity for non-polar terpenes and esters, whereas other plant proteins interact with distinct flavor groups (as shown in Table 1). Future research should prioritize comparative investigations across protein sources to unravel underlying interaction mechanisms and develop targeted strategies that enhance sensory performance while preserving the nutritional and functional integrity of plant-based foods.

4 | Insights Into the Mechanisms and Mathematical Models for Characterizing Plant Protein-Flavor Interactions

4.1 | Flavor Perception Mechanism in Plant-Based Protein Foods (PBPFs)

The perception of flavors in PBPFs is a dynamic interplay between physiological processes and physicochemical interactions, shaped by olfactory pathways, salivary activity and taste perception (Frank et al. 2012; Mestres et al. 2005) (Figure 2). Olfactory perception integrates orthonasal and retronasal olfactory pathways, with the latter dominating in plant protein foods. Orthonasal detection involves volatiles inhaled directly from food surfaces, while retronasal perception relies on volatiles released during chewing and transported retrograde to olfactory receptors via the nasopharynx (Wang et al. 2024). In PBPFs, gel strength and network density govern volatile release: dense, rigid gels hinder diffusion and delay flavor perception, while softer, looser gels disintegrate quickly, allowing faster volatile release and stronger retronasal impact (Nawaz et al. 2019). Beyond volatiles, recent evidence suggests that non-volatile sweet compounds can also reach the olfactory epithelium through aerosol particles generated during oral processing, with matrix viscosity and surface tension modulating this transport pathway (He et al. 2025). Odorant molecules bind to the olfactory mucosa, diffuse through mucus to olfactory sensory neurons (OSNs) expressing odorant receptors, triggering a G-protein signaling cascade ($G_{\alpha olf}$/ACIII/PKA) in OSN cilia (Han et al. 2023; Wang et al. 2025). This generates action potentials transmitted via axons to the olfactory bulb, where mitral and tufted cells relay signals directly to the primary and secondary olfactory cortices, bypassing the thalamus. The secondary cortex integrates olfactory data, enabling adaptive flavor-guided responses through this thalamus-independent peripheral-to-central pathway (Kharlamova et al. 2023). Thus, while the neurophysiology of odor detection is conserved, the extent of volatile liberation from plant protein matrices—modulated by processing-induced structural changes such as extrusion, fermentation, or gelation—largely determines flavor intensity.

During mastication, texture-dependent mechanisms critically modulate flavor release: firmer textures, such as protein gels, reduce chewing efficiency and prolong oral residence time, delaying the release of volatile compounds (Hollowood et al. 2002; Mestres et al. 2005). Conversely, softer matrices accelerate structural disintegration, increasing surface area exposure and enhancing flavor diffusion into saliva and air phases (Déléris et al. 2011). Compared with animal proteins, plant proteins often form less elastic but more brittle gels, which fracture differently during chewing, thereby altering flavor release kinetics (Tang et al. 2024). Saliva, enriched with enzymes (α-amylase, proteases), mucins, and ions, govern flavor dynamics through dual mechanisms, hydrating protein networks to liberate trapped volatiles while simultaneously altering binding equilibria. For example, hydrophobic interactions between salivary mucins and aroma compounds trap volatiles on the oral mucosa, enabling gradual post-swallow release, a phenomenon termed "aroma persistence" (Muñoz-González et al. 2022). In PBPFs, additional interactions with polyphenols and tannins from plant matrices intensify astringency by precipitating salivary proteins, thus altering lubrication and modulating flavor persistence (Rossetti et al. 2008). Additionally, interindividual variability in salivary composition, including flow rate, pH, and viscosity, introduces significant flavor perceptual differences. Sodium-rich artificial saliva disrupts protein-volatile interactions to amplify flavor release, whereas high-viscosity saliva impedes aroma diffusion by reducing volatile mobility (Huang et al. 2023). Beyond these physicochemical factors, qualitative differences in salivary proteins also play a crucial role. Proline-rich proteins exhibit high affinity for polyphenols and certain aldehydes, thereby reducing their volatility, while mucins form viscous glycoprotein networks that entrap aroma compounds and modulate retronasal perception. Individual variability in the abundance and isoforms of these proteins can thus markedly shift volatile binding capacity, contributing to strong interindividual differences in flavor perception (Schwartz et al. 2022).

Taste perception in plant protein foods is mediated by the recognition of specific molecules by distinct types of taste receptor

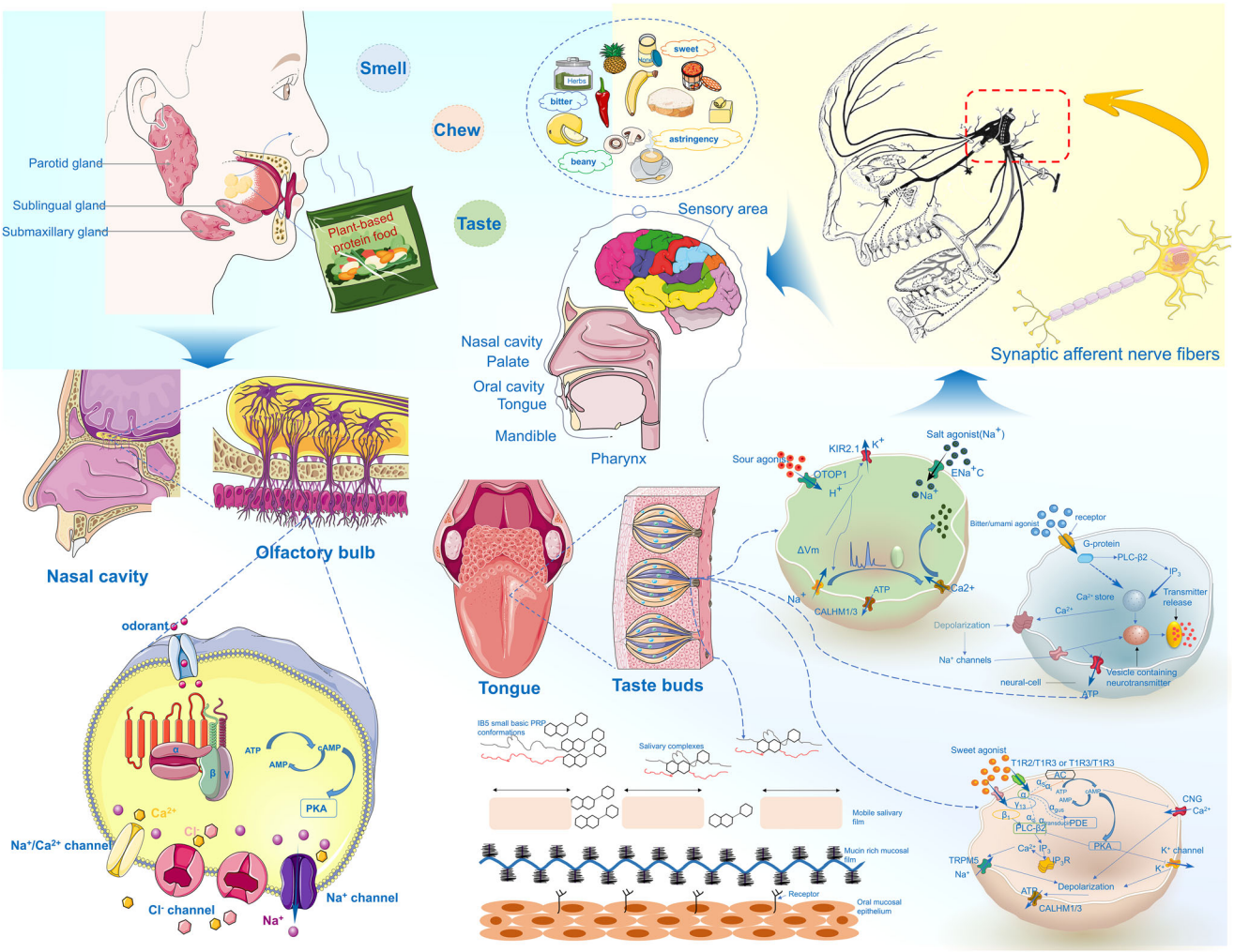


FIGURE 2 | The perception of flavors in plant-based protein foods shaped by olfactory pathways, salivary activity and taste perception.

cells (TRCs) in taste buds and subsequent signal transduction. Sweet, bitter, and umami tastes are detected by Type II TRCs through G protein-coupled receptors (T1R and T2R families). These receptors activate the phospholipase Cβ_2 (PLCβ_2) pathway, triggering IP3-mediated Ca^{2+} release from intracellular stores. This cascade leads to cell depolarization via TRPM5 channels and ATP release as a neurotransmitter, which activates adjacent afferent nerve fibers. In contrast, salty and sour tastes are mediated by specific ion channels: epithelial sodium channels (ENaCs) for salty taste and OTOP1 proton channels for sour taste. In PBPFs, sodium ions not only elicit saltiness but also disrupt protein–volatile complexes and mask intrinsic beany or bitter notes, linking taste perception to structural modulation (Luo et al. 2019). Type III TRCs transmit sour signals through direct synaptic release of serotonin (5-hydroxytryptamine). Taste information is relayed via cranial nerves to the nucleus tractus solitarius in the brainstem, ultimately being integrated in the cerebral cortex to form conscious taste perception (Tian et al. 2023). While the neural coding of taste is universal, the perceived quality of PBPFs strongly depends on how their protein matrices retain or release bitter peptides, salts, and flavor-active volatiles (Fan et al. 2021).

Despite advances in flavor perception mechanisms in PBPFs, critical knowledge gaps persist in individual-specific oral-nasal biomechanics (e.g. masticatory kinematics, retronasal airflow patterns) and neurocognitive integration of texture-flavor cues. Future research should not only decode neural pathways but also establish direct structure–perception links by integrating tribological simulations, metabolomic profiling of saliva-protein-volatile triads, and sensory evaluation of processing-induced protein architectures. Such a neurogastronomic framework will be essential to engineer next-generation plant protein composites with multisensory appeal.

4.2 | Mechanisms of Plant Protein-Flavor Interactions

The interaction between plant proteins and flavor compounds is governed by a complex combination of reversible non-covalent and irreversible covalent binding mechanisms, which critically influence flavor perception in PBPF systems (Figure 3).

4.2.1 | Non-Covalent Binding of Plant Protein and Flavor Compounds

Non-covalent interactions between plant proteins and flavor compounds, including hydrophobic forces, hydrogen bonding,

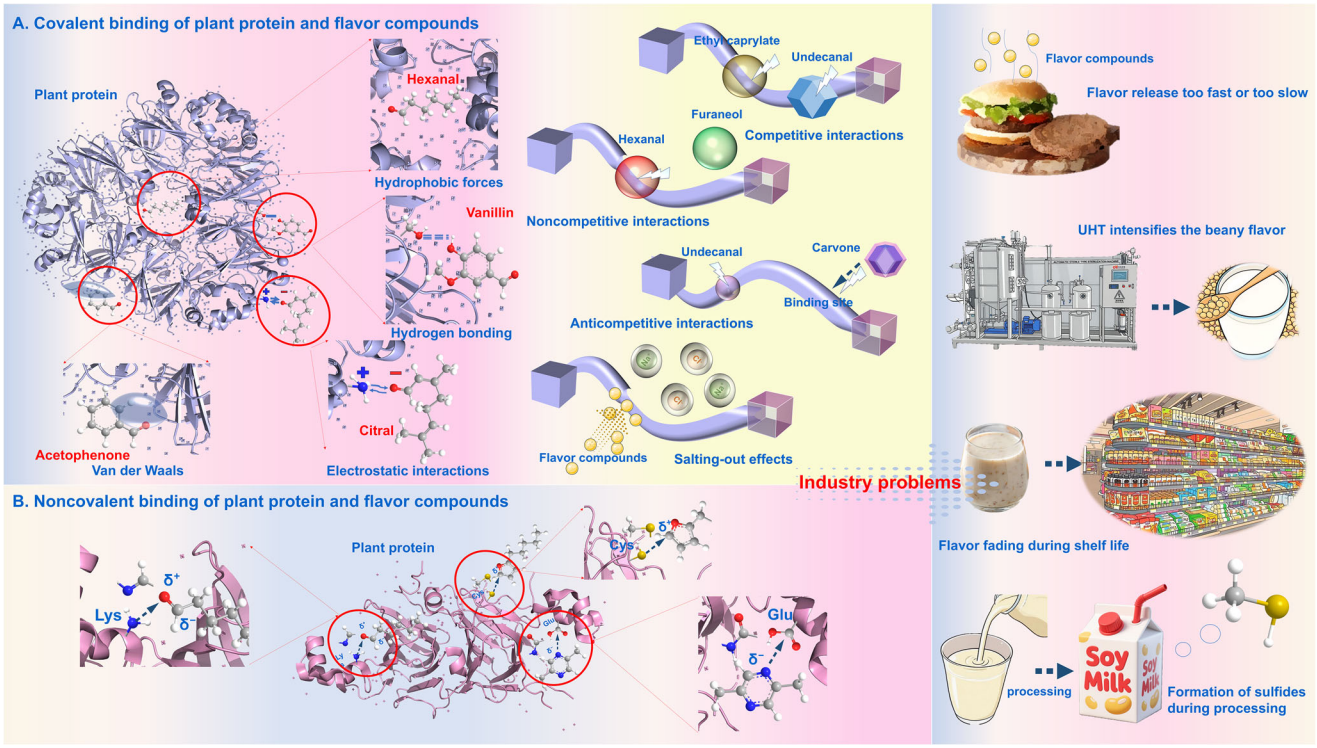


FIGURE 3 | Non-covalent binding and covalent binding of plant protein and flavor compounds, and the resulting issues in the food industry.

electrostatic interactions, and van der Waals forces, govern the reversible and dynamic equilibrium of flavor retention and release. These interactions are thermodynamically spontaneous, driven by the hydrophobicity, isomerism, and functional groups (e.g. hydroxyl, carboxyl) of flavor compounds depending on the chemical structure of the volatiles (Zhang et al. 2021). Hydrophobic compounds exhibit stronger binding affinities, often diffusing into protein interiors after initial surface interactions (Xiang et al. 2023). For example, GC–MS analyses of sunflower seed milk reveal strong terpene-binding affinity that corresponds with trained panel reports of reduced "pine-like" aroma intensity (Tangyu et al. 2023). Studies on soy protein isolate (SPI) and pea protein isolate (PPI) also demonstrate hydrophobic interactions dominate the binding of aldehydes (e.g. (E)-2-octenal) and alcohols (e.g. (Z)-2-penten-1-ol) (Ruth and Roozen 2010).

Multi-flavor interactions exhibit four modes, competitive (different compounds compete for the same binding sites), noncompetitive (compounds bind to independent sites without interference), anticompetitive (compounds bind to different sites but cause mutual interference), and salting-out effects (high salt reduces solubility and promotes protein–flavor binding), dictated by molecular structure, protein flexibility, and environmental factors. Competitive interactions are crucial for industrial flavoring applications. Compounds with higher hydrophobicity or stronger hydrogen-bonding can significantly displace others from protein binding sites. For example, delta-non-alactone and furaneol compete with hexanal for binding sites during SPI processing (Schwartz et al. 2022). Such competitive binding results in reduced grassy and beany intensity scores under high-concentration neutral (plant-based meat) or low-concentration acidic (plant protein beverage) conditions and enhanced creamy or fruity notes. The competitive binding between PPI and sulfur-containing flavor compounds is driven by both molecular structure and concentration, cyclic lenthionine binds most strongly due to its hydrophobicity, while concentration-dependent site saturation triggers competitive inhibition (Sun et al. 2025). These interactions alter PPI's conformation, enhancing meaty aromas and surpressing beany flavors. Ethyl caprylate and undecanal bind noncompetitively to shared SPI sites at low concentrations, undecanal and carvone occupy distinct sites, inducing anticompetitive binding via protein unfolding. Cadinene and phellandrene exhibit salting-out effects under high ionic strength, where reduced solubility enhances protein binding (Guo et al. 2019). Similar mechanisms operate in pea proteins, where pyrazines interact with surface hydrophobic cavities via van der Waals forces and hydrogen bonds (Guo et al. 2024). Fluorescence quenching and molecular docking reveal pyrazine derivatives quench pea protein fluorescence through static quenching (formation of stable non-fluorescent complexes) or dynamic quenching (collisional quenching during excitation), and static quenching is supported by stable binding at hydrophobic and polar residues (Guo et al. 2024). A hydrophobicity hierarchy further regulates binding strength: aldehydes surpass ketones and alcohols due to structural complementarity with hydrophobic protein domains, as seen in (E)-2-octenal's strong affinity in pea proteins (Wang and Arntfield 2017). Conversely, low-hydrophobicity esters show weak retention due to water competition (Guo et al. 2019).

