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Fermentation profiles and probiotic viability in plant-based yogurt alternatives compared to traditional dairy yogurts: A Critical Review

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The global trend toward plant-based diets has driven significant innovation in non-dairy fermented products, particularly yogurt alternatives. This review critically compares how substrate composition influences fermentation kinetics, texture development, and probiotic survival in dairy versus plant-based yogurt analogues. Scientific literatures were mostly reviewed systematically from PubMed, Scopus, and Web of Science, on substrate composition, fermentation and its impact on starter culture performance, metabolic activities, and probiotic survival. The review highlights challenges in achieving optimal acidification, texture development, and sensory properties in plant matrices compared to dairy systems. It was observed that plant-based matrices often exhibit 20–30% slower acidification rates and up to a 40% reduction in probiotic viability compared to dairy yogurt. Furthermore, strategies for enhancing probiotic viability in plant-based yogurt alternatives, including substrate modification, strain selection, and protective technologies, were evaluated. Significantly, there are inadequate *in vivo* studies on gut microbiota modulation by plant-based yogurts, representing a crucial research frontier, to guide continued innovation in this rapidly evolving sector. This study highlights pathways for improving fermentation performance and probiotic stability in plant-based yogurts by blending complementary plant proteins and providing practical guidance for developing high-quality dairy alternatives.

Keywords: Plant-based yogurt, substrate engineering, fermentation, probiotics, sensory optimization, functional foods.

INTRODUCTION

Traditional dairy yogurt, with its long history of consumption across diverse cultures, remains a significant source of essential nutrients and potential probiotic benefits in modern diets (Tamime and Robinson, 2007). However, the last decade has witnessed an unprecedented surge in consumer demand for plant-based alternatives driven by various factors including lactose intolerance, milk allergies, ethical concerns regarding animal welfare, environmental sustainability considerations, and shifting dietary preferences (McClements *et al.,* 2019; Sethi *et al.,* 2016). The global plant-based yogurt market was valued at approximately USD 2.3 billion in 2021 and is projected to reach USD 6.5 billion by 2030, growing at a CAGR of 11.2% (Roselli *et al.,* 2021).

This market expansion has catalyzed extensive research into the development of non-dairy yogurt alternatives that can deliver nutritional benefits, sensory appeal, and probiotic functionality comparable to their dairy counterparts (Zannini *et al.,* 2018). However, plant matrices present distinct physicochemical environments that significantly differ from milk in terms of carbohydrate profiles, protein content and structure, lipid composition, mineral availability, and natural antimicrobial compounds (Jeske *et al.,* 2018). These compositional differences directly affect fermentation, from culture growth

Table 1. Compositional comparison of dairy milk and major plant-based yogurt substrates (per 100g of unfortified base).

Component	Cow Milk	Soy	Coconut	Almond	Oat
Protein (g)	3.3	3.5-4.0	0.5-1.0	1.5-2.5	1.2-1.6
Fat (g)	3.9	2.0-2.5	4.0-24.0*	10.0-15.0	0.8-1.5
Carbohydrates (g)	4.7	2.5-3.0	1.5-4.0	1.0-3.0	6.5-8.0
Primary carbohydrate	Lactose	Oligosaccharides	Fiber	Fiber	β-glucans
Calcium (mg)	120	25-40	10-12	15-45	5-10
pH	6.7	6.6-7.0	6.1-6.5	6.6-7.0	6.5-6.8
Buffering capacity	High	Medium	Low	Low	Medium
Primary antimicrobial compounds	Lactoperoxidase, lactoferrin	Isoflavones	Fatty acids	Flavonoids	Avenanthramides

Varies significantly based on dilution factor Data compiled from: Haug *et al.,* 2007; Mäkinen *et al.,* 2016; Paul *et al.,* 2019; Ranadheera *et al.,* 2018; Roselli *et al.,* 2021.

and metabolite production to texture and probiotic survival during processing and storage (Leroy and De Vuyst, 2004; Makinen *et al.,* 2016).

While researchers have made considerable progress in addressing challenges specific to plant-based yogurt alternatives, the field remains dynamic with continuous innovations in substrate engineering, culture optimization, and processing technologies (Marco *et al.,* 2017; Ranadheera *et al.,* 2018). This review aims to consolidate current scientific knowledge regarding fermentation profiles and probiotic viability in plant-based yogurt alternatives compared to traditional dairy yogurts, with particular emphasis on the four most commercially prevalent plant sources: soy, coconut, almond, and oat. The selection of oat, soy, coconut, and almond substrates for a comprehensive review of plant-based yogurt alternatives reflects their diverse nutritional profiles, market popularity, unique fermentation characteristics, and broad consumer appeal. These substrates represent a wide range of nutritional compositions—from soy's high protein content to oat's soluble fiber, almond's healthy fats, and coconut's distinctive fatty acids—while also catering to different dietary preferences and health trends. Their scientific significance lies in the distinct challenges they present for probiotic survival and culture growth, making them ideal candidates for an in-depth investigation into the fermentation dynamics and functional characteristics of plant-based yogurt alternatives.

Systematic methodology approach beginning with a clearly defined research question and explicit inclusion / exclusion criteria. Comprehensive literature searches were conducted across PubMed, Scopus, Web of Science, and Google Scholar using targeted keywords, focusing on peer-reviewed articles published. The findings were synthesized narratively to identify patterns, consistencies, contradictions, and knowledge gaps across the literature, providing an integrated analysis of current understanding in the field.

This review examines the compositional differences between dairy and plant-based substrates, analyzes their effects on fermentation dynamics and probiotic viability, and highlights key research gaps to guide future innovation in plant-based yogurt alternatives.

Compositional Characteristics of Plant-Based Substrates versus Dairy Milk

Macronutrient Profiles

The fundamental differences between plant-based substrates and dairy milk begin at the macronutrient level, which directly influences fermentation dynamics and microbial growth (Table 1). Cow's milk typically contains 3.3% protein, 4.7% lactose, and 3.9% fat, providing a well-balanced nutrient profile for lactic acid bacteria (LAB) growth (Haug *et al.,* 2007). In contrast, unfortified plant-based substrates exhibit considerable variation in their macronutrient composition, which presents specific challenges for fermentation processes.

Soy-based substrates contain approximately 3.5-4.0% protein, comparable to cow's milk, with proteins predominantly in the form of globulins (glycinin and β-conglycinin) rather than the casein and whey proteins found in dairy (Paul *et al.,* 2019). However, soy substrates are mostly deficient in lactose, containing instead various oligosaccharides, primarily stachyose (4.1%) and raffinose (1.1%), which many traditional yogurt cultures cannot readily metabolize (Mital and Steinkraus, 1979; Scalabrini *et al.,* 1998).

Coconut-based substrates present a distinctly different profile, typically containing less than 1% protein but approximately 24% fat when prepared from coconut cream, or significantly less (2-4%) when diluted for commercial beverages (Ranadheera *et al.,* 2018). The high fat content, primarily medium-chain triglycerides, may protect probiotic organisms during gastrointestinal transit.

