



Review Article

Prebiotics in animal nutrition: Harnessing agro-industrial waste for improved gut health and performance

M. Cristina Ravanal ^{a, b, c, †}, Carolina A. Contador ^{d, e, †}, Wing-Tak Wong ^{d, e}, Qile Zhang ^{d, e},
 Analese Roman-Benn ^{a, f, g}, Kong Shun Ah-Hen ^a, Pilar E. Ulloa ^h, Hon-Ming Lam ^{d, e, *}

^a Institute of Food Science and Technology, Faculty of Agricultural and Food Sciences, Austral University of Chile (UACH), Valdivia 5090000, Chile

^b Faculty of Agronomy and Natural Systems, Pontificia Universidad Católica de Chile, Santiago 7820436, Chile

^c Institute for Sustainable Development, Pontificia Universidad Católica de Chile, Santiago 7820436, Chile

^d School of Life Sciences and Centre for Soybean Research of the State Key Laboratory of Agrobiotechnology, The Chinese University of Hong Kong, Shatin, Hong Kong SAR 000000, China

^e Institute of Environment, Energy and Sustainability, The Chinese University of Hong Kong, Shatin, Hong Kong SAR 000000, China

^f Graduate School, Faculty of Agricultural and Food Sciences, Austral University of Chile (UACH), Isla Teja Campus, Valdivia 5090000, Chile

^g Food Policy Division, Ministry of Health, Georgetown 05924, Guyana

^h Center for Applied Research in Veterinary and Agricultural Sciences, University of the Americas, Santiago 7500975, Chile

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ABSTRACT

This review provides an overview of the current research on prebiotics and their applications in animal nutrition and health. Various types of prebiotics are introduced and classified, with an analysis of agro-industrial residues as sources. The potential of prebiotics as substrates for the growth and/or activity of probiotic microorganisms, as well as their applications in animal feeds, were examined. This analysis also considered the health-promoting advantages linked to different production techniques and bioactive compounds. The mechanisms by which prebiotics alter gastrointestinal tract microbiota are discussed, specifically in terms of combating pathogenic bacteria and modulating immune cells in the gut. Investigations of the impact of prebiotics in both polygastric and monogastric animals are reported, highlighting their effects on the gut ecosystem and animal performance. This review concludes that agro-industrial residues are valuable sources of prebiotics that possess numerous beneficial health-promoting properties suitable for animal nutrition. These prebiotics can serve as a relevant substitute in the ongoing search for alternative strategies to prevent and control the presence of pathogenic bacteria in animals, particularly considering the restriction on antimicrobial growth promoters. However, further research is necessary to explore the interaction between prebiotics and probiotics in animal care and well-being, to establish systematic management of production and practical applications of these functional feed additives.

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* Corresponding author.

E-mail address: honming@cuhk.edu.hk (H.-M. Lam).

[†] These authors equally contribute to this work.

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1. Introduction

The practice of using antibiotics as feed additives in animal farming, with the purpose of promoting animal growth and balancing gut flora, has been banned to tackle the dissemination of antibiotic-resistant bacteria and their potential food-borne transmission to humans (Haulisah et al., 2021). However, the elimination of antimicrobial growth promoters has been a challenge for animal nutrition industry, as some adverse consequences have emerged for the production, health, and welfare of animals (Khan et al., 2022). Therefore, significant research efforts have been focused on the development of antibiotic alternatives to maintain or

improve animal health and performance. Modulation of the gut microbiota with feed additives such as prebiotics and probiotics have become a need to maximize productivity and maintain animal health and welfare. Among these, prebiotics are a promising alternative. Their inclusion in livestock and poultry feed have shown the capability to improve host health and productivity through the selective stimulation of beneficial gut microbiota (Solís-Cruz et al., 2019). In this regard, agro-industrial waste plays a role as a source of feed ingredients in animal nutrition (Pinotti et al., 2020). In particular, agro-industrial waste is often rich in carbohydrates and fibre, which are considered prebiotics that can promote the proliferation of beneficial microbes in the large intestine. Agro-industrial wastes from fruits (e.g., mango peels, citrus peels, apple pomace) and vegetables (e.g., garlic straw, potato processing waste, onion skins) have been explored to produce prebiotics (Rahmani et al., 2017) that are employed as feed supplements. The term “prebiotics” was first coined by Gibson and Roberfroid (1995) and described as the “non-digested food components that, through stimulation of growth and/or activity of a single type or a limited amount of microorganisms residing in the gastrointestinal tract, improve the health condition of a host” (Gibson and Roberfroid, 1995). Through the years, this description has evolved, and the latest criterion to distinguish a prebiotic was created by the International Scientific Association of Probiotics and Prebiotics (ISAPP) (Gibson et al., 2017). The definition states that a prebiotic is “a substance that is selectively utilized by host microorganisms conferring a health benefit” (Gibson et al., 2017). This description broadens the prebiotic category to encompass not only carbohydrates, but also polyphenols and polyunsaturated fatty acids. The recognition that the applications of prebiotics are not restricted to the human gastrointestinal tract and includes animal nutrition highlights the broader benefits beyond human health.

On the other hand, the discovery of the health benefits of microorganisms can be traced back to 1907 when Russian scientist Elie