The Aromatic Footprint of *Lactiplantibacillus plantarum*: Volatilome Intraspecific Diversity and Variability Across Food Matrices

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Abstract

Background

Lactiplantibacillus plantarum is a metabolically versatile lactic acid bacterium widely used in fermented foods. Although its probiotic, biocontrol, and fermentation traits are well documented, knowledge of its volatilome across food matrices remains fragmented.

Scope and approach

This review synthesises peer-reviewed monoculture fermentation studies on volatile organic compounds produced by *L. plantarum* across eight food categories: dairy, meat, fish and seafood, fruit juices, vegetables, cereals, agricultural by-products, and plant-based milk alternatives. Volatile profiles were compared by chemical class, individual compound, strain identity, and food matrix to identify conserved metabolic traits, matrix-dependent behaviours, and sources of intraspecific variability. Co-fermentation studies with yeasts and other bacteria were also considered to contextualise the metabolic limits and complementary functions of *L. plantarum* monocultures.

Key findings and conclusions

Across matrices, *L. plantarum* consistently generated pyruvate-derived metabolites, with acetoin and acetic acid emerging as recurrent markers of fermentative activity. Aldehyde behaviour was matrix dependent, increasing in dairy, meat, and cereals but decreasing in fruit juices and plant-based milks, where they are often associated with off-flavours. Three recurring patterns emerged: strain-dependent variability in 2,3-butanediol production, strain-specific rather than constitutive acetaldehyde synthesis, and time-dependent ester accumulation. Volatile performance depended strongly on strain–matrix interactions; cross-niche inoculation often enhanced aroma complexity, whereas performance in one substrate did not predict outcomes in another. Co-fermentation expanded volatile diversity, particularly by promoting ester formation and reducing sulphur-related off-odours. Overall, this review supports a strain- and matrix-specific framework for rational flavour-by-design fermentation.

Keywords: volatile organic compounds; flavour; food fermentation; *Lactiplantibacillus plantarum*; food matrix; starter culture; strain selection

The Aromatic Footprint of *Lactiplantibacillus plantarum*: Volatilome Intraspecific Diversity and Variability Across Food Matrices

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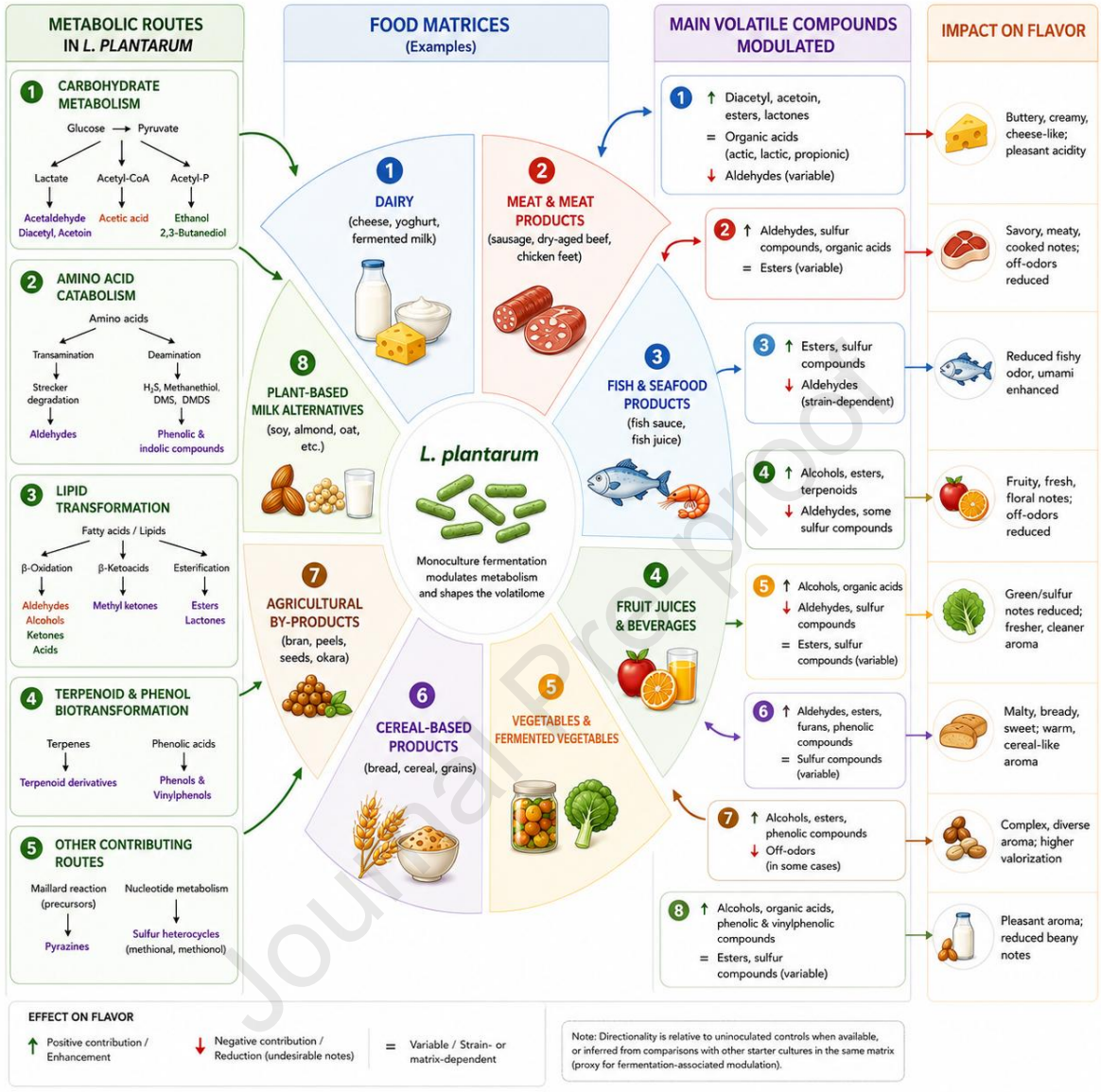
17 **Graphical Abstract**



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1. Introduction

Fermented foods have played a fundamental role in human nutrition for millennia, providing not only preservation benefits but also enhanced nutritional value, bioactive compounds, and distinctive sensory characteristics (Tamang et al., 2020). Among the microorganisms responsible for food fermentation, lactic acid bacteria (LAB) occupy a central position due to their metabolic versatility, safety profile, and ability to produce a wide range of flavour-active compounds (Garcia et al., 2020). Within the LAB group heterogeneous category, *Lactiplantibacillus plantarum* has emerged as one of the most extensively studied species, especially among lactobacilli, attracting considerable research attention across diverse food systems. The remarkable adaptability of *L. plantarum* can be attributed to its relatively large genome size (~3.3 Mb) compared to other LAB, which encodes a broad repertoire of metabolic pathways enabling colonization of diverse ecological niches (from raw vegetables and fermented plant foods to dairy products, meat, fish, and even the human gastrointestinal tract) (Kleerebezem et al., 2003; Seddik et al., 2017). This "nomadic" lifestyle, as described by Martino et al. (2016), results from a genome evolution that appears independent of ecological pressures, unlike other specialised LAB, which exhibit a reduction in genome size as a consequence of environmental adaptation. The metabolic flexibility of *L. plantarum* is reflected in its ability to switch between homofermentative and heterofermentative pathways depending on available substrates and environmental conditions (Zheng et al., 2020). Although *L. plantarum* has a broad metabolic potential, its phenotypic expression is strongly influenced by the specific substrate and environmental conditions. Consequently, volatile production should not be considered an exclusively strain-specific trait, but rather the result of the interaction between strain-specific metabolic potential and matrix composition. Differences in precursor availability and physicochemical conditions can therefore modulate the metabolic pathways

expressed during fermentation, contributing to distinct volatile and flavour profiles across food matrices (Papadimitriou et al., 2016).

While the probiotic properties, antimicrobial activities, and general fermentation performance of *L. plantarum* have been thoroughly documented (Filannino et al., 2014; Todorov & Franco, 2010; Xing et al., 2025; Russo et al., 2017), comparatively less attention has been devoted to systematically characterizing its volatile metabolome, the complete set of volatile organic compounds (VOCs) produced during fermentation. VOCs are critical determinants of food quality, as they directly influence aroma perception and consumer acceptance (Mazzucotelli et al., 2022). In *bacteria*, VOCs mainly arise as intermediates or end products of primary metabolic pathways, including carbohydrate, amino acid, and lipid metabolism. These pathways generate a wide range of volatile compounds, including alcohols, aldehydes, ketones, organic acids, esters, sulfur-containing compounds, terpenoids, furans, and pyrazines. Owing to its remarkable metabolic versatility, *L. plantarum* is able to produce a broad spectrum of these VOCs, whose composition depends on the strain, substrate, and environmental conditions (Jiang et al., 2025). However, despite extensive research, a systematic, comparative characterization of the volatilome of *L. plantarum* across different matrices and conditions is still lacking. Most published works consist of context-specific case studies (Krieger-Weber et al., 2020; Xing et al., 2025) rather than systematic investigations, making it challenging to identify common metabolic patterns, strain-dependent variations, and matrix-specific effects on volatile biosynthesis.

This review aims to address this knowledge gap by synthesising data from peer-reviewed studies that investigated VOCs produced by *L. plantarum* in monoculture fermentation. The analysis encompasses eight major food categories: dairy (cheese, yoghurt and fermented milk), meat, fish and seafood products, fruit juices, vegetable juices, cereal-based products, agricultural by-products, and plant-based milk alternatives. The last two categories are

heterogeneous and were selected for their emerging relevance in food science and for their uniformity in intended use. For these categories as well, the product's raw material origin is the same, consistent with the findings of the other studies analyzed. Together, these findings provide a comprehensive overview of the volatile signature of *L. plantarum* fermentation, identifying common metabolic patterns and highlighting research gaps warranting future investigation.

2. Literature selection criteria

To facilitate a consistent mapping of the volatile contribution of *L. plantarum*, this review focuses primarily on studies investigating monoculture fermentations. Restricting the analysis to monoculture experiments minimizes confounding effects arising from microbial interactions and allows a more reliable assessment of VOCs directly associated with the metabolic activity of *L. plantarum*. The ultimate aim is to identify recurring volatile signatures that may represent a core volatilome of the species across different fermentation systems.

To further distinguish microbial VOC production from the intrinsic volatile background of the substrate, studies including a direct comparison between inoculated samples and non-inoculated controls were prioritized whenever available. Where a direct comparison with an uninoculated control was unavailable, strain-level or inter-treatment comparisons were used as proxies to infer directionality; these cases should be interpreted as relative modulation patterns rather than absolute changes from a true non-fermented baseline.

3. Genomic flexibility and metabolic potential

The generation of volatile aroma compounds by *L. plantarum* is rooted in four main metabolic networks: central carbon metabolism via pyruvate, amino acid and lipid catabolism, and a range of secondary biotransformation reactions, including terpenoid, phenolic, and heterocyclic

compound formation, which further diversify the species' aroma-forming capacity (Di Cagno et al., 2013; Siezen et al., 2012). Understanding these pathways is essential for predicting and interpreting the volatile profile of this species across different food matrices and fermentation conditions. The capacity of *L. plantarum* to exploit these different metabolic routes and to modulate their relative contributions according to substrate and strain characteristics is closely associated with the genomic flexibility and strain-level genetic diversity of this species.

Comparative genomic studies have shown that *L. plantarum* possesses an unusually large and flexible gene repertoire, composed of a conserved core genome associated with essential cellular functions and a highly variable accessory genome enriched in traits related to environmental adaptation (Martino et al., 2016). In particular, strain-to-strain variability has been observed in genes involved in carbohydrate transport and metabolism, exopolysaccharide biosynthesis, bacteriocin production, and other adaptive functions, indicating that different strains may possess distinct capacities for substrate utilisation and metabolic responses (Molenaar et al., 2005). More recent pan-genomic analyses confirmed that *L. plantarum* has an open and unusually large pan-genome, with extensive variation among strains. Interestingly, the distribution of variable genes was not strictly associated with the ecological origin of isolates, supporting the concept of a metabolically flexible and "nomadic" species able to adapt to diverse environments (Martino et al., 2016).

This genomic plasticity underlies strain-dependent metabolic potential and may contribute to differences in volatile production across fermentation systems. Comparative analyses of *L. plantarum* genomes have highlighted variability in enzyme families involved in flavour-related metabolism, including aromatic aminotransferases, alcohol dehydrogenases, hydroxyacid dehydrogenases, and esterases, with several of these functions represented by multiple gene copies in *L. plantarum* WCFS1 compared with other lactobacilli (Liu et al., 2008). These differences may influence the capacity of individual strains to transform carbohydrate-, amino

acid-, and lipid-derived precursors into aroma-active metabolites. However, genomic information should be interpreted as an indicator of metabolic potential rather than as a direct predictor of volatile production, since gene presence alone does not guarantee pathway activation (Yuan et al., 2024).

This distinction between genomic potential and functional output has been demonstrated by Yuan et al. (Yuan et al., 2024), who showed that genes involved in the conversion of L-phenylalanine to phenylethyl alcohol were present in most strains examined. In contrast, phenylacetaldehyde accumulation was detected only in one strain. The authors suggested that strain-specific differences in transcriptional regulation or enzyme activity of aryl-alcohol dehydrogenase may determine whether the aldehyde intermediate accumulates or is further converted into the corresponding alcohol. Similarly, Du et al. (Du et al., 2022) showed that genomic information can reveal potential aroma-forming pathways, while the final volatile profile depends on substrate availability, pathway regulation, enzyme activity, and fermentation conditions.

Therefore, the aroma-forming capacity of *L. plantarum* should be considered the result of an interaction among the genomic repertoire, context-dependent pathway regulation, and the chemical environment of the fermentation matrix. This perspective also provides a mechanistic basis for using strains from different ecological niches in fermentation processes. When introduced into non-native substrates, strains may encounter different nutrient profiles and environmental conditions that influence metabolic regulation and precursor conversion, potentially resulting in complementary volatile profiles and increased aroma complexity.

3.1 Pyruvate as a Central Metabolic Hub

Pyruvate is a central element of its metabolic network, acting as a key branching point that connects primary carbon metabolism to the biosynthesis of several odor-active molecules

(Figure 1). Under typical fermentative conditions, carbon flux is predominantly directed toward lactate production (Axelsson, 2004). However, alternative pyruvate-dissipating pathways can significantly contribute to aroma formation. In particular, pyruvate can be converted into α-acetolactate, which can then undergo two competing fates: enzymatic decarboxylation to acetoin, with subsequent reduction to 2,3-butanediol, or spontaneous oxidative decarboxylation to diacetyl (Hang et al., 2026). Both diacetyl and acetoin are relevant compounds widely associated with buttery and creamy sensory notes in fermented foods (Smid & Kleerebezem, 2014). However, excessive diacetyl concentrations can impart unpleasant off-flavours, whereas acetoin accumulation helps to temper the sharpness of buttery notes, contributing a milder aroma profile (Hang et al., 2026).

In *L. plantarum*, the partitioning of pyruvate among different metabolic routes is strongly influenced by the cellular redox balance and directly contributes to flavour development (Hang et al., 2026; Molenaar et al., 2005). Conditions favouring NAD^+ regeneration promote oxidative pathways leading to diacetyl and acetoin formation, whereas reducing conditions redirect metabolism toward lactate production. Overall, carbon partitioning is governed by the interplay between redox balance and gene expression, which ultimately determines the relative fluxes toward organic acids or aroma-active metabolites (Hang et al., 2026). This trade-off between acidification and flavour production is a key consideration in strain selection for food fermentation applications. Several studies have investigated the production of these compounds and found that citrate, naturally occurring in plant tissues (Dan et al., 2019), can stimulate diacetyl production more effectively than glucose alone. In *L. plantarum*, citrate metabolism is also connected to an incomplete tricarboxylic acid (TCA) pathway: citrate can be converted to oxaloacetate with concomitant acetate formation, while oxaloacetate can enter the reductive branch leading to malate, fumarate, and succinate (Ferain et al., 1996; Tsuji et al., 2013). Malate can additionally be converted to lactate with the release of CO_2 through

malolactic fermentation (Krieger-Weber et al., 2020). Nevertheless, citrate is a poor carbon source and may not adequately support LAB growth; consequently, higher citrate concentrations are not necessarily linked to greater biomass accumulation (Christensen & Pederson, 1958). Beyond its role in aroma formation, diacetyl production, as a neutral compound, is also associated with the cellular stress response to high pyruvate concentrations, contributing to pH regulation and acting as a detoxification mechanism (Jyoti et al., 2003). Additionally, pyruvate can be transformed into acetyl-CoA, which can subsequently support acetate formation or be converted into acetaldehyde, which is further reduced to ethanol, contributing to redox balance during fermentation (Marathe & Ghosh, 2009). Acetaldehyde imparts typical yoghurt-like notes, with optimal concentrations being critical for flavour balance (Dan et al., 2019).