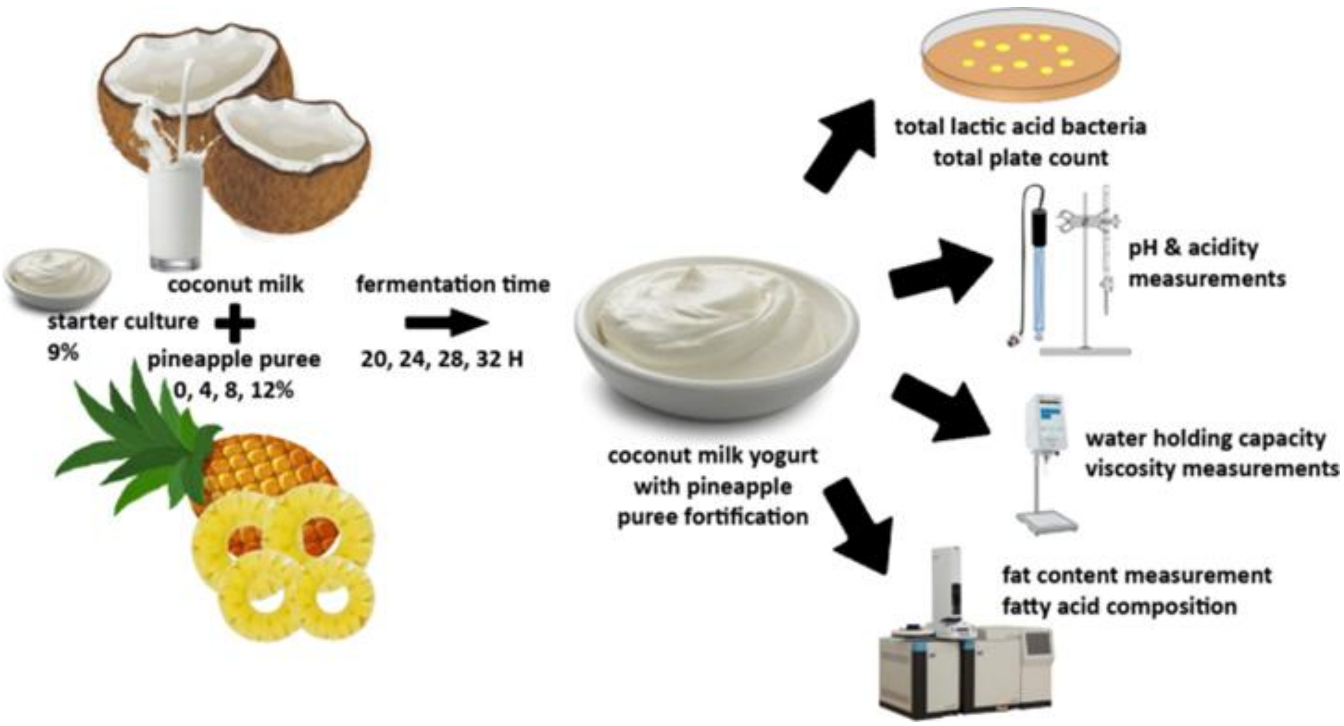

Figure 1. Coconut milk fortified with pineapple puree and fermented for yogurt production analysis (Parhusip *et al.,* 2024).

However, this may pose challenges for homogenous fermentation and texture development (Ranadheera *et al.,* 2015).

Almond-based substrates contain moderate protein levels (1.5-2.5%) and relatively high fat content (10-15% in unfortified base), with predominantly unsaturated fatty acids that may affect membrane fluidity in bacterial cells (Bernat *et al.,* 2014). The carbohydrate content is low, consisting mainly of dietary fiber and minimal fermentable sugars, necessitating carbohydrate supplementation for effective fermentation.

Oat-based substrates offer a distinctive carbohydrate profile rich in β-glucans (approximately 2-8%) with significant implications for texture and potential prebiotic effects (Mårtensson *et al.,* 2002). With moderate protein content (1.2-1.6%) predominantly in the form of globulins and avenins, oat substrates provide a viable matrix for LAB growth, particularly when supplemented with additional fermentable carbohydrates (Mäkinen *et al.,* 2016).

Recent studies by Nguyen *et al.* (2019) and Roselli *et al.* (2021) demonstrated that these inherent compositional differences significantly affect not just the growth and metabolic activity of starter cultures but also the nutritional profile of the final products. Roselli *et al.* (2021) observed that plant proteins undergo less proteolysis during fermentation compared to milk proteins, resulting in different bioactive peptide profiles with potentially different functional properties.

Micronutrient and Growth Factor Availability

Micronutrient availability is another critical factor influencing fermentation efficiency and probiotic survival. Dairy milk naturally contains a comprehensive profile of vitamins and minerals essential for LAB growth, including B vitamins, magnesium, zinc, and calcium (Haug *et al.,* 2007). Additionally, dairy provides specific growth factors such as peptides, nucleotides, and organic acids that stimulate bacterial growth (Haenlein, 2004).

In contrast, plant-based substrates exhibit significant variability in micronutrient profiles (Figure 1). Soy substrates contain appreciable levels of potassium, phosphorus, and magnesium but are comparatively low in calcium and vitamin B_{12} unless fortified (Reilly *et al.,* 2006). Moreover, the presence of phytic acid (1-2%) in soy can chelate mineral ions, potentially reducing their bioavailability to microorganisms. Also, inhibiting bacterial growth by limiting access to essential cofactors needed for enzymatic activity and metabolism. (Sandberg, 2002).

Oat substrates provide substantial manganese, phosphorus, and thiamine, but lack several B vitamins critical for LAB metabolism (Mäkinen *et al.,* 2016). Almond-based substrates contribute riboflavin and vitamin E but are deficient in B_{12} and certain trace minerals (Bernat *et al.,* 2014). Coconut-based substrates are generally low in water-soluble vitamins and minerals compared to other plant sources and dairy milk.

Recent metabolomic analyses by Mekanna *et al.* (2024) revealed significant differences in the profiles of small molecular weight compounds between dairy and plant-based substrates that affect bacterial metabolism. They identified over 45 metabolites present in dairy milk but absent or at substantially lower concentrations in unfortified plant substrates, many of which play crucial roles in bacterial growth pathways.

Antimicrobial Compounds and Inhibitory Factors

Plant-based substrates naturally contain various bioactive compounds that may inhibit or modulate microbial growth. Polyphenols, present in significant quantities in many plant substrates, can exert antimicrobial effects against certain LAB strains through multiple mechanisms, including disruption of cell membranes, enzyme inhibition, and substrate deprivation (Lacombe *et al.,* 2013; Tabasco *et al.,* 2012).

Furthermore, soy substrates contain isoflavones (primarily daidzein and genistein) at concentrations of 1.2-4.2 mg/g, which have demonstrated moderate inhibitory effects against certain probiotic strains (Pérez-Gregorio *et al.,* 2011). Studies by Wei *et al.* (2007) showed differential sensitivity among *Lactobacillus* species to isoflavone-rich extracts, with *L. acidophilus* showing greater resistance compared to *L. rhamnosus* strains.

Similarly, almond-based substrates contain proanthocyanidins and flavonoids that can affect bacterial growth. Interestingly, Bernat *et al.* (2014) observed that certain LAB strains, particularly *L. plantarum*, demonstrated the ability to metabolize these compounds, potentially reducing their inhibitory effects during prolonged fermentation.

Moreover, oat substrates contain avenanthramides, unique polyphenolic alkaloids with documented antimicrobial properties against certain gram-positive bacteria (Lim*,* 2018). Studies by Russo *et al.* (2014b) demonstrated strain-specific sensitivity among probiotics, with bifidobacteria showing greater susceptibility compared to *Lactobacillus species*.

Beyond polyphenols, plant substrates may contain saponins, tannins, and lectins with varying degrees of antimicrobial activity. Additionally, the presence of endogenous enzymes, such as peroxidases and polyphenol oxidases, can generate reactive compounds during processing that further impact microbial stability (Marco *et al.,* 2017).

Recent research by Zhang *et al.* (2018) using advanced metabolomic approaches has identified previously uncharacterized antimicrobial peptides in plant substrates that demonstrate inhibitory effects against certain probiotic strains. Their work highlights the complex interplay between substrate composition and microbial ecology in plant-based fermentation systems.

Starter Culture Performance in Plant-Based Matrices

Growth Kinetics and Acidification Patterns

The fundamental performance parameters of yogurt starter cultures—*Streptococcus thermophilus* and *Lactobacillus delbrueckii* subsp. *bulgaricus*—differ significantly between dairy and plant-based substrates. In dairy environments, these organisms exhibit a well-documented symbiotic relationship (proto-cooperation) that enhances acidification rates and flavor development (Sieuwerts *et al.,* 2008). S. *thermophilus* initially dominates, metabolizing lactose and producing formate and CO_2, which stimulates *L. bulgaricus* growth. In turn, *L. bulgaricus* contributes to protein hydrolysis, releasing peptides and amino acids that further enhance *S. thermophilus* growth (Settachaimongkon *et al.,* 2014).