The equilibrium dynamics of non-covalent flavor-protein interactions necessitate meticulous formulation strategies in food applications. For example, it's common in the industry to age protein-rich products (1–3 days), which allows flavors to equilibrate between free and bound states, thereby refining sensory profiles post-production (Reineccius 2022). However, the dynamic

nature of these interactions introduces formulation challenges: initial flavor intensity often declines as compounds redistribute into protein matrices, requiring compensatory adjustments to account for equilibrium shifts. While this reversibility enables controlled flavor release during storage and consumption, it can also heighten sensitivity to processing variables (e.g. heating, pH) and matrix components (e.g. salts, solvents). Consequently, optimizing plant-based foods demands tailored approaches to harmonize flavor retention, bioavailability, and stability, balancing the transient benefits of non-covalent binding against its inherent thermodynamic vulnerabilities.

4.2.2 | Covalent Binding of Plant Protein and Flavor Compounds

While non-covalent interactions are generally more frequent, covalent interactions between plant proteins and flavor compounds also play the critical role in flavor retention or loss, in turn significantly affecting food sensory quality and shelf life (Reineccius 2022; Zhang et al. 2021). The sensory consequences of covalent binding are usually assessed through time-intensity sensory curves, where irreversible loss of volatile compounds aligns with decreased perceived aroma intensity over product storage, leading to noticeable flavor fading (Kuesten et al. 2024). The irreversible nature of covalent binding is exemplified by reactions such as sulfhydryl-disulfide interchange. For example, dibutyl-disulfide reacts with PPIs to generate volatile by-products (e.g. 1-butanethiol, a pungent, cabbage-like off-aroma) under reducing conditions (Yang et al. 2023). Such interactions highlight the dynamic role of cysteine residues in flavor-protein adduct formation. In addition, covalent adduct formation can—via Schiff base reactions (aldehydes with lysine), Michael additions (thiols and α,β-unsaturated carbonyls), and disulfide bond cleavage—has been associated with rancid, bitter, or astringent notes in protein foods, and such reactions can be further linked to specific sensory descriptors, including intensified "sulfurous" or "burnt" notes, as evidenced by GC–O analysis combined with trained panel evaluations (Yang, Zhang et al. 2023). Among reactive flavor classes, aldehydes, thiols, and α-diketones (e.g. diacetyl) exhibit the highest covalent reactivity due to their electrophilic functional groups, which target nucleophilic residues like lysine, cysteine, and arginine in proteins (Suppavorasatit and Cadwallader 2012). Beyond direct protein-flavor reactions, other reactive species such as polyphenols, lipid oxidation products, and Maillard intermediates may also form covalent adducts (Ma et al. 2024). Quantifying these reactive interactions alongside sensory thresholds enables prediction of when covalent binding will perceptibly alter flavor quality. Covalent flavor-protein binding varies by chemical class, such as dibutyl disulfide forms irreversible disulfide bonds (resisting denaturation), octanal has dual covalent/non-covalent binding, and benzaldehyde/2-octanone/hexyl acetate rely on reversible interactions (Wang and Arntfield 2016). Environmental factors include thermal processing (accelerates covalent bonds via aldehyde/thiol reactivity), reducing agents (enable disulfide exchange), and salts. Stabilizing salts (e.g. Na_2SO_4) provide structural support for covalent binding, while destabilizing salts (e.g. $Cl_3CCOONa$) expose nucleophilic residues to boost covalent retention (Zhang et al. 2021). Even ambient storage triggers slow covalent reactions, which over time manifest as muted aroma and rancidity in long-shelf-life products. Monitoring flavor changes during storage via sensory panels, combined with targeted GC-MS analysis, is the common approach to quantify the real-world impact of these covalent processes.

In summary, covalent flavor-protein interactions significantly impact sensory quality during flavor formation. They are governed by the reactivity of specific flavor functional groups, the abundance of nucleophilic protein residues, and environmental factors. Integrating physicochemical assays with sensory evaluation, such as GC-O, electronic nose, and relative odor activity value analysis, provides a comprehensive view of how molecular binding translates to consumer-perceived flavor quality. However, covalent binding in plant proteins can selectively deplete key flavor components—where mild binding may help suppress undesirable beany notes, but extensive binding weakens flavor intensity, alters heat-processed flavor profiles, and generates off-flavors through crosslinking or reaction by-products. Therefore, precise control of protein composition and processing conditions is essential to balance sensory authenticity and product stability.

4.3 | Analytical Models for Evaluating Plant Protein-Flavor Interactions

The investigation of plant protein-flavor interactions relies on analytical models that elucidate binding mechanisms, quantify thermodynamic parameters, and predict the behavior under varying conditions.

4.3.1 | Scatchard and Hill Models in Thermodynamic Analysis

Central to these analyses are the Scatchard and Hill equations, which describe linear and cooperative binding behaviors respectively (Kühn et al. 2007). The Scatchard equation, expressed as (Cao et al. 2021; Scatchard 1949):

$$\frac{\upsilon}{[L]} = nK - \upsilon K$$

$$\frac{\upsilon}{n-\upsilon} = K\,[L]$$

where υ represents the moles of flavor compound bound per mole of protein, $[L]$ is the free ligand concentration (mol/L), n denotes the number of binding sites, and K is the binding constant. For enhanced linear regression analysis, the equation can be transformed into a double-reciprocal Klotz plot:

$$\frac{1}{\upsilon} = \frac{1}{n} + \frac{1}{nK\,[L]}$$

Here, $[L]$ is derived from gas chromatography (GC) peak areas calibrated against a standard curve. The bound ligand concentration υ is calculated using:

$$\upsilon = \frac{[L]_t - [L]}{C_p}$$

where $[L]_t$ is the total ligand concentration (free + bound) and C_p is the protein concentration. The parameters n, nK, and K are obtained by fitting experimental data to the Klotz plot. The binding constant K is determined as the ratio nK/n, with standard errors (SEs) estimated using variance equations derived from linear regression analysis:

$$\mathrm{var}\,(n) \approx \frac{\mathrm{SE}_a^2}{a^4}$$

$$\mathrm{var}\,(K) \approx \left(\frac{a}{b}\right)^2 \left(\frac{\mathrm{SE}_a^2}{a^2} + \frac{\mathrm{SE}_b^2}{b^2} - \frac{2 \cdot \mathrm{cov}\,(a,b)}{ab}\right)$$

$$\mathrm{var}\ \ (nK) = \frac{\mathrm{SE}_b^2}{b^4}$$

where ($a = 1/n$) and ($b = 1/nK$) represent the intercept and slope of the Klotz plot, respectively.

For plant proteins with multiple nonequivalent binding sites, cooperative interactions between ligands can arise. This behavior is modeled using the Hill equation (Hill 1910):

$$\frac{1}{\nu} = \frac{1}{n(K\,[L])^h} + \frac{1}{n}$$

where the Hill coefficient h quantifies cooperativity:

($h = 1$): Non-cooperative (independent) binding.

($h > 1$): Positive cooperativity (binding at one site enhances subsequent binding).

($h < 1$): Negative cooperativity (binding reduces affinity for additional ligands).

Where h is the Hill coefficient reflecting interactions between individual binding sites within their population; h is not necessarily an integer. The double reciprocal form of the Hill equation was used to determine the binding parameters (Zha et al. 2021b).

4.3.2 | Thermodynamic Interpretation of Binding Constants

The binding constant K provides critical insights into the thermodynamic driving forces of interactions. The Gibbs free energy (ΔG), enthalpy (ΔH) and entropy (ΔS) are calculated as:

$$\Delta G = -RT \ln K$$

$$\Delta H = \frac{-R\mathrm{d} \ln K}{\mathrm{d}\,(1/T)}$$

$$\Delta S = \frac{\Delta H - \Delta G}{T}$$

Spontaneous binding processes ($\triangle G < 0$) are classified into two mechanistic categories (Mahmoudpour et al. 2020):

1. **Enthalpy-driven processes** ($\triangle H < 0$): Dominated by van der Waals forces and hydrogen bonding, these interactions are favored at lower temperatures.
2. **Entropy-driven processes** ($\triangle S > 0$): Governed by hydrophobic interactions, these are enhanced at elevated temperatures or under conditions that promote protein unfolding (e.g. heat treatment), which exposes hydrophobic binding sites.

4.3.3 | Integrating Equilibrium, Thermodynamics, and Computation

The integration of Scatchard and Hill models with thermodynamic analyses offers a robust framework for elucidating plant protein-flavor interactions. While Scatchard analysis suffices for simple binding systems, the Hill equation becomes indispensable in characterizing cooperative effects at high ligand concentrations. This dual approach not only clarifies binding mechanisms but also guides the optimization of food processing conditions (e.g. temperature, protein modification) to modulate flavor retention. Guo et al. demonstrated the utility of these models in studying flavor binding to SPI. Specifically, linear Scatchard plots ($h = 1$) indicated non-cooperative binding with no conformational changes in SPI at low flavor concentrations (0.04–0.16 mM), whereas higher concentrations (0.4–1.6 mM) exhibited nonlinear Hill behavior ($h > 1$) for citronellol, citronellal, and their esters, signifying positive cooperativity and structural reorganization of SPI (Guo et al. 2020). These findings have shown that ligand saturation can alter protein tertiary structure, exposing hydrophobic domains.

Recent research emphasizes the synergistic use of equilibrium binding studies, thermodynamic profiling, and computational modeling to provide a comprehensive understanding of protein-flavor interactions. For instance, equilibrium binding studies showed that the binding affinity (nK) between PPI and strawberry flavor compounds decreased with rising temperature, with γ-decalactone showing the strongest affinity due to its hydrophobicity (Wongprasert et al. 2024). Thermodynamic parameters indicated spontaneous binding, mainly driven by hydrophobic interactions for vanillin and γ-decalactone, whereas hydrogen bonding and van der Waals forces dominated for furaneol and (Z)-3-hexen-1-ol. Molecular docking supported these findings, accurately predicting binding sites and affinities and revealing key non-covalent interactions (Wongprasert et al. 2024). In addition, molecular dynamics (MD) simulations have been effectively coupled with Scatchard/Hill analyses and isothermal titration calorimetry (ITC) data to visualize conformational changes associated with cooperative binding (ΔH) or hydrophobic site exposure (ΔS) predicted by the models (Barallat-Pérez et al. 2024; Nunes et al. 2020). This integrated workflow confirms model predictions and offers atomic-level insights difficult to obtain experimentally.

Recent advances in predictive analytics can further refine our ability to decode plant protein-flavor interactions by link-

ing molecular architecture to binding behavior. Quantitative structure-sctivity relationship (QSAR) and partial least squares regression models systematically correlate molecular descriptors, such as hydrophobicity, topological indices, and electronic parameters, with experimental binding affinities, enabling high-throughput screening of flavor retention patterns without labor-intensive trials. For example 3D-QSAR analyses in earlier studies highlighted the dual role of hydrophobicity and hydrogen bonding in protein–flavor retention (Tromelin and Guichard 2003). More recently, a QSAR model covering 33 flavor compounds and five plant proteins identified hydrophobicity, electronic properties, and molecular geometry as key drivers of binding (Barallat-Pérez et al. 2024). Such models simplify flavor formulation by predicting optimal ligand-protein pairs without extensive experimentation.

Although studies have developed mathematical models to characterize protein-flavor interactions through diverse methodologies, critical knowledge gaps remain (Guo et al. 2020; Guo et al. 2019). First, existing models oversimplify real food systems, neglecting competitive interactions between proteins, lipids, and carbohydrates. For instance, flavor partitioning in dairy systems revealed hydrophobic dominance, but plant proteins may exhibit distinct synergies (Viry et al. 2018). Second, computational models often ignore solubility limitations or concentration-dependent binding shifts. Validating QSAR predictions is essential in practical protein solutions, particularly across flavor concentration gradients. Finally, comparative studies across diverse protein sources (e.g. pea, lentil, or chickpea) are needed to establish universal binding frameworks (Kumar et al. 2025). Addressing these challenges will refine predictive accuracy and enable tailored flavor design in complex plant protein foods.

5 | Key Factors Affecting Plant Protein-Flavor Interactions

Plant protein-flavor interactions are governed by intrinsic factors (inherent properties of proteins and flavor compounds) and extrinsic factors (processing, pH and ion strength etc.) (Figure 4 and Table 2).

5.1 | Intrinsic Factors Impact on Plant Protein-Flavor Interactions

5.1.1 | Plant Proteins

The structural and physicochemical properties of plant proteins critically shape their interactions with flavor compounds. Protein conformation, surface hydrophobicity, and oligomeric organization collectively govern how flavor molecules bind, stabilize, or release within protein matrices. Plant protein structural rearrangements triggered by hydrophobic flavor penetration or covalent bonding (e.g. aldehydes with lysine residues) expose buried hydrophobic regions and enhance non-covalent interactions, meanwhile occasionally destabilizing folded states (Xiang et al. 2023). Surface hydrophobicity, modulated by oxidative modifications (e.g. malondialdehyde), optimizes flavor retention at low oxidation levels by exposing hydrophobic domains but diminishes at higher oxidation due to aggregation (Wang et al. 2018). Oligomeric proteins, such as pea 7S and 11S globulins, exhibit subunit-specific binding behaviors: 11S globulins favor long-chain aldehydes via larger hydrophobic pockets, while 7S subunits accommodate smaller molecules through structural flexibility (Wang et al. 2018). Synergistic effects between covalent and non-covalent interactions further dictate flavor retention, with long-chain aldehydes like trans-2-undecenal showing enhanced binding via combined mechanisms (Wang et al. 2018). These universal mechanisms manifest differently across protein sources, as detailed in Section 3. Significantly, excessive covalent modification risks protein aggregation, underscoring the need to balance interaction modes. Strategic manipulation of protein matrices guided by advanced structural and thermodynamic analyses, can offer pathways to optimize flavor stability and controlled release in plant protein products, addressing challenges such as off-flavors and inconsistent sensory profiles.