3.2 Amino Acid Catabolism

L. plantarum possesses an extensive proteolytic system that releases amino acids and peptides from food proteins, generating a pool of precursors for volatile compound formation (Fig. 1) (Marathe & Ghosh, 2009). This pathway is particularly relevant in protein-rich matrices such as dairy, meat, and legume-based plant milks. Branched-chain amino acids (BCAA), leucine, isoleucine, and valine, are first transaminated to α-keto acids, which are subsequently decarboxylated to branched-chain aldehydes. These can be reduced to the corresponding alcohols or oxidised to carboxylic acids (Liu et al., 2008; Ardó, 2006). Leucine catabolism yields 3-methylbutanal and 3-methyl-1-butanol (isoamyl alcohol), associated with malty, fruity, and floral notes; isoleucine and valine generate 2-methylbutanal and 2-methylpropanal, contributing a sweaty and cheesy character (Ardó, 2006). The relative flux through these pathways depends strongly on the free amino acid pool available in the matrix, which in turn

depends on the strain proteolytic activity and the protein composition of the substrate (Ardö, 2006).

Aromatic amino acids (phenylalanine, tyrosine, tryptophan) follow the same transamination-decarboxylation route, yielding benzaldehyde, phenylacetaldehyde, and phenylethyl alcohol, which contribute floral, rose-like, and honey notes. Sulphur-containing amino acids (methionine and cysteine) generate methanethiol as a key intermediate, giving rise to dimethyl sulphide (DMS), dimethyl disulphide (DMDS), dimethyl trisulphide (DMTS), and thio-esters, associated with garlic, cabbage, and meaty aromas (Fig. 2) (Liu et al., 2008). These sulphur compounds are technologically relevant because they are often associated with off-flavours at elevated concentrations, particularly in brassica vegetable fermentations. Threonine catabolism provides an additional route to acetaldehyde, particularly relevant in protein-rich matrices where free threonine is readily available (Ardó, 2006). Moreover, this amino acid is also a source of 2,3-pentadione, which contributes to buttery and vanilla flavours, along with diacetyl, particularly relevant in yogurt or milky alternatives (Smid et al., 2014).

3.3 Lipid biotransformation

Lipolysis and subsequent fatty acid catabolism represent another major source of volatile compounds, particularly in fat-rich matrices. The oxidation of unsaturated fatty acids yields lipid-derived aldehydes: hexanal from linoleic acid, and heptanal, octanal, and nonanal from oleic acid (Fig. 1). The esterase and lipase activities of *L. plantarum* can then reduce these aldehydes to their corresponding alcohols via specific oxidoreductases, attenuating undesirable green or beany off-flavours (Shahidi & Hossain, 2022; Xing et al., 2025). This aldehyde-to-alcohol biotransformation is a technologically critical capability of *L. plantarum*, particularly valued in plant-based milk applications. The direction of this biotransformation is matrix-dependent and reflects both the reductive capacity of the strain and the susceptibility of the

matrix to lipid oxidation. Differences in fatty acid composition determine the availability of lipid-derived aldehyde precursors, ultimately influencing the resulting volatile profile. Esters are generated through the esterification of fatty acids with alcohols, catalyzed by the esterase activity of *L. plantarum*, thereby contributing fruity and fresh sensory notes (Huang et al., 2025; Bai et al., 2023). Ester production is typically more pronounced during extended fermentation times, a consideration of direct practical importance: short fermentation protocols commonly used in industrial settings may not allow sufficient ester accumulation to contribute to the aroma profile meaningfully.

3.4 Secondary metabolic contributions to aroma formation

Beyond the core metabolic pathways described in Fig. 1 and Fig. 2, *L. plantarum* contributes to aroma formation through strain-dependent enzymatic activities that modulate the transformation of matrix-derived precursors into volatile compounds. These processes mainly include biotransformation reactions, enzymatic release of bound molecules, and indirect involvement in chemical conversions occurring within the fermentation matrix. A first contribution concerns the biotransformation of plant-derived terpenoid compounds. *L. plantarum* strains have been reported to modify monoterpenes such as α-pinene and d-limonene into oxygenated derivatives, including myrtenol, and to release glycosidically bound terpenes (e.g., linalool, geraniol, nerol) via glycosidase activity. These reactions are particularly relevant in fruit and plant-based fermentations, where they increase the pool of free volatiles and enhance fruity and floral sensory notes (Di Cagno et al., 2017; Ricci et al., 2018).

Nitrogen-containing heterocyclic compounds such as pyrazines may also be detected in fermented matrices associated with LAB activity. Pyrazines can originate from the condensation of α-dicarbonyl compounds, including acetoin and related intermediates, with amino-derived α-aminocarbonyl species. In addition, they may form via Strecker-type

degradation of amino acid-derived α-keto acids, where transamination products undergo cyclisation and oxidation to yield alkylpyrazines. Although pyrazine formation is classically associated with thermal Maillard reactions, their presence in fermented foods under mild conditions suggests indirect microbial involvement through amino acid metabolism (Weisskopf et al., 2021).

Lipid-derived volatile compounds further contribute to aroma complexity in *L. plantarum* fermentations. Furan derivatives, particularly 2-pentylfuran, originate from oxidative degradation of linoleic acid via hydroperoxide intermediates and β-scission reactions. These compounds are associated with green and beany notes and exhibit low odour thresholds. Lactones are formed via intramolecular esterification of hydroxy fatty acids derived from lipid metabolism, particularly through β-oxidation pathways (Shahidi and Hossain, 2022).Phenolic acid metabolism is one of the most well-characterised strain-dependent activities of *L. plantarum*. This pathway involves the decarboxylation of hydroxycinnamic acids, such as ferulic and p-coumaric acids, leading to the formation of vinyl derivatives (e.g., 4-vinylguaiacol and 4-vinylphenol), which may be further reduced to their corresponding ethyl derivatives. The reduction step is catalysed by vinylphenol reductase, an enzyme recently characterised in *L. plantarum*, confirming its ability to convert vinylphenols into ethylphenols. However, ethylphenol production in fermented matrices appears highly dependent on substrate composition and fermentation conditions, and in some cases these compounds are not detected despite the presence of the metabolic pathway (Markkinen et al., 2021). This highlights a strong strain- and matrix-dependent regulation of phenolic aroma formation.

3.5 Factors Driving Variability in Aroma Formation

Beyond substrate composition and strain-specific metabolic traits, fermentation conditions represent an additional source of variability influencing VOC formation. Across the studies

reviewed here, incubation temperature ranged from 18 °C to 37 °C and fermentation duration from 12 h to several days, or up to 90 days in fish sauce, with these parameters generally determined by matrix-specific processing requirements rather than systematically varied. Within the same food matrix, however, temperature and fermentation time can themselves lead to distinct volatile profiles irrespective of substrate composition. For example, in sea buckthorn juice, the reduction of esters and terpenes was attributed to incubation temperature (Markkinen et al., 2021), whereas in oat flour the fermentation time associated with the most favourable aroma profile differed between *L. plantarum* strains, with one strain reaching optimal performance after 12 h and another after 20 h (Wronkowska et al., 2022), illustrating that strain genotype and fermentation conditions interact to shape aroma development. Another important procedural difference concerns the fermentation endpoint: dairy fermentations were commonly terminated upon reaching a target pH, whereas most other food matrices were fermented for a predefined incubation period. This difference in process design influences the time available for volatile accumulation and further complicates direct comparisons among studies. Consequently, the matrix-dependent differences examined in the following sections should be interpreted as the combined outcome of substrate composition, strain-specific metabolic and genomic traits, and fermentation conditions, including temperature, duration, and endpoint criteria, rather than as the consequence of any single factor considered in isolation.

4. Overview of Volatile Compound Patterns Across Food Categories

The metabolic networks described in Section 2 and illustrated in Figures 1 and 2 represent the theoretical biochemical potential of *L. plantarum*. However, VOC production during fermentation is not static; it emerges from the dynamic interaction between this enzymatic repertoire and the specific precursor availability of each food matrix. Section 3 serves as a

functional bridge between these fundamental biochemical pathways and their empirical phenotypic expression across the eight food categories as detailed in Table 1.

Compounds classified as higher or lower abundance refer to VOCs already present in the corresponding uninoculated matrix whose concentrations were modulated by fermentation, whereas compounds reported as newly detected indicate VOCs absent in the uninoculated control and detected only after fermentation, suggesting their formation or accumulation to detectable levels as a consequence of *L. plantarum* metabolic activity. Where a direct comparison with an uninoculated control was not available, strain-level or inter-treatment comparisons were used as a proxy to infer directionality, and these cases should be interpreted as relative modulation patterns rather than absolute changes from a true non-fermented baseline.

To contextualise the matrix-specific discussions that follow, Figure 3 summarises the most frequently reported VOCs across all fermentation systems considered, classified according to their direction of change relative to the uninoculated control. Where a direct comparison with an uninoculated control was not available, strain-level contrasts were used to assign directionality, as no additional studies on the same matrix fermented with *L. plantarum* were identified in the literature. Acetic acid and acetoin were the only compounds showing a consistently unidirectional pattern across all food categories, predominantly at higher or de novo levels regardless of substrate, reflecting their origin from central carbohydrate metabolism, a pathway conserved across virtually all *L. plantarum* strains regardless of substrate composition (Xing et al., 2025). For all other VOCs, both frequency and direction of change are strongly matrix-dependent, as discussed in the following sections. Reporting frequency should not be interpreted as a surrogate for sensory relevance, as aroma impact depends on compound concentration, odour threshold, and matrix-specific interactions, and

only 16 of the 50 studies included in Table 1 reported odour activity values (OAV or ROAV) or sensory evaluation data alongside instrumental analyses.

4.1 Volatile Compounds in Dairy Products

L. plantarum modulates the volatile fraction of dairy products through ketone biosynthesis, organic acid accumulation, and lipolysis-driven ester and methyl ketone production. Dairy matrices provide a favourable environment for aroma formation due to the concurrent availability of pyruvate from lactose catabolism, fatty acid precursors from lipolysis, and amino acids released during proteolysis. Diacetyl and acetoin were the most consistently produced volatile compounds across all dairy systems examined. Their concentrations increased in fermented milk, yogurt, and cream cheese, although production magnitude was strongly strain-dependent. Particularly high levels were reported for strains WJ108 and F120, isolated from traditional Chinese sauerkraut, in yogurt, and for the probiotic strain Kita-3 in cream cheese, which outperformed commercial starter cultures (Zhang, X. et al., 2024; Tian et al., 2025; Tologana et al., 2023). Both compounds are biosynthesised from pyruvate via the α-acetolactate pathway, driven by upregulation of α-acetolactate synthase and NADH oxidase, and their ratio constitutes a relevant quality parameter, since diacetyl is considerably more aromatically potent than acetoin, which attenuates its sharpness, leading to a more balanced, creamy profile (Du et al., 2022). A competing pathway redirects pyruvate to lactate, ethanol, or formate, resulting in fresher, less aromatic profiles. The low-diacetyl strain SC-4 exemplifies this behaviour, producing high levels of 2,3-butanediol, a downstream product of diacetyl, which accounts for its low residual diacetyl concentration in yoghurt (Tian et al., 2025). Medium-chain methyl ketones such as 2-heptanone, 2-octanone, and 2-nonanone also increased or decreased in a strain-dependent manner, reflecting active β-oxidation and decarboxylation pathways in lipid-rich environments (Tian et al., 2025; Zhang, X. et al., 2024).

A notable exception emerged in synbiotic ice cream, where *L. plantarum* Dad-13, when combined with inulin, exclusively produced macrocyclic ketones, 2-hydroxycyclopentadecanone and oxacyclotetradecan-2-one, not detected in any other dairy systems. This observation indicates that changing product formulation with the same strain can substantially reshape the volatile profile (Saputro et al., 2023).

Organic acid accumulation complemented ketone production across all dairy matrices. Acetic acid was the most consistent organic acid reported in fermented milk (Zhang, X. et al., 2024), yoghurt (Tian et al., 2025), and cream cheese (Tologana et al., 2023). Medium-chain fatty acids, including hexanoic, octanoic, and decanoic acids, accumulated in fermented bovine milk and cream cheese, derived from lipolysis and contributing cheese-like and mildly sour notes (Zhang et al., 2024; Tologana et al., 2023). In yoghurt, divergent organic acid profiles were observed, with the F120 strain producing benzoic acid alongside octanoic acid, and the HLB-5 strain characterised by elevated acetic acid (Tian et al., 2025). This confirms the organic acid signature in dairy reflects the interplay between lipolytic capacity and carbohydrate metabolism of individual strains.

Aldehydes showed the most variable behaviour among volatile classes in dairy. Zhang, X. et al. (2024) reported elevated levels of nonanal and decanal in strains T1 and CSK, both originating from oleic acid oxidation and associated with rose and citrus notes. This finding highlights the concentration-dependent nature of aldehyde sensory perception, as these compounds are typically associated with off-flavours at higher concentrations. Acetaldehyde, the compound most associated with the characteristic fresh yoghurt note, was produced at relevant concentrations only by strain SC-4 in yoghurt, remaining at trace levels in all other strains tested (Tian et al., 2025). This suggests that its production is strain-specific rather than a constitutive trait of the species, highlighting the need to selectively screen strains for acetaldehyde when targeting yoghurt-like fresh aromatic profiles (Tian et al., 2025). Esters

increased in a strain- and product-dependent manner, with the broadest spectrum documented in cream cheese fermented with Kita-3. This strain promoted the de novo formation of ethyl hexanoate, pentyl pentanoate, and propyl hexanoate, which were undetectable in both the commercial starter (control) and the Dad-13 strain, indicating strain-specific esterase activity. Both strains produced ethyl 2-hexanoate, though at a markedly higher level in Kita-13.The resulting ester profile conferred a fruity character that effectively masked the unpleasant fatty acid and phenolic compounds that typically accumulate during ripening (Tologana et al., 2023). In yoghurt, esters were not a relevant class in most strains, consistent with the shorter fermentation time (Tian et al., 2025), suggesting that ester production in dairy requires both extended fermentation and high fatty acid availability as provided by cheese ripening conditions. Additionally, lactones associated with creamy, buttery, and fruity flavours further contributed to modulating the overall aroma profile in cream cheese (Tologana et al., 2023). Alcohols represented a secondary volatile class with strain-specific contributions. In particular, 3-methyl-1-butanol, derived from leucine catabolism via the branched-chain amino acid pathway, reached its highest concentration in Kita-13 cream cheese, confirming its relevance to the fresh, mild bovine character associated with Mozzarella-style cheeses (Tologana et al., 2023). In contrast, 1-heptanol, a product of fatty acid reduction contributing grassy, nutty, and fatty-fermented notes, was identified as a strain-specific marker of MN-9 in yoghurt (Tian et al., 2025) and also of Kita-13 in cream cheese (Tologana et al., 2023).

4.1.1 Practical Implications for Dairy products

The dairy matrix is often described as a favorable environment for *L. plantarum* aroma production, this metabolic potential does not necessarily translate into optimal growth, which is strongly strain-dependent. For instance, Zhang H. et al. (2024) reported poor growth and viability of *L. plantarum* ST-III in milk, likely due to limited nitrogen and vitamin availability. From a production standpoint, diacetyl, acetoin and acetaldehyde act as complementary

sensory modulators, contributing buttery, creamy, and fresh yoghurt-like notes, respectively. Their synergistic balance is more relevant than individual concentrations, given that odour thresholds vary considerably across matrices (van Aardt et al., 2001). A reference ratio of 4.00:16.0:32.0 mg/L for diacetyl, acetaldehyde, and acetoin has been proposed for optimised dairy flavour, though matrix-specific calibration remains necessary (Tian et al., 2020). Therefore, strain selection should align with the desired sensory target: strains that produce more diacetyl and acetoin may be preferred for buttery, creamy dairy products, whereas acetaldehyde-producing strains are better suited to fresh, yoghurt-like notes. Since acetaldehyde production is non-constitutive in *L. plantarum*, strains must be specifically screened when yoghurt-like freshness is targeted, while its concentration should be carefully controlled to prevent strong or pungent off-notes. Beyond carbonyl compounds, ester biosynthesis represents a key lever for flavour complexity, as esters can effectively mask off-notes and improve overall sensory acceptance. However, ester formation typically requires extended fermentation times and is favored by fat-rich matrices that supply the alcohol and acid precursors necessary for esterification, suggesting that both strain selection and substrate formulation act as complementary drivers of flavour development (Tologana et al., 2023). The present review further suggests that strains exhibiting higher esterase activity, such as Kita-3, may be particularly valuable for ripened or high-fat dairy products, where increased ester formation can enhance flavour complexity and mask undesirable fatty or phenolic notes. Cross-niche strain selection, such as screening sauerkraut-derived isolates for dairy applications (Tian et al., 2025), has consistently yielded superior volatile profiles compared to dairy-native isolates, reinforcing ecological origin as an important selection criterion for starter culture development. Finally, the co-substrate effect observed in synbiotic ice cream, where the addition of inulin redirected *L. plantarum* volatile metabolism toward macrocyclic ketones absent in other dairy products (Saputro et al., 2023), highlights a underexplored aspect of dairy

fermentation volatilomics: prebiotic or functional ingredients added to the formulation may redirect volatile biosynthesis in ways that are not predictable from monoculture studies on plain milk alone, and this variable should be accounted for in the design of functional dairy products. This is exemplified by the probiotic strain Dad-13, whose volatile profile varied markedly between cream cheese and synbiotic ice cream, highlighting that the metabolic expression of a given strain is highly dependent on product formulation.