Mistry and Hassan (1992), including more recently, Wang *et al.* (2018a), demonstrated significantly slower acidification rates in unfortified soy substrate compared to dairy milk. Wang *et al.* (2018b) reported that *S. thermophilus* required 42% more time to reduce the pH to 4.5 in soy substrate compared to milk, while *L. bulgaricus* showed even greater growth inhibition, with cell counts approximately 1.5 log CFU/mL lower after 8 h of fermentation.

Similar challenges have been documented in other plant substrates. Bernat *et al.* (2014) observed extended fermentation times of 10-14 h to reach pH 4.5 in unfortified almond substrate, compared to 4-6 h typically required for dairy yogurt. Their study revealed that *L. bulgaricus* was particularly affected, showing minimal growth in almond substrate unless supplemented with glucose and yeast extract.

Coconut-based substrates present unique challenges due to their high fat and low protein content. Ranadheera *et al.* (2018) documented unusual acidification patterns, with initial rapid pH reduction followed by prolonged plateaus, attributed to the limited buffering capacity of coconut substrate compared to dairy milk. They also noted that standard starter cultures produced approximately 40% less lactic acid in coconut substrate compared to dairy milk after 8 h of fermentation.

Conversely, oat-based substrates have shown promising results for traditional yogurt cultures. Mårtensson *et al.* (2002) and Nionelli *et al.* (2018) demonstrated that the presence of β-glucans and other soluble fibers in oat substrate may enhance the growth of certain LAB strains. However, Nionelli *et al.* (2018) found that acidification patterns remained irregular compared to dairy, with slower initial pH reduction but comparable final acidity after prolonged fermentation.

Recent studies using advanced bioinformatic approaches have provided deeper insights into these phenomena. Transcriptomic analyses by Mekanna *et al.* (2024) revealed significant upregulation of stress response genes and downregulation of carbohydrate metabolism genes when *L. bulgaricus* was grown in soy substrate compared to milk. Similarly, Chen *et al.* (2017) used comparative proteomics to demonstrate substantial differences in protein expression profiles of *S. thermophilus* when fermenting dairy versus almond substrate, with notable differences in carbohydrate transport systems and amino acid biosynthesis pathways.

Metabolite Production and Flavor Development

Fermentation metabolites such as organic acids and volatiles determine the distinctive flavor of yogurt, including organic acids, acetaldehyde, diacetyl, acetoin, and various volatile compounds (Chen et al., 2017). The production of these compounds differs markedly between dairy and plant-based substrates due to variations in precursor availability and metabolic pathways. These metabolite shifts not only alter flavor profiles but may also impact consumer perception and acceptability of plant-based yogurts.

In dairy yogurt, acetaldehyde (typically 10-15 mg/kg) is considered the primary flavor compound, derived mainly from threonine metabolism by *L. bulgaricus* (Zourari *et al.,* 1992). However, Bao *et al.* (2012) demonstrated that acetaldehyde production in soy yogurt was approximately 60% lower than in dairy yogurt when using traditional starter cultures. Their metabolomic analysis revealed that this reduction was correlated with lower threonine availability and altered threonine aldolase activity in the soy environment.

Similarly, Walsh *et al.* (2016) observed significant differences in volatile compound profiles between coconut yogurt and dairy yogurt, with notably lower concentrations of diacetyl and acetoin but elevated levels of fatty acid-derived compounds, including octanoic and decanoic acids, which contributed to distinct flavor characteristics. Their sensory evaluation indicated that these differences resulted in flavor profiles described as "less yogurt-like" by trained panelists.

The production of exopolysaccharides (EPS), which contribute to texture and mouthfeel, also varies significantly between substrates. Macedo *et al.* (2008) demonstrated that certain strains of *S. thermophilus* produced 40-60% less EPS in soy substrate compared to milk, which they attributed to differences in carbohydrate precursor availability. Conversely, Zannini *et al.* (2018) observed enhanced EPS production by certain *L. plantarum* strains in oat substrate, potentially due to the presence of β-glucans that may serve as primers for EPS synthesis.

Recent metabolomic studies have provided comprehensive profiles of fermentation metabolites across different substrates. Chen *et al.* (2017) identified over 200 volatile compounds in fermented dairy, soy, and almond yogurts, revealing substrate-specific patterns. Their study demonstrated that plant-based yogurts contained higher levels of aldehydes and phenolic compounds derived from plant materials but were deficient in typical dairy-derived volatiles such as certain ketones and sulfur compounds.

Innovative work by Mekanna *et al.* (2024) using stable isotope labeling and metabolic flux analysis has revealed fundamental differences in carbon metabolism between dairy and plant-based fermentations. They demonstrated that central carbon metabolism pathways are redirected in plant environments, resulting in altered end-product profiles that directly impact sensory characteristics. Specifically, they observed enhanced production of succinic acid and ethanol in plant-based fermentations, indicating a shift toward mixed acid fermentation rather than the predominantly homolactic fermentation typical in dairy environments.

Texture Development and Microstructure Formation

Texture development in yogurt results from complex interactions between milk proteins (primarily caseins) and the acidic environment created during fermentation, leading to the formation of a characteristic gel structure (Lee and Lucey, 2017). In dairy systems, the acidification process causes casein micelles to destabilize and aggregate when the pH approaches the isoelectric point (pH 4.6), forming a three-dimensional protein network that entraps water and fat globules (Lucey, 2017).

Plant-based substrates present fundamentally different protein systems that form distinctly different structural networks during acidification. Soy proteins (primarily glycinin and β-conglycinin) undergo pH-dependent aggregation but form weaker gel networks compared to casein micelles. Due to the absence of casein micelles, plant proteins like glycinin and globulins form looser and less cohesive gels. Confocal laser scanning microscopy (CLSM) studies by Li *et al.* (2014) revealed that soy yogurt exhibits a more heterogeneous protein network with larger aggregate particles compared to the fine-stranded network characteristic of dairy yogurt.

Also, almond proteins present even greater challenges for gel formation due to their globular nature and lower concentration in typical formulations. Scanning electron microscopy (SEM) analysis by Bernat *et al.* (2014) demonstrated that almond yogurt forms a discontinuous protein network with significant phase separation unless stabilized with additional hydrocolloids. Recent work by Roselli *et al.* (2021) using atomic force microscopy (AFM) provided nanoscale evidence that almond proteins form primarily particulate gels rather than the fine-stranded gels typical of casein systems.

Moreover, coconut-based yogurts present unique textural challenges due to their low protein and high fat content. Ranadheera *et al.* (2019) demonstrated through rheological analyses that coconut yogurts exhibit significantly lower gel strength and higher susceptibility to syneresis compared to dairy yogurts, necessitating the addition of stabilizers for acceptable texture development. While oat-based systems benefit from the presence of β-glucans, which can form viscous solutions and contribute to texture development independent of protein gelation (Mäkinen *et al.,* 2016). Mårtensson *et al.* (2002) demonstrated that β-glucan interactions with oat proteins during fermentation resulted in increased viscosity and water-holding capacity, though the resulting structures differed fundamentally from dairy yogurt as shown by their rheological characterization.

Innovative research by Chen *et al.* (2017) using neutron scattering and dynamic rheology has provided deeper insights into the structural development of plant protein networks during acidification. Their work revealed that plant protein gelation follows different kinetic parameters compared to casein systems, with distinct aggregation mechanisms that directly impact texture development. Specifically, they observed that plant proteins form primarily through particulate aggregation rather than the continuous network formation typical of casein systems.

Recent advances in three-dimensional imaging techniques have further elucidated structural differences. Wang *et al.* (2018b) utilized X-ray microtomography to generate 3D visualizations of different yogurt microstructures, demonstrating fundamental differences in pore size distribution, connectivity, and tortuosity between dairy and plant-based systems. These structural differences directly impact not only textural properties but also the microbial microenvironment, potentially affecting probiotic viability during storage. Understanding these structural differences is critical for developing stabilizer systems and processing parameters tailored to plant-based matrices.