5.1.2 | Flavor Compounds

The molecular properties of flavor compounds, including functional groups, hydrophobicity, chain length, substituent patterns, and structural complexity, significantly shape their interactions with plant proteins (Barallat-Pérez et al. 2023). These characteristics determine the binding affinity, stability, and release dynamics of flavor molecules in protein matrices, directly impacting the sensory quality of plant protein foods (Snel et al. 2023). Functional groups play a pivotal role in defining interaction mechanisms. Aldehyde-containing compounds, such as octanal and furfural, have a higher binding affinity to plant proteins compared to alcohols or ketones (Shen et al. 2020). Similarly, octanal binds more tightly to SPI than 1-octen-3-ol or 2-octanone, as observed in studies about aldehyde reactivity dominated binding kinetics (Zhang et al. 2022). Moreover, furfural has higher affinity for SPI than 5-methylfurfural, which underscores the importance of aldehyde positioning in optimizing steric and electronic compatibility with protein binding sites (Guo et al. 2024). Hydrophobicity, quantified by the octanol-water partition coefficient (LogP), is another critical factor. Compounds with high LogP values exhibit enhanced binding to hydrophobic regions within plant proteins (Wongprasert et al. 2024) (Table 1). For example, thermal processing slightly enhances hexanal-SPI binding by denaturing the protein and exposing hydrophobic regions (Barallat-Pérez et al. 2023). Yet, hydrophobicity alone does not guarantee stable binding at all concentrations. α-pinene and terpinene exhibit salting-out effects at high molar ratios to SPI, reflecting concentration-dependent phase behavior. Chain length and molecular volume further refine binding specificity. Long-chain aldehydes (e.g. (*E*)-2-octenal) bind more strongly to PPI than shorter-chain analogs (e.g. hexanal, 2-penten-1-ol), as their extended hydrophobic structures better align with nonpolar protein pockets (Wang and Arntfield 2014).

Structural complexity, such as branched or cyclic configurations, can also modulate interactions. Subtle structural variations, including substituent position and molecular rigidity, add layers of complexity. Aromatic or cyclic compounds (e.g. furans, pyrazines) often have higher affinities than linear molecules due to π-π stacking or van der Waals interactions with aromatic residues in proteins (Guo et al. 2024). Moreover, pyrazine derivatives with multiple methyl groups (e.g. 2,3,5-trimethylpyrazine)

TABLE 2 | Factors affecting plant protein-flavor interactions and major results.

Factors	Experimental methods	Protein sources	Flavors	Results	Reference
Plant proteins	Headspace GC analysis, partition coefficient K, flavor release dynamics	Soy, pea, canola proteins	2-nonanone, octanal, β-ionone, γ-decalactone	Soy proteins (with glycinin showing higher binding capacities than β-conglycinin), pea proteins, and faba bean proteins exhibit varied flavor-binding behaviors influenced by their structural conformations and amino acid compositions.	(Kun et al. 2017)
	SPME-GC/MS, fluorescence quenching, molecular docking	Soy protein	Octanal, 1-octen-3-ol, 2-octanone	The structural conformation SPI, characterized by increased β-sheet/β-turn content and aggregation-induced hydrophobic exposure, enhances its interaction with volatile flavor compounds, particularly favoring aldehyde groups through hydrogen bonding with residues like His65 and Tyr109 in 7S/11S subunits.	(Zhang, Zhang et al. 2022)
	Thermal reaction of peptides with sugars, flavor compound analysis	Soy, sunflower, rice bran, corn proteins	Pyrazines, pyrazinones, thiazoles, thiophenes	The chain length, amino acid composition, and sequence of plant protein-derived peptides influence their Maillard reaction pathways with reducing sugars, thereby modulating the formation of flavor-active compounds such as pyrazines and enhancing umami and meaty aroma profiles in food systems.	(Fu et al. 2020)
	Pea protein hydrolysate reacted with arabinose and cysteine; sensory and physicochemical evaluation	Pea protein	Furfural, octanal, nonanal, benzaldehyde, 3-methyl-2-thiophene, 2-pentylfuran, 2-pentylpyridine	The Maillard reaction products of pea protein hydrolysate enhanced salty and umami tastes while reducing sodium content in beef flavors, with altered rheological properties promoting flavor release through increased volatile aldehydes, acids, and ketones.	(Zheng et al. 2023)
Flavor substances	Incubated linear aroma compounds with whey, pea, soy, lupin protein isolates and measured binding by headspace GC-MS.	Pea, soy, lupin proteins	Hexanal, 2-hexanone-carbonyl, trans-2-hexenal-unsaturated aldehyde, 1-hexanol-alcohol)	Flavor structure dominated binding; aldehydes and unsaturated compounds showed stronger binding; protein source and fat content had minor effects.	(Barallat-Pérez et al. 2023)
	HS-SPME-GC/MS and static HS-GC. Analyzed binding data using Klotz (double-reciprocal) plots for low concentrations and Hill plots for high concentrations to derive binding constants (K) and binding site numbers.	Soy protein	Citronellal, citronellol, citronellyl propionate, citronellyl acetate	Flavor-SPI binding shifted from linear to cooperative as concentration increased. At low levels, citronellal showed stronger linear binding than citronellol. At high concentrations, binding became nonlinear, with a Hill coefficient ~1.98 for citronellal, indicating positive cooperativity and ~11 binding sites. Citronellal showed the strongest overall affinity, citronellol the weakest.	(Guo et al. 2020)

(Continues)

TABLE 2 | (Continued)

Factors	Experimental methods	Protein sources	Flavors	Results	Reference
	Dual-flavor interactions at high and low concentrations using SPME-GC-MS and static HS-GC	Soy protein	Hexanal, undecanal, carvone	Flavor binding varied by molecular structure and concentration. Both competitive and cooperative interactions observed depending on flavor type.	(Guo et al. 2023)
	Low (0.04–0.16 mM) and high (0.4–1.6 mM) flavor concentrations with SPME-GC-MS + modeling	Soy protein	Citronellal, citronellyl acetate/propionate, citronellol, α-pinene, terpinene	Low concentration: linear binding; High concentration: protein conformational changes and cooperative binding observed. Salting-out effects noted for terpenes.	(Jun et al. 2019)
Processing methods	Post-printing microwave heating (3 power levels) on 3D-printed SPI-carrageenan gel	Soy protein	Vanilla (vanillin), 1-octen-3-ol, maltol, ethyl maltol, eugenal	Microwave promoted the generation of new flavor volatiles and improved flavor intensity, SPI gel with carrageenan enhanced printability and flavor perception.	(Phuhongsung et al. 2020)
	Ultrasonic-thermal synergistic treatment (350 W, 120°C, 150 s)	Soy protein	Hexanal, (E)-2-hexenal, 1-octen-3-ol, (E)-2-nonenal, 2-pentylfuran	Ultrasonic-thermal synergistic treatment alters soy protein isolate's secondary structure (reducing β-sheet, increasing β-turn) and surface hydrophobicity, thereby weakening its binding capacity with volatile flavor compounds through modified hydrophobic interactions and structural flexibility, ultimately reducing beany flavor by 61–95% in key aldehydes and alcohols.	(Kong et al. 2024)
	Heat-treated at 65°C (30 min), 75°C (15 min), 95°C (2–30 min), analyzed by GC-O/MS	Soy protein	Hexanal, 1-octen-3-ol, (E)-2-nonenal, 2-pentylfuran, aldehydes, ketones	Heat-induced structural changes modulated off-flavor release. SPI at 95°C initially increased off-flavors but prolonged treatment (30 min) reduced them via aggregate formation and Maillard products.	(Xu et al. 2024)
	Twin-screw extrusion (160°C, 25 rpm) + GC-MS, GC-O, HPLC	Oat protein	Aldehydes, heterocycles (e.g. hexanal, 2,4,6-nonatrienal), umami/bitter amino acids	Extrusion shifted flavor profile from grassy/green to nutty/pleasant odors; increased aldehydes and umami amino acids; decreased bitterness. Structural transformation to V-type crystal also observed.	(Zhang et al. 2023)
	Grinding for 0–8 h; characterization by GC-MS, FTIR, SEM	Soy protein	Aldehydes, alcohols, acids, ketones, alkanes	Smaller particle size, more irregular morphology, improved solubility/emulsification. Grinding increased total volatiles, suggesting stronger flavor retention and potential release modulation.	(Zhao et al. 2020)
	Ultrasonic versus thermal treatment (200–500 W, 7 min) + HS-SPME-GC-MS	Soy protein	Hexanal, (E)-2-nonenal, (Z)-2-heptenal, (E)-2-hexenal	Ultrasound reduced beany flavors more effectively than thermal. Structural unfolding increased hydrophobic exposure and improved solubility/emulsification. Flavor–structure correlations differed between treatments.	(Kong et al. 2023)

(Continues)

TABLE 2 | (Continued)

Factors	Experimental methods	Protein sources	Flavors	Results	Reference
	Low-moisture extrusion at different energy inputs; analysis via GC-O-MS and microstructure tools	Soy protein	Hexanal, 2-pentylfuran, 1-hexanol	Specific mechanical energy (609 kJ/kg) and temperature (155°C) created porous protein networks with improved flavor retention. Volatile losses modulated by cavity structures and protein-flavor binding dynamics.	(Yang, Ying et al. 2023)
	Fermentation of oat, sunflower seed, pea, and faba milk by 15 LAB strains	Oat/pea/faba/sunflower protein	Hexanal, 1-hexanol, 2-pentylfuran, terpenes	LAB reduced off-flavors (hexanal, alcohols); specific strains (e.g. *S. thermophilus*) produced buttery/cheesy volatiles. Fermentation enhanced aroma spectrum and sensory perception.	(Tangyu et al. 2023)
pH	Binding test of SPI with flavor compounds under pH 3.0, 6.0, 9.0	Soy protein	Hexyl acetate, heptyl acetate, linalool, limonene, geraniol, myrcene	Binding capacity increased with pH; alkaline conditions exposed hydrophobic sites. Limonene/myrcene showed "salting-out" effects.	(Guo, He et al. 2019)
	Binding of 2-hexanone, 2-heptanone, 2-octanone with PPI different pHs	Pea protein	2-hexanone, 2-heptanone, 2-octanone	Binding followed: pH 5 > pH 7 > pH 9 > pH 11 > pH 3.	(Wang & Arntfield, 2015)
	Alkaline extraction at pH 8.5, 9.0, 9.5	Yellow pea protein	Butanol, 1-octen-3-ol, hexanal, 1-octen-3-one, 2-methoxy-3-isopropyl pyrazine	Optimal pH 9.0 led to lowest beany flavor and LOX activity; pH affected solubility and aggregate formation without changing secondary structure.	(Gao et al. 2020)
Ion strength	Binding of 2-hexanone, 2-heptanone, 2-octanone with PPI under NaCl, $CaCl_2$.	Pea protein	2-hexanone, 2-heptanone, 2-octanone	NaCl (0.25–1 M) enhanced flavor binding; anions' lyotropic series influenced results. 2-octanone showed stronger binding.	(Wang and Arntfield 2015)
	Rheological measurements, differential scanning calorimetry, and chemical treatments (salts, denaturants, reducing agents)	Pea protein	/	Sodium salts with chaotropic anions (e.g. SCN^-) may weaken hydrophobic interactions and disrupt native conformations and then modify flavor-binding sites, whereas kosmotropic anions (e.g. SO_4^{2-}) tend to stabilize compact structures and potentially limit flavor accessibility	(Sun and Arntfield 2012)
	Dynamic rheology, light microscopy, and differential scanning calorimetry, under varying salt concentrations (NaCl, $CaCl_2$, NaSCN, Na_2SO_4).	Faba bean protein	/	Anions like Cl^- (mid-series) may subtly alter protein flexibility compared to strongly stabilizing (F^-) or destabilizing (SCN^-) ions, thereby diversifying flavor adsorption dynamics	(Arntfield et al. 1990)

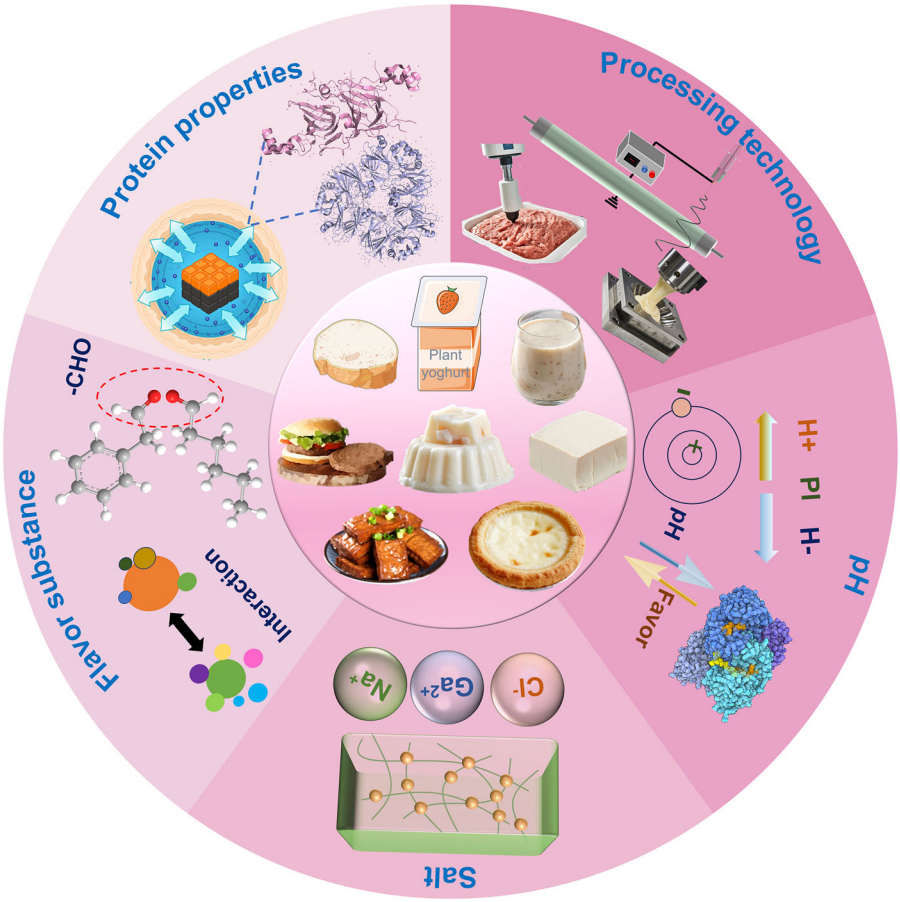


FIGURE 4 | Factors that influence the plant protein-flavor interactions, including plant protein properties, flavor compounds, processing methods, pH and salts type/ion strength.

bind more strongly to PPI than simpler analogs (e.g. 2-methylpyrazine), due to greater hydrophobic surface area and steric stabilization within binding pockets (Guo et al. 2024).

Collectively, the structural and physicochemical diversity of plant proteins and flavor compounds creates a multifaceted interaction landscape. These insights guide the design of plant protein foods with optimized flavor profiles, emphasizing the selection of hydrophobic and structurally complex molecules for stable flavor retention. Future studies should explore how stereochemical variations, dynamic binding processes, and competitive displacement in multicomponent systems further refine flavor delivery in protein matrices.

5.2 | Extrinsic Factors Impact on Plant Protein-Flavor Interactions

Extrinsic factors, processing methods, pH, and ionic strength, play crucial roles in shaping protein-flavor interactions. These factors are relevant not only during protein isolation, determining the structural and sensory characteristics of protein ingredients, but also further influence flavor retention and release in plant-based products in processing.

5.2.1 | Processing Methods

5.2.1.1 | Ultrasonic Treatment. Ultrasonic treatment has emerged as a promising non-thermal technology, leveraging its unique physical effects, including high shear forces, turbulence, and cavitation, to alter protein structures and flavor interactions. At the isolation stage, ultrasound enhances protein yield and reduces lipid-derived volatiles, while in product formulation it modifies protein conformation and flavor retention (Hussain et al. 2023; Mehta et al. 2022). Studies demonstrate that ultrasonic energy disrupts intermolecular forces in plant proteins, such as hydrogen bonds, disulfide bonds, and hydrophobic interactions, leading to subunit dissociation and conformational changes. This process generates partially unfolded or moderately denatured protein structures, which expose hydrophobic regions and create binding sites (Zhang et al. 2021). These structural modifications enhance molecular flexibility and improve functional properties (e.g. solubility, emulsification, and foaming capacity), thereby influencing flavor retention through steric hindrance or weak interactions (Liao et al. 2022). Compared to conventional thermal treatment, ultrasound selectively reduces α-helix content while increasing β-sheet, β-turn, and random coil structures, promoting protein unfolding (Kong et al. 2023). Thermal processing primarily affects the polarity surrounding tryptophan residues, altering flavor-binding properties (Zhao et al. 2021). Furthermore, ultrasonic-thermal synergistic processing applied to tofu gels can intensify structural changes, increasing sur-

face hydrophobicity and fluorescence intensity while reducing flavor-binding capacity. This approach significantly decreases the concentrations of key volatile compounds, such as hexanal, (*E*)-2-hexenal, and 1-octen-3-ol, while eliminating (*E*)-2-nonenal and 2-pentylfuran (Zhang et al. 2022). It is worth noting that ultrasound generated free radicals, which accelerated lipid oxidation and modified volatile profiles and consequently reduced undesirable beany flavor compounds. To balance techno-functional enhancements with sensory quality, parameter optimization (e.g. power density, duration, and salt concentration) is critical to mitigate oxidative side effects while maximizing flavor retention.