Importantly, within the dairy studies included in this review, volatile profiling was not supported by a comprehensive sensory validation. In the absence of combined OAV calculations and sensory analysis, the reported modulation of volatile compounds should be regarded as an indicator of aroma potential rather than direct evidence of improved flavour quality. Future studies should integrate chemical and sensory approaches to validate the technological relevance of strain-dependent volatile production.

4.2 Volatile Compounds in Meat Products

L. plantarum modulates the volatile fraction of meat products through pyruvate-derived ketone biosynthesis, aldehyde biotransformation, and organosulphur compound metabolism. However, the same metabolic activities that enhance flavour in controlled fermentation may also contribute to quality deterioration under spoilage conditions, revealing a dual role of this species in meat systems. Diacetyl increased markedly, while acetoin was produced de novo in sucuk fermented with the autochthonous strain *L. plantarum* GM77 compared to spontaneous fermentation, reflecting active pyruvate metabolism directed toward α-acetolactate synthesis (Kaya and Kaban, 2024). However, this trend was not universal across meat matrices. In dry-aged beef, *L. plantarum* inoculation reduced acetoin levels, which, in this context was considered a spoilage marker rather than a desirable metabolite given its association with off-flavours at elevated concentrations (Yang et al., 2025). This divergence confirms that the

443 sensory role of acetoin in meat is concentration- and product-dependent, functioning as a
444 positive aroma contributor in fermented sausages but as a quality defect indicator in aged beef.
445 Aldehyde metabolism similarly showed product-specific patterns. In sucuk, heptanal, octanal,
446 and nonanal increased, suggesting stimulation of lipid oxidation pathways, while the
447 phenylalanine-derived aldehyde 2-methyl-3-phenylpropanal, associated with undesirable off-
448 flavours at high concentrations, was substantially reduced, pointing to a catabolic activity of *L.*
449 *plantarum* GM77 toward this compound (Kaya and Kaban, 2024). In dry-aged beef,
450 benzaldehyde increased, while 6-methyl-5-hepten-2-one and 2,6-diethylpyrazine were newly
451 formed. The latter is associated with the roasted, Maillard-derived character typical of cooked
452 or aged meat (Yang et al., 2025). In contrast, in spoiled ready-to-eat chicken feet, aldehydes
453 responsible for fresh chicken aroma, notably citral, neral and nonanal, decreased significantly,
454 indicating microbial biotransformation into the corresponding alcohols or acids, and their
455 declining trend was proposed as a potential marker of chicken deterioration (Jia et al., 2025).
456 Organic acid and alcohol accumulation further differentiated controlled fermentation from
457 spoilage. In spoiled chicken feet, *L. plantarum* promoted significant increases in acetic and
458 octanoic acid, contributing sour and vinegary off-notes, alongside excessive accumulation of
459 monoterpene alcohols including linalool, α-terpineol, geraniol, citronellol, isogeraniol, and
460 neryl alcohol, whose elevated levels introduced pungent and fermented off-flavours (Jia et al.,
461 2025). Ester content also increased under spoilage conditions, driven by the high availability
462 of alcohol and acid precursors together with active esterase systems (Jia et al., 2025). In sucuk,
463 although members of the *L. plantarum* group are generally known for ester production, no
464 consistent ester trend was observed with *L. plantarum* strain GM77. A notable finding,
465 however, was the strong increase in methyl thiirane coupled with a decrease in dimethyl
466 disulphide, indicating active biotransformation of garlic-derived organosulphur precursors
467 from spice ingredients (Kaya and Kaban, 2024).

4.2.1 Practical Implications for Meat Products

The available evidence indicates that *L. plantarum* impact on meat volatiles is fundamentally context-dependent, with the boundary between flavour enhancement and spoilage being determined by product type, microbial ecology, and process control. Importantly, only one study in meat systems (Yang et al., 2025) combined volatile profiling with odour activity values (OAVs) and electronic nose analysis. This integrated approach represents a methodological advancement, enabling the identification of odor-active compounds and providing a global fingerprint of aroma changes, thereby offering a more direct interpretation of the sensory relevance of *L. plantarum*-driven volatile modulation. In controlled dry-fermented sausage production, the strain's capacity to increase diacetyl and acetoin while reducing undesirable aldehydes such as 2-methyl-3-phenylpropanal and to transform garlic-derived organosulphur compounds represents a clear technological advantage for flavour optimisation (Kaya and Kaban, 2024). In dry-aged beef, modulation of acetoin, together with the formation of benzaldehyde and Maillard-derived heterocyclic compounds, suggests a potential contribution to the roasted, nutty, and almond-like character of aged products. However, the sensory role of acetoin remains matrix-dependent (Yang et al., 2025). Conversely, the spoilage case of ready-to-eat chicken feet demonstrates that uncontrolled *L. plantarum* growth generates the same metabolic outputs, such as organic acids, terpene alcohols and esters, at concentrations that cross the threshold from desirable to detrimental, with citral and neral depletion serving as potential early indicators of quality loss (Jia et al., 2025). This dual behaviour highlights the need for strict process control in meat applications, including temperature regulation, competitive flora design, and monitoring of key volatile markers, to ensure that *L. plantarum* metabolism remains within the window of sensory benefit rather than spoilage-associated volatile accumulation.

4.3 Volatile Compounds in Fish and Seafood Products

L. plantarum modulates the volatile fraction of traditional fermented fish products through ester production, aldehyde biotransformation, and organic acid accumulation, although its capacity to reduce fishy malodours in monoculture fermentations remains limited. Ethyl esters of medium-chain fatty acids were the most distinctive contribution, with strain *L. plantarum* 1-24-LJ promoting accumulation of fruity ethyl esters predominantly towards the end of a 28-day Suanzhayu fermentation, confirming the time-dependent nature of ester production (Zhang et al., 2023). This delayed accumulation may be related to the progressive availability of ester precursors during fermentation. In particular, the gradual release and accumulation of fatty acids, together with the availability of alcohols, may favour ester synthesis through LAB-associated esterase and alcoholysis reactions during the later stages of fermentation (Holland et al., 2005). In sterile grass carp juice, *L. plantarum* L6 also produced an ester-dominated fraction, though insufficient to compensate for persistent fishy off-odours (Ma et al., 2025), while in *Zhayu* fermentation, no significant increasing trend was observed for esters except for methyl bromoacetate and phthalate, whose relevance to aroma quality remains limited (Xu et al., 2023). Alongside ester modulation, aldehyde behaviour varied markedly across fish products. In *Suanzhayu*, *L. plantarum* 1-24-LJ promoted the release of nonanal and hexanal, contributing fatty and grassy notes, together with 1-octen-3-ol and 2-pentylfuran, the latter two of which are responsible for mushroom, beany, earthy, and metallic aromas commonly associated with meat fermentation (Zhang et al., 2023). In fish sauce, however, *L. plantarum* XL23 reduced several aldehydes characteristic of traditional sauce, including 3-methylbutanal and related compounds responsible for caramelised notes, and removed the entire alkane fraction, representing a trade-off between microbiological control and preservation of sensory authenticity (Dinc et al., 2024). Organic acid accumulation further modulated aroma in fish sauce. *L. plantarum* XL23 substantially increased acetic acid and butanoic acid levels, while

hexanoic acid was detected exclusively in the inoculated group, reflecting active organic acid metabolism (Dinc et al., 2024); in *Zhayu*, *L. plantarum* L1 produced octanoic acid at elevated levels, contributing fruity and chocolate-like notes (Xu et al., 2023). Beyond these major volatile classes, modulation of alcohol and heterocyclic compounds added further layers of complexity. In *Zhayu*, *L. plantarum* L1 markedly reduced 2,3-butanediol, which was associated with pungent off-notes and correlated with spoilage-related genera, resulting in a milder sensory profile, while simultaneously increasing 2-pentylfuran and 2-butyl-3-methylpyrazine, which contributed pleasant roasted and nutty nuances through Strecker degradation pathways (Xu et al., 2023). The (−)-trans-myrtanol, rarely reported in fermented fish products, was also found at higher levels in inoculated Zhayu samples; this compound is commonly encountered in essential oils and is known for its inhibitory activity against pathogenic microorganisms (Xu et al., 2023). In contrast, in grass carp juice *L. plantarum* L6 failed to reduce compounds contributing to fishy malodour, including 1-octen-3-ol and 1-hexanol. Long-chain n-alkanes, such as hexadecane and heptadecane, were detected at high concentrations and, although associated with fresh and fermented fish products, have no aromatic impact due to their high odour thresholds (Ma et al., 2025). Notably, desirable aroma compounds such as the lactone γ-dodecalactone and 2-pentylfuran were absent or present at low levels in monoculture and accumulated only upon co-cultivation with other microorganisms (Ma et al., 2025).

4.3.1 Practical Implications for Fish Products

The available evidence indicates that *L. plantarum* monoculture delivers measurable but incomplete aroma modulation in fish matrices. On the one hand, the strain contributes positively through fruity ester accumulation, suppression of spoilage-associated compounds such as 2,3-butanediol, generation of organic acids that simultaneously lower pH and introduce desirable flavour notes, and production of bioactive terpene alcohols such as (−)-trans-myrtanol with antimicrobial potential (Xu et al., 2023). On the other hand, its inability to degrade key

543 fishy malodour compounds, particularly 1-octen-3-ol and 1-hexanol, represents a critical
544 limitation for applications where off-odour reduction is a primary objective (Ma et al., 2025).
545 The observation that desirable lactones, such as γ-dodecalactone, accumulate only during co-
546 cultivation with yeasts demonstrates that comprehensive aroma improvement in fish matrices
547 requires microbial interactions. Furthermore, eliminating aldehydes responsible for traditional
548 caramelised notes in fish sauce (Dinc et al., 2024) underscores the need to calibrate inoculation
549 strategies against product-specific sensory benchmarks, as excessive microbial standardisation
550 risks erasing the flavour signatures that define traditional fermented fish products. Strain
551 selection should therefore be guided not only by safety and acidification performance, but also
552 by volatile metabolite profiling tailored to each product category.
553 Accordingly, the future development of starter cultures for fermented fish products may require
554 a transition from single-strain selection to rationally designed microbial consortia, in which
555 complementary metabolic activities are exploited to achieve balanced aroma profiles.
556 The interaction between *L. plantarum* and complementary microorganisms, particularly yeasts,
557 offers a promising strategy to enhance volatile profiles via microbial cross-feeding and
558 metabolic complementarity. These findings indicate that microbial consortia may provide
559 greater control over aroma development than single-strain fermentation in complex fish
560 matrices.
561 However, the technological relevance of these changes remains difficult to establish without
562 sensory-oriented validation. Sensory relevance has been evaluated in only one fish
563 fermentation study included in this review. In Suanzhayu, OAV analysis identified 16 volatile
564 compounds with potential aroma activity, highlighting nonanal, hexanal, 1-octen-3-ol and 2-
565 pentylfuran as key contributors associated with *L. plantarum* inoculation. This approach
566 provides a more robust interpretation of volatile modulation by linking compound abundance

with aroma contribution, although further studies integrating OAV calculations with sensory evaluation are required to confirm their perceptual impact.

4.4 Volatile Compounds in Agricultural By-Products

Agricultural by-products represent a chemically heterogeneous group of substrates, and the volatile response to *L. plantarum* fermentation proved equally variable, with off-odour reduction as the most consistent outcome, and terpene biotransformation as the most substrate-dependent. Off-odour reduction was the most consistent trend across matrices: in tuna cooking liquid, *L. plantarum* RP26 decreased ketones such as 2-nonanone, nitrogen compounds such as trimethylamine, and sulphur compounds such as dimethyl trisulfide, all commonly associated with fatty and fishy off-odours, while simultaneously promoting the accumulation of aldehydes such as (E)-2-dodecenal and 2-butyl-2-octenal alongside 2-undecanone, which collectively contribute grassy and fruity notes (Ma et al., 2023). In orange peel fermentation, L. plantarum Harvest LB-1 substantially reduced the aldehydes octanal, hexanal, (E)-2-hexenal, nonanal, and decanal, which are typically responsible for green, pungent, and bitter sensory attributes (Deba-Rementeria et al., 2022). In rice bran, *L. plantarum* 423 likewise decreased the overall aldehyde content, whereas in wheat bran, an opposite trend was observed, with octanal propylene glycol acetal becoming the predominant carbonyl-derived compound and contributing sweet orange aroma notes (Wang et al., 2020). This substrate-dependent divergence demonstrates that carbonyl compound metabolism in *L. plantarum* is not intrinsically unidirectional but is strongly shaped by precursor availability in the fermentation matrix. Alongside carbonyl modulation, terpene biotransformation followed highly strain- and substrate-specific patterns. In hemp seed bran, *L. plantarum* 98B exhibited exceptional capacity for producing β-linalool, alongside p-cymen-8-ol, Δ-3-carene, cis-β-farnesene, borneol, and eucalyptol. In contrast, several terpenes characteristic of the unfermented hemp

bran, including geraniol, β-pinene, α-farnesene, 9-methyldecalin, and β-selinene, were substantially depleted or absent, suggesting microbial consumption or biotransformation of intrinsic substrate terpenes (Nissen et al., 2021). In orange peel, *L. plantarum* Harvest LB-1 reduced linalool, α-terpineol, geranial and neral, and carvone, attenuating citrusy and floral notes, while selectively increasing δ-3-carene (Deba-Rementeria et al., 2022). These contrasting outcomes indicate that *L. plantarum* acts simultaneously as a terpene producer and consumer, with the net balance determined by the terpenoid precursor pool of the raw material. Beyond terpenes, organic acid and phenol accumulation contributed further layers of aroma complexity. In hemp seed bran, *L. plantarum* LB325 progressively increased the production of volatile short-chain fatty acids, including acetic, propionic, and butyric acids, which are recognised as postbiotics generated through fibre degradation and are associated with gut health benefits (Nissen et al., 2021). In rice bran, *L. plantarum* 423 promoted a marked increase in phenolic compounds, with 4-ethylphenol emerging as the dominant volatile phenol and contributing herbal flavour characteristics, an effect not observed in wheat bran fermented with the same strain (Wang et al., 2020). Regarding esters, in orange peel, hexyl butanoate and butyl butyrate decreased during *L. plantarum* Harvest LB-1 fermentation, contributing to the overall attenuation of fruity notes (Deba-Rementeria et al., 2022). Notably, volatile modulation by *L. plantarum* can also carry functional consequences beyond aroma. In hemp seed bran, *L. plantarum* LB325 showed no detectable production of myrcene and only negligible amounts of p-cymene, two compounds strongly associated with antimicrobial and prebiotic activity, consistent with the relatively lower prebiotic score recorded for this strain (Nissen et al., 2021). Despite compositional differences across substrates, electronic nose analysis of rice and wheat bran fermentation broths revealed similar overall aroma profiles, suggesting that global volatile patterns rather than individual compound abundance better reflect the aroma of fermented by-products (Wang et al., 2020).

4.4.1 Practical Implications for Agricultural By-Products

The available evidence positions *L. plantarum* as a versatile tool for the sensory upgrading of agricultural by-products, yet with important caveats for process design. However, the sensory relevance of these volatile modifications remains largely unexplored. Among the agricultural by-product studies included in this review, volatile characterization generally relied on compound identification and relative abundance, while approaches integrating OAVs or sensory validation remain lacking. Consequently, increases or reductions in specific volatile compounds should be interpreted as changes in aroma potential rather than confirmed improvements in sensory quality. The strain's consistent ability to reduce off-odour ketones, nitrogen compounds, and sulphur volatiles makes it particularly promising for deodorising protein-rich waste streams such as tuna cooking liquid, where off-flavour removal is the primary technological objective (Ma et al., 2023). In fruit-derived by-products, the capacity to shorten fermentation time from weeks to days while attenuating excessively pungent or bitter aldehydes offers clear advantages for industrial scalability, although the concurrent reduction of desirable monoterpene alcohols, monoterpene aldehydes, and esters means that inoculation protocols must be carefully calibrated to avoid over-processing (Deba-Rementeria et al., 2022). The strong substrate-dependency observed across cereal brans, where the same strain produced opposite aldehyde trends in rice versus wheat matrices (Wang et al., 2020), underscores that volatile outcomes cannot be extrapolated from one by-product to another without dedicated profiling. Furthermore, the case of hemp seed bran illustrates that strain selection should account not only for aroma but also for functional properties: the exceptional β-linalool production by *L. plantarum* LB325 came at the expense of myrcene and p-cymene, two compounds positively correlated with prebiotic activity (Nissen et al., 2021). This trade-off between sensory and bioactive outcomes implies that multi-strain consortia or sequential inoculation strategies may be necessary when both flavour enhancement and functional

enrichment are targeted simultaneously. Overall, effective valorisation of agricultural by-products through *L. plantarum* fermentation requires a matrix- and strain-specific approach, guided by integrated volatile, odour activity and functional profiling rather than generalised assumptions about flavour improvement.