Probiotic Viability Challenges in Plant-Based Yogurt Alternatives

Comparative Survival During Fermentation and Storage

The viability of probiotic bacteria throughout processing and storage is critical to delivering health benefits, with minimum recommended levels typically ranging from 10^6 to 10^9 CFU/g at the time of consumption (Hill *et al.,* 2014). Comparative studies of probiotic survival in dairy versus plant-based yogurts have revealed substrate-dependent patterns that present both challenges and opportunities. For instance, *L. plantarum* generally shows good viability in almond and oat substrates, while *L. acidophilus* struggles in coconut and soy matrices.

In a landmark study, Farnworth *et al.* (2007) documented that *L. rhamnosus* GR-1 maintained higher viability in soy yogurt compared to dairy yogurt during 28 days of refrigerated storage, with approximately 0.8 log CFU/g less reduction in the soy matrix. They attributed this enhanced survival to the protective effects of soy oligosaccharides and potentially prebiotic fiber components. However, a contrasting study by Bedani *et al.* (2013) observed that *L. acidophilus* LA-5 exhibited significantly reduced viability in soy yogurt compared to dairy yogurt, with a difference of approximately 1.2 log CFU/g after 28 days of storage. This discrepancy highlights the strain-specific nature of probiotic-substrate interactions.

Similar variations have been observed across other plant substrates. Wang *et al.* (2018b) evaluated the survival of five common probiotic strains in almond yogurt compared to dairy yogurt during 21 days of refrigerated storage. Their results revealed that *L. plantarum* exhibited superior survival in almond substrate (0.4 log CFU/g reduction versus 1.3 log CFU/g in dairy), while *B. animalis* subsp. lactis Bb-12 showed poorer viability (2.1 log CFU/g reduction versus 0.7 log CFU/g in dairy).

Coconut-based yogurts present unique challenges for probiotic viability due to their high fat content and antimicrobial fatty acids. Ranadheera *et al.* (2015) demonstrated that medium-chain fatty acids in coconut, particularly lauric acid, exerted strain-specific antimicrobial effects against certain probiotic bacteria. Their study showed that *L. casei* Shirota maintained comparable viability in coconut and dairy yogurts, while *L. acidophilus* LA-5 showed significantly reduced survival in the coconut matrix.

Oat substrate has generally demonstrated favorable results for probiotic viability. Kedia *et al.* (2008) observed enhanced survival of *B. breve* and *L. reuteri*in oat-based yogurt compared to dairy yogurt during 28 days of storage, which they attributed to the prebiotic effects of oat β-glucans. Their findings were later supported by Russo *et al.* (2014), who documented superior survival of various Bifidobacterium strains in oat-based fermented products.

Recent comprehensive studies by Chen *et al.* (2017) evaluated probiotic viability across multiple substrate types and probiotic species using standardized methodologies. Their results, summarized in Table 2, demonstrate the complex interplay between specific strains and substrates, highlighting the need for careful strain selection based on the intended plant matrix.

Advanced molecular techniques have provided deeper insights into the mechanisms underlying differential survival. Transcriptomic studies by Mekanna *et al.* (2024) revealed upregulation of stress response genes and changes in membrane composition when *L. rhamnosus* GG was cultivated in plant-based substrates compared to dairy. Similarly, metagenomic analyses by Zhang *et al.* (2018) demonstrated differences in gene expression profiles of probiotics in various substrates, particularly genes related to carbohydrate metabolism, stress

Table 2. Comparative reduction in probiotic viability (log CFU/g) after 28 days of refrigerated storage (4°C) in different yogurt substrates.

Probiotic Strain	Dairy log CFU/g	Soy log CFU/g	Coconut Log CFU/g	Almond log CFU/g	Oat Log CFU/g
L. acidophilus LA-5	0.8	2.0	2.4	1.5	1.2
L. rhamnosus GG	1.2	0.6	1.8	1.4	0.5
B. animalis subsp. lactis Bb-12	0.7	1.1	1.8	2.1	0.4
L. casei Shirota	1.0	1.2	1.1	1.6	0.9
L. plantarum 299v	1.3	0.9	1.5	0.4	0.3

(Farnworth *et al.,* 2007; Bedani*et al.,* 2013; Ranadheera*et al.,* 2018; Wang *et al.,* 2018b; Chen *et al.,* 2017).

response, and cell envelope modification.

pH and Acid Tolerance in Plant Matrices

Post-acidification during storage represents a significant challenge for probiotic viability in fermented products, with continued acid production potentially reducing pH to levels inhibitory for certain strains (Shah, 2000). The acid tolerance of probiotics in plant-based yogurts differs from dairy systems due to variations in buffering capacity, acid profiles, and protective factors.

Dairy milk exhibits significant buffering capacity due to its protein and mineral content, which moderates pH changes during fermentation and storage (Salaün *et al.,* 2005). In contrast, many plant-based substrates demonstrate lower buffering capacity, potentially resulting in more rapid pH reduction and greater stress on probiotic organisms. Wang *et al.* (2018a) documented that unfortified almond milk exhibited approximately 40% lower buffering capacity compared to dairy milk, resulting in more rapid pH decline during fermentation and storage.

Beyond absolute pH values, the specific organic acid profile impacts probiotic viability. Dairy yogurt acidification results predominantly from lactic acid production, whereas plant-based fermentations often yield more diverse acid profiles. Chen *et al.* (2017) demonstrated that soy yogurt contained significantly higher concentrations of acetic acid compared to dairy yogurt when fermented with identical cultures. This is significant as undissociated acetic acid has stronger antimicrobial activity than lactic acid at equivalent pH values due to its ability to penetrate microbial membranes more easily (Wang *et al.,* 2012).

Recent work by Zhang *et al.* (2018) utilizing high-performance liquid chromatography (HPLC) and gas chromatography-mass spectrometry (GC-MS) has provided comprehensive organic acid profiles across different yogurt types. Their analysis revealed substrate-specific patterns in acid production that correlated with probiotic viability during storage. Notably, they observed that coconut yogurt contained elevated levels of certain medium-chain fatty acids with documented antimicrobial properties, which correlated with reduced survival of acid-sensitive probiotic strains.

Comprehensive studies by Mekanna *et al.* (2024) have demonstrated strain-specific responses to acidification in different substrates. They observed that *L. rhamnosus* strains maintained higher viability in soy yogurt compared to dairy yogurt at equivalent pH values, suggesting that factors beyond pH alone influence survival. Their transcriptomic analysis revealed differential expression of acid tolerance response genes depending on the substrate, indicating that the molecular mechanisms of acid adaptation may vary between dairy and plant environments.

These findings emphasize the need to consider both pH and acid type when selecting probiotic strains for plant-based formulations, in order to attain a desirable result and reduce losses.

Oxidative Stress and Antioxidant Systems

Oxidative stress represents another significant challenge for probiotic viability in fermented products. Yogurt manufacturing processes introduce dissolved oxygen, while improper packaging and storage can allow continued oxygen permeation, potentially damaging sensitive probiotic organisms, particularly anaerobic bifidobacteria (Tabasco *et al.,* 2011).

Plant-based and dairy substrates differ significantly in their inherent redox potential and antioxidant capacity, which influences oxidative stress levels experienced by probiotics. Many plant substrates contain various polyphenolic compounds with antioxidant properties that may protect probiotic organisms from oxidative damage (Wang *et al.,* 2012). Zhang *et al.* (2018) demonstrated that certain isoflavones in soy substrate significantly reduced intracellular reactive oxygen species (ROS) accumulation in *L. rhamnosus*, potentially enhancing survival during storage.

Similarly, Bernat *et al.* (2014) observed that the phenolic compounds in almond substrate provided protective effects against oxidative stress for certain probiotic strains. Their electron paramagnetic resonance (EPR) analysis demonstrated that almond yogurt exhibited significantly higher radical scavenging activity compared to dairy yogurt, which correlated with enhanced survival of oxygen-sensitive bifidobacteria strains.