5.2.1.2 | Extrusion processing. Extrusion processing, as a high-efficiency thermomechanical technology, profoundly alters the structure-function relationships of plant proteins and their interactions with flavor compounds through synergistic effects of high temperature, high pressure, and intense shear forces (Kadam et al. 2025). Studies reveal that extrusion transforms protein structure from a compact texture into an irregular, spongy matrix with V-type crystal formation. This reorganization triggers dynamic changes in volatile compounds, leading to increased levels of aldehydes (e.g. hexanal) and heterocyclic compounds (e.g. pyrazines) after extrusion (Chen et al. 2023). Consequently, the extrusion processing of oat flour induces a flavor transition from the raw oat green odors to nutty, grassy, and bean-like odors driven by thermal and shear effects. Additionally, the process elevates umami amino acids (e.g. glutamic acid) while reducing bitter amino acids (e.g. leucine), enhancing the overall flavor (Zhang et al. 2023). Extrusion parameters, such as mechanical energy and texturization temperature, critically regulate the microstructure and flavor retention of plant proteins. During extrusion of plant-based meat analogs, soybean proteins undergo structural rearrangements that expose hydrophobic regions, hereby promoting hydrophobic interactions with beany flavor compounds (e.g. hexanal and (*E*)-2-nonenal) and facilitating their physical entrapment within a uniform, dense air chamber structure of high porosity (Yang et al. 2023). Moreover, high extrusion temperatures exaggerate lipid oxidation in raw plant materials or uncontrolled Maillard reactions (producing bitter peptides), thermal degradation releases amino acids that undergo deamination and decarboxylation, forming aldehydes and sulfides (Samard et al. 2019). Therefore, it is necessary for the process optimization (e.g. temperature, moisture control, screw configuration) to balance functional enhancement and flavor stability. Structural characterization further indicates that a reduction in α-helix and β-sheet content diminishes molecular compactness, exposing additional hydrophobic regions that enhance interactions with flavor molecules (Sun et al. 2022). Collectively, these interrelated phenomena highlight the critical influence of extrusion processing on the structural reorganization of plant proteins and then the consequent change of flavor attributes in plant protein products.

5.2.1.3 | Other treatments. Microwave and ultrafine grinding represent two distinct approaches in modulating plant protein-flavor interactions through physicochemical modifications. Microwave treatment, when applied as a post-processing technology in protein-flavor systems, leverages rapid thermal energy to reconfigure structural networks, enabling controlled flavor release while maintaining protein functionality. For example, in 4D-printed soy protein-carrageenan gels, optimized microwave power facilitates shape transformation and stabilizes volatile flavor compounds (Phuhongsung et al. 2020). Ultrafine grinding relies on prolonged mechanical shear to alter protein secondary structures, increasing α-helix, β-sheet and random coil content, and enhancing surface properties, thereby improving solubility and emulsifying capacity (Zhao et al. 2020). Extended grinding duration can increase total volatile compounds, primarily aldehydes and alcohols, by exposing flavor precursors, while excessive processing risks oxidative flavor degradation. Both methods demonstrate how thermal-mechanical (microwave) and purely mechanical (grinding) forces differentially influence protein-flavor binding and release dynamics, providing foundational insights for integrating additional processing strategies in flavor optimization.

Collectively, diverse processing technologies for PBPFs can modulate protein structures and thereby influence flavor retention and release through distinct physicochemical pathways (Chen et al. 2025). While these methods enhance functional properties, they also introduce challenges related to oxidative degradation and flavor stability. Future research should focus on the synergistic integration of multiple processing techniques, advanced characterization of dynamic protein-flavor interactions, and the optimization of parameters using data-driven approaches. Additionally, sustainable and precision-tailored processing strategies will be critical for developing next-generation plant-based foods with superior sensory and nutritional profiles.

5.2.2 | pH

The pH environment critically governs plant protein-flavor interactions by altering protein conformation, surface charge, and enzymatic activity. For instance, studies on PPI extraction reveal that lipoxygenase activity is lowest at pH 9.0, thereby minimizing the formation of beany flavor compounds such as hexanal, 1-octen-3-ol, and 2-methoxy-3-isopropyl pyrazine (Gao et al. 2020). Similarly, research on SPI shows pH-induced structural changes increase protein flexibility and exposure of hydrophobic regions enhancing binding with esters (e.g. hexyl acetate) and alcohols (e.g. linalool) at higher pH, while hydrophobic terpenes like limonene exhibit a "salting-out" effect as binding weakens (Guo et al. 2019). Flavor retention typically peaks near the isoelectric point (pH 4–5), where protein aggregation promotes hydrophobic interactions, but decreases under alkaline conditions (pH 9–11) as solubility increases and binding with hydrophobic volatiles weakens (Cui et al. 2020). In addition, pH regulates the net charge of plant proteins relative to the isoelectric point (pI): limited binding occurs near the pI due to low solubility and reduced charge, while deviations from the pI enhance electrostatic interactions, which may be moderated by ionic shielding (Kuijpers et al. 2025). These effects arise from pH-dependent alterations in electrostatic and hydrophobic interactions, as extreme pH conditions disrupt native conformations and alter binding sites (Weel et al. 2003). Importantly, the progressive increase in flavor retention from pH 3.0 to 9.0 due to greater hydrophobic site availability, indicating that protein unfolding at alkaline pH facilitates flavor entrapment, whereas acidic conditions may promote electrostatic repulsion or favor hydrogen bonding, depending

on flavor polarity, which can be leveraged in protein-based beverage formulation (Guo et al. 2019). These findings underscore the interplay between pH-mediated protein flexibility, surface hydrophobicity, and flavor release kinetics, and highlight the importance of precise pH control to avoid irreversible protein aggregation or flavor degradation.

5.2.3 | Ion Strength

The ionic environment, particularly salt type and concentration, plays a pivotal role in plant protein–flavor interactions by altering protein conformation and molecular forces. Salts modulate protein structure through electrostatic shielding and hydrophobic effects governed by the lyotropic (Hofmeister) series, where different anions can either destabilize or stabilize protein folding. For example, sodium salts with chaotropic anions (e.g. SCN^-) may weaken hydrophobic interactions and disrupt native conformations and then modify flavor-binding sites, whereas kosmotropic anions (e.g. SO_4^{2-}) tend to stabilize compact structures and potentially limit flavor accessibility (Sun and Arntfield 2012). Moreover, salt type also influences plant protein gelation and flavor interactions, as evidenced by NaCl, KCl, and $CaCl_2$ producing distinct elastic properties in carrageenan gels, and divalent cations like Mg^{2+} and Ca^{2+} enhancing flavor compound binding through charge bridging or structural stabilization (Souza et al. 2023). In plant protein-based systems, salt addition can simultaneously screen surface charges, therefore reducing electrostatic repulsion between proteins and flavor compounds, and perturb water structure to amplify hydrophobic interactions. For instance, moderate NaCl concentration (0.251 M) may promote protein unfolding and expose hydrophobic sites that enhance nonpolar flavor binding, while high salt levels ($CaCl_2$ ≥0.25 M, NaCl >1 M) might induce protein aggregation that occludes binding sites, leading to variable effects on flavor retention through shifts in electrostatic repulsion, hydrogen bonding, and hydrophobic patch exposure (Wang and Arntfield 2015). Furthermore, the Hofmeister effect adds complexity to these interactions; anions like Cl^- (mid-series) may subtly alter protein flexibility compared to strongly stabilizing (F^-) or destabilizing (SCN^-) ions, thereby diversifying flavor adsorption dynamics (Arntfield et al. 1990). These dual electrostatic and hydrophobic mechanisms highlight the need to study salt-specific effects on plant protein matrices to optimize sensory quality, with applications in cell-cultured meat scaffolds—affecting 3D gel or electrospun fiber formation—and plant-based cheese, where salt–protein interactions guide flavor release.

6 | The Opportunities and Challenges of Plant Protein-Flavor Interactions in Food Industry

The interactions of plant proteins and flavor compounds presents both opportunities and challenges in food product development. As functional flavor carriers, plant proteins bind and stabilize key aroma molecules to enable flavor delivery in plant protein products. Conversely, this binding affinity may cause flavor masking or undesired retention, requiring meticulous formulation and processing consideration (Qian et al. 2025; Wongprasert et al. 2024). This dual role highlights both their potential in enhancing product quality and the technical barriers that must be overcome.

6.1 | Opportunities of Plant Protein-Flavor Interactions

The interaction between plant proteins and flavor compounds offers multifaceted functional benefits in the food industry, driven by dynamic molecular-level binding and release mechanisms. Plant proteins utilize their structural features, such as hydrophobic domains and hierarchical porous networks, to efficiently capture flavor molecules via physical adsorption or chemical bonding (Bi et al. 2020). These mechanisms allow for controlled release during processing, storage, and consumption, thereby enhancing sensory persistence. For instance, pea protein-strawberry flavoring complexes can be applicable in flavor formulation for plant-based protein aqueous foods, and almond protein-vanillin nanofibers used as the thermostable delivery system for flavor (Wongprasert et al. 2024). Additionally, hydrolyzed peptides interacting with Maillard reaction compounds contribute to roasted aromas and textural improvements in plant-based analogs (Barallat-Pérez et al. 2023; Sun et al. 2023). Such interactions not only support clean-label innovation by reducing synthetic additives but also improve oxidative stability and bioavailability of certain flavor precursors (Jin et al. 2023).

6.2 | Challenges of Plant Protein-Flavor Interactions

Despite their benefits, plant protein-flavor interactions also lead to several challenges that compromise sensory quality, with the persistence of characteristic beany notes, which largely arise from lipid oxidation catalyzed by endogenous lipoxygenase (LOX) (Roland et al. 2017). Limited solubility of proteins such as PPI, together with residual polar lipids, often generates grassy or rancid undertones that reduce consumer acceptance (Li et al. 2024). Additionally, strong binding affinities may trap desirable aroma compounds, leading to unbalanced flavor profiles and masking of target notes. Non-volatile compounds such as flavonoids or phenolic acids can further intensify these problems by stabilizing volatile off-flavor precursors (Roland et al. 2017). Moreover, covalent binding between proteins and volatiles may distort oxidation assessments, since common methods (e.g. TBARS, hexanal quantification) often underestimate the extent of deterioration (Abeyrathne et al. 2021), complicating both shelf-life management and targeted interventions (Reineccius 2022). Thus, the challenge lies less in understanding the chemical mechanisms—which are well established—and more in translating this knowledge into effective sensory optimization and reliable quality control.

6.3 | Strategies to Modulate Flavors in Plant-Based Protein Foods

As mentioned, the impact of plant protein-flavor interactions on off-flavor generation, the following sections will systematically examine flavor modulation approaches (as illustrated in Figure 5).

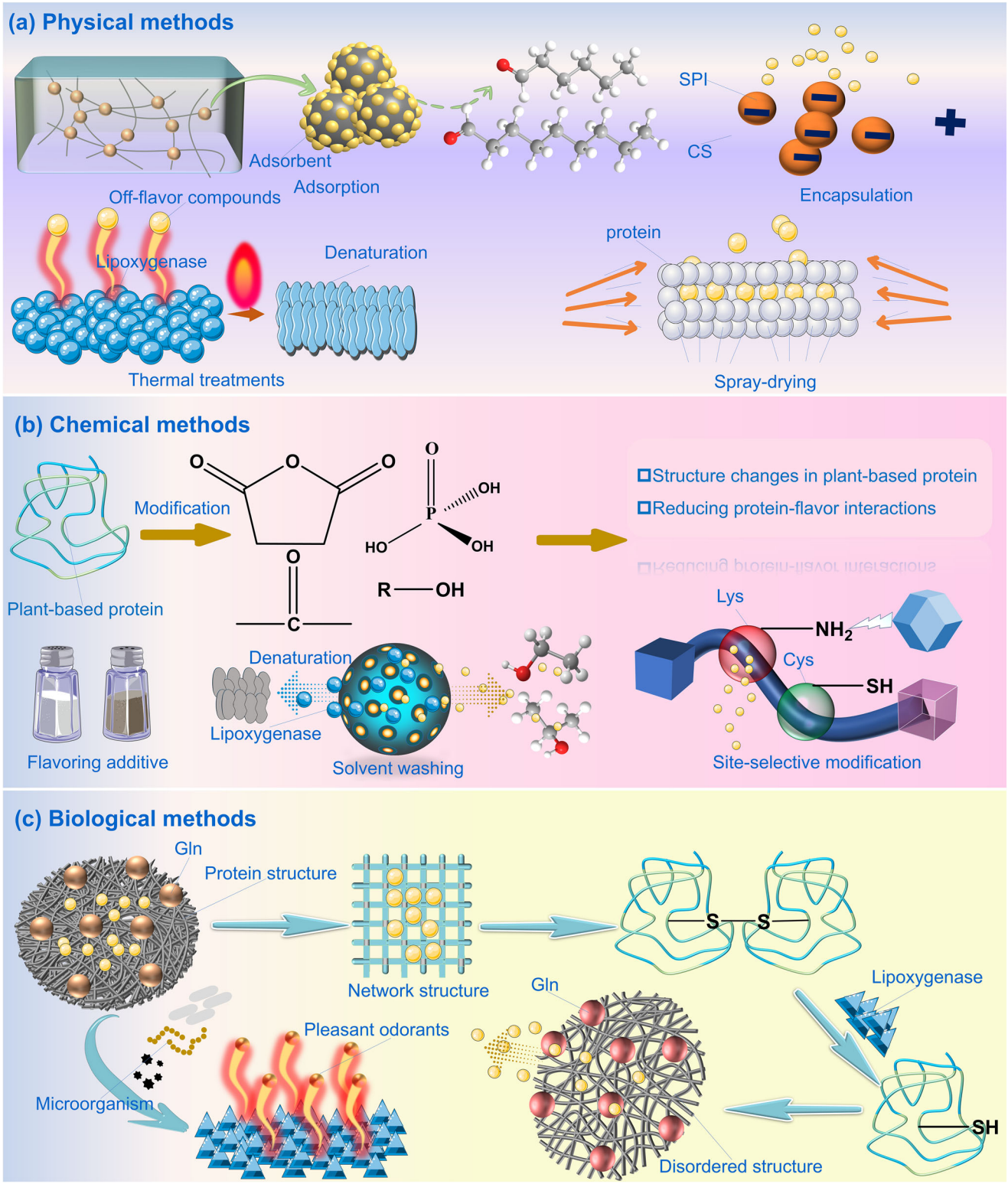


FIGURE 5 | Strategies to modulate flavors of plant-based protein foods: (A) physical methods, (B) chemical methods, and (C) biological methods.