4.5 Volatile Compounds in Fruit Juices

Across all fruit juice matrices examined, *L. plantarum* fermentation exhibited a common metabolic pattern characterised by aldehyde reduction, accumulation of alcohols and ketones, and increased organic acid production, although the extent of these changes was strongly dependent on strain and substrate. Aldehyde depletion represented the most frequent trend observed across all matrices examined. In pomegranate juice, *L. plantarum* C2, POM1, and LP09 significantly reduced branched-chain aldehydes such as 2-methyl-propanal, 3-methyl-butanal, butanal, and pentanal, which are associated with cooked and off-flavour notes. They also reduced sulphur compounds, including methanethiol, dimethyl sulphide, and dimethyl disulphide, which are known to contribute to unpleasant odours. In addition, furan compounds, especially furfural, which are linked to Maillard reactions and coffee- or caramel-like off-aromas, were reduced. These compounds are commonly found in commercial pasteurized juices, and their formation can be further promoted by the juice's acidic conditions (Di Cagno et al., 2017). A comparable pattern was observed in sea buckthorn juice, where six *L. plantarum* strains reduced green-associated aldehydes such as hexanal, heptanal, octanal, and nonanal (Markkinen et al., 2021), and in watermelon juice, where *L. plantarum* JHT78 decreased unsaturated aldehydes including 2-octenal and 6-nonenal (Shi et al., 2023). Studies attributed this reduction to microbial conversion of aldehydes to their corresponding alcohols, a biotransformation that attenuates perceived green character rather than simply replacing it, since the resulting alcohols typically have higher odour thresholds than their aldehyde

667 precursors (Markkinen et al., 2021).In elderberry juice, some aldehydes were also reduced
668 relative to the unfermented control and isovaleraldehyde (3-methyl-butanal) emerged as one of
669 the key volatile markers distinguishing *L. plantarum*-fermented samples (Ricci et al., 2018).
670 However, not all aldehydes followed a decreasing trend, as demonstrated by the increase in 3-
671 methyl-2-butenal in sea buckthorn juice, which contributed fruity notes (Markkinen et al.,
672 2021).
673 The alcohols generated through aldehyde conversion, together with those produced *de novo*,
674 consistently enriched the volatile profile of fermented juices. In pomegranate juice, 1-butanol,
675 1-hexanol, and ethanol contributed sweet and fruity notes (Di Cagno et al., 2017), while in
676 elderberry juice, hexanol, (Z)-3-hexen-1-ol, and (E)-2-hexen-1-ol, carriers of fresh green notes
677 characteristic of this fruit, were most abundantly produced by dairy-derived strains, particularly
678 *L. plantarum* 285 (Ricci et al., 2018). In sea buckthorn juice, 3-methyl-1-butanol, ethanol, and
679 benzyl alcohol increased, introducing fermented and floral notes (Markkinen et al., 2021), and,
680 in watermelon juice, 1-penten-3-ol and phenylethyl alcohol were identified as key fermentation
681 markers (Shi et al., 2023). Ketone accumulation was equally consistent: diacetyl and acetoin,
682 both biosynthesised from pyruvate originating from citrate or carbohydrate metabolism,
683 increased in elderberry (Ricci et al., 2018), sea buckthorn (Markkinen et al., 2021), and
684 pomegranate juice (Di Cagno et al., 2017), contributing buttery and creamy notes. Acetoin
685 accumulation in *L. plantarum* has often been attributed to limited 2,3-butanediol
686 dehydrogenase activity, which restricts the conversion of acetoin into 2,3-butanediol
687 (Markkinen et al., 2021). However, this metabolic trait appears to be strain-dependent, as
688 comparative genomic analyses have identified *L. plantarum* strains carrying genes associated
689 with butanediol dehydrogenase/diacetyl reductase activity, enabling the further conversion of
690 acetoin to 2,3-butanediol (Choi et al., 2021). In pomegranate juice, additional methyl ketones,
691 including 2-propanone, 2-pentanone, 2-heptanone, and 2-nonanone, were markedly elevated

(Di Cagno et al., 2017), while in sea buckthorn juice, 2-undecanone was detected exclusively in fermented samples, making it a specific marker of *L. plantarum* metabolic activity in this substrate (Markkinen et al., 2021).

Terpene modulation was strongly strain-dependent and influenced by the ecological origin of the isolate. In pomegranate juice, *L. plantarum* POM1 and LP09 substantially increased limonene, β-myrcene, γ-terpinene, α-terpinene, terpinolene, and p-cymene, their release being attributed to enzymatic hydrolysis of glycosidically bound precursors (Di Cagno et al., 2017). In elderberry juice, dairy-derived strains significantly enhanced the production of β-linalool and β-damascenone compared to plant-derived isolates, reflecting strain-specific differences in terpene release and biosynthetic capacity(Ricci et al., 2018). In contrast, in sea buckthorn juice, terpene and ester decline was driven primarily by incubation temperature rather than microbial activity, as the same decrease occurred in both inoculated and non-inoculated controls (Markkinen et al., 2021), demonstrating that process parameters can override strain-specific metabolic contributions to the volatile profile.

Organic acid accumulation was both desirable and potentially detrimental. Acetic acid emerged as the key differentiating compound in elderberry juice, being most strongly associated with *L. plantarum* fermentation (Ricci et al., 2018), and increased markedly in sea buckthorn juice through both the acetate kinase route and citrate metabolism (Markkinen et al., 2021), as well as in watermelon juice, where the overall acid increase was considered beneficial for shelf-life extension (Shi et al., 2023). However, excessive acetic acid accumulation introduces a vinegar-like off-note, raising quality concerns (Markkinen et al., 2021). In sea buckthorn juice, medium-chain fatty acids, including hexanoic, heptanoic, octanoic, and nonanoic acids, also increased, possibly due to increased hydrolysis of the corresponding esters by lipase and/or esterase activities of *L. plantarum*. While this hydrolysis liberates aromatic acids, the concurrent accumulation of free fatty acids introduces rancid and cheesy off-notes (Markkinen

et al., 2021). With respect to esters, a slight increase was observed in pomegranate juice, linked to the higher availability of alcohol precursors (Di Cagno et al., 2017), and in elderberry juice, where ethyl acetate, methyl isovalerate, isoamyl isovalerate, and methyl salicylate contributed fruity notes (Ricci et al., 2018), while watermelon juice similarly showed ester enhancement following fermentation (Shi et al., 2023). Beyond aroma-related effects, some volatile changes were also associated with functional outcomes, including reduced astringency perception in watermelon juice through acetaldehyde-mediated tannin interactions (Shi et al., 2023). (Di Cagno et al., 2017).

4.5.1 Practical Implications for Fruit Juices

The available evidence indicates that *L. plantarum* is a promising tool for reshaping the volatile profiles of fruit juices, with fruit matrices providing the strongest evidence within this review that volatile changes can translate into perceptible sensory effects. Indeed, compared with other food categories, fruit juice studies more frequently incorporated sensory evaluation, electronic nose analysis, and, in selected cases, OAV assessment, allowing a more robust interpretation of the aroma relevance of fermentation-induced volatile changes. However, sensory outcomes remain highly dependent on the interaction between strain, substrate composition, and fermentation conditions. The conserved aldehyde-to-alcohol conversion represents the most predictable and broadly applicable metabolic contribution, consistently attenuating green and cooked off-notes across berry, stone fruit, and tropical matrices (Di Cagno et al., 2017; Markkinen et al., 2021; Shi et al., 2023). However, the concurrent accumulation of acetic acid and medium-chain fatty acids through ester hydrolysis poses a tangible risk of introducing vinegar-like, rancid, and cheesy off-notes that may offset the aromatic benefits (Markkinen et al., 2021). Strain origin appears to influence metabolic performance, as dairy-derived isolates enhanced the release of terpenes, norisoprenoids, ketones, and alcohols in elderberry juice more effectively than plant-derived strains (Ricci et al., 2018), indicating that ecological origin does

not necessarily predict suitability for a specific fermentation substrate. These findings indicate that ecological origin alone does not necessarily predict a strain's suitability for fermenting a specific substrate. In particular, during elderberry juice fermentation, the cheese-derived strain *L. plantarum* 285 showed higher VOC production and a broader VOC profile than strains originating from plant environments (Ricci et al., 2018). Similar observations have been reported in other fermented foods, where using strains from different ecological niches (a cross-fermentation approach) has been shown to improve flavour development (Alemayehu et al., 2014).

One possible explanation is that strains introduced into a non-native environment may activate different adaptive and stress-response mechanisms, thereby affecting their metabolic pathways. Indeed, under stressful conditions, food-associated LAB have been reported to enhance the production of aroma-related metabolites (Papadimitriou et al., 2016). In the case of elderberry juice, the enhanced formation of compounds characteristic of its native aroma profile, such as β-linalool, β-damascenone, 2-phenylethanol, hexanol, and 3-hexen-1-ol, suggests that the selection of strains from different ecological origins could represent a strategy to modulate, restore, or enhance the original aroma profile after processing-related losses.

Process optimisation is equally critical, as fermentation parameters may override strain-specific metabolic effects. In sea buckthorn juice, the decline of terpenes and esters occurred independently of inoculation, indicating that incubation temperature exerted a stronger influence than microbial activity on volatile evolution. Thus, temperature and fermentation duration should be optimised before attributing volatile changes exclusively to strain performance. (Markkinen et al., 2021).Overall, successful application of *L. plantarum* in fruit juice fermentation should require an integrated strategy combining strain selection based on volatile, ecological origin of the isolate, and process optimisation. Future work should focus

on limiting volatile acid and free fatty acid accumulation while maximising terpene release and aldehyde reduction.

4.6 Volatile Compounds in Vegetable Juices and Fermented Vegetables

Vegetable matrices brought out some of the most striking capabilities of *L. plantarum*: the complete elimination of beany off-flavours in legumes, selective terpene modulation in root vegetables, and outstanding ester biosynthesis in fermented cabbage. Aldehyde modulation was a recurrent feature across vegetable matrices, although the direction and magnitude of changes were strongly substrate-dependent. In mung beans, three *L. plantarum* strains significantly decreased hexanal, hexanol, and 1-octen-3-ol, the main contributors to undesirable beany flavour, with the volatile profile shifting from an aldehyde-dominated character in unfermented beans to an ester-dominated one in fermented samples, described as fruity and grassy with no beany flavour (Yi et al., 2021). Several additional aldehydes, including nonanal, octanal, 2-furfural, and 3-methylbutanal, decreased or were no longer detected, although *L. plantarum* YI-Y2013 showed weaker aldehyde reduction, which correlated with its limited amino acid metabolism (Yi et al., 2021). In carrot juice, *L. plantarum* WZ-01 demonstrated a different aldehyde pattern, promoting the formation of hexanal and heptanal, benzaldehyde, and 2-nonenal, alongside octanone and damascenone, while acetoin nearly doubled (Zhang et al., 2019). This divergent aldehyde behaviour between legume and root vegetable matrices confirms that *L. plantarum* aldehyde metabolism is substrate-dependent rather than uniformly reductive.

Terpene modulation was particularly pronounced in matrices rich in terpenoid precursors. In carrot juice, *L. plantarum* WZ-01 completely eliminated β-pinene, β-phellandrene, and ocimene, responsible for the characteristic green carrot-like off-flavour, after 72 h of fermentation, while significantly reducing α-pinene, sabinene, and β-myrcene (Zhang et al.,

2019). In sauerkraut, *L. plantarum* fermentation remarkably increased terpene concentrations, particularly linalool, citral, and linalool oxide, associated with floral and fruity notes, likely through glycosidase-mediated release from non-volatile precursors or de novo biosynthesis (Yang et al., 2020). In cabbage juice, *L. plantarum* E10 similarly enhanced linalool and phenylethyl alcohol (Liang et al., 2025), suggesting that terpene release may represent a relevant metabolic capacity of *L. plantarum* in brassica fermentations.

Ester biosynthesis emerged as a defining feature of *L. plantarum* in vegetable fermentation. In sauerkraut, *L. plantarum* produced the highest ester abundance among all lactic acid bacteria tested, including isoamyl acetate, ethyl octanoate, ethyl lactate, and ethyl acetate, contributing banana-like, apple-like, milky, and strawberry-like notes, respectively, a finding attributed to the optimal esterase activity of *L. plantarum*, which is particularly active at low temperatures commonly encountered in food fermentations (Yang et al., 2020). The production of isoamyl acetate was associated with elevated levels of the higher alcohol isoamyl alcohol, derived from leucine catabolism, supporting the role of amino acid-derived alcohols as precursors for ester biosynthesis (Yang et al., 2020). In mung beans, the esters isoamyl acetate, ethyl acetate, and ethyl hexanoate similarly increased during fermentation (Yi et al., 2021), while in red beetroot juice *L. plantarum* ATCC 3543 demonstrated the highest capacity for volatile compound formation among all strains tested, with exclusive formation of different new compounds including alcohols, ketones, acids, furan and esters (Foss et al., 2023).

Organic acid and alcohol accumulation contributed further aroma dimensions. In sauerkraut, *L. plantarum* was associated with the highest hexanoic acid content, imparting sweet cheese and rancid notes, while acetic acid, the most abundant acid overall, was produced at higher levels by other lactic acid bacteria with heterofermentative metabolism (Yang et al., 2020). In red beetroot juice, acids were the most abundant volatile class, followed by phenols, ketones, and alcohols (Foss et al., 2023). Higher alcohols showed strain-specific profiles in sauerkraut:

isoamyl alcohol accumulated consistently with leucine catabolism, and phenylethyl alcohol derived from phenylalanine catabolism, as supported by the correspondingly lower levels of these amino acids in *L. plantarum*-fermented sauerkraut (Yang et al., 2020). In mung beans, 2,3-butanediol increased during fermentation (Yi et al., 2021), although this finding contrasts with other matrices where *L. plantarum* is reported to lack the specific enzyme for this conversion. Alongside volatile modulation, *L. plantarum* fermentation of sauerkraut resulted in the lowest levels of isothiocyanates coupled with the highest levels of nitriles and indoles, nitrogen-containing heterocyclic compounds with potential chemopreventive properties (Yang et al., 2020), demonstrating that volatile biotransformation by *L. plantarum* can carry functional implications beyond aroma.

A notable limitation was identified in cabbage juice fermentation, where *L. plantarum* E10 showed only limited capacity to reduce dimethyl trisulphide and dimethyl disulphide, the most representative and unpleasant sulphuric volatiles of fresh cabbage juice; effective elimination of these off-odours required other strategies. This finding highlights that selection of *L. plantarum* strains for vegetable fermentation should consider not only their capacity to generate desirable volatiles but also their ability to remove matrix-specific off-odours.

4.6.1 Practical Implications for Vegetables

L. plantarum can be an effective tool for deodorising vegetable matrices and building fermented flavour complexity, although specific off-flavour challenges may exceed its monoculture capacity. The species demonstrated attenuation of beany off-flavour in mung beans through combined aldehyde and alcohol reduction, coupled with ester enrichment that redirected the volatile profile toward fruity and grassy notes acceptable to consumers (Yi et al., 2021), and marked reduction of carrot top off-flavour through selective degradation of monoterpene hydrocarbons (Zhang et al., 2019). These results position *L. plantarum* as a reliable single-strain solution when the target off-flavour compounds fall within its metabolic

reach. However, sulphur compound reduction in brassica matrices represents a clear boundary: dimethyl trisulphide and dimethyl disulphide persisted during *L. plantarum* monoculture fermentation of cabbage juice. The effective removal of these off-flavours required co-fermentation with other microorganisms. The outstanding esterase activity demonstrated in sauerkraut, particularly at low temperatures (Yang et al., 2020), suggests that cold-chain vegetable fermentations may represent an optimal industrial niche for exploiting *L. plantarum* ester biosynthesis. Furthermore, the capacity to simultaneously reduce isothiocyanates while increasing nitriles and indoles with bioactive potential (Yang et al., 2020) opens opportunities to position *L. plantarum*-fermented vegetables as functional foods, provided that these bioactive volatile biotransformations are validated through dedicated in vivo studies. Overall, strain selection for vegetable fermentation should integrate volatile metabolite profiling with assessment of amino acid metabolism capacity, given that strains with weak amino acid catabolism showed correspondingly weaker aldehyde reduction (Yi et al., 2021), and process design should account for the co-substrate and co-culture requirements specific to each vegetable matrix.

4.7 Volatile Compounds in Cereal-Based Products

Unlike most food matrices examined in this review, cereal fermentations were characterised by a consistent increase in aldehydes following *L. plantarum* fermentation, rather than their depletion. Aldehydes represented the predominant volatile class across all cereal matrices examined, suggesting that substrate-specific lipid oxidation pathways override the aldehyde-reducing metabolism commonly observed in other food systems. In oat flour, hexanal, derived from lipid oxidation, increased substantially during fermentation with *L. plantarum* W42 and IB, while several additional aldehydes appeared exclusively in fermented samples, including 3-methylbutanal, (E)-2-hexenal and (Z)-2-heptenal (Wronkowska et al., 2022). A comparable

trend was observed in wheat sourdough, where *L. plantarum* P1 produced the highest hexanal concentration among all lactic acid bacteria tested, suggesting enhanced lipid oxidation activity (Liu et al., 2020).