However, these interactions are complex and strain-dependent. Recent research by Chen *et al.* (2017) utilizing flow cytometry with fluorescent indicators for intracellular oxidative stress demonstrated variable responses among probiotic strains to different plant substrates. They observed that while *L. plantarum* showed reduced oxidative stress markers in polyphenol-rich plant substrates compared to dairy, certain Bifidobacterium strains exhibited increased stress markers in the same environments.

Advanced metabolomic approaches by Mekanna *et al.* (2024) have provided deeper insights into these phenomena, revealing substrate-specific impacts on cellular redox homeostasis in probiotics. Redox homeostasis in probiotics is the maintenance of balanced oxidation-reduction conditions through antioxidant systems that protect cells from oxidative damage while supporting metabolic function and survival. Their analyses of key metabolites involved in oxidative stress responses, including glutathione, thioredoxin, and various antioxidant enzymes, demonstrated that the molecular mechanisms of oxidative stress resistance vary significantly between dairy and plant environments. The presence of polyphenols in soy and almond matrices may be leveraged to formulate yogurts with enhanced oxidative stability for sensitive probiotic strains.

Nutrient Limitation and Starvation Stress

Nutrient availability during long-term storage represents another critical factor influencing probiotic viability. As fermentable carbohydrates are depleted during initial fermentation and early storage, probiotics may experience starvation stress that compromises membrane integrity and reduces viability (Guerzoni *et al.,* 2001).

Plant and dairy substrates differ substantially in their carbohydrate profiles and nutrient availability during storage. Dairy milk contains predominantly lactose, which is readily metabolized by most LAB, while plant substrates contain more diverse carbohydrate profiles, including various oligosaccharides, resistant starches, and dietary fibers (Marco *et al.,* 2017).

Studies by Wang *et al.* (2018b) demonstrated that certain plant oligosaccharides, particularly those found in soy substrate, can be metabolized slowly during refrigerated storage by specific probiotic strains with appropriate enzymatic capabilities. Their metabolomic analysis revealed gradual reduction in raffinose and stachyose concentrations during storage of soy yogurt containing *L. plantarum*, correlating with enhanced survival compared to dairy yogurt.

Similarly, Russo *et al.* (2014) documented the utilization of β-glucan degradation products by certain Bifidobacterium strains during storage of oat yogurt, potentially providing a sustained carbohydrate source that supported prolonged viability. Their enzymatic analyses demonstrated that strains possessing β-glucanase activity exhibited superior survival in oat substrates compared to strains lacking this capability.

Beyond carbohydrates, amino acid availability during storage impacts probiotic survival. Recent proteomic research by Chen *et al.* (2017) revealed significant differences in protein hydrolysis patterns between dairy and plant-based yogurts during storage. Their analysis demonstrated that the release of peptides and free amino acids followed different kinetics in plant matrices compared to dairy, potentially affecting nutrient availability to probiotics during extended storage periods. Proteomic data revealed that peptide and amino acid release occurred more slowly in plant matrices than in dairy, potentially affecting sustained nutrient availability for probiotics.

Strategies for Enhancing Probiotic Viability in Plant-Based Yogurt Systems

Substrate Modification and Fortification

The inherent limitations of plant-based substrates for supporting probiotic growth and viability have driven research into substrate modification strategies. Various approaches have been developed to enhance the nutritional value and protective properties of plant matrices for probiotic organisms (Table 3).

Carbohydrate supplementation represents one of the most common modification strategies. While traditional dairy yogurt cultures readily metabolize lactose, many plant-based alternatives lack sufficient fermentable carbohydrates to support robust fermentation. Martensson *et al.* (2002) demonstrated that glucose supplementation (2% w/v) to oat substrate significantly enhanced the growth rate of yogurt cultures, reducing fermentation time by approximately 40%. Similarly, Wang *et al.* (2018b) observed that fructooligosaccharide (FOS) addition Protein fortification strategies have also shown promising results. Jeske *et al.* (2018) evaluated the impact of pea protein isolate addition (1-3% w/v) on the fermentation properties and probiotic viability in oat-based yogurt alternatives. Their results demonstrated that protein supplementation significantly enhanced the buffering capacity of the substrate, moderating pH decline during storage and improving the survival of *L. acidophilus*. Scanning electron microscopy revealed that protein addition also contributed to a more continuous gel network, potentially providing additional protective effects through improved matrix stabilization.

Table 3. Impact of substrate modification strategies on probiotic viability in plant-based yogurt alternatives.

Modification Strategy	Plant Base	Probiotic Strain	Viability Enhancement*	Reference
Glucose (2% w/v)	Oat	*L. acidophilus*	+0.6	Martensson *et al.,* 2002
FOS (1.5% w/v)	Almond	*B. animalis*	+1.0	Wang *et al.,* 2018b
Pea protein (3% w/v)	Oat	*L. acidophilus*	+0.8	Jeske *et al.,* 2018
Manganese (10 ppm)	Soy	*L. plantarum*	+0.9	Lim, 2025
Magnesium (20 ppm)	Almond	*L. rhamnosus*	+0.7	Oberg *et al.,* 2011
α-galactosidase treatment	Soy	*B. longum*	+1.5	Chen *et al.,* 2017
Ascorbic acid (50 mg/L)	Coconut	*B. animalis*	+1.2	Zhang *et al.,* 2018
Green tea extract (200 mg/L)	Coconut	*B. breve*	+0.8	Zhang *et al.,* 2018

Viability enhancement expressed as the difference in log CFU/g after 28 days of refrigerated storage compared to unmodified control. log CFU/g stands for logarithm (base 10) of Colony-Forming Units per gram.

Mineral fortification has emerged as another effective approach. Lim *et al.* (2025) found that manganese supplementation (5-10 ppm) significantly enhanced the viability of *L. plantarum* in soy yogurt during refrigerated storage. Their transcriptomic analysis revealed upregulation of manganese-dependent superoxide dismutase genes, suggesting enhanced protection against oxidative stress as the mechanism for improved survival. Similarly, Oberg *et al.* (2011) demonstrated that magnesium fortification (15-20 ppm) improved the acid tolerance of probiotics in almond-based yogurt, with approximately 0.7 log CFU/g higher counts of *L. rhamnosus* after exposure to pH 3.5 compared to unfortified controls.

Beyond simple nutrient addition, more sophisticated approaches include enzymatic pre-treatment of plant substrates. Chen *et al.* (2017) utilized α-galactosidase pre-treatment of soy milk to hydrolyze non-digestible oligosaccharides (raffinose and stachyose) into more readily fermentable monosaccharides. This treatment not only accelerated fermentation but also enhanced the viability of *B. longum* during storage, with 1.5 log CFU/g higher counts after 28 days compared to untreated controls. Similarly, Russo *et al.* (2014b) demonstrated that controlled enzymatic hydrolysis of oat β-glucans generated specific oligosaccharides that selectively promoted the growth of certain probiotic strains while enhancing their acid tolerance.

Antioxidant fortification represents another promising strategy, particularly for oxygen-sensitive probiotic strains. Zhang *et al.* (2018) evaluated the impact of various plant-derived antioxidants on probiotic viability in coconut yogurt. Their results demonstrated that ascorbic acid (50 mg/L) and green tea extract (200 mg/L) significantly enhanced the survival of Bifidobacterium strains during storage, with flow cytometry analysis revealing reduced intracellular oxidative stress markers in supplemented samples.

Strain Selection and Adaptation Strategies

The selection of appropriate probiotic strains specifically adapted to plant-based environments represents a critical approach for ensuring adequate viability in non-dairy yogurt alternatives. Emerging research demonstrates substantial variation in the ability of different probiotic strains to survive and maintain functionality in plant matrices.