6.3.1 | Physical Methods

Adsorption and encapsulation techniques have emerged as effective physical approaches to address off-flavors in plant-based proteins. Adsorbents such as Amberlite-XAD16N, Sepabeads-SP207, and Diaion-HP20 reduce aldehydes and alcohols in lentil protein isolates by 32–41%, associated with a reduction in beany odor in the deodorization step (Guldiken et al. 2021). β-cyclodextrin further enhances flavor removal by forming inclusion complexes with hydrophobic compounds; when combined with phospholipase A_2, it can decrease key beany volatiles like benzaldehyde and hexanal (Guldiken et al. 2021). Encapsulation strategies, such as SPI/chitosan complex coacervates and Pickering emulsions, leverage electrostatic interactions and hydrogen bonding

to entrap volatile compounds, significantly mitigating flavor loss of PBMA during thermal processing (Li et al. 2024; Zeng et al. 2024). These methods rely on modifying interfacial properties or molecular interactions to stabilize flavor compounds within protein matrices.

Spray-drying and thermal treatments offer complementary solutions. Spray-drying with amorphous carriers (e.g. gum arabic or maltodextrin) disrupts β-sheet conformations in PPI, improving solubility and reducing off-flavor compounds like 1-octen-3-ol by 2-3-fold, which corresponded to weakened earthy/musty perception (Lan et al. 2019). Thermal treatments (75-95°C) induce protein unfolding, exposing hydrophobic regions that bind off-flavors; however, prolonged heating risks Maillard reactions or aggregation, necessitating precise temperature control (Xu et al. 2024). Supercritical carbon dioxide (SC-CO_2) utilizes a dual-regulation mechanism based on density and diffusivity: high pressure for cutting off the source of off-flavors in soybean flour, while low pressure with high diffusivity enables targeted removal of volatile molecules (Kaur and Ubeyitogullari 2024). This is further enhanced by structural disruption, ultimately achieving efficient elimination of beany odor compounds (reducing concentration to 9% of that in the untreated sample). There is also research utilizing high pressure (200 MPa) to alter the conformation of SPI, facilitating its efficient hydrolysis by Corolase PP (Guan et al. 2024). This process dynamically regulates the degradation pathway of bitter peptides while synergistically enhancing emulsion stability and antioxidant activity. Ultimately, it achieves significant bitterness reduction and flavor optimization.

In practice, physical methods such as spray-drying and extrusion are already used in large-scale production of plant-based meats and protein powders (Ong et al. 2025). Challenges such as oxidation during spray-drying or temperature-dependent flavor release highlight the need for integrated antioxidant strategies and process optimization to balance functionality and sensory quality in industrial applications. Therefore, future research should focus on improving carrier stability, optimizing processing parameters, and developing scalable hybrid approaches that ensure flavor retention.

6.3.2 | Chemical Methods

Chemical modification serves as an effective strategy to address undesirable flavors in plant-based protein products by altering protein-flavor interactions and enhancing functional properties (Wang et al. 2021). Acylation, phosphorylation, amidation, esterification, and non-enzymatic glycation are widely used to modulate protein structure and flavor binding affinities (Zha et al. 2021b). For instance, acylation via acetylation or succinylation modifies the isoelectric point and charge distribution of proteins, reducing hydrophobic interactions with flavor compounds, thereby mitigating beany off-flavors (Zha et al. 2021b). Succinylation, in particular, induces protein unfolding and charge repulsion, diminishing flavor retention (Wang et al. 2018). Similarly, enzymatic deamination using protein-glutaminase weakens covalent or hydrophobic bonds between proteins and flavor molecules, shifting interactions to weaker van der Waals forces or hydrogen bonds, which reduced aldehydic harshness in liquid plant-based foods such as plant milks (Suppavorasatit and Cadwallader 2012). In heat-processed plant protein products, amidation and esterification chemically modify acidic amino acid residues (Asp/Glu) to modulate protein functionality and flavor binding through structural unfolding and charge modification, whereas phosphorylation introduces phosphoryl groups, enhancing heat stability while potentially reducing water solubility. However, these methods have potential issues regarding the toxicity of reagents used and the lack of data on their safe usage in the food industry (Zha et al. 2021a). Nonenzymatic glycation through Maillard reaction not only improves solubility and antioxidant activity but also reduces off-flavors by generating new aroma compounds, relating to sweet and roasted flavors (Zha et al. 2021a).

Additionally, site-selective chemical modifications enable precise control over flavor-binding by targeting specific amino acid residues or protein termini. For example, modifying lysine residues with electrophilic reagents or leveraging the unique reactivity of N-/C-termini can reduce off-flavor retention while maintaining structural integrity in plant-based beverages (Zha et al. 2021b). Solvent-assisted extraction further complements chemical strategies. Alcohol washing (e.g. ethanol/isopropanol) effectively removes lipid-derived off-flavors in PPI by leveraging solvent polarity to solubilize volatile compounds, achieving up to 94% reduction in total volatile content (Wang et al. 2020). Moreover, in the preparation of SPI, introducing furaneol with thermal processing during protein resolubilization competitively binds off-flavors (e.g. hexanal, (*E*)-2-nonenal) from binding sites. It is evident from molecular docking that furaneol can accelerate their release, effectively reducing grassy, beany and oil oxidation odors as validated by the sensory panel (Xu et al. 2025). Additive masking enhances sensory profiles through incorporation of natural spices (e.g. garlic, pepper), Maillard reaction products (e.g. sulfur-containing heterocyclics), or plant extracts (e.g. vanilla, curcumin) (Nagassa et al. 2024). For instance, SPI complexes with raspberry juice shift flavor profiles from "beany" to "citrus," demonstrating synergistic flavor modulation (Kelemen et al. 2022). Recent studies on hybrid meat-mimicking analogs (HMMAs) further highlight chemical and structural modifications: polysaccharides such as carrageenan enhance Maillard reactivity through carbonyl groups (Qiu et al. 2025). However, the dense matrix networks formed during extrusion hinder volatile diffusion, necessitating yeast extract to offset flavor loss, however the long-term stability of flavor retention remains unresolved due to dynamic protein-network interactions (Jiang et al. 2025).

Overall, only mild chemical approaches such as ethanol washing and natural flavor masking are used commercially, as more complex modifications face regulatory and clean-label constraints. Future research should focus on integrated chemical approaches that offer a multifaceted toolkit to tailor plant protein functionality and flavor profiles, but still with clean labels.

6.3.3 | Biological Methods

Biological methods, particularly enzymatic modification and microbial fermentation, have emerged as sustainable and pre-

cise strategies to mitigate off-flavors in plant protein foods. Enzymatic deamidation, catalyzed by glutaminase, modifies glutamine residues into glutamic acid, altering protein conformation to weaken hydrophobic interactions with aldehydes and shift binding to weaker van der Waals forces, thereby facilitating flavor release (Xiang et al. 2023). For instance, protein-glutaminase treatment reduced hexanal and 2-pentylfuran in SPI by 80.2% and 95.2% respectively, and then lowering beany intensity for the high-moisture extrudates (Li et al. 2024). Similarly, proteolysis via alcalase disrupts hydrophobic domains, releasing trapped esters and ketones while enhancing aldehyde retention due to exposed reactive groups (e.g. lysine), which could weak grassy notes and potentially facilitate nutty-like odors. Transglutaminase (TGase)-mediated cross-linking improves gelation and thermal stability of plant proteins, indirectly modulating flavor release by altering matrix viscosity and diffusion barriers (Zha et al. 2021b). Microbial fermentation offers dual benefits by degrading off-flavor compounds and generating desirable flavors. Lactic acid bacteria and yeast strains, such as *Lactobacillus plantarum* and *Saccharomyces cerevisiae*, enzymatically convert hexanal and decadienal into less odorous alcohols (hexanol, octanol) via alcohol dehydrogenase or metabolize proteins and carbohydrates into flavor-enhancing metabolites (e.g. diacetyl, lactic acid), thereby replacing grassy-green notes with softer fruity and creamy notes (Xiang et al. 2023). *Streptococcus thermophilus* and *Leuconostoc mesenteroides* in plant-based protein products, produce buttery (2,3-butanedione) or cheesy (branched-chain fatty acids) odors, masking residual off-flavors (Xiang et al. 2023). Fermentation of pea milk with *Lactobacillus johnsonii* reduced grassy odors by 92.6 % and elevated (-)-mytenol by 50-fold, leading to floral and woody aroma profile validated by sensory tests (Tangyu et al. 2023). Proteomic analyses of *Bacillus subtilis*-fermented soymilk further linked flavor modulation to amino acid metabolism, where threonine pathways generated pyrazines, generating roasted notes (Hu et al. 2024).

Recently, numerous studies have demonstrated that hybrid approaches integrating biological and chemical or physical methods demonstrate synergistic effects, which could achieve enhanced outcomes that are otherwise unattainable through single method. For example, combining enzymatic hydrolysis (alcalase) with chemical acylation (acetylation/succinylation) can selectively modulate flavor retention: acetylation masks $-NH_2$ and —OH groups to reduce binding, and succinylation introduces negative charges to weaken hydrophobic interactions. Concurrently, hydrolysis releases esters but increases disulfide retention via exposed –SH groups, necessitating balanced modifications for optimal flavor profiles (Shi et al. 2021). Physical-biochemical hybrids, such as TGase-crosslinked or heat-induced gels, regulate flavor release through matrix design. Especially, TGase-induced plant protein gels with higher rigidity slow the diffusion of nonpolar flavors, whereas softer heat-induced gels enhance aroma perception by facilitating molecular mobility, which can be applied in low-fat or reduced-salt plant-based foods to compensate for flavor loss (McClements 2017; Pu et al. 2019). In addition, bioengineered additives like *Pichia*-derived porcine myoglobin (PMb) exemplify targeted flavor modulation in plant meat analogues, 0.5% PMb in soy-wheat blends suppresses aldehydes significantly while elevating ketones and pyrazines, bringing roasted aroma via volatile synergy and suppressing beany odors validated by sensory panel (Qian et al. 2025).

Biological methods highlight the potential of tailored enzymatic treatments, strain-specific fermentation, and matrix engineering to mitigate off-flavor, which already used commercially in plant-based yogurts, burgers, and cheese analogs, making biological approaches among the most industrially viable. However, challenges such as residual bitterness from proteolysis, strain compatibility and scalability require further optimization to meet industrial demands for clean-label and appealing-sensory attributes (Zha et al. 2021b). Future advance can focus on integrating hybrid techniques (e.g. AI-enabled bio–physicochemical metabolic design) to synergistically disrupt off-flavor formation, release, and perception (Li et al. 2024).

7 | Conclusion and Perspectives

The interactions between plant proteins and flavor compounds in PBPFs vary significantly across protein sources. Legume proteins exhibit strong hydrophobic and covalent interactions with aldehydes and sulfur-containing compounds, while cereal/pseudocereal proteins engage in moderate, reversible binding via hydrogen bonds and electrostatic forces. Nut and seed proteins demonstrate lipid-modulated flavor release, and emerging sources like algae present unique challenges due to structural complexities. Significantly, not all the protein-flavor interactions in plant-based foods have been identified. Even with identical proteins and flavor molecules, differences in the physical state of the protein matrix, such as liquid versus gel, can lead to markedly different flavor retention and release behaviors. Gel structures restrict flavor mobility while emulsions facilitate faster release, this structural heterogeneity complicates the standardization and comparison of findings.

The perception of flavors in PBPFs is a dynamic interplay between physiological processes and physicochemical interactions, shaped by olfactory pathways, salivary activity and taste perception. Mechanistically, the interactions between plant proteins and flavor compounds are governed by reversible non-covalent forces and irreversible covalent bonds. Prior studies have employed diverse analytical methodologies, such as ITC, surface plasmon resonance (SPR), fluorescence quenching, and GC-MS, to investigate these interactions. However, these techniques vary in sensitivity, resolution, and applicability, contributing to challenges in result comparability. Analytical models such as the Scatchard equation and Hill model could be employed to quantify the binding thermodynamics. The Scatchard model assumes independent and equivalent binding sites, thus overlooking cooperative interactions, while the Hill model incorporates cooperativity but presumes site homogeneity-both simplifications can limit their ability to fully represent complex protein-flavor systems.

Intrinsic factors like protein conformation, surface hydrophobicity, and flavor compound polarity dictate binding specificity of plant protein-flavor interactions, while extrinsic factors, processing conditions, pH and ionic strength, dynamically modulate interactions. In the plant protein foods, these interactions present dual outcomes: controlled binding enhances flavor stability, but

irreversible associations often result in off-flavors. Moreover, inconsistencies in results across studies often arise due to differences in matrix formats, protein extraction and isolation methods. These experimental divergences limit the cross-comparability of findings and hinder consensus in binding behavior.

Based on this, multifaceted addressing strategies are employed, including physical methods (encapsulation, spray-drying), chemical methods (structural modification, Maillard reaction masking, solvent-assisted extraction), biological methods (enzymatic hydrolysis, fermentation), and hybrid techniques. However, these strategies also present limitations: physical methods may lead to low flavor retention during storage or processing; chemical and biological modifications can inadvertently alter nutritional quality or introduce off-target effects. Additionally, the scalability and cost-effectiveness of hybrid techniques remain challenges for industrial application.

Future research should prioritize computational models (e.g. molecular docking, machine learning) to predict interaction between specific protein domains and flavor molecules. Analytical advancements should hinge on more precision tools like AI-driven QSAR models to predict binding dynamics. In this context, the behavior and underlying mechanisms of characteristic key flavor compounds across various protein matrices deserve particular attention, as matrix-specific interactions may significantly influence flavor perception and delivery. In addition, digital oral processing dynamics, simulating mastication forces and lingual shear, could also predict flavor release kinetics. Moreover, advanced technologies are also required for protein-flavor modulation, encapsulation systems (e.g. double emulsions with alginate-chitosan matrices) might enable pH-triggered release of lipid-soluble flavors during oral processing. Pulsed electric fields could selectively disrupt protein-flavor complexes while preserving nutritional integrity. And emerging tools like CRISPR-Cas9-mediated protein editing may enable targeted modifications of amino acid residues to reduce covalent binding with off-flavor compounds for flavor modulation. Furthermore, 4D printing of anisotropic plant protein structures could mimic meat fibrous texture and release flavor orderly with embedding flavor reservoirs.

The authors recommend the integration of "flavoromics" with sustainable processing and structural bioengineering approaches to bridge gaps in flavor acceptance in plant-based products. Equally, aligning these innovations with clean label principles, minimizing artificial additives, simplifying ingredient lists, and enhancing naturality, will be pivotal in earning consumer trust. In addition, systematic sensory validation is essential to complement computational tools by explicitly linking molecular predictions with perceptual outcomes such as thresholds, hedonic scores, and retronasal perception. Combining sensory tests and consumer evaluations will ensures that mechanistic insights are effectively translated into products that deliver flavor quality consistent with consumer expectations. Through harmonizing molecular insights, protein topology optimization, green technologies, and sensory validation, future research can position plant protein foods as flavorful, nutritious, and sustainable staples in global diets.

Author Contributions

Xinran Dai: investigation, visualization, writing – original draft, writing – review and editing. **Jiaping Zhang**: writing – original draft. **Zhaoshi Chen**: writing – original draft, writing – review and editing. **Muhammad Awais**: writing – review and editing. **Bei Fan**: supervision, funding acquisition. **Marie-Laure Fauconnier**: conceptualization, writing – review and editing. **Liya Liu**: conceptualization, funding acquisition, writing – review and editing. **Fengzhong Wang**: funding acquisition, supervision.

Acknowledgments

The work was supported by the National Key Research and Development Program of China (2023YFE0107000), National Key Research and Development Program of China (2022YFF1102100), and Xinjiang Uygur Autonomous Region "Tianchi Talent" Training Plan Project (2023, 2025).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

No data was used for the research described in the article.

References

Abeyrathne, E., K. Nam, and D. U. Ahn. 2021. "Analytical Methods for Lipid Oxidation and Antioxidant Capacity in Food Systems." *Antioxidants* 10, no. 10: 1587. http://doi.org/10.3390/antiox10101587.