Alcohol production consistently accompanied aldehyde accumulation across cereal matrices. In wheat sourdough, *L. plantarum* P1 generated significantly higher concentrations of 1-pentanol,1-hexanol and 3-methyl-1-butanol (Liu et al., 2020). The simultaneous accumulation of hexanal and 1-hexanol in the same sourdough suggests that lipid oxidation and aldehyde reduction occurred concurrently, with hexanal formation likely exceeding its subsequent conversion to the corresponding alcohol (Liu et al., 2020). In durum wheat sourdough, fermentation increased the release of ethanol, 1-pentanol, 2-methyl-2-buten-1-ol, and 1-decanol (Ferri et al., 2016), while in KAMUT® khorasan wheat dough, 1-hexanol accumulated alongside 2-pentylfuran and the lactone 2(3H)-furanone (Ferri et al., 2016). In oat flour, 1-hexanol and acetic acid were the primary accumulating compounds, along with hexanal (Wronkowska et al., 2022). These parallel aldehyde-alcohol profiles across wheat, ancient grain, and oat matrices suggest that lipid oxidation coupled with alcohol dehydrogenase-mediated reduction represents a major route of volatile formation during cereal fermentation with *L. plantarum*. Organic acid and ketone production added further aroma dimensions. Acetic acid increased in oat flour (Wronkowska et al., 2022), KAMUT® khorasan wheat dough, where it accumulated alongside hexanoic and octanoic acids (Ferri et al., 2016), and wheat sourdough, where butanoic and pentanoic acids also increased (Liu et al., 2020). Acetoin was detected in all fermented cereal samples across studies (Liu et al., 2020; Ferri et al., 2016; Wronkowska et al., 2022), supporting pyruvate-derived ketone biosynthesis as a common metabolic outcome of *L. plantarum* in cereal matrices, while 1-hydroxy-2-propanone was additionally reported in wheat sourdough (Liu et al., 2020). In contrast, ester production was notably absent or negligible: *L. plantarum* P1 demonstrated the capacity to produce buttery-

note compounds in wheat sourdough while lacking the ability to generate esters associated with fruity and floral aromas (Liu et al., 2020), and in durum wheat dough, esters did not characterise the fermented samples (Ferri et al., 2016). This ester deficiency in cereals contrasts sharply with the ester-rich profiles reported for *L. plantarum* in vegetable and dairy fermentations. It likely reflects the limited availability of medium-chain fatty acid and alcohol precursors necessary for esterification in cereal matrices. A noteworthy finding from durum wheat and KAMUT® khorasan wheat fermentation was that alcohols and carbonyl compounds were positively correlated with polyphenol content, suggesting that the aroma-active fraction of *L. plantarum* fermentation is not isolated from the health-promoting metabolic activity of the strain (Ferri et al., 2016). Additionally, in oat flour, the strain-specific marker methoxyphenyl oxime was detected exclusively in *L. plantarum* W42-fermented samples, highlighting the strain-dependent nature of volatile production within the same species (Wronkowska et al., 2022).

Substrate-dependency was particularly pronounced in cereal fermentation. The effect of *L. plantarum* on the volatile profile was more marked in durum wheat than in KAMUT® khorasan wheat, where the substrate itself exerted a dominant influence on the metabolic outcome, partly masking strain-dependent differences (Ferri et al., 2016). Optimal strain-substrate combinations differed between the two flour types: strains 98A and 6BHI provided the best sensorial and health-promoting characteristics in durum wheat dough, while strains 94A and 206 showed the highest performance in KAMUT® khorasan wheat dough, confirming that strain selection for sourdough fermentation cannot be decoupled from the choice of substrate (Ferri et al., 2016). Similarly, the optimal fermentation time differed between strains in oat flour: *L. plantarum* W42 reached the highest volatile content at 12 hours, whereas IB required 20 hours (Wronkowska et al., 2022).

4.7.1 Practical Implications for Cereals

The practical application of *L. plantarum* in cereal fermentation requires a different strategy from that adopted for other food matrices. Unlike dairy, fruit, and vegetable systems, where the species primarily reduces aldehydes and promotes ester formation, cereal fermentations are characterised by lipid oxidation-driven production of aldehydes and alcohols. Consequently, *L. plantarum* is inherently suited for generating fatty, green, and malty aroma notes rather than the fruity and floral profiles. The consistently limited ester production observed across all cereal substrates examined suggests that fruity aroma complexity is in cereal-based products would require either extended fermentation times beyond the 12–24 hours typically employed (Liu et al., 2020), co-fermentation with ester-producing species, or substrate enrichment with alcohol and fatty acid precursors to promote esterification. The strong substrate-dependency documented across wheat, ancient grain, and oat matrices (Ferri et al., 2016; Wronkowska et al., 2022) underscores that strain selection must be performed in the target cereal rather than extrapolated from screening in standard laboratory media, since the same strain can yield markedly different volatile outcomes depending on the flour type. The positive correlation between aroma-active volatiles and polyphenol content (Ferri et al., 2016) offers opportunities for dual-purpose strain selection targeting both sensory and health-promoting outcomes. From a process standpoint, fermentation kinetics require strain-specific optimisation, as the window for maximum volatile accumulation varies from 12 to 20 hours depending on the strain. (Wronkowska et al., 2022) Finally, methodological factors should also be considered when interpreting volatile data. In particular, sample preparation procedures, such as autoclaving, may contribute to the baseline volatile profile, which must be accounted for when assessing the net contribution of *L. plantarum* fermentation to aroma development.

4.8 Volatile Compounds in Plant-Based Milk Alternatives

Plant-based milk alternatives emerged as one of the most promising application areas for *L. plantarum*, given its conserved capacity to reduce beany and grassy off-flavours while simultaneously promoting the buttery and creamy notes associated with conventional dairy yoghurt. Aldehydes reduction was the most consistent metabolic pattern across all matrices examined. In soymilk, *L. plantarum* X7021 demonstrated superior capability in degrading the three main beany flavour compounds, hexanal, 1-octen-3-ol, and 2-pentylfuran, compared to commercial yoghurt starters. This metabolic advantage was attributed to its extensive oxidoreductase system encoded in its genome, which included approximately 44 sequences annotated as oxidoreductases, particularly members of the short-chain dehydrogenases and aldo/keto reductases families (Du et al., 2022). The biotransformation of hexanal to both hexanoic acid and hexanol was directly observed in a soy matrix (Du et al., 2022). In walnut milk, hexanal decreased significantly while nonanal was no longer detected, consistent with the general tendency of aldehydes to be rapidly reduced to alcohols or oxidised to acids in fermented matrices (Liu et al., 2022). Across four plant-based milk alternatives, *L. plantarum* NCC 2988 effectively decreased aldehydes responsible for bean-like and grassy off-flavours, including hexanal, heptanal, nonanal, and 2-nonenal, through reductive conversion to the corresponding primary alcohols (1-hexanol, 1-heptanol, 1-octanol, and 1-nonanol). This biotransformation is considered beneficial because alcohols exhibit higher odour thresholds and contribute sweeter, fruitier aroma notes than their aldehyde precursors (Tangyu et al., 2023). In contrast, almond beverage fermentation resulted in a more complex aldehyde profile, including hexanal and benzaldehyde, the latter being a key contributor to the characteristic almond-like aroma of the matrix, along with additional volatile compounds generated during fermentation REF. Similarly, aldehydes remained the dominant volatile class in coconut water fermented with *L. plantarum* A33, with nonanal exhibiting the highest relative OAV and contributing fatty, citrus, and green notes (Xu et al., 2025). In a rice-based fermented beverage,

965 benzaldehyde was the only aldehyde detected (Giri et al., 2018), confirming that aldehyde
966 metabolism by *L. plantarum* is strongly influenced by substrate composition.
967 Alcohol accumulation consistently accompanied aldehyde reduction across plant-based milk
968 alternatives (Liu et al., 2022; Tsibourginoudi et al., 2026). In walnut milk, dramatic increases
969 were observed in hexanol, pentanol, and isoamyl alcohol, while 2,3-butanediol, heptanol, and
970 the aromatic alcohols benzyl alcohol and phenylethyl alcohol were detected exclusively after
971 fermentation (Liu et al., 2022). Similarly, in almond beverage, increases in the medium-chain
972 alcohols (1-hexanol, 1-heptanol and 1-octanol) were accompanied by the exclusive appearance
973 of 3-methyl-1-butanol (isoamyl alcohol), benzyl alcohol, 1-nonanol, and 2-methyl-2-propanol
974 after fermentation (Tsibourginoudi et al., 2026). In a rice-based beverage, isoamyl alcohol was
975 the most relevant alcohol, contributing sweet, banana-like notes (Giri et al., 2018).
976 Ketone biosynthesis through pyruvate metabolism represented a consistent feature across nut-
977 and legume-based matrices. In both walnut milk and soymilk, diacetyl and acetoin were the
978 predominant ketones, arising from citrate and pyruvate metabolism and imparting desirable
979 buttery and creamy notes (Liu et al., 2022; Du et al., 2022). Diacetyl exhibits an aroma potency
980 approximately 100-fold greater than acetoin; however, acetoin complements its sensory impact
981 by softening the sharp buttery character and contributing to a more balanced, creamy profile
982 (Du et al., 2022). Additional ketones, 2,3-pentanedione and 2,5-hexanedione were detected
983 exclusively in fermented walnut milk, confirming their microbial origin (Liu et al., 2022). In
984 soymilk, sucrose supplementation further enhanced diacetyl accumulation by stimulating
985 glycolysis and increasing pyruvate availability, while simultaneously reducing acetoin
986 production due to non-enzymatic conversion from α-acetolactate to diacetyl (Du et al., 2022).
987 Terpene modulation was substrate-dependent and particularly pronounced in matrices rich in
988 terpenoid precursors. In sunflower seed milk, *L. plantarum* NCC 2988 displayed active
989 terpenoid metabolism, converting terpene alkenes such as α-pinene and D-limonene into their

corresponding alcohols, resulting in approximately a 50-fold increase in (−)-myrtenol and contributing pleasant minty and woody notes (Tangyu et al., 2023). In faba milk, the same strain contributed to increased formation of linalool, a highly valued terpenoid associated with citrus and floral aromas (Tangyu et al., 2023). Beyond terpene modulation, organic acid and ester production varied markedly across matrices. *L. plantarum* NCC 2988 proved particularly effective in enhancing cheesy and sour flavour notes in legume-based milks through the formation of branched-chain fatty acids, 2-methyl butanoic acid and 3-methyl butanoic acid, a finding of industrial relevance given the current consumer demand for non-dairy cheese alternatives (Tangyu et al., 2023).

In walnut milk, acetic acid, butyric acid, and hexanoic acid were found only after fermentation, with acetic acid remaining within the concentration range considered optimal for fermented dairy-like products (Liu et al., 2022). In soymilk, *L. plantarum* X7021 showed stronger acetic acid production than the yoghurt starter, with acetic acid synthesised mainly through bypasses of the pyruvate and acetyl-CoA cycle (Du et al., 2022). Ester profiles were highly substrate-dependent: in rice-based beverages, esters dominated the entire volatile profile, with succinic acid diethyl ester and octanoic acid ethyl ester as the most abundant compounds (Giri et al., 2018), while in walnut milk, ethyl lactate increased markedly, contributing floral and fruity notes (Liu et al., 2022). In contrast, in coconut water, fruity esters were absent or at very low levels in *L. plantarum* monoculture (Xu et al., 2025). Notably, in coconut water, 2-butanethiol was detected exclusively in *L. plantarum*-fermented samples with high OAV, representing a distinctive metabolic marker of lactic acid bacteria fermentation. Similarly, 5-hydroxyoctanoic acid lactone, which contributes peach, coconut, and dairy notes, was detected only after *L. plantarum* fermentation, suggesting a specific lipolytic activity of this strain in coconut water (Xu et al., 2025). This further confirms that substrate composition is a primary determinant of volatile outcomes.

4.8.1 Practical Implications for Plant-Based Milk Alternatives

L. plantarum is a particularly versatile tool for flavour improvement of plant-based milk alternatives, with demonstrated capacity to address the beany and grassy off-flavours that represent a major barrier to consumer acceptance of these products. Importantly, the volatile changes identified were confirmed by sensory evaluation in several studies, demonstrating that the reduction of off-flavour aldehydes and the formation of buttery, creamy, fruity, and floral aroma compounds translated into perceptible improvements in flavour quality across different plant-based beverages, including pea, oat, faba bean, sunflower seed, and walnut milks. The species conserved aldehyde-to-alcohol biotransformation, mediated by a genomically encoded oxidoreductase system (Du et al., 2022), provides a reliable metabolic mechanism for reducing hexanal, 1-octen-3-ol, and related off-flavour compounds across legume- and nut-based matrices, while the concurrent accumulation of diacetyl and acetoin introduces the buttery and creamy notes that consumers associate with conventional dairy yogurt. However, the efficacy and metabolic output of *L. plantarum* vary substantially with substrate composition: nut- and legume-based milks with higher fat and protein content yield more complex volatile profiles than cereal-based alternatives (Dąbrowski et al., 2022), and the species exhibits a more substrate-responsive and individually tunable flavour metabolism compared to other lactic acid bacteria, making it a particularly promising candidate for flavour-by-design approaches (Tangyu et al., 2023). The capacity to enhance cheesy and sour notes through branched-chain amino acid catabolism in legume milks offers specific opportunities for developing plant-based cheese alternatives (Tangyu et al., 2023). Nevertheless, *L. plantarum* monoculture shows clear limitations in matrices where fruity esters are essential for the desired flavour profile, as demonstrated in coconut water, where co-fermentation with yeasts is a good strategy to achieve a complete aromatic profile (Xu et al., 2025). Sucrose supplementation represents an additional

lever for modulating the diacetyl-to-acetoin ratio and enhancing buttery character in soymilk (Du et al., 2022), while fermentation time optimisation, with 12 hours identified as optimal in walnut milk (Liu et al., 2022), is critical for maximising aroma complexity without excessive organic acid accumulation. Overall, strain selection for plant-based milk fermentation should integrate volatile metabolite profiling with assessments of oxidoreductase activity and branched-chain amino acid metabolism capacity, and process design should account for precursor availability in each plant matrix, since the same strain can yield markedly different volatile outcomes depending on the substrate.

5. Conclusions

The evidence reviewed in this work shows that *L. plantarum* exhibits versatile but matrix-dependent volatile metabolism, influenced by strain genotype, substrate composition, and processing conditions. Across different food systems, a common metabolic pattern emerges, including production of pyruvate-derived ketones (mainly diacetyl and acetoin), reduction of aldehydes to the corresponding alcohols through oxidoreductase activity, and accumulation of organic acids. Together, these processes constitute a recurrent metabolic pattern associated with the species' volatile profile.

The same strain may increase aldehydes in cereal fermentations but reduce them in fruit juices, promote ester formation in vegetables while producing very few esters in sourdough, or improve flavour under controlled fermentation while contributing to spoilage in uncontrolled conditions. Rather than discouraging cross-application studies, this matrix dependency should guide strain selection. Strains with specific enzymatic traits, such as strong esterase or oxidoreductase activity, can be selected for new food systems where these metabolic functions are desirable, although their volatile impact still requires matrix-specific validation. These observations further confirm that volatile output depends on the interaction between strain

metabolic potential and substrate precursor availability, making aroma performance poorly transferable across matrices.

The ecological adaptability of *L. plantarum* further supports its use in aroma modulation across different foods. Its large genome and metabolic flexibility allow the species to colonise and adapt to environments including dairy, plant, meat, and fish products. In several studies, strains isolated from ecological niches different from the target product generated more complex volatile profiles than autochthonous isolates, suggesting that cross-niche strain screening is a promising strategy for starter culture selection. In addition, strain origin does not always predict performance, as dairy isolates may enhance terpene release in fruit products, while strains from fermented vegetables can produce high levels of diacetyl in dairy systems. Nevertheless, monocultures of *L. plantarum* often provide only partial improvement in aroma. Reducing complex off-flavours, such as fishy notes and sulphur compounds in brassica vegetables, and forming an ester-rich aroma profile often require co-fermentation with other microorganisms to achieve effective sensory control. Some metabolites, including 2,3-butanediol, also appear to be highly strain-dependent and should therefore be evaluated individually in each fermentation system.

Another important limitation in the current literature is the heavy reliance on conventional analytical methods, mainly GC-MS, which generally provide only endpoint or discrete measurements of volatile composition rather than continuous monitoring of aroma evolution over time. Real-time techniques such as Proton Transfer Reaction– Time of Flight – Time-of-Flight Mass Spectrometry (PTR-ToF-MS) could greatly improve understanding of aroma development by continuously monitoring volatile formation and degradation during fermentation (Corvino et al., 2024). In addition, many studies quantify volatile compounds without assessing their real sensory relevance through odour activity values or sensory thresholds. Although several studies confirmed instrumental findings through sensory

evaluation, this approach remains underutilised, and future investigations should systematically integrate volatile profiling with sensory analysis to establish the practical relevance of aroma changes. Future research should therefore combine real-time volatilome monitoring, sensory analysis, odour activity evaluation, and genomic characterisation of aroma-related pathways to support more rational strain selection for specific food applications. Ultimately, integrating metabolomics, genomics, and sensory science will enable the transition from empirical starter selection to predictive flavour design based on the metabolic potential of individual *L. plantarum* strains.

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TABLES AND FIGURES

Tables

Table 1. Summary of volatile organic compounds produced by *Lactiplantibacillus plantarum* during monoculture fermentation across eight food categories. Directionality is defined relative to the corresponding uninoculated control when available. When no uninoculated control was included, directionality was inferred from comparisons between *L. plantarum* and alternative starter cultures applied to the same food matrix. In these cases, it should be interpreted as a proxy for fermentation-associated modulation rather than as an absolute change relative to a non-fermented baseline. VOCs are grouped into three categories: enriched, depleted, and newly detected compounds after fermentation. Within each study, strains exhibiting the same VOC modulation are grouped in a single row, whereas strains with distinct modulation patterns are listed separately.