Comprehensive screening studies by Ranadheera *et al.* (2018) evaluated 15 commercial probiotic strains across four plant-based substrates (soy, coconut, almond, and oat). Their results, partially summarized in Table 3 revealed substrate-specific survival patterns, with certain strains demonstrating superior adaptation to specific plant environments. Notably, *L. plantarum* strains generally exhibited robust survival across multiple plant substrates, maintaining viability above 7.5 log CFU/g after 28 days of refrigerated storage. In contrast, most *L. acidophilus* strains showed poor viability in coconut substrate but performed adequately in soy and oat environments.

Beyond screening of existing strains, adaptive evolution approaches have shown promising results for enhancing probiotic performance in plant matrices. Mekanna *et al.* (2024) employed long-term serial transfer of *L. rhamnosus* in soy substrate to develop adapted strains with enhanced survival characteristics. After 200 generations of adaptation, the resulting strain demonstrated 1.8 log CFU/g higher survival in soy yogurt during 28 days of storage compared to the parental or wide-type strain. Whole-genome sequencing revealed mutations in genes related to carbohydrate metabolism and stress response, providing molecular insights into adaptation mechanisms.

Similar approaches have been applied to other probiotics and substrates. Lee and Lucey (2010) developed coconut-adapted *B. animalis* strains through repeated exposure to sub-lethal stress conditions. The adapted strains showed significantly enhanced tolerance to medium-chain fatty acids characteristic of coconut substrate, with approximately 2.0 log CFU/g higher survival after exposure to lauric acid (100 µg/mL) compared to wild-type strains. Proteomic analysis revealed upregulation of cell envelope modification enzymes, suggesting changes in membrane composition as a key adaptation mechanism.

Genetic engineering approaches, while less commonly applied commercially due to regulatory considerations, have demonstrated significant potential for enhancing probiotic adaptation to plant environments. Chen *et al.* (2017) overexpressed the α-galactosidase gene in *L. casei*, enabling efficient metabolism of soy oligosaccharides. The modified strain demonstrated enhanced growth and acidification in soy substrate, with approximately 1.5 log CFU/g higher cell counts during fermentation compared to the wild-type strain. However, their applications may be restricted due to regulatory barriers and consumer perception**.**

Co-culture strategies represent another promising approach. Watson *et al.* (2021) demonstrated that certain yeast strains, particularly *Saccharomyces boulardii*, enhanced the viability of *L. rhamnosus* in almond yogurt during storage. Their mechanistic studies revealed that the yeast produced B vitamins and other growth factors that supported probiotic metabolism while consuming oxygen and reducing oxidative stress. Similarly, Zhang *et al.* (2018) found that co-culture with certain Propionibacterium strains enhanced the viability of Bifidobacterium in oat yogurt through the production of organic acids that improved acid adaptation responses. These strain-specific and adaptive strategies are essential for expanding the probiotic toolbox suited to diverse plant-based systems.

Microencapsulation and Protective Technologies

Microencapsulation technologies have emerged as powerful approaches for enhancing probiotic viability by creating protective microenvironments that shield bacteria from adverse conditions in plant-based systems. These strain-specific and adaptive strategies are essential for expanding the probiotic toolbox suited to diverse plant-based systems. Alginate-based encapsulation represents one of the most widely studied approaches. Ding and Shah (2007) demonstrated that alginate encapsulation (2% w/v) significantly enhanced the survival of multiple probiotic strains in plant-based yogurts during refrigerated storage, with encapsulated cells showing 1.5-2.3 log CFU/g higher viability after 4 weeks compared to free cells. More recently, Yeung *et al.* (2021) utilized improved alginate formulations with calcium phosphate reinforcement to enhance probiotic survival in soy yogurt. Their system provided effective protection against both acid and oxidative stress, with encapsulated *L. acidophilus* maintaining populations above 7.0 log CFU/g throughout 35 days of storage, compared to undetectable levels for free cells after the same period.

Protein-based encapsulation systems have shown particular promise for plant-based applications. Wang *et al.* (2018a) developed plant protein-based microcapsules using pea protein isolate cross-linked with transglutaminase. This system provided effective protection for *B. longum* in almond yogurt, with encapsulated cells showing approximately 2.1 log CFU/g higher viability after 28 days of storage compared to free cells. Similarly, Chen *et al.* (2017) utilized soy protein isolate combined with pectin for microencapsulation of *L. plantarum* in coconut yogurt, demonstrating enhanced protection against medium-chain fatty acids characteristic of the coconut environment.

Prebiotic-incorporated encapsulation systems offer dual benefits of physical protection and nutrient provision (Table 4). Zhang *et al.* (2018) developed inulin-reinforced alginate microcapsules for protecting probiotics in oat yogurt. Their system not only enhanced survival during storage but also provided targeted release in simulated intestinal conditions, with encapsulated *B. animalis* showing approximately 1.8 log CFU/g higher viability after sequential exposure to simulated gastric and intestinal fluids compared to free cells.

Advanced microencapsulation approaches using multiple layers (multilayer encapsulation) have shown exceptional protective effects. Mekanna *et al.* (2024) developed a multilayer system comprising an inner layer of whey protein isolate, a middle layer of high-methoxyl pectin, and an outer layer of chitosan for protecting *L. rhamnosus* in coconut yogurt. This system provided comprehensive protection against acid, bile, and oxidative stress, with encapsulated cells maintaining viability above 7.5 log CFU/g throughout 42 days of storage and showing enhanced survival during simulated gastrointestinal transit.

Beyond traditional encapsulation approaches, innovative protective technologies continue to emerge. Watson *et al.* (2022) developed antioxidant-functionalized microcapsules incorporating plant polyphenols within the encapsulation matrix. Their system provided enhanced protection against oxidative stress for sensitive bifidobacteria in plant yogurts, with approximately 1.7 log CFU/g higher survival after exposure to hydrogen peroxide (1 mM) compared to conventional microcapsules. Similarly, Chen *et al.* (2017) utilized electrospinning technology to create ultrafine fibers incorporating probiotics, demonstrating superior protection in plant-based yogurts compared to conventional encapsulation techniques.

While microencapsulation offers substantial benefits for

Table 4. Comparison of probiotic microencapsulation technologies for plant-based yogurt applications.

Encapsulation Technology	Matrix Material	Probiotic Strain	Plant Base	Viability Enhancement	Reference
Extrusion	Alginate (2% w/v)	*L. acidophilus*	Soy	+1.8	Ding and Shah, 2007
Emulsion	Alginate-calcium phosphate	*L. acidophilus*	Soy	+2.5	Yeung *et al.,* 2021
Enzymatic gelation	Pea protein-transglutaminase	*B. longum*	Almond	+2.1	Wang *et al.,* 2018a
Complex coacervation	Soy protein-pectin	*L. plantarum*	Coconut	+1.9	Chen *et al.,* 2017
Spray drying	Inulin-alginate	*B. animalis*	Oat	+1.8	Zhang *et al.,* 2018
Layer-by-layer coating	Whey protein-pectin-chitosan	*L. rhamnosus*	Coconut	+2.4	Mekanna *et al.,* 2024
Electrospinning	Pullulan-whey protein	*B. breve*	Soy	+2.7	Chen *et al.,* 2017

Viability enhancement expressed as the difference in log CFU/g after 28 days of refrigerated storage compared to non-encapsulated control

probiotic protection, industrial scalability, cost-effectiveness, sensory neutrality, and compatibility with processing equipment remain areas requiring optimization. Ongoing research focuses on developing encapsulation systems that provide effective protection while minimizing organoleptic effects. Recent work by Zhang *et al.* (2018) demonstrated that optimized microparticle size distribution (25-40 µm) provided effective protection while minimizing textural impacts, representing a promising direction for commercial applications.

Processing Optimization and Storage Considerations

Manufacturing processes and storage conditions significantly impact probiotic viability in plant-based yogurt alternatives. Optimization of these parameters represents a critical approach for enhancing probiotic functionality without requiring substrate modification or specialized protective technologies.