Akkad, R., E. Kharraz, J. Han, J. D. House, and J. M. Curtis. 2019. "Characterisation of the Volatile Flavour Compounds in Low and High Tannin Faba Beans (Vicia faba var. minor) Grown in Alberta, Canada." *Food Research International* 120: 285–294. http://doi.org/10.1016/j.foodres.2019.02.044.

Arntfield, S. D., E. D. Murray, and M. A. H. Ismond. 1990. "Influence of Salts on the Microstructural and Rheological Properties of Heat-Induced Protein Networks From Ovalbumin and Vicilin." *Journal of Agricultural and Food Chemistry* 28, no. 6: 1335–1343. http://doi.org/10.1021/jf00096a008.

Bader, S., M. Czerny, P. Eisner, and A. Buettner. 2009. "Characterisation of Odour-Active Compounds in Lupin Flour." *Journal of the Science of Food and Agriculture* 89, no. 14: 2421–2427. http://doi.org/10.1002/jsfa.3739.

Bailliere, J., D. Laureys, P. Vermeir, et al. 2022. "10 Unmalted Alternative Cereals and Pseudocereals: A Comparative Analysis of Their Characteristics Relevant to the Brewing Process." *Journal of Cereal Science* 106: 103482. http://doi.org/10.1016/j.jcs.2022.103482.

Barallat-Pérez, C., B. Hollebrands, H. G. Janssen, et al. 2024. "Development of a QSAR Model to Predict Protein-Flavor Binding in Protein-Rich Food Systems." *Food Chemistry* 467: 142268.

Barallat-Pérez, C., H. G. Janssen, S. Martins, V. Fogliano, and T. Oliviero. 2023. "Unraveling the Role of Flavor Structure and Physicochemical Properties in the Binding Phenomenon With Commercial Food Protein Isolates." *Journal of Agricultural and Food Chemistry* 71, no. 50: 20274–20284. http://doi.org/10.1021/acs.jafc.3c05991.

Bi, S., X. X. Xu, D. S. Luo, et al. 2020. "Characterization of Key Aroma Compounds in Raw and Roasted Peas (Pisum sativum L.) by Application of Instrumental and Sensory Techniques." *Journal of Agricultural and Food Chemistry* 68, no. 9: 2718–2727. http://doi.org/10.1021/acs.jafc.9b07711.

Cao, Y. N., Z. Huang, L. L. Luo, J. Y. Li, P. Li, and X. Liu. 2021. "Rapid and Selective Extraction of Norfloxacin From Milk Using Magnetic Molecular Imprinting Polymers Nanoparticles." *Food Chemistry* 353: 129464. http://doi.org/10.1016/j.foodchem.2021.129464.

Chen, C., J. Zhou, Q. Zhou, et al. 2023. "Research Progress on Aroma Compounds in Almonds and Factors Influencing Its Flavor Quality." *Food Science* 44, no. 19: 320–329.

Chen, Q. L., J. C. Zhang, H. D. Liu, T. Q. Li, and Q. Wang. 2023. "Mechanism of High-Moisture Extruded Protein Fibrous Structure Formation Based on the Interactions Among Pea Protein, Amylopectin, and Stearic Acid." *Food Hydrocolloids* 136: 108254. http://doi.org/10.1016/j.foodhyd.2022.108254.

Chen, S. M., W. J. Jiao, and J. F. Wu. 2025. "Current Insights Into Heat Treatment for Improving Functionalities of Soy Protein: A Review." *Comprehensive Reviews in Food Science and Food Safety* 24, no. 2: e70141. http://doi.org/10.1111/1541-4337.70141.

T/CIFST 002.–. 2021, General Standard for Plant-Based Foods.

CODEX STAN 1.–. 1985, General Standard for the Labelling of Prepackaged Foods.

Cui, L. Q., J. Kimmel, L. Zhou, J. J. Rao, and B. C. Chen. 2020. "Combining Solid Dispersion-Based Spray Drying With Cyclodextrin to Improve the Functionality and Mitigate the Beany Odor of Pea Protein Isolate." *Carbohydrate Polymers* 245: 116546. http://doi.org/10.1016/j.carbpol.2020.116546.

Déléris, I., A. Saint-Eve, F. Dakowski, et al. 2011. "The Dynamics of Aroma Release During Consumption of Candies of Different Structures, and Relationship With Temporal Perception." *Food Chemistry* 127, no. 4: 1615–1624. http://doi.org/10.1016/j.foodchem.2011.02.028.

do Livramento, K. G., F. M. Borem, A. C. José, et al. 2017. "Proteomic Analysis of Coffee Grains Exposed to Different Drying Process." *Food Chemistry* 221: 1874–1882.

Fan, N. N., H. M. Shewan, H. E. Smyth, G. E. Yakubov, and J. R. Stokes. 2021. "Dynamic Tribology Protocol (DTP): Response of Salivary Pellicle to Dairy Protein Interactions Validated Against Sensory Perception." *Food Hydrocolloids* 113: 106478. http://doi.org/10.1016/j.foodhyd.2020.106478.

Ferawati, F., C. Witthft, and M. Bergstrm. 2020. "Characterization of Volatile Compounds in Swedish Yellow and Gray Peas: Implications for New Legume-Based Ingredients." *Legume Science* 2, no. 4: e55. http://doi.org/10.1002/leg3.55.

Frank, D. C., G. T. Eyres, U. Piyasiri, and C. M. Delahunty. 2012. "Effect of Food Matrix Structure and Composition on Aroma Release During Oral Processing Using In Vivo Monitoring." *Flavour and Fragrance Journal* 27, no. 6: 433–444. http://doi.org/10.1002/ffj.3113.

Fu, Y., Y. Zhang, O. P. Soladoye, and R. E. Aluko. 2020. "Maillard Reaction Products Derived From Food Protein-Derived Peptides: Insights Into Flavor and Bioactivity." *Critical Reviews in Food Science and Nutrition* 60, no. 20: 3429–3442.

Gao, Z. L., P. Y. Shen, Y. Lan, et al. 2020. "Effect of Alkaline Extraction pH on Structure Properties, Solubility, and Beany Flavor of Yellow Pea Protein Isolate." *Food Research International* 131: 109045. http://doi.org/10.1016/j.foodres.2020.109045.

Guan, H. N., C. M. Feng, M. Ren, X. J. Xu, D. Y. Liu, and X. Q. Diao. 2024. "Emulsifying Property, Antioxidant Activity, and Bitterness of Soybean Protein Isolate Hydrolysate Obtained by Corolase PP Under High Hydrostatic Pressure." *Food Science and Human Wellness* 13, no. 3: 1271–1278. http://doi.org/10.26599/fshw.2022.9250106.

Guldiken, B., R. Green, and M. T. Nickerson. 2021. "The Impact of Different Adsorbents on Flavour Characteristics of a Lentil Protein Isolate." *European Food Research and Technology* 247, no. 3: 593–604. http://doi.org/10.1007/s00217-020-03648-z.

Guo, J., Z. Y. He, S. F. Wu, M. M. Zeng, and J. Chen. 2019. "Binding of Aromatic Compounds With Soy Protein Isolate in an Aqueous Model: Effect of pH." *Journal of Food Biochemistry* 43, no. 10: e12817. http://doi.org/10.1111/jfbc.12817.

Guo, J., Z. Y. He, S. F. Wu, M. M. Zeng, and J. Chen. 2020. "Effects of Concentration of Flavor Compounds on Interaction Between Soy Protein Isolate and Flavor Compounds." *Food Hydrocolloids* 100: 105388. http://doi.org/10.1016/j.foodhyd.2019.105388.

Guo, J., Z. Y. Hen, S. F. Wu, M. M. Zeng, and J. Chen. 2019. "Binding of Aroma Compounds With Soy Protein Isolate in Aqueous Model: Effect of Preheat Treatment of Soy Protein Isolate." *Food Chemistry* 290: 16–23. http://doi.org/10.1016/j.foodchem.2019.03.126.

Guo, J., M. Zeng, and J. Chen. 2023. "Binding of Dual-Flavour Compounds by Soy Protein Isolate in Aqueous Model Systems." *International Journal of Food Science and Technology* 58, no. 1: 432–441.

Guo, Y. N., Q. Gong, F. W. Sun, et al. 2024. "Interaction Mechanism of Pea Proteins With Selected Pyrazine Flavors: Differences in Alkyl Numbers and Flavor Concentration." *Food Hydrocolloids* 147: 109314. http://doi.org/10.1016/j.foodhyd.2023.109314.

Han, S. A., J. K. Kim, D. Y. Cho, Z. M. Patel, and C. S. Rhee. 2023. "The Olfactory System: Basic Anatomy and Physiology for General Otorhinolaryngologists." *Clinical and Experimental Otorhinolaryngology* 16, no. 4: 308–316. http://doi.org/10.21053/ceo.2023.00185.

Harper, A. R., R. C. J. Dobson, V. K. Morris, and G. J. Moggre. 2022. "Fermentation of Plant-Based Dairy Alternatives by Lactic Acid Bacteria." *Microbial Biotechnology* 15, no. 5: 1404–1421. http://doi.org/10.1111/1751-7915.14008.

He, Y., J. M. Qiu, J. S. Chen, W. Y. Shi, and J. G. Shi. 2025. "Aerosol Generation of Sweeteners Solutions During a Drinking Process." *Food Hydrocolloids* 159: 110603. http://doi.org/10.1016/j.foodhyd.2024.110603.

Hill, A. V. 1910. "The Possible Effects of the Aggregation of the Molecules of Haemoglobin on Its Dissociation Curves." *The Journal of Physiology* 40: 4–7.

Hollowood, T. A., J. M. Davidson, L. DeGroot, R. S. T. Linforth, and A. J. Taylor. 2002. "Taste Release and Its Effect on Overall Flavor Perception." In *Chemistry of Taste: Mechanisms, Behaviors, and Mimics*. Edited by P. Given and D. Paredes, 166–178. ACS Publications.

Hu, M., J. Wang, Y. X. Gao, B. Fan, F. Z. Wang, and S. Y. Li. 2024. "Proteomic Analysis of the Characteristic Flavor Components in Bacillus Subtilis BSNK-5-Fermented Soymilk." *Foods* 13, no. 15: 2399. http://doi.org/10.3390/foods13152399.

Huang, Z. J., Y. Y. Qu, X. H. Hua, F. Z. Wang, X. Jia, and L. J. Yin. 2023. "Recent Advances in Soybean Protein Processing Technologies: A Review of Preparation, Alterations in the Conformational and Functional Properties." *International Journal of Biological Macromolecules* 248: 125862. http://doi.org/10.1016/j.ijbiomac.2023.125862.

Hussain, M., M. A. Gantumur, M. F. Manzoor, et al. 2023. "Sustainable Emerging High-Intensity Sonication Processing to Enhance the Protein Bioactivity and Bioavailability: An Updated Review." *Ultrasonics Sonochemistry* 97: 106464. http://doi.org/10.1016/j.ultsonch.2023.106464.

ISO 23662. 2021, Definitions and Technical Criteria for Foods and Food Ingredients Suitable for Vegetarians or Vegans and For Labelling and Claims.

Jiang, W. R., X. Y. Yang, and L. Li. 2025. "In-Depth Analysis of the Relationship Between Matrix Network Structure and Flavor Diffusion of Meat Analogs: Based on Interactions and Extrusion Processes." *Food Hydrocolloids* 163: 111064. http://doi.org/10.1016/j.foodhyd.2025.111064.

Jin, C. M., H. J. Zhang, F. Y. Ren, and J. Wang. 2023. "Preparation and Characterization of Wheat Gluten Nanofiber Films Based on Electrospinning and Maillard Crosslinking." *LWT-Food Science and Technology* 186: 115208. http://doi.org/10.1016/j.lwt.2023.115208.

Jun, G., Z. He, S. Wu, M. Zeng, and J. Chen. 2019. "Effects of Concentration of Flavor Compounds on Interaction Between Soy Protein Isolate and Flavor Compounds." *Food Hydrocolloids* 100: 105388.

Kadam, A., M. G. Scanlon, and F. Koksel. 2025. "Extrusion of Oilseed-Based Ingredients: Unlocking New Potential for Sustainable Protein Solutions." *Comprehensive Reviews in Food Science and Food Safety* 24, no. 3: e70185. http://doi.org/10.1111/1541-4337.70185.

Kaur, S., and A. Ubeyitogullari. 2024. "The Impact of Supercritical Carbon Dioxide Processing on the Aroma and Physicochemical Properties of Soybean Flour." *Future Foods* 10: 100476. http://doi.org/10.1016/j.fufo.2024.100476.

Kelemen, V., A. Pichler, I. Ivic, I. Buljeta, J. Simunovic, and M. Kopjar. 2022. "Brown Rice Proteins as Delivery System of Phenolic and Volatile Compounds of Raspberry Juice." *International Journal of Food Science and Technology* 57, no. 4: 1866–1874. http://doi.org/10.1111/ijfs.15023.

Khalifa, I., Z. H. Li, A. Nawaz, et al. 2025. "Recent Innovations for Improving the Techno-Functional Properties of Plant-Based Egg Analogs and Egg-Mimicking Products to Promote Their Industrialization and Commercialization." *Comprehensive Reviews in Food Science and Food Safety* 24, no. 1: e70086. http://doi.org/10.1111/1541-4337.70086.

Kharlamova, A. S., O. S. Godovalova, E. G. Otlyga, and A. E. Proshchina. 2023. "Primary and Secondary Olfactory Centres in Human Ontogeny." *Neuroscience Research* 190: 1–16. http://doi.org/10.1016/j.neures.2022.12.005.

Khrisanapant, P., B. Kebede, S. Y. Leong, and I. Oey. 2019. "A Comprehensive Characterisation of Volatile and Fatty Acid Profiles of Legume Seeds." *Foods* 8, no. 12: 651. http://doi.org/10.3390/foods8120651.

Klost, M., G. Giménez-Ribes, and S. Drusch. 2020. "Enzymatic Hydrolysis of Pea Protein: Interactions and Protein Fractions Involved in Fermentation Induced Gels and Their Influence on Rheological Properties." *Food Hydrocolloids* 105: 105793. http://doi.org/10.1016/j.foodhyd.2020.105793.

Kong, Y., L. N. Sun, Z. N. Wu, et al. 2023. "Effects of Ultrasonic Treatment on the Structural, Functional Properties and Beany Flavor of Soy Protein Isolate: Comparison With Traditional Thermal Treatment." *Ultrasonics Sonochemistry* 101: 106675. http://doi.org/10.1016/j.ultsonch.2023.106675.

Kong, Y., Z. N. Wu, Y. H. Li, et al. 2024. "Analyzing Changes in Volatile Flavor Compounds of Soy Protein Isolate During Ultrasonic-thermal Synergistic Treatments Using Electronic Nose and HS-SPME-GC-MS Combined With Chemometrics." *Food Chemistry* 445: 11.

Kuesten, C., J. Bi, H. D. Zanetti, and J. Dang. 2024. "Using Functional Data Analysis (FDA) for Time-Intensity (T-I) Evaluation of Perceptual Efficacy, Exemplified by a Supplement Tablet Longitudinal Study." *Food Quality and Preference* 115: 105126. http://doi.org/10.1016/j.foodqual.2024.105126.

Kühn, J., X. Q. Zhu, T. Considine, and H. Singh. 2007. "Binding of 2-Nonanone and Milk Proteins in Aqueous Model Systems." *Journal of Agricultural and Food Chemistry* 55, no. 9: 3599–3604. http://doi.org/10.1021/jf063517o.

Kuijpers, S. A., E. D. Garina, M. I. Gobes, et al. 2025. "Impact of pH-Shifting on Multiscale Structural Anisotropy of High-Moisture Extrudates of Soy Proteins." *Food Hydrocolloids* 168: 111456. http://doi.org/10.1016/j.foodhyd.2025.111456.