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
DAIRY	Bovine milk	T1, CSK	37 °C until coagulation and acidification	acids (octanoic acid, hexanoic acid)	nonanal, decanal, dodecanal, 2-heptanone, 2-nonanone	undecanal, 2-undecanone, acetic acid, heptanoic acid, alcohols (phenylethyl alcohol)	HS-SPME/GC-MS; % peak area; comparison with uninoculated sample	Octanoic and acetic acids contributed, respectively, to cheese-like and sour notes	Zhang et al. (2024)
DAIRY	Yoghurt milk	WJ108, F120, J-3-2, SN-100, MN-9, HLB-5 *(HD group)*	37 °C until pH 4.5	diacetyl, acetoin, 2-heptanone, 2-nonanone, octanoic acid, acetic acid, benzoic acid	2-octanone, acetaldehyde		HS-SPME/GC-MS; µg/L (IS: 2-octanol); comparison between 14 strains	Wide strain-level variation in diacetyl yield; buttery/creamy profile in HD strains linked to *alsS* and *nox* upregulation; aldehyde and alcohol accumulation in LD strains associated with *ldh*, *adhe* and *pfld* dominance	Tian et al. (2025)
		SN-84, WJ36, XC-3, BH29 *(MD group)*		diacetyl, acetoin, 2-heptanone	benzoic acid				
		SC-4, F111, F23, PC-26 *(LD group)*		acetaldehyde, 2-octanone, 2,3-butanediol, 1-heptanol	diacetyl, acetoin				

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
DAIRY	Ice cream	Dad-13	37 °C/24h	methyl 10-octadecenoate	–	2-hydroxy-cyclopentadecanone, oxacyclotetradecan-2-one, anthracene/2-trifluoroacetoxydodecane/4-propionyloxytridecane	HS-SPME/GC-MS; % peak area (IS: 1,2-dichlorobenzene); comparison between 0 %, 1 % and 2 % of inulin	Inulin supplementation modified the VOC profile; ketones and esters were exclusively detected in synbiotic samples	Saputro et al. (2023)
DAIRY	Cream cheese	Dad-13	37 °C until pH <4.7	diacetyl, acetoin, butanoic acid, hexanoic acid, heptanoic acid, octanoic acid, decanoic acid, 2-heptanone, 2-nonanone, 2-undecanone, heptyl acetate, δ-decalactone	acetic acid, pentanoic acid, 3-methyl-1-butanol,2-pentanol, ethyl octanoate	2-pentanone, 2-hexanone, 8-nonen-2-one, ethyl 2-hexanoate	HS-SPME/GC-MS; % peak area (IS: 3-heptanone); comparison between commercial starter and single strain	VOC profile richer than commercial products	Tologana et al. (2023)
		Kita-3		propanoic acid, butanoic acid, pentanoic acid, hexanoic acid, heptanoic acid, octanoic acid, decanoic acid, 3-methyl-1-butanol, 2-heptanone, 2-undecanone, diacetyl, acetoin, heptyl acetate, ethyl octanoate	acetic acid, 2-pentanol, δ-decalactone	1-heptanol, 2-pentanone, 2-hexanone, 2-octanone, 8-nonen-2-one, ethyl hexanoate, pentyl pentanoate, propyl hexanoate, ethyl 2-hexanoate, γ-caprolactone, γ-nonalactone			
MEAT	Sucuk	GM77	18-24 °C / 14 days	heptanal, octanal, diacetyl, acetic acid, 1-methyl-1H-pyrrole, methyl thiirane, ethyl lactate, β-myrcene	toluene, 1-methyl-4-(1methylethyl)-benzene, aliphatic hydrocarbons, ethyl acetate, ethyl 2,4-hexadienoate, β-pinene, 2-methyl-3-phenylpropanal, dimethyl disulfide	nonanal, acetoin, acetone, α-propylbenzene methanol	HS-SPME/GC-MS; comparison with uninoculated sample; arbitrary area units ($\times 10^6$)	Off-flavour compounds reduced	Kaya & Kaban (2024)
MEAT	Dry-aged beef	R2	21 days	octanal, nonanal, 2-butanone, 2-heptanone, benzaldehyde, 2-pentyl-furan,	acetoin, 3-methylbutanal, 2-methylbutanal, ethyl acetate,	decanal, 6-methyl-5-hepten-2-one, 2,6-diethyl-pyrazine, p-xylene	HS-SPME/GC-O-MS; OAVs (IS: 2-methyl-3-heptanone); comparison with uninoculated sample¸ OAV >0.1; electronic nose	Acetoin content decreased; pyrazine formation enhanced	Yang et al. (2025)
MEAT	Chicken feet	*	25 °C / 15 days	acetic acid, octanoic acid, linalool, α-terpineol, geraniol, citronellol,	aldehydes (citral, neral, nonanal)	–	HS-SPME/GC-MS; μg/kg (IS: 1,2-	Lp as a spoilage indicator	Jia et al. (2025)

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
				isogeraniol, and neryl alcohol, esters			dichlorobenzene); comparison with uninoculated sample; time-series during storage (days 0, 3, 6, 9, 12)	contributing to off-flavour development	
FISH	*Suanzhayu*	1-24-LJ	25 °C / 28 days	nonanal, hexanal, 1-hexanol, 1-heptanol, 1-octen-3-ol, 3-octanol, 1-octanol, phenylethyl alcohol, , 3-octanone, hexanoic acid, octanoic acid, 2-pentyl-furan, ethyl esters, 2,6-diethyl-pyrazine	limonene, heptanoic acid, 2-ethyl-1-hexanol	–	HS-SPME/GC-MS; OAVs (IS: cyclohexanone); comparison with uninoculated sample; time-series during storage (0-28 days)、OAV >1	Ester compounds dominated the volatile profile	Zhang et al. (2023)
FISH	*Zhayu*	L1	32 °C / 10 days	(-)-trans-myrtanol, 2-pentylfuran, octanoic acid, methylbromoacetate, phthalate, 2-butyl-3-methylpyrazine	5-methyl-2-heptanol, 1-propanol, 3-methylthiopropanol, 2,3-butanediol, esters	–	HS-SPME/GC-O-MS; %peak value; comparison with uninoculated sample;	Pungent off-odour effectively reduced, improving fish flavour and safety	Xu et al. (2023)
FISH	Grass carp juice	L6	37 °C / 48h	4-methyl-1-hexanol, 1-nonanol, 1-octen-3-ol, 1-hexanol, 2,5-hexanedione, esters	hexadecanal, hexanal, 2-octenal, nonanal,	, 3,4-dimethylbenzyl alcohol, (s)-(+)-6-methyl-1-octanol, pentanoic acid, formic acid, diethyl phthalate, diisobutyl phthalate, methyl palmitate, 1,3-diacetin, alkanes	HS-SPME/GC-MS; VOC/IS peak area ratio (IS: 3-hexanone 10); comparison across yeast and co-culture	Fishy odour not reduced in monoculture; co-fermentation required	Ma et al. (2025)
FISH	Fish sauce	XL23	37 °C / 90 days	acetic acid, butanoic acid, propanoic acid, methional, benzaldehyde, 2-furanmethanol	3-methylbutanal, benzenemethanol , benzeneacetaldehyde , alkanes	ethyl formate, 1,3-butanediol, 2,3-butanediol, phenylethyl alcohol, octaethylene glycol, hexanoic acid	HS-SPME/GC-MS; ng/mL (IS: cyclohexanol); comparison with uninoculated sample	Fishy/sour profile modified	Dinc et al. (2024)
BY-PRODUCTS	Tuna cooking liquid	RP26	30 °C / 72h	ethanol, heptylidene acetone, cyclododecyne, (E)-2-dodecenal, 2-butyl-2-octenal, 2-undecanone	aldehydes (hexanal, (E)-2-hexenal, 2-butenal), 2-nonanone, ethyl myristate, alkanes, 2-ethylfuran, 2-pentylfuran trimethylamine, dimethyltrisulfide	3-methyl-1-butanol, ethyl vinyl carbinol, alcohols (phenylethyl alcohol, 1-heptanol), esters	HS-SPME/GC-MS: μg/g (IS: 4-methyl-2-pentanol); comparison with uninoculated sample	Fishy off-odour effectively reduced	Ma et al. (2023)

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
BY-PRODUCTS	Orange peel	Harvest LB-1	21 °C / 10 days	1-decanol, δ-3-carene, valencene, 4-terpineol	1-octanol, octanal, hexanal, nonanal, 2-hexenal, decanal, linalool, α-terpineol, neral, carvone, geranial, butyl butyrate, hexyl butanoate	–	HS-SPME/GC-MS; mg/mL (IS: benzyl acetate); comparison with uninoculated sample	Bitter aroma attenuated	Deba-Rementeria et al. (2022)
BY-PRODUCTS	Rice bran	423	37 °C / 48h	phenols (4-ethylphenol)	aldehydes, alcohols, ketones, hydrocarbons		HS-SPME/GC-MS; comparison with uninoculated sample; time-series during fermentation (0-48h); electronic nose	Enhanced odor intensity without altering qualitative volatile profiles	Wang et al. (2020)
BY-PRODUCTS	Wheat bran	423	37 °C / 48h	aldehydes (octanal propylene glycol acetal), phenols	alcohols, ketones, hydrocarbons	–	HS-SPME/GC-MS; %peak area comparison with uninoculated sample; time-series during fermentation (0-48h), electronic nose	Enhanced odor intensity without altering qualitative volatile profiles	Wang et al. (2020)
BY-PRODUCTS	Hemp seed bran	98b	37 °C / 72h	β-linalool, borneol, p-cymen-8-ol, citronellol, eucalyptol, Δ-3-carene, cis-β-farnesene, citral, 1-octen-3-ol, acetic acid, propionic acid, butyric acid	geraniol, β-pinene and α-farnesene, 9-methyldecalin, and β-selinene, myrcene, eugenol, p-cymene,	–	HS-SPME/GC-MS; mg/kg per organic acids, ratio peak area/total peak area for terpenes (IS: 4-methyl-2-pentanol); comparison with uninoculated sample; time-series during fermentation (0-72h)	β-Linalool is the most abundant VOC; prebiotic activity of terpenes and organic acids	Nissen et al. (2021)
BY-PRODUCTS	Mango peel	JGR2, PTM46	37 °C / 72h			phenylethyl alcohol, carveol, pentanoic acid	Solvent extraction (ethyl acetate) + TMS derivatization/GC-MS/FID; µg/mL	Antimicrobial organic acids and aroma-active compounds support mango peel	Sarang & Kulkarni (2025)

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
							(IS: tridecanoic acid); comparison with uninoculated sample	valorization as additives to food and feed	
FRUIT JUICE	Elderberry	285 (dairy origin)	30 °C / 48h	diacetyl, acetoin, phenylethyl alcohol, limonene, 1-hexanol, (Z)-3-hexen-1-ol, β-linalool, β-damascenone, acetic acid, 4-ethylphenol	isovaleraldehyde, 3-methyl-1-butanol, isovaleric acid, ionone, benzaldehyde	–	HS-SPME/GC-MS; µg/mL (IS: toluene); comparison with uninoculated sample	Strain 285 is a good candidate for producing aromatic compounds	Ricci et al. (2018)
		4186 (dairy origin)	30 °C / 48h	diacetyl, acetoin, phenylethyl alcohol, 3-methyl-1-butanol, limonene, β-linalool, acetic acid, isovaleric acid,	isovaleraldehyde, ionone, benzaldehyde, 1-hexanol, (Z)-3-hexen-1-ol,				
		POM1(plant origin)	30 °C / 48h	diacetyl, acetoin, phenylethyl alcohol, 3-methyl-1-butanol, limonene, β-linalool, acetic acid, isovaleric acid, 1-hexanol, (Z)-3-hexen-1-ol,	isovaleraldehyde, ionone, benzaldehyde,				
		C1 (plant origin)	30 °C / 48h	diacetyl, acetoin, phenylethyl alcohol, 3-methyl-1-butanol, limonene, β-linalool, acetic acid, isovaleric acid, 1-hexanol, (Z)-3-hexen-1-ol,	isovaleraldehyde, ionone, benzaldehyde				
		1LE1 (plant origin)	30 °C / 48h	diacetyl, acetoin, phenylethyl alcohol, 3-methyl-1-butanol, limonene, β-linalool, acetic acid, isovaleric acid, 1-hexanol, (Z)-3-hexen-1-ol,	isovaleraldehyde, ionone, benzaldehyde				
FRUIT JUICE	Cashew apple	TISTR 543	30 °C / 72h	3-methyl-1-butanol, 1-hexanol, acetoin, isovaleric acid, ethanol	benzaldehyde, 2,6-dimethyl-4-heptanol, 4-methyl-4-heptanol, ethyl octanoate, acetic acid, ethyl hexanoate		HS-SPME/GC-MS; % peak area, comparison with inoculated sample; time-series during	Aroma profile shifted toward sweet, fruity and whiskey-like notes	Kaprasob et al. (2018)

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
							fermentation (0-48h)		
FRUIT JUICE	Watermelon	JHT78	37 °C / 36h	ethanol, 1-hexanol, 2,6-nonadien-1-ol, 1-octen-3-ol, 1-penten-3-ol, 5-hepten-2-one, acetaldehyde, acetic acid, hexanoic acid, linalool, ethyl acetate, phenylethyl alcohol, trans-2-(2-pentenyl) furan	aldehydes (heptanal, hexanal, nonanal, octanal, 2-hexenal, 2,6-nonadienal, 2-octenal), p-cresol, 2-nonen-1-ol, 3,6-nonadien-1-ol, 3-buten-2-one	–	HS-SPME/GC-MS; % peak area (IS: 2-octanol); comparison with uninoculated sample; sensory evaluation	The typical fermented character is enhanced, improving the overall flavour complexity	Shi et al. (2023)
FRUIT JUICE	Sea buckthorn	6 DSM strains	30 °C / 36-72h	3-methyl-2-butenal, alcohols (3-methyl-1-butanol, benzyl alcohol, ethanol), ketones (acetoin, diacetyl), acids (acetic acid, 3-methylbutanoic acid, hexanoic acid, heptanoic acid, octanoic acid and nonanoic acid)	aldehydes(hexanal, heptanal, octanal, nonanal), esters and terpenes	2-undecanone	HS-SPME/GC-MS; µg/L (IS: ethyl propionate); comparison with uninoculated sample	Buttery notes enhanced via MLF; aldehydes reduced (herbal notes) but branched-chain aldehydes retained (fruity notes); ester and terpene loss attributed to incubation temperature; acetic acid and free fatty acid accumulation as off-note risk	Markkinen et al. (2021)
FRUIT JUICE	Apple (Fuji)	WFC 502	37 °C / 48h	ethanol, trans-2-hexenol , 1-hexanol, 1-octanol, β-damascenone, acids	1,3-octanediol, aldehydes (2-hexenal, nonanal, benzaldehyde), esters, phenol, α-farnesene	2-methyl-1-butanol, 2-pentanol, 3-methyl-3-buten-1-ol, 2-methyl-2-buten-1-ol, (E)-3-hexen-1-ol, acetoin, hexanoic acid, eugenol	HS-SPME/GC-MS; µg/L (IS: 3-octanol); comparison with uninoculated sample	Enrichment of sweet, fruity and floral aroma notes via alcohol, ketone and acid biosynthesis	Liang et al. (2022)
FRUIT JUICE	Pomegranate	C2, POM1, LP09	30 °C / 120h	acetaldehyde, benzaldehyde, 1-butanol, 1-hexanol, ethanol, ketones (diacetyl, 2-propanone, 2-pentanone, 2-heptanone, 2-nonanone, and 4-methyl-2-heptanone), 2-methyl-1-propene and 2-methyl-1,3-butadiene, terpenes (limonene, β-myrcene, γ-terpinene, α-terpinene, α-	BCAA aldehydes, sulfur compounds (methanethiol, dimethyl sulphide and dimethyl disulphide), furans (furfural)	–	PT/GC-MS; log arbitrary area units (no IS); comparison with uninoculated sample; sensory evaluation	Floral, fruity, and anise notes enhanced	Di Cagno (2017)