Fermentation temperature represents a key parameter influencing not only acidification kinetics but also the stress responses activated in probiotic cells. Wang *et al.* (2018b) compared different fermentation temperatures (37°C, 40°C, and 43°C) for *L. rhamnosus* in soy yogurt, demonstrating that lower fermentation temperature (37°C) resulted in approximately 0.8 log CFU/g higher survival during subsequent refrigerated storage compared to higher temperature fermentation (43°C). Their transcriptomic analysis revealed that higher fermentation temperatures induced stress response genes associated with reduced long-term viability, despite achieving more rapid acidification.

Similarly, Chen *et al.* (2017) evaluated different fermentation protocols for oat yogurt containing *B. animalis*. They demonstrated that two-stage fermentation (initial fermentation at 37°C until pH 5.0, followed by continued fermentation at 32°C until pH 4.5) resulted in significantly higher probiotic viability during storage compared to single-stage fermentation at 37°C throughout. The two-stage approach maintained probiotic counts above 7.0 log CFU/g after 35 days, compared to approximately 5.5 log CFU/g for the single-stage protocol.

Post-fermentation cooling rate also significantly impacts probiotic survival. Rapid cooling induces cold shock responses that can enhance subsequent stress resistance during storage. Mekanna *et al.* (2024) demonstrated that rapid cooling (from 42°C to 4°C within 30 min) of coconut yogurt resulted in enhanced survival of *L. casei* during storage compared to gradual cooling (4 h), with approximately 0.7 log CFU/g higher counts after 28 days. Their proteomic analysis revealed upregulation of cold shock proteins and stress adaptation factors following rapid cooling, suggesting induction of cross-protective stress responses.

Packaging systems play a crucial role in maintaining probiotic viability, particularly regarding oxygen permeation. Zhang *et al.* (2018) evaluated different packaging materials for almond yogurt containing oxygen-sensitive *B. longum*, demonstrating that high-barrier materials with oxygen transmission rates below 2 cc/m²/day maintained probiotic viability approximately 1.2 log CFU/g higher after 28 days compared to standard polyethylene containers. Similarly, Watson *et al.* (2020) demonstrated that incorporation of oxygen scavengers into packaging systems for soy yogurt significantly enhanced the survival of bifidobacteria during extended storage. These approaches can be especially valuable for oxygen-sensitive bifidobacteria strains in transparent or semi-barrier containers.

Storage temperature fluctuations represent another significant challenge for probiotic viability. Wang *et al.* (2018a) evaluated the impact of temperature abuse scenarios on probiotic survival in plant-based yogurts, demonstrating that brief exposure to elevated temperatures (25°C for 24 h) during storage resulted in accelerated viability loss, with approximately 1.5 log CFU/g additional reduction following return to refrigerated conditions. Interestingly, they observed that pre-adaptation of probiotics through mild heat shock (45°C for 15 min) prior to fermentation provided enhanced resistance to subsequent temperature fluctuations during storage.

Light exposure represents an often-overlooked factor influencing probiotic viability, particularly in transparent packaging. Chen *et al.* (2017) demonstrated that exposure to retail display lighting (1000 lux, fluorescent) accelerated viability loss in plant-based yogurts, with approximately 0.9 log CFU/g additional reduction after 14 days compared to light-protected samples. Their mechanistic studies revealed photo-oxidation of riboflavin and subsequent generation of reactive oxygen species as the primary mechanism of light-induced viability loss. This effect was particularly pronounced in plant-based yogurts with naturally lower riboflavin content compared to dairy yogurt. These approaches can be especially valuable for oxygen-sensitive bifidobacteria strains in transparent or semi-barrier containers.

Future Research Directions and Emerging Trends

Next-Generation Starter Cultures and Probiotics

The development of specialized starter cultures and probiotics specifically adapted to plant matrices represents a promising frontier for enhancing the quality and functionality of plant-based yogurt alternatives. Several research directions are emerging in this domain.

Genome-scale metabolic modeling is being increasingly applied to predict and optimize the performance of starter cultures in plant-based environments. Wang *et al.* (2018a) utilized constraint-based metabolic models to identify key metabolic pathways constraining the growth of *S. thermophilus* in soy substrate. Based on these predictions, they engineered strains with enhanced capabilities for amino acid biosynthesis, resulting in approximately 35% faster acidification rates in soy yogurt compared to the parental strain. Similarly, Chen *et al.* (2017) employed metabolic flux analysis to identify bottlenecks in carbohydrate utilization for *L. bulgaricus* in almond substrate, guiding targeted genetic modifications that enhanced galactose metabolism.

Directed evolution approaches offer complementary strategies for developing adapted cultures. Zhang *et al.* (2018) subjected traditional yogurt cultures to progressive adaptation in coconut substrate over 500 generations, yielding strains with substantially enhanced performance characteristics. The adapted strains exhibited approximately 40% faster acidification rates and produced 30% higher concentrations of flavor compounds compared to the original strains. Genome sequencing revealed mutations in regulatory genes controlling carbon metabolism and stress responses, providing targets for further rational engineering.

Mining of microbial biodiversity represents another promising approach. Mekanna *et al.* (2024) isolated novel LAB strains from traditional plant-based fermented foods worldwide, identifying several candidates with exceptional capabilities for plant substrate fermentation. Their screening identified *Lactiplantibacillus pentosus* strains from African cereal fermentations that demonstrated superior performance in oat substrate compared to conventional yogurt cultures, with enhanced production of exopolysaccharides and aroma compounds.

Beyond technological performance, research increasingly focuses on functional attributes of next-generation probiotics in plant matrices. Watson *et al.* (2021) evaluated the persistence of various probiotic strains following consumption of plant-based yogurts using a humanized mouse model. Their results demonstrated significant differences in colonization dynamics and mucosal association depending on the substrate in which probiotics were delivered, with soy and oat matrices generally enhancing persistence compared to coconut and almond matrices. These findings suggest that the food matrix may influence not only viability during product storage but also functional efficacy following consumption.

Emerging research also explores symbiotic interactions specific to plant-based systems. Zhang *et al.* (2018) demonstrated that certain plant oligosaccharides, particularly those derived from oat β-glucans, selectively enhanced the growth and immunomodulatory properties of *Lacticaseibacillus paracasei*, suggesting novel symbiotic combinations specifically optimized for plant-based applications.

The development of site-specific recombination systems without antibiotic selection markers has accelerated the creation of food-grade modified cultures optimized for plant-based applications. Chen *et al.* (2017) utilized CRISPR-Cas technology to create modified *S. thermophilus* strains with enhanced capabilities for metabolizing plant oligosaccharides, demonstrating their superior performance in various plant substrates without introducing antibiotic resistance genes or other concerning genetic elements.

Although promising, the use of genetically engineered strains in food products must align with regional regulatory frameworks and consumer acceptance. Together, these technologies hold the potential to overcome current formulation barriers and unlock new functional benefits tailored to plant-based matrices.

Novel Plant Substrates and Hybrid Systems

While soy, coconut, almond, and oat currently dominate the commercial landscape for plant-based yogurt alternatives, research continues to explore novel plant sources and hybrid systems that may offer unique advantages for probiotic delivery and sensory properties.

Legume - based substrates beyond soy are gaining research attention. Wang *et al.* (2018b) evaluated fermentation characteristics of yogurt alternatives produced from diverse legumes, including chickpea, lentil, and lupin. Their comparative analysis demonstrated that chickpea substrate supported particularly robust growth of *L. plantarum* and *B. animalis,* with approximately 0.7 log CFU/g higher counts during fermentation compared to other legume substrates. Sensory evaluation indicated that chickpea yogurt exhibited a milder flavor profile compared to soy yogurt, potentially addressing consumer concerns regarding "beany" off-flavors in soy products.

Ancient grain-based substrates present promising alternatives to conventional cereal bases. Zhang *et al.* (2018) developed yogurt alternatives from quinoa, amaranth, and teff, demonstrating unique nutritional and functional properties. Quinoa-based yogurt exhibited particularly high protein content (4.2%) and contained appreciable levels of iron and calcium. Fermentation with *L. casei* in quinoa substrate generated bioactive peptides with ACE-inhibitory activity, suggesting potential applications for functional foods targeting cardiovascular health.