Kumar, N., S. Hong, Y. Zhu, et al. 2025. "Comprehensive Review of Chickpea (Cicer arietinum): Nutritional Significance, Health Benefits, Techno-Functionalities, and Food Applications." *Comprehensive Reviews in Food Science and Food Safety* 24, no. 2: e70152. http://doi.org/10.1111/1541-4337.70152.

Kun, W., D. Susan, and Arntfield. 2017. "Effect of Protein-Flavour Binding on Flavour Delivery and Protein Functional Properties: A Special Emphasis on Plant-Based Proteins." *Flavour & Fragrance Journal* 32, no. 2: 92–101.

Lan, Y., J. B. Ohm, B. C. Chen, and J. J. Rao. 2020. "Physicochemical Properties and Aroma Profiles of Flaxseed Proteins Extracted From Whole Flaxseed and Flaxseed Meal." *Food Hydrocolloids* 104: 105731. http://doi.org/10.1016/j.foodhyd.2020.105731.

Lan, Y., M. W. Xu, J. B. Ohm, B. C. Chen, and J. J. Rao. 2019. "Solid Dispersion-Based Spray-Drying Improves Solubility and Mitigates Beany Flavour of Pea Protein Isolate." *Food Chemistry* 278: 665–673. http://doi.org/10.1016/j.foodchem.2018.11.074.

Li, J., Q. Shen, A. Albahi, H. S. Liang, J. Li, and B. Li. 2024. "Chitosan Mitigates the Beany Flavor and Improves the Functional Properties of Soy Protein Isolate via the Electrostatic Interaction." *Food Hydrocolloids* 155: 110164. http://doi.org/10.1016/j.foodhyd.2024.110164.

Li, J. M., X. W. Zhang, S. J. Luo, et al. 2024. "Heterologous Expression of Protein-Glutaminase in Escherichia coli Nissle 1917 for Improved Flavor Properties of Soy Protein and Its Implications on High-Moisture Extrudates." *Food Bioscience* 57: 103591. http://doi.org/10.1016/j.fbio.2024.103591.

Li, S. Q., J. Yan, J. H. Yang, et al. 2024. "Modulating Peppermint Oil Flavor Release Properties of Emulsion-Filled Protein Gels: Impact of Cross-Linking Method and Matrix Composition." *Food Research International* 185: 114277. http://doi.org/10.1016/j.foodres.2024.114277.

Li, Y. G., Q. Y. Zhang, X. X. Liu, et al. 2025. "Flavor Interactions in Wine: Current Status and Future Directions From Interdisplinary and Crossmodal Perspectives." *Comprehensive Reviews in Food Science and Food Safety* 24, no. 3: e70199. http://doi.org/10.1111/1541-4337.70199.

Liao, X. Y., S. S. Wang, Y. Q. Li, et al. 2022. "Effects of "Nine Steaming Nine Sun-drying" on Proximate Composition, Protein Structure and Volatile Compounds of Black Soybeans." *Food Research International* 155: 111070. http://doi.org/10.1016/j.foodres.2022.111070.

Lima, E. C. S., M. B. S. Feijo, M. C. J. Freitas, E. R. dos Santos, A. U. O. Sabaa-Srur, and L. S. M. Moura. 2013. "Sensorial Evolution of Cassava Flour (Manihot esculenta crantz) Added to Protein Concentrate Cassava Leaves." *Food Science & Nutrition* 1, no. 5: 357–362. http://doi.org/10.1002/fsn3.16.

Liu, M. 2024. *Study on the Application of Haematococus pluvialis on High Moisture Plant Based Meat Analogues Unpublished Master*. Qilu University of Technology.

Liu, Y. Z., D. C. Cadwallader, and M. Drake. 2023. "Identification of Predominant Aroma Components of Dried Pea Protein Concentrates and Isolates." *Food Chemistry* 406: 134998. http://doi.org/10.1016/j.foodchem.2022.134998.

Luo, N., A. Q. Ye, F. M. Wolber, and H. Singh. 2019. "Structure of Whey Protein Emulsion Gels Containing Capsaicinoids: Impact on In-Mouth Breakdown Behaviour and Sensory Perception." *Food Hydrocolloids* 92: 19–29. http://doi.org/10.1016/j.foodhyd.2019.01.019.

Luo, Q. S. 2024. *Pecan Allergen Isolation and Plant-Based Yogurt Preparation*. Nanchang University.

Ma, Q. Y., Q. D. Xu, N. Chen, and W. C. Zeng. 2024. "Establishing a Novel Covalent Complex of Wheat Gluten With Tea Polyphenols: Structure, Digestion, and Action Mechanism." *International Journal of Biological Macromolecules* 281: 136184. http://doi.org/10.1016/j.ijbiomac.2024.136184.

Mahmoudpour, M., F. Javaheri-Ghezeldizaj, R. Yekta, et al. 2020. "Thermodynamic Analysis of Albumin Interaction With Monosodium Glutamate Food Additive: Insights From Multi-Spectroscopic and Molecular Docking Approaches." *Journal of Molecular Structure* 1221: 128785. http://doi.org/10.1016/j.molstruc.2020.128785.

McClements, D. J. 2017. "Recent Progress in Hydrogel Delivery Systems for Improving Nutraceutical Bioavailability." *Food Hydrocolloids* 68: 238–245. http://doi.org/10.1016/j.foodhyd.2016.05.037.

Mehta, N., S. Jeyapriya, P. Kumar, et al. 2022. "Ultrasound-Assisted Extraction and the Encapsulation of Bioactive Components for Food Applications." *Foods* 11, no. 19: 2973. http://doi.org/10.3390/foods11192973.

Mestres, M., N. Moran, A. Jordan, and A. Buettner. 2005. "Aroma Release and Retronasal Perception During and After Consumption of Flavored Whey Protein Gels With Different Textures. 1. In Vivo Release Analysis." *Journal of Agricultural and Food Chemistry* 53, no. 2: 403–409. http://doi.org/10.1021/jf048596n.

Mohan, V. R., P. S. Tresina, and E. D. Daffodil. 2016. "Antinutritional Factors in Legume Seeds: Characteristics and Determination." *Encyclopedia of Food and Health* 2016: 211–220.

Müller, M., O. Holderer, K. Schwärzer, et al. 2025. "Proteins Derived From Green Biomass: Alfalfa (Medicago sativa L.) and Water Lentil

Concentrate (Lemna minor L.) in the Focus as Stabilizers for Emulsions." *Food Hydrocolloids for Health* 8: 100233. http://doi.org/10.1016/j.fhfh.2025.100233.

Muñoz-González, C., M. Brule, C. Martin, G. Feron, and F. Canon. 2022. "Molecular Mechanisms of Aroma Persistence: From Noncovalent Interactions Between Aroma Compounds and the Oral Mucosa to Metabolization of Aroma Compounds by Saliva and Oral Cells." *Food Chemistry* 373. http://doi.org/10.1016/j.foodchem.2021.131467.

Murat, C., M. H. Bard, C. Dhalleine, and N. Cayot. 2013. "Characterisation of Odour Active Compounds Along Extraction Process From Pea Flour to Pea Protein Extract." *Food Research International* 53, no. 1: 31–41. http://doi.org/10.1016/j.foodres.2013.03.049.

Nagassa, M., S. D. He, S. Y. Liu, et al. 2024. "Exploring Off-Flavour Compounds in Soy-Based Meats: Mechanisms and Removal Methods." *Flavour and Fragrance Journal* 39, no. 6: 319–335. http://doi.org/10.1002/ffj.3803.

GB 28050-2011. National Food Safety Standard — General Rules for Nutrition Labeling of Prepackaged Foods.

Nawaz, A., Z. Y. Xiong, Q. Li, et al. 2019. "Evaluation of Physicochemical, Textural and Sensory Quality Characteristics of Red Fish Meat-Based Fried Snacks." *Journal of the Science of Food and Agriculture* 99, no. 13: 5771–5777. http://doi.org/10.1002/jsfa.9845.

Nunes, N. M., Y. L. Coelho, J. S. Castro, et al. 2020. "Naringenin-Lactoferrin Binding: Impact on Naringenin Bitterness and Thermodynamic Characterization of the Complex." *Food Chemistry* 331: 127337. http://doi.org/10.1016/j.foodchem.2020.127337.

Ong, D. S. M., X. Y. Hua, A. H. P. Theng, et al. 2025. "Influence of Mixed Plant Protein Combinations on the Physicochemical, Textural, Structural and Nutritional Properties of Extruded High-Moisture Meat Analogues." *Journal of Food Engineering* 399: 112633. http://doi.org/10.1016/j.jfoodeng.2025.112633.

Pérez, C. B., T. Oliviero, V. Fogliano, H. G. Janssen, and S. Martins. 2023. "Flavour Them up! Exploring the Challenges of Flavoured Plant-Based Foods." *Flavour and Fragrance Journal* 38, no. 3: 125–134. http://doi.org/10.1002/ffj.3734.

Phuhongsung, P., M. Zhang, and B. Bhandari. 2020. "4D Printing of Products Based on Soy Protein Isolate via Microwave Heating for Flavor Development." *Food Research International* 137: 109605. http://doi.org/10.1016/j.foodres.2020.109605.

Pu, X. L., R. Linforth, M. M. Dragosavac, and B. Wolf. 2019. "Dynamic Aroma Release From Complex Food Emulsions." *Journal of Agricultural and Food Chemistry* 67, no. 33: 9325–9334. http://doi.org/10.1021/acs.jafc.9b02304.

Qian, Y., G. J. Liang, J. L. Dong, et al. 2025. "Effect of Myoglobin on the Flavor, Color and Texture of High-Moisture Soy Protein Concentrate-Wheat Gluten Extrudates." *Food Chemistry* 473: 143102. http://doi.org/10.1016/j.foodchem.2025.143102.

Qiu, C., Y. X. Meng, Z. H. Zhang, et al. 2025. "Enhancement of Soy Protein Functionality by Conjugation or Complexation With Polysaccharides or Polyphenols: A Review." *Comprehensive Reviews in Food Science and Food Safety* 24, no. 1: e70095. http://doi.org/10.1111/1541-4337.70095.

Reineccius, G. A. 2022. "Flavor Interactions With Proteins." *Current Opinion in Food Science* 47: 100884.

Roland, W. S. U., L. Pouvreau, J. Curran, F. van de Velde, and P. M. T. de Kok. 2017. "Flavor Aspects of Pulse Ingredients." *Cereal Chemistry* 94, no. 1: 58–65. http://doi.org/10.1094/cchem-06-16-0161-fi.

Rossetti, D., G. E. Yakubov, J. R. Stokes, A. M. Williamson, and G. G. Fuller. 2008. "Interaction of Human Whole Saliva and Astringent Dietary Compounds Investigated by Interfacial Shear Rheology." *Food Hydrocolloids* 22, no. 6: 1068–1078. http://doi.org/10.1016/j.foodhyd.2007.05.014.

Ruth, S. M. v., and J. P. Roozen. 2010. "Delivery of Flavours From Food Matrices." In *Food Flavour Technology, Second Edition*. Edited by A. J. Taylor and R. S. T. Linforth, Ch 7. Wiley.

Samard, S., B. Y. Gu, and G. H. Ryu. 2019. "Effects of Extrusion Types, Screw Speed and Addition of Wheat Gluten on Physicochemical Characteristics and Cooking Stability of Meat Analogues." *Journal of the Science of Food and Agriculture* 99, no. 11: 4922–4931. http://doi.org/10.1002/jsfa.9722.

Scatchard, G. 1949. "The Attractions of Proteins for Small Molecules and Ions." *Annals of the New York Academy of Sciences* 51: 660–672.

Schwartz, M., H. Brignot, G. Feron, et al. 2022. "Role of Human Salivary Enzymes in Bitter Taste Perception." *Food Chemistry* 386: 132798. http://doi.org/10.1016/j.foodchem.2022.132798.

Shahbaz, M., N. Raza, M. Islam, et al. 2023. "The Nutraceutical Properties and Health Benefits of Pseudocereals: A Comprehensive Treatise." *Critical Reviews in Food Science and Nutrition* 63, no. 29: 10217–10229. http://doi.org/10.1080/10408398.2022.2071205.

Shen, H., J. S. Elmore, M. M. Zhao, and W. Z. Sun. 2020. "Effect of Oxidation on the Gel Properties of Porcine Myofibrillar Proteins and Their Binding Abilities With Selected Flavour Compounds." *Food Chemistry* 329: 127032. http://doi.org/10.1016/j.foodchem.2020.127032.

Shen, P. Y., Z. L. Gao, M. W. Xu, J. B. Ohm, J. J. Rao, and B. C. Chen. 2020. "The Impact of Hempseed Dehulling on Chemical Composition, Structure Properties and Aromatic Profile of Hemp Protein Isolate." *Food Hydrocolloids* 106: 105889. http://doi.org/10.1016/j.foodhyd.2020.105889.

Shi, Y., A. Singh, D. D. Kitts, and A. Pratap-Singh. 2021. "Lactic Acid Fermentation: A Novel Approach to Eliminate Unpleasant Aroma in Pea Protein Isolates." *LWT-Food Science and Technology* 150: 111927. http://doi.org/10.1016/j.lwt.2021.111927.

Singh, B., J. P. Singh, A. Kaur, and N. Singh. 2017. "Phenolic Composition and Antioxidant Potential of Grain Legume Seeds: A Review." *Food Research International* 101: 1–16. http://doi.org/10.1016/j.foodres.2017.09.026.

Snel, S. J. E., M. Pascu, I. Bodnár, S. Avison, A. J. van der Goot, and M. Beyrer. 2023. "Flavor-Protein Interactions for Four Plant Proteins With Ketones and Esters." *Heliyon* 9, no. 6: e16503. http://doi.org/10.1016/j.heliyon.2023.e16503.

Soto-Vaca, A., A. Gutierrez, J. N. Losso, Z. M. Xu, and J. W. Finley. 2012. "Evolution of Phenolic Compounds From Color and Flavor Problems to Health Benefits." *Journal of Agricultural and Food Chemistry* 60, no. 27: 6658–6677. http://doi.org/10.1021/jf300861c.

Souza, H. K. S., W. Kraiem, A. Ben Yahia, A. Aschi, and L. Hilliou. 2023. "From Seaweeds to Hydrogels: Recent Progress in Kappa-2 Carrageenans." *Materials* 16, no. 15: 5387. http://doi.org/10.3390/ma16155387.

Sun, A., L. N. Chen, W. Wu, O. P. Soladoye, Y. H. Zhang, and Y. Fu. 2023. "The Potential Meat Flavoring Generated From Maillard Reaction Products of Wheat Gluten Protein Hydrolysates-Xylose: Impacts of Different Thermal Treatment Temperatures on Flavor." *Food Research International* 165: 112512. http://doi.org/10.1016/j.foodres.2023.112512.

Sun, A., W. Wu, O. P. Soladoye, et al. 2022. "Maillard Reaction of Food-Derived Peptides as a Potential Route to Generate Meat Flavor Compounds: A Review." *Food Research International* 151: 110823. http://doi.org/10.1016/j.foodres.2021.110823.

Sun, H. L., J. Y. Liang, Y. R. Qian, X. Chen, and L. Y. Zhao. 2025. "Interactions of Pea Protein With Three Sulfur-Containing Flavor Compounds: Insights Into Molecule Structural, Non-Covalent, and Binding Mechanisms." *Food Hydrocolloids* 166: 111326. http://doi.org/10.1016/j.foodhyd.2025.111326.

Sun, X. D., and S. D. Arntfield. 2012. "Molecular Forces Involved in Heat-Induced Pea Protein Gelation: Effects of Various Reagents on the Rheological Properties of Salt-Extracted Pea Protein Gels." *Food Hydrocolloids* 28, no. 2: 325–332. http://doi.org/10.1016/j.foodhyd.2011.12.014.