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
				terpinolene, and p-cymene)					
FRUIT JUICE	Tomato	Lp-56	37 °C / 24h	6-methyl-5-hepten-2-one, guaiacol, acetic acid, octanoic acid, phenols	dimethyl sulfide, 1-octen-3-ol, aldehydes (hexanal, 2-hexenal, trans-2-octenal), 1-penten-3-one, ethyl acetate and phenylethyl acetate	linalool, geraniol, β-ionone, 2-nonanone	HS-SPME/GC-MS; µg/L (IS: 3-octanol); comparison with uninoculated sample	Recovery of aroma after thermal sterilization and reduction of green/cooked off-flavours	Jiang et al. (2025)
FRUIT JUICE	Grape	LP-56	37 °C / 48h	hexanal, nonanal, 2-hexenol, 1-hexanol, benzoic acid, acids (octanoic acid, hexanoic acid, 2-methylvaleric acid, 2-ethylcaproic acid, nonanoic acid, acetic acid, ethyl acetate, ethyl octanoate, β-damascenone,	2-hexenal, phenylethyl alcohol, linalool, geraniol	–	HS-SPME/GC-MS; µg/L (IS: 2-methylvaleric); comparison with uninoculated sample; time-series (0,24 and 48h); electronic nose and tongue	Terpenes reduced; acids and esters increased; monoculture insufficient for optimal fermentation	Sheng et al. (2022)
FRUIT JUICE	Strawberry	LP56	34 °C / 23h	benzaldehyde, 2-nonanone, (E)-3-penten-2-one, acetophenone, hexanoic acid, acetic acid, linalool, nerolidol, hexyl acetate	(E)-2-hexenal	–	HS-SPME/GC-MS; µg/L (IS: 2-octanol); comparison with uninoculated sample; time-series (0-23h); OAV>1; sensory evaluation	Linalool was the major aroma-active compound	Tong et al. (2025)
FRUIT JUICE	Apricot	LP56	37 °C / 12h	decanal, 2-undecanone, β-pinene, ,	linalool, β-ionone, 2-amylfuran	α-pinene, eugenol	HS-SPME/GC-MS; µg/L (IS: 3-octanol); comparison with uninoculated sample; time-series (0-12h); OAV>1; sensory evaluation	Terpene-dominated profile; sensory acceptability improved	Sun et al. (2022)
FRUIT JUICE	Hawthorn	Lpl.58	37 °C / 24h	1-pentanol, 1-nonanol, 1-decanol, 1-octanol, acetic acid, benzaldehyde, 2-nonanone	hexanal, ethyl decanoate, ethyl dodecanoate	2-pentanol, 2-methyl-1-butanol, (Z)-4-dodecen-1-ol, 4-methyl-1-(1-methylethyl)-3-cyclohexen-1-ol	HS-SPME/GC-MS; µg/L (IS: n.i.); comparison with uninoculated sample	Strain-dependent VOC remodelling; hexanal consistently reduced across all strains; Lpl.69 and	Sun et al. (2023)

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
		Lpl.55		1-pentanol, 1-nonanol, 1-decanol, 1-octanol, acetic acid, benzaldehyde	hexanal, 2-hexenal, nonanal, ethyl decanoate, ethyl dodecanoate	2-pentanol, 2-methyl-1-butanol, (Z)-4-dodecen-1-ol, 4-methyl-1-(1-methylethyl)-3-cyclohexen-1-ol		Lpl.HY-1 showed broader terpenoid enhancement and higher aroma complexity compared to Lpl.55 and Lpl.58	
		Lpl.69		1-pentanol, 1-nonanol, 1-decanol, 1-octanol, linalool, terpineol, acetic acid, octanoic acid, benzaldehyde, d-limonene	hexanal, 2-hexenal, nonanal, ethyl decanoate	2-pentanol, 2-methyl-1-butanol, (Z)-4-dodecen-1-ol, 4-methyl-1-(1-methylethyl)-3-cyclohexen-1-ol			
		Lpl.HY-1		1-pentanol, 1-nonanol, 1-decanol, 1-octanol, linalool, terpineol, acetic acid, octanoic acid, benzaldehyde, ethyl octanoate, d-limonene, benzyl alcohol	hexanal, ethyl decanoate	2-pentanol, decanal, 2-methylbutanoic acid, (Z)-4-dodecen-1-ol, 4-methyl-1-(1-methylethyl)-3-cyclohexen-1-ol			
FRUIT JUICE	Pear	90	37 °C / 48h	linalool, acetaldehyde, 2-hexenal, heptanal, nonanol, α-terpineol, dextro-limonene,	hexanal, heptanal, butyl acetate, ethyl esters, nonanal, 1-nonen-3-ol, tert-butanol	β-ocimene, γ-terpinene	HS-SPME/GC-MS; µg/L (IS: 2-octanol); comparison with uninoculated sample; sensory evaluation	Lowest VOC diversity; unique terpenoids formed; no acetic acid produced	Wang et al. (2022)
VEGETABLE	Carrot	WZ-01	37 °C / 72h	acetoin, linalool, 2,3-butanediol	1-octanol, β-pinene, β-phellandrene, ocimene, α-pinene, sabinene, β-myrcene	hexanal, heptanal, benzaldehyde, 2-nonenal, octanone, β-damascenone, furfural, 2-pentanecarboxylic acid	HS-SPME/GC-MS; % peak area; comparison with uninoculated sample	Carrot-top off-flavour reduced; monoterpene degradation	Zhang et al. (2019)
VEGETABLE	Beetroot	ATCC 3543	30 °C / 24h	acetoin, 2-heptanone, 2-nonanone, acetic acid	4-ethyl-e-methoxyphenol, 4-methylpyridine, 2,3-butanediol, 2,4-dimethylfuran, 2-pentanone,	decanal, 1-butanol, 3-methyl-1-butanol, 1-hexanol, 1-heptanol, 2-butanone, 2-heptanone, 3-nonen-2-one, 2-pentylfuran, butanoic acid, hexanoic acid, octanoic acid, phenylethyl alcohol, butanoic acid butyl ester, methyl nonyl ethyl	HS-SPME/GC-MS; µg/mL (IS: d4-pyrazine); comparison with uninoculated sample	Highest VOC diversity among tested strains	Foss et al. (2023)
VEGETABLE	Cabbage	E10	25 °C / 72h	hexanoic acid, octanoic acid, nonanoic acid, decanoic acid, diacetyl,	dimethyl tetrasulfide, butyl butanoate, dimethyl trisulfide,		HS-SPME/GC-MS; µg/g (IS: amyl acetate);	Partial reduction of off-odours	Liang et al. (2025)

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
				acetoin, geraniol, 4-terpineol, cyclohexanone, 1-octen-3-ol, decanal, undecanal, benzaldehyde, eucalyptol, β-damascenone, 2-heptanone, 3-methyl-1-butanolethyl acetate	hexanal, (E)-2-hexanal, heptanal, (e,e)-2,4-heptadienal, 2-ethylfuran, 2-pentylfuran, 1-penten-3-ol		comparison with uninoculated sample; time-series (0, 24. 48 and 72h; OAV>1		
VEGETABLE	Kimchi	h32	28 °C / 108h	hexanal, heptanal, nonanal, decanal, benzaldehyde	alkanes	2-methyl-n- butyraldehyde, (E)-2-hexenal, , butyl trialkyl sulfate and butyl tetradecyl sulfate	HS-SPME/GC-MS; % peak area; comparison with uninoculated sample	Enhancement of aroma complexity and sensory quality	Qiao et al. (2025)
VEGETABLE	Mung bean	22699, 23169 and YI-Y2013	37 °C / 48h	2,3-butanediol, 3-methyl-butan-1-ol, 2-hydroxypropanoate, butanal, 2-propanone, acetoin, 2-pentylfuran, ethyl acetate, ethyl hexanoate	hexanal, nonanal, octanal, 3-methylbutanal, 2-furfural, phenylacetaldehyde, 1-octen-3-ol, 1-hexanol, esters, 2-butanone, 2-heptanone	isoamyl acetate, acetic acid	GC-IMS; peak intensity; comparison with uninoculated sample; ROAV; sensory evaluation; electronic nose	Beany flavour effectively reduced	Yi et al. (2021)
VEGETABLE	Sauerkraut	Lpl	18-20 °C / 30 days	nonanal, decanal, octanal, acetaldehyde, dimethyl sulfide, dimethyl trisulfide, methanethiol, ocimene, terpineol, geraniol, 1-octen-3-ol, 3-methyl-1-butanol, phenylethyl alcohol, hexanoic acid, octanoic acid, acetoin, isoamyl acetate, ethyl acetate, ethyl lactate, linalool, citral	hexanal, heptanal, undecanal, dodecanal, isothiocyanates, 2-pentanone	–	HS-SPME/GC-MS; μg/g (IS: amyl acetate); comparison with uninoculated sample; time-series (0, 24. 48 and 72h)	Highest ester content among LAB tested	Yang et al. (2020)
VEGETABLE	Table olives	C11C8, F1.16, and F3.5	18 °C / 80 days	3-methyl-1-butanol, phenylethyl alcohol, acetoin, acetic acid, ethyl acetate, lactic acid ethyl ester	4-ethylphenol, 2,3-butanediol, 3,7-dimethyl-1-octanol, muurolene, and phenol-2methoxy	–	HS-SPME/GC-MS; μg/g (IS: 2-octanol); comparison with uninoculated sample	*Zapatera* defect prevented; off-flavour inhibition	Vaccaluzzo et al. (2022)
CEREALS	Sourdough (wheat)	P1	30 °C / 12h	hexanal, (E)-2-hexenal, heptanal, 1-hexanol, 1-pentanol, acetoin, 1-	1-octen-3-ol	–	HS-SPME/GC-MS; peak area; comparison	Highest hexanal and hexanol among strains tested	Liu et al. (2020)

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
				hydroxy-2-propanone, butanoic acid, pentanoic acid			between different strains		
CEREALS	Sourdough (alfalfa)	ATCC 8014	37°C / 24h	nonanal, 2-hexanal, 2-octenal, heptanal, benzaldehyde, 1-pentanol, 2-heptanone, 4-hepten-1-ol, hexanoic acid ethyl ester, 2-pentylfuran, dimethyl trisulfide, benzenacetadehyde and 4-hepten-1-ol	1-octanol, acetophenone , 1-octen-3-ol, octanal	–	ITEX-DHS/GC–MS; comparison between different strains; sensory evaluation	Bread developed off-flavours compared to *S. cerevisiae*	Păușan et al. (2026)
CEREALS	Sourdough (Durum wheat and KAMUT® khorasan)	94A, 133, 124, 189A, 98A, 98B, 206, 801, 5BHI, 6BHI	35°C / 16h	ethanol, 1-pentanol, 2-methyl-2-buten-1-ol, 1-decanol (durum); acetic acid, octanoic acid, 1-hexanol, 2-pentyl furan, 2(3h)-furanone (kamut)	2,4-decadienal and 10-methylnonadecane (durum), pentanal and hexanoic acid (kamut)		HS-SPME/GC-MS; % peak area; comparison with uninoculated sample	Optimal strain-substrate: 98A/6BHI (durum), 94A/206 (KAMUT)	Ferri et al. (2016)
CEREALS	Oat flour	W42	37 °C / 24h	hexanal, heptanal, benzaldehyde, 1-hexanol, 1-pentanol, 2-heptanone,	nonanal, 3-octen-2-one	acetoin, 3-methylbutanal, 3,5-octadien-2-ol, d-limonene, dodecane, (E)-2-hexanal, , (E)-2-octenal, acetic acid, (e,e)-3,5-octadien-2-one,	HS-SPME/GC-MS; µg/mL (IS: d4-pyrazine); comparison with uninoculated sample; time-series (0-24h)	Optimal fermentation: W42 at 12h, IB at 20h	Wronkowska et al. (2022)
		IB		hexanal, 1-hecanol, acetic acid	d-limonene, hexanoic acid, 2-ethyl-1-hexanol, benzaldehyde	3-methylbutanal, 2-ethylfuran, 3,5-octadien-2-ol, 2-heptanone, acetoin, 1-heptanol, heptanal, (E)-2-hexenal, (Z)-2-heptenal, (E)-2-octenal			
PLANT MILKS	Walnut milk	LP56	30 °C / 16h	1-hexanol, 3-methyl-1-butanol, phenylethyl alcohol, diacetyl, acetoin, , ethyl lactate	hexanal, nonanal, 2-pentanol, octyl butyrate, hexyl isovalerate, d-limonene	2,3-butanediol, heptanol, benzyl alcohol, butyric acid, phenylethyl alcohol, acetic acid, hexanoic acid, isooctanoic acid, octyl formate, ethyl lactate, phenethyl acetate, octanal	HS-SPME/GC-MS; µg/L (IS: nonanoic acid methyl ester); comparison with uninoculated sample; time-series (0-16h); sensory evaluation	Enhanced aroma complexity and marked reduction of grassy off-notes; optimal fermentation at 12h	Liu et al. (2022)
PLANT MILKS	Soy milk	X7021	37 °C / 12h		hexanal , , 1-octen-3-ol, 2-pentylfuran, 2-ethyl furan, 2-heptanone, 4-	diacetyl, acetoin, 2-nonanone, acetic acid, hexanoic acid, octanoic	HS-SPME/GC-MS; relative abundance (IS:	Superior beany flavour reduction achieved; no pre-	Du et al. (2022)

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
					pentenal, 2-heptanal, 2-methylbutanal, 3-ene-1-butanol, 1-penten-3-ol	acid, acetaldehyde, maltol, 1-pentanol, 1-hexanol, 2-octanol, 5-methyl-1-heptanol	nonanoic acid methyl ester); comparison with uninoculated sample; sensory evaluation	existing compounds increased; de novo formation of buttery/creamy notes (diacetyl, acetoin) and acetic acid	
PLANT MILKS	Chickpea milk	LP-56	37 °C / 24h	(E)-2-heptenal, 1-octen-3-ol, 1-butanol 3-methyl, 1-pentanol, maltol, nonanoic acid, octanoic acid	hexanal, esters (, octanoic acid ethyl ester), acetone, methyl ester, 1,4-butanediol, benzoic acid	1-hexanol, benzyl alcohol, 1-heptanol, linalool, 1-nonanol, acetic acid, 3-methylbutanoic acid, hexanoic acid, 2-heptanone, acetoin, 2-nonanone, 1-octen-3-one, 2-undecanone	HS-SPME/GC-MS; peak area; comparison with uninoculated sample	Beany off-flavour was significantly reduced	Zhang et al. (2022)
PLANT MILKS	Pea milk	NCC 2988	30 °C / 24h	1-hexanol, 1-heptanol, 1-octen-3-ol, 1-octanol, 1-pentanol, nonanoic acid, 2,4-decadienal	hexanal, heptanal, nonanal, 2-octenal benzaldehyde, 4-ethyl-benzaldehyde 1-nonanol	benzyl alcohol, 2-octen-1-ol, 3-ethyl-4-nonanol, acetic acid, 3-methylbutanoic acid, 2-methylbutanoic acid, hexanoic acid, octanoic acid, acetic acid,	HS-SPME/GC-MS; relative peak area (%); no IS; comparison with uninoculated control; sensory evaluation	Strongest bean-like off-flavour reduction; cheesy/sour profile via BCAA-derived acids; absence of yogurt-like compounds (diacetyl, acetoin)	Tangyu et al. (2023)
PLANT MILKS	Faba milk	NCC 2988	30 °C / 24h	1-hexanol,3-methylbutanoic acid, linalool, 2-heptenal, benzyl alcohol, 1-octen-3-ol	aldehydes (hexanal, 2-methylbutanal, 3-methylbutanal, heptanal, nonanal)	3-methyl-1-butanol, 2-methyl-1-butanol, phenylethyl alcohol, 2-ethyl-1-hexanol, 1-nonanol, eugenol, diacetyl, acetoin, 3-octanone	HS-SPME/GC-MS; relative peak area (%); no IS; comparison with uninoculated control; sensory evaluation	Complete removal of malty/fatty off-notes; floral and citrus enhancement (linalool biosynthesis); cheesy/sour notes introduced	Tangyu et al. (2023)
PLANT MILKS	Sunflower seed milk	NCC 2988	30 °C / 24h	(-)-myrtenol, pinocarveol, 2-methyl-butanol, 1-hexanol, 2-m, ethyl-1-butanol, 2-nonanone, nonaoic acid	aldehydes (hexanal, 2-methyl-butanal, 3-methylbutanal, nonanal), alkenes (α-pinene, β-terpinene) D-limonene	diacetyl, acetoin	HS-SPME/GC-MS; relative peak area (%); no IS; comparison with uninoculated control; sensory evaluation	Elimination of grassy off-notes; woody, minty and balsamic profile via terpenoid bioconversion; buttery notes	Tangyu et al. (2023)
PLANT MILKS	Oat milk	NCC 2988	30 °C / 24h	2-methyl-butanol, 1-heptanol, acetoin, hexanoic acid, octanoic acid, ethyl acetate	aldehydes (hexanal, 2-methylbutanal, 3-methylbutanal, nonanal, 1-octen-3-ol, alkenes (α -pinene)	acetic acid, 3-methylbutanoic acid, 2-methyl-1-butanol, 2-methyl-3-hexanol	HS-SPME/GC-MS; relative peak area (%); no IS; comparison with uninoculated	Partial attenuation of green/grassy off-notes; mild fruity, buttery character	Tangyu et al. (2023)

Category	Matrix	Strain	Fermentation parameters	VOCs enriched after fermentation	VOCs depleted after fermentation	Vocs newly formed during fermentation	Analytical method	Key Findings	Reference
							control; sensory evaluation		
PLANT MILKS	Coconut water	A33	21 °C / 36h	aldehydes (nonanal), octanoic acid, nonanoic acid, ethyl caprate, esters	2-ethylhexanol,	2,4-dimethyl-3-pentanol, acetic acid, 2-ketoglutaric acid, lactone, benzaldehyde, 2-butanethiol, menthol, 5-hydroxyoctanoic acid lactone, β-damascenone, esters	HS-SPME/GC-MS; μg/mL (IS: 2-methyl-3-heptanone); comparison with uninoculated sample; ROAV >1	Insufficient ester formation and no harmonious flavour profile	Xu et al. (2025)
PLANT MILKS	Rice beverage	L7	35 °C / 6 days	benzaldehyde, 3-methyl-1-butanol, ethanol, butanol, propanedioic acid, succinic diethyl ester, octanoic ethyl ester	acids (propanoic acid, butanoic acid, hexadecanoic acid)	acetic acid	LLE/GC-MS (BSTFA derivatization); % peak area	Ester-dominated profile of total VOCs	Giri et al. (2018)
PLANT MILKS	Almond beverage	ATCC14917,	30 °C / 48h	ethyl decanoate, 1-hexanol, 1-heptanol, 1-octanol, 2-heptenal, (E)-2-decenal, (E,E)-2,4-decadienal, 2-ethyl-3-methyl-pyrazine, 1-acetylpyrazine	–	ethyl acetate, benzyl acetate, 2-methyl-2-propanol, 3-methyl-1-butanol, benzyl alcohol, 1-nonanol, hexanal, benzaldehyde, 4-methyl-benzaldehyde, vanillin, triacetin	HS-SPME/GC-MS; ppm (IS: 4-methyl-2-pentanol); comparison with uninoculated sample	Yogurt-like profile with diverse newly formed VOCs	Tsibourginoudi et al. (2026)

Abbreviations: BCAA = branched-chain amino acids; MCFA = medium-chain fatty acids; MLF = malolactic fermentation; OAV = Odour Activity Value; ROAV = relative odour active value; GC-O-MS = gas chromatography-olfactometry-mass spectrometry; PT-GC-MS = purge and trap-gas chromatography-mass spectrometry; ITEX-DHS-GC-MS= In-Tube Extraction Dynamic Headspace-gas chromatography-mass spectrometry. *Strain not specified in the original publication.