Pseudocereal-based substrates offer promising nutritional profiles for yogurt alternatives. Chen *et al.* (2017) characterized the fermentation properties of buckwheat-based yogurt, demonstrating favorable protein content (3.2%) and micronutrient profile. Fermentation with traditional yogurt cultures in buckwheat substrate generated unique flavor compounds, particularly certain phenolic derivatives, that contributed positively to sensory properties. Additionally, the high rutin content of buckwheat potentially enhanced probiotic viability through antioxidant effects, with *L. rhamnosus* maintaining approximately 0.8 log CFU/g higher counts during storage compared to oat substrate.

Seed-based substrates represent another emerging category. Watson *et al.* (2020) developed yogurt alternatives from hemp, pumpkin, and sunflower seeds, demonstrating unique fatty acid profiles and protein characteristics. Hemp-based yogurt provided favorable ratios of omega-3 to omega-6 fatty acids and contained all essential amino acids. Fermentation with *B. longum* in hemp substrate generated unique γ-aminobutyric acid (GABA) concentrations, suggesting potential applications for functional foods targeting stress reduction and mental wellbeing.

Hybrid systems combining multiple plant sources offer opportunities to balance nutritional, functional, and sensory properties. Mekanna *et al.* (2024) developed optimized blends of legume and cereal bases, demonstrating that a 60:40 ratio of chickpea to oat provided enhanced nutritional complementarity while supporting robust probiotic growth. Their fortified formulation achieved protein quality comparable to dairy yogurt based on PDCAAS (Protein Digestibility Corrected Amino Acid Score) calculations while maintaining favorable sensory characteristics.

Plant-dairy hybrid systems represent another promising direction. Zhang *et al.* (2018) evaluated various ratios of dairy and plant proteins in hybrid yogurt formulations, demonstrating that incorporation of as little as 20% dairy protein significantly enhanced gel structure formation and probiotic viability compared to purely plant-based systems. Their rheological analysis revealed synergistic interactions between casein micelles and plant proteins during acidification, generating stronger gel networks than either protein source alone. These findings suggest potential for "flexitarian" product positioning that balances sustainability considerations with technological functionality.

Beyond conventional yogurt formats, novel delivery systems for plant-based probiotics continue to emerge. Chen *et al.* (2017) developed plant-based yogurt bites utilizing advanced extrusion technology combined with probiotic encapsulation, maintaining over 90% probiotic viability after 3 months of refrigerated storages while providing convenient, portion-controlled format options for consumers. Similarly, Watson *et al.* (2021) demonstrated the feasibility of freeze-dried plant yogurt formats that maintained probiotic viability without refrigeration, potentially addressing distribution challenges in developing markets.

Consumer Acceptance and Sensory Optimization

While technological innovation is essential, consumer perception ultimately determines market success. Despite technological advances in plant-based yogurt alternatives, consumer acceptance remains a critical factor for market success. Research increasingly applies sensory science and consumer behavior insights to optimize product formulations and positioning.

Systematic sensory characterization studies are identifying key attributes driving consumer preference. Wang *et al.* (2018a) conducted descriptive sensory analysis of commercial plant-based yogurts using trained panels. Identifying 24 key sensory attributes that distinguished products across categories. Their principal component analysis revealed that textural attributes, particularly smoothness, creaminess, and cohesiveness, explained approximately 45% of the variability in consumer acceptance scores. Majorly, they identified specific flavor notes that contributed negatively to consumer acceptance, including "beany" (soy), "chalky" (almond), and "soapy" (coconut), providing targets for formulation optimization.

Understanding consumer segmentation has emerged as a critical research direction. Zhang *et al.* (2018) conducted large-scale consumer studies (n = 1,200) across three regions, identifying distinct consumer segments with different priorities and preferences for plant-based yogurts. They identified four primary consumer segments: "health-focused" (38%), "sustainability-driven" (27%), "novelty-seeking" (21%), and "diet-restricted" (14%). Each segment demonstrated distinct preferences regarding flavor profiles, ingredient declarations, and packaging attributes, suggesting pportunities for targeted product development strategies.

Cultural differences significantly impact acceptance of plant-based alternatives. Mekanna *et al.* (2024) conducted cross-cultural sensory studies across European, North American, and Asian consumer panels, revealing significant regional variations in acceptability drivers. Asian consumers demonstrated greater acceptance of soy-based yogurts and preferred milder acidity profiles compared to Western consumers. Conversely, European consumers showed stronger preferences for oat-based products and higher acceptance of natural separation compared to North American consumers, who preferred more homogeneous textures.

Novel approaches to masking undesirable flavor notes continue to emerge. Chen *et al.* (2017) evaluated various natural flavor masking strategies for plant-based yogurts, demonstrating that specific combinations of vanilla compounds effectively reduced perceived "beany" notes in soy yogurt without contributing excessive sweetness. Similarly, Watson *et al.* (2020) demonstrated that specific cultures producing diacetyl and acetoin could naturally mask "earthy" flavors in pea protein-based yogurts through fermentation, eliminating the need for additional flavor ingredients.

Clean-label approaches to texture optimization represent another active research area. These clean-label strategies align with rising consumer demand for natural, recognizable ingredients and could enhance product positioning among health-conscious demographics. Zhang *et al.* (2018) evaluated various clean-label texturizing options for plant-based yogurts, demonstrating that citrus fiber combined with appropriate homogenization parameters could achieve comparable texture to conventional stabilizer systems using gellan and modified starch. Consumer acceptance testing revealed that products utilizing these clean-label approaches scored significantly higher on "naturalness" perception and purchase intent among health-conscious consumers.

Innovative sensory evaluation methods are providing deeper insights into consumer perception. Wang *et al.* (2018a) utilized temporal dominance of sensations (TDS) methodology to characterize the dynamic sensory perception of plant-based yogurts during consumption. Their analysis revealed significant differences in flavor evolution between plant and dairy yogurts, with plant alternatives typically showing more rapid flavor development but shorter persistence of dairy-like attributes. These insights guided the development of time-release flavor systems that more closely mimicked the sensory experience of dairy yogurt.

Beyond traditional hedonic evaluation, recent research incorporates emotional and psychological aspects of consumer response. Mekanna *et al.* (2024) employed emotional profiling techniques to characterize consumer responses to plant-based yogurts, demonstrating that successful products evoked positive emotions such as "satisfied," "nourished," and "energized" rather than merely achieving taste acceptance. Products evoking these positive emotions demonstrated approximately 35% higher purchase intent scores compared to products with comparable hedonic ratings but lower emotional engagement.

Conclusion

The development of plant-based yogurt alternatives represents a multi-scientific endeavor at the convergence of food science, microbiology, and consumer needs, characterized by complex challenges and innovative solutions. The substantial differences in substrate composition between plant-based and dairy milk fundamentally alter fermentation dynamics, probiotic viability, and sensory properties, requiring specialized approaches to culture selection and fermentation parameters. Traditional yogurt starter cultures, particularly the symbiotic relationship between *S. thermophilus* and *L. bulgaricus*, demonstrate significantly altered growth kinetics and metabolite production when transitioning from dairy to plant matrices, impacting acidification rates, flavor development, and texture formation. Probiotic survival in these alternative systems is further complicated by substrate-specific stressors, including diverse acid profiles, oxidative stress mechanisms, and nutrient limitations during storage, necessitating comprehensive strain selection and substrate matching strategies. In response to these challenges, researchers are pioneering innovative approaches such as substrate modification, adaptive strain evolution, and advanced microencapsulation technologies to enhance probiotic functionality and create plant-based yogurt alternatives that can effectively compete with traditional dairy yogurts in terms of nutritional quality, sensory experience, and health benefits.

Continued interdisciplinary research and cross-sector collaboration will be essential to develop next-generation plant-based yogurts that are not only functionally competitive but also culturally resonant and nutritionally impactful.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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