Suppavorasatit, I., and K. R. Cadwallader. 2012. "Effect of Enzymatic Deamidation of Soy Protein by Protein-Glutaminase on the Flavor-Binding Properties of the Protein Under Aqueous Conditions." *Journal of Agricultural and Food Chemistry* 60, no. 32: 7817–7823. http://doi.org/10.1021/jf301719k.

Tang, Q., Y. H. Roos, and S. Miao. 2024. "Structure, Gelation Mechanism of Plant Proteins Versus Dairy Proteins and Evolving Modification Strategies." *Trends in Food Science & Technology* 147: 104464.

Tangyu, M., M. Fritz, J. P. Tan, et al. 2023. "Flavour by Design: Food-Grade Lactic Acid Bacteria Improve the Volatile Aroma Spectrum of Oat Milk, Sunflower Seed Milk, Pea Milk, and Faba Milk Towards Improved Flavour and Sensory Perception." *Microbial Cell Factories* 22, no. 1: 133. http://doi.org/10.1186/s12934-023-02147-6.

Temthawee, W., A. Panya, K. R. Cadwallader, and I. Suppavorasatit. 2020. "Flavor Binding Property of Coconut Protein Affected by Protein-Glutaminase: Vanillin-Coconut Protein Model." *LWT-Food Science and Technology* 130: 109676. http://doi.org/10.1016/j.lwt.2020.109676.

Tian, W. N., Y. S. Huang, Z. L. Song, et al. 2023. "Flexible Control of Bigel Microstructure for Enhanced Stability and Flavor Release During Oral Consumption." *Food Research International* 174: 113606. http://doi.org/10.1016/j.foodres.2023.113606.

Tromelin, A., and E. Guichard. 2003. "Use of Catalyst in a 3D-QSAR Study of the Interactions Between Flavor Compounds and β-Lactoglobulin." *Journal of Agricultural and Food Chemistry* 51, no. 7: 1977–1983. http://doi.org/10.1021/jf0207981.

Viry, O., R. Boom, S. Avison, M. Pascu, and I. Bodnár. 2018. "A Predictive Model for Flavor Partitioning and Protein-Flavor Interactions in Fat-Free Dairy Protein Solutions." *Food Research International* 109: 52–58. http://doi.org/10.1016/j.foodres.2018.04.013.

Wang, B., Q. Zhang, N. Zhang, et al. 2021. "Insights Into Formation, Detection and Removal of the Beany Flavor in Soybean Protein." *Trends in Food Science & Technology* 112: 336–347. http://doi.org/10.1016/j.tifs.2021.04.018.

Wang, F. R., J. Q. Fan, H. L. Shen, Y. L. Yang, and Y. R. Guo. 2020. "Formation Mechanism of Pyrazine Compounds in the Sunflower Oil." *Science and Technology of Food Industry* 41, no. 02: 330–335+344. http://doi.org/10.13386/j.issn1002-0306.2020.02.053.

Wang, J., M. M. Zhao, C. Y. Qiu, and W. Z. Sun. 2018. "Effect of Malondialdehyde Modification on the Binding of Aroma Compounds to Soy Protein Isolates." *Food Research International* 105: 150–158. http://doi.org/10.1016/j.foodres.2017.11.001.

Wang, K., and S. D. Arntfield. 2014. "Binding of Carbonyl Flavours to Canola, Pea and Wheat Proteins Using GC/MS Approach." *Food Chemistry* 157: 364–372. http://doi.org/10.1016/j.foodchem.2014.02.042.

Wang, K., and S. D. Arntfield. 2015. "Effect of Salts and pH on Selected Ketone Flavours Binding to Salt-Extracted Pea Proteins: the Role of Non-Covalent Forces." *Food Research International* 77: 1–9.

Wang, K., and S. D. Arntfield. 2016. "Probing the Molecular Forces Involved in Binding of Selected Volatile Flavour Compounds to Salt-Extracted Pea Proteins." *Food Chemistry* 211: 235–242. http://doi.org/10.1016/j.foodchem.2016.05.062.

Wang, K., and S. D. Arntfield. 2017. "Effect of Protein-Flavour Binding on Flavour Delivery and Protein Functional Properties: A Special Emphasis on Plant-Based Proteins." *Flavour and Fragrance Journal* 32, no. 2: 92–101. http://doi.org/10.1002/ffj.3365.

Wang, L. Q., J. N. Huang, Z. H. Liu, and C. Wang. 2025. "Decoding the Secrets of Odor-Active Compounds in Dark Tea." *Comprehensive Reviews in Food Science and Food Safety* 24, no. 3: e70206. http://doi.org/10.1111/1541-4337.70206.

Wang, X. Y., Y. M. Pei, J. Y. Wu, X. B. Zhong, H. Y. Liu, and Y. S. Xue. 2025. "Innovative Mycelium-Based Food: Advancing One Health Through Nutritional Insights and Environmental Sustainability." *Comprehensive Reviews in Food Science and Food Safety* 24, no. 2: e70166. http://doi.org/10.1111/1541-4337.70166.

Wang, Y., B. Guldiken, M. Tulbek, J. D. House, and M. Nickerson. 2020. "Impact of Alcohol Washing on the Flavour Profiles, Functionality and Protein Quality of Air Classified Pea Protein Enriched Flour." *Food Research International* 132: 109085. http://doi.org/10.1016/j.foodres.2020.109085.

Wang, Y. Q., F. Tuccillo, A. M. Lampi, et al. 2022. "Flavor Challenges in Extruded Plant-Based Meat Alternatives: A Review." *Comprehensive Reviews in Food Science and Food Safety* 21, no. 3: 2898–2929. http://doi.org/10.1111/1541-4337.12964.

Wang, Y. Q., H. F. Wang, H. Xiang, et al. 2024. "Unlocking the Opportunities for Creating Sustainable, Flavorful and Healthy High-Protein "Blue Foods": Focusing on the Impacts of Protein-Flavor Interactions." *Trends in Food Science & Technology* 148: 104523. http://doi.org/10.1016/j.tifs.2024.104523.

Weel, K. G. C., A. E. M. Boelrijk, J. J. Burger, et al. 2003. "Effect of Whey Protein on the In Vivo Release of Aldehydes." *Journal of Agricultural and Food Chemistry* 51, no. 16: 4746–4752. http://doi.org/10.1021/jf034188s.

Wongprasert, T., P. Mathatheeranan, P. Siripitakpong, et al. 2024. "Effect of Functional Groups in Strawberry Flavoring on Pea Protein-Flavor Interactions: Potential Applicable in Flavor Formulation for Plant-Based Protein Aqueous Foods." *Food Chemistry-X* 23: 101702. http://doi.org/10.1016/j.fochx.2024.101702.

Wu, N. N., L. J. Wang, X. Q. Yang, S. W. Yin, Z. Teng, and E. L. Zheng. 2011. "Comparison of Flavor Volatiles and Come Functional Properties of Different Soy Protein Products." *Journal of the American Oil Chemists Society* 88, no. 10: 1621–1631. http://doi.org/10.1007/s11746-011-1825-9.

Xiang, L. B., B. Jiang, Y. L. Xiong, et al. 2023. "Beany Flavor in Pea Protein: Recent Advances in Formation Mechanism, Analytical Techniques and Microbial Fermentation Mitigation Strategies." *Food Bioscience* 56: 103166. http://doi.org/10.1016/j.fbio.2023.103166.

Xiang, L. B., W. Y. Zhu, B. Jiang, J. J. Chen, L. Zhou, and F. Zhong. 2023. "Volatile Compounds Analysis and Biodegradation Strategy of Beany Flavor in Pea Protein." *Food Chemistry* 402: 134275. http://doi.org/10.1016/j.foodchem.2022.134275.

Xie, H. X., and L. Grossmann. 2025. "Tenderness in Meat and Meat Alternatives: Structural and Processing Fundamentals." *Comprehensive Reviews in Food Science and Food Safety* 24, no. 1: e70033. http://doi.org/10.1111/1541-4337.70033.

Xu, J., Q. M. Chen, Y. Qiu, et al. 2025. "Insight Into the Effect of 4-Hydroxy-2,5-Dimethyl-3(2H)-Furanone on the Changes of Off-Flavors in the Preparation of Soy Protein Isolate: Potential Mechanisms of Their Reduction." *Food Chemistry* 471: 142782. http://doi.org/10.1016/j.foodchem.2025.142782.

Xu, J., Q. M. Chen, M. M. Zeng, et al. 2024. "Effect of Heat Treatment on the Release of Off-Flavor Compounds in Soy Protein Isolate." *Food Chemistry* 437: 137924. http://doi.org/10.1016/j.foodchem.2023.137924.

Xu, J. X., X. Y. Xu, Z. H. Yuan, et al. 2022. "Effect of Hemp Protein on the Physicochemical Properties and Flavor Components of Plant-Based Yogurt." *LWT-Food Science and Technology* 172: 114145. http://doi.org/10.1016/j.lwt.2022.114145.

Xu, M. W., Z. Jin, Y. Lan, J. J. Rao, and B. C. Chen. 2019. "HS-SPME-GC-MS/Olfactometry Combined With Chemometrics to Assess the Impact of Germination on Flavor Attributes of Chickpea, Lentil, and Yellow Pea Flours." *Food Chemistry* 280: 83–95. http://doi.org/10.1016/j.foodchem.2018.12.048.

Yang, L. Y., Z. W. Ying, H. Li, et al. 2023. "Extrusion Production of Textured Soybean Protein: The Effect of Energy Input on Structure and Volatile Beany Flavor Substances." *Food Chemistry* 405: 134728. http://doi.org/10.1016/j.foodchem.2022.134728.

Yang, L. Y., T. Y. Zhang, H. Li, T. P. Chen, and X. Q. Liu. 2023. "Control of Beany Flavor From Soybean Protein Raw Material in Plant-Based Meat Analog Processing." *Foods* 12, no. 5: 923. http://doi.org/10.3390/foods12050923.

Yin, W. J., M. M. Zhu, X. W. Chen, S. D. Sun, and Y. H. Wang. 2024. "Preparation and Characteristics of High-Protein and Fat-Reduced Vegetarian Mayonnaise Co-Stabilized by Natural Quillaja Saponin and Soybean Protein Isolate." *Food Science* 45, no. 09: 22–28.

Yin, X. Y., J. X. Li, L. Zhu, and H. Zhang. 2024. "Advances in the Formation Mechanism of Set-Type Plant-Based Yogurt Gel: A Review." *Critical Reviews in Food Science and Nutrition* 64, no. 26: 9412–9431. http://doi.org/10.1080/10408398.2023.2212764.

Ying, X. H., X. Xu, Y. N. Ouyang, et al. 2011. "Analysis of Characteristic Compound in Aroma Rice by Gas Chromatography/Mass Spectrometry With Solid-Phase Microextraction." *Journal of Analytical Science* 27, no. 01: 69–71.

Yu, J. C., Y. J. Z. Wu, and W. S. Shin. 2025. "From Waste to Value: Integrating Legume Byproducts Into Sustainable Industrialization." *Comprehensive Reviews in Food Science and Food Safety* 24, no. 3: e70174. http://doi.org/10.1111/1541-4337.70174.

Zeng, X. Q., Y. Li, P. Li, et al. 2024. "Encapsulation of Roast Beef Flavor by Soy Protein Isolate/Chitosan Complex Pickering Emulsions to Improve Its Releasing Properties During the Processing of Plant-Based Meat Analogues." *Food Chemistry* 450: 139313. http://doi.org/10.1016/j.foodchem.2024.139313.

Zha, F., J. Rao, and B. Chen. 2021a. "Modification of Pulse Proteins for Improved Functionality and Flavor Profile: A Comprehensive Review." *Comprehensive Reviews in Food Science and Food Safety* 20, no. 3: 3036–3060. https://doi.org/10.1111/1541-4337.12736.

Zha, F. C., J. J. Rao, and B. C. Chen. 2021b. "Modification of Pulse Proteins for Improved Functionality and Flavor Profile: A Comprehensive Review." *Comprehensive Reviews in Food Science and Food Safety* 20, no. 3: 3036–3060. http://doi.org/10.1111/1541-4337.12736.

Zhang, B., J. W. Zhang, X. B. Yu, J. Peng, L. Q. Pan, and K. Tu. 2022. "Evaluation of the Adsorption Capacity and Mechanism of Soy Protein Isolate for Volatile Flavor Compounds: Role of Different Oxygen-Containing Functional Groups." *Food Chemistry* 386: 132745. http://doi.org/10.1016/j.foodchem.2022.132745.

Zhang, D. H., Y. P. Cai, F. Lao, and J. H. Wu. 2025. "Protein Structural Properties, Proteomics and Flavor Characterization Analysis of Rice During Cooking." *Food Chemistry* 465: 142101. http://doi.org/10.1016/j.foodchem.2024.142101.

Zhang, D. H., Y. H. Zhang, X. Pan, et al. 2023. "Effect of Extrusion on the Structural and Flavor Properties of Oat Flours." *Journal of Cereal Science* 113: 103742. http://doi.org/10.1016/j.jcs.2023.103742.

Zhang, J., D. C. Kang, W. G. Zhang, and J. M. Lorenzo. 2021. "Recent Advantage of Interactions of Protein-Flavor in Foods: Perspective of Theoretical Models, Protein Properties and Extrinsic Factors." *Trends in Food Science & Technology* 111: 405–425. http://doi.org/10.1016/j.tifs.2021.02.060.

Zhang, L., X. Wang, W. J. Qu, et al. 2022. "Evaluation of Dual-Frequency Multi-Angle Ultrasound on Physicochemical Properties of Tofu Gel and Its Finished Product by TOPSIS-Entropy Weight Method." *Ultrasonics Sonochemistry* 90: 106196. http://doi.org/10.1016/j.ultsonch.2022.106196.

Zhao, C. B., Z. J. Chu, Z. C. Miao, et al. 2021. "Ultrasound Heat Treatment Effects on Structure and Acid-Induced Cold Set Gel Properties of Soybean Protein Isolate." *Food Bioscience* 39: 100827. http://doi.org/10.1016/j.fbio.2020.100827.

Zhao, X. Y., L. Sun, X. W. Zhang, H. K. Liu, and Y. P. Zhu. 2020. "Effects of Ultrafine Grinding Time on the Functional and Flavor Properties of Soybean Protein Isolate." *Colloids and Surfaces B-Biointerfaces* 196: 111345. http://doi.org/10.1016/j.colsurfb.2020.111345.

Zheng, Z., L. Zhang, M. Zhang, A. S. Mujumdar, and Y. Liu. 2023. "Maillard Reaction Products of Pea Protein Hydrolysate as a Flavour Enhancer for Beef Flavors: Effects on Flavor and Physicochemical Properties." *Food Chemistry* 417: 8.

Zhou, M., Y. M. Li, Z. Q. Yuan, et al. 2023. "Effect of Tartary Buckwheat and Highland Barley Flours on the Quality of Glutinous Rice Cakes Determined by Nutritional Composition, Physical Structure, Sensory Perception and Flavour." *International Journal of Food Science and Technology* 58, no. 5: 2400–2410. http://doi.org/10.1111/ijfs.16377.

Zhu, W. Y., B. Jiang, F. Zhong, J. J. Chen, and T. Zhang. 2021. "Effect of Microbial Fermentation on the Fishy-Odor Compounds in Kelp (*Laminaria japonica*)." *Foods* 10, no. 11: 2532. http://doi.org/10.3390/foods10112532.

Zuo, C. X., W. L. Li, Y. S. Chen, et al. 2024. "*Research Progress and Development Trend of Walnut Milk Preparation Technology*." Tongfang CNKI (Beijing) Technology Co.