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Figures

Figure 1. Pyruvate metabolism, fatty acid catabolism, and general and branched-chain amino acid (BCAA) catabolism in *Lactiplantibacillus plantarum*. Abbreviations: AAT, alcohol acyltransferase; ACK, acetate kinase; AcDH, acetaldehyde dehydrogenase; ADH, alcohol dehydrogenase; ALDC, α-acetolactate decarboxylase; ALDH, aldehyde dehydrogenase; ALS, α-acetolactate synthase; BDH, 2,3-butanediol dehydrogenase; BOX, β-oxidation; DAR, diacetyl reductase; ES, esterase; FAD, fatty acid desaturase; GDH, glutamate dehydrogenase; HPL, hydroperoxide lyase; KADC, β-ketoacyl decarboxylase; KDC, α-keto acid decarboxylase; LDH, lactate dehydrogenase; LOX, lipoxygenase; PDH, pyruvate dehydrogenase; PTA, phosphotransacylase; R, reductase; TL, thiolase. Coloured compounds indicate their sensory impact: green, pleasant compounds; blue; orange, unpleasant if exceeding the sensory threshold.

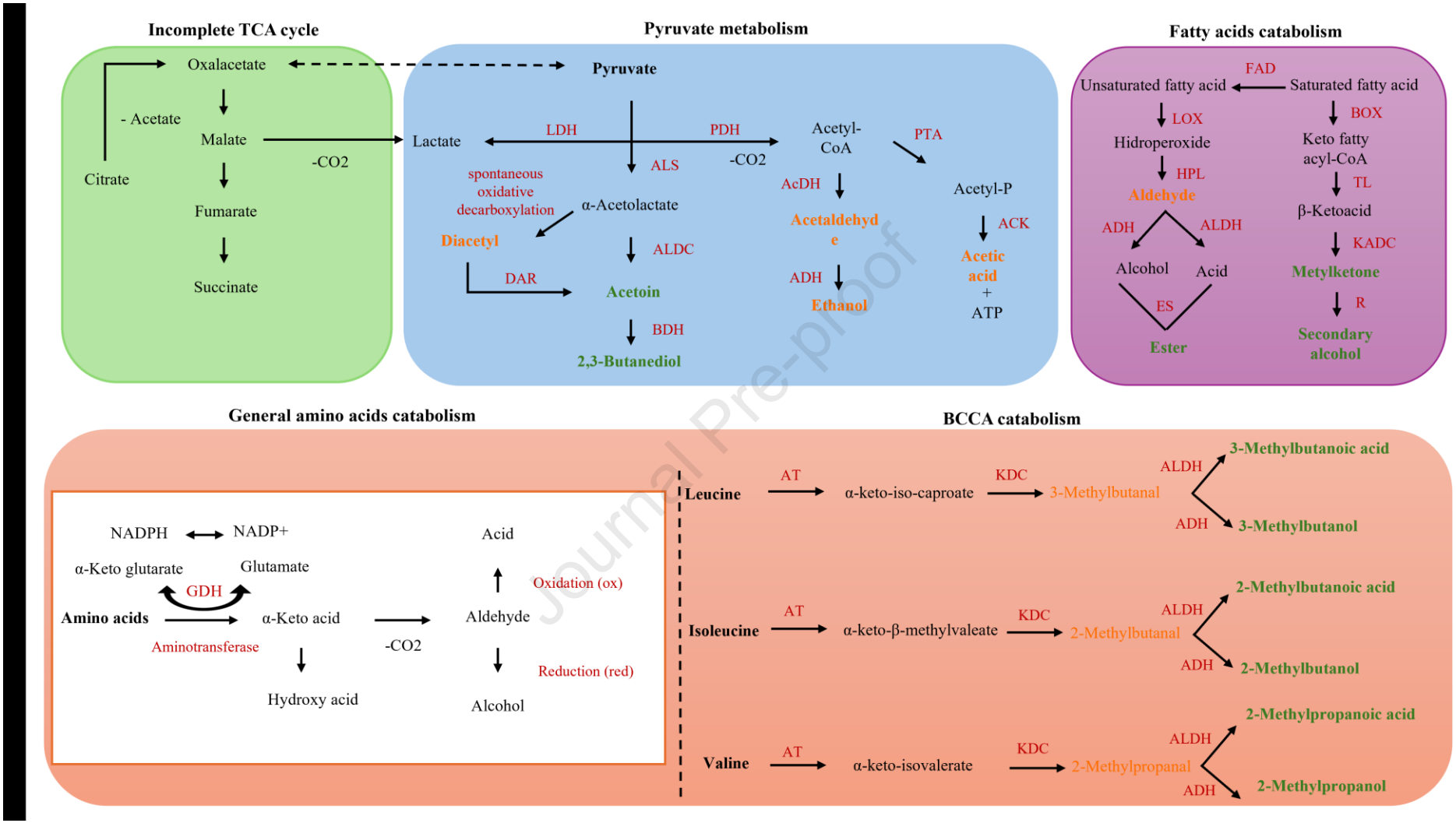

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Figure 2. Sulfur amino acid, threonine, and aspartate metabolism in *Lactiplantibacillus plantarum*. Abbreviations: ADH, alcohol dehydrogenase; AHSH, acetylhomoserine sulfhydrylase; ALDH, aldehyde dehydrogenase; AT, aminotransferases; BDH, 2,3-butanediol dehydrogenase; CBL, cystathionine β-lyase; CBS, cystathionine β-synthase; CGL, cystathionine γ-lyase; CGS, cystathionine γ-synthase; CysE, serine acetyltransferase; CysK, cysteine synthase; DR, diacetyl reductase; HSAT, homoserine O-acetyltransferase; HSDH, homoserine dehydrogenase; HSK, homoserine kinase; HSST, homoserine succinyltransferase; HycDH, hydroxyacid dehydrogenase; MDH, malate dehydrogenase; MetE, 5-methyltetrahydropteroyltriglutamate—homocysteine S-methyltransferase; MetH, homocysteine S-methyltransferase; PLP, pyridoxal phosphate; TA, threonine aldolase; TE, thioesterase; KMBA, 4-methylthio-2-oxobutanoate; HMBA, 2-hydroxy-4-methylsulfanyl-butyric acid; DMS, dimethyl sulfide; DMDS, dimethyl disulfide; DMTS, dimethyl trisulfide. Coloured compounds indicate their sensory impact: green, pleasant compounds; blue, off-flavour; orange, unpleasant if exceeding sensory threshold.

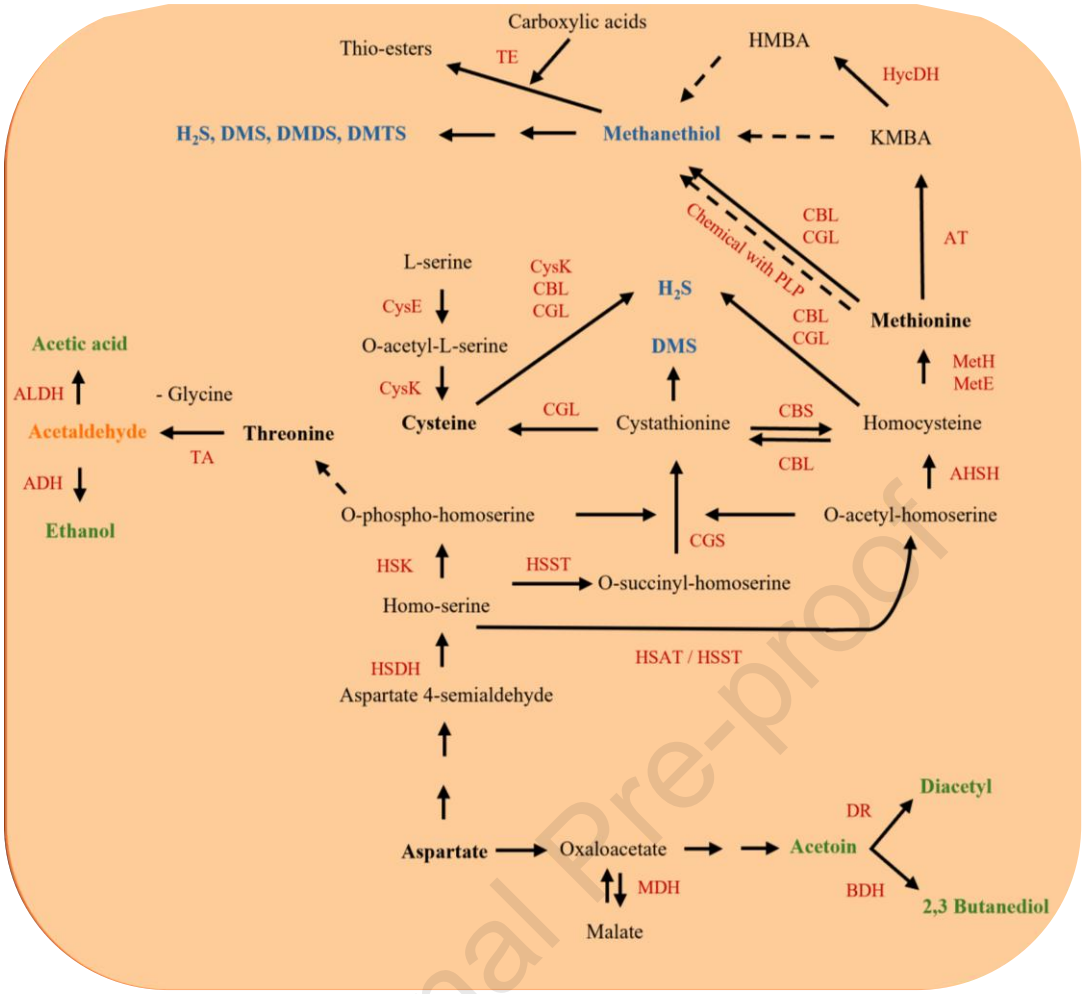

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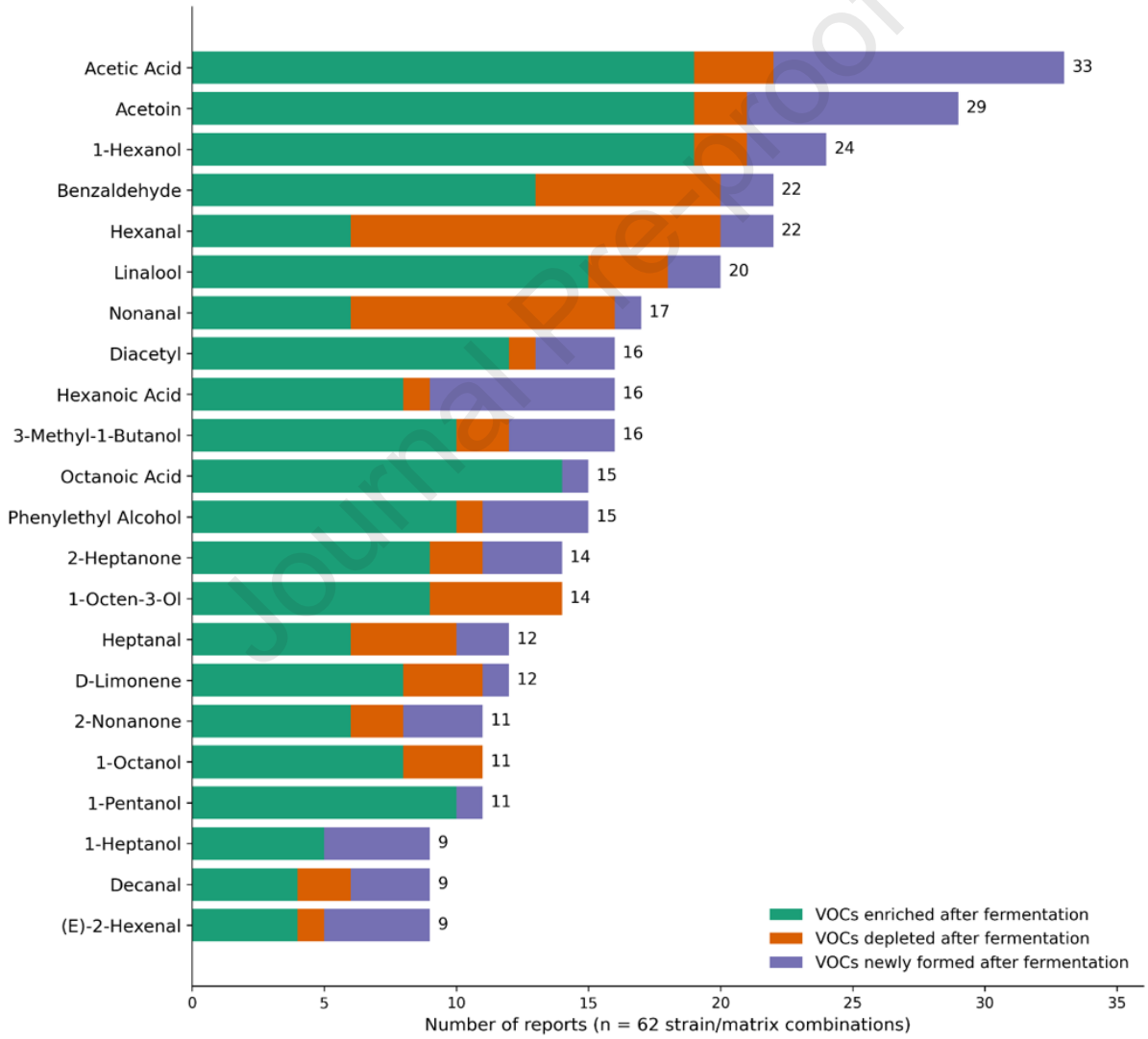
Figure 3. The most frequently reported volatile organic compounds (VOCs) associated with *Lactiplantibacillus plantarum* fermentation across the strain/matrix combinations included in Table 1. For each compound, the total bar length indicates the number of studies reporting that compound in association with *L. plantarum* fermentation, partitioned by the direction of change relative to the respective comparator reported in each study: VOCs enhanced (green), depleted (orange), or newly formed (purple) after fermentation. Compounds are ranked in descending order of total number of reports.



Highlights

- A cross-matrix framework to interpret *L. plantarum* volatilome data is provided.
- Identified recurring methodological limitations in volatilome studies.
- Synthesised evidence linking substrate composition to volatile signatures.
- Knowledge gaps limiting predictive flavor design are highlighted.
- Proposed directions for strain selection and fermentation optimization.

CRediT authorship contribution statement

A. Corvino: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Software, Validation, Visualisation, Writing – original draft preparation. **G. Spano:** Conceptualization, Methodology, Investigation, Formal analysis, Supervision, Validation, Visualisation, Writing – review and editing. **F. Biasioli:** Conceptualization, Methodology, Investigation, Project administration, Supervision, Validation, Visualisation, Funding acquisition, Writing – review and editing. **V. Capozzi:** Conceptualization, Methodology, Investigation, Formal analysis, Funding acquisition, Project administration, Validation, Visualisation, Writing – review and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

A. Corvino: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Software, Validation, Visualisation, Writing – original draft preparation,

G. Spano: Conceptualization, Methodology, Investigation, Formal analysis, Supervision, Validation, Visualisation, Writing – review and editing.

F. Biasioli: Conceptualization, Methodology, Investigation, Project administration, Supervision, Validation, Visualisation, Funding acquisition, Writing – review and editing.

V. Capozzi: Conceptualization, Methodology, Investigation, Formal analysis, Funding acquisition, Project administration, Validation, Visualisation, Writing – review and editing.

Declaration of Interest Statement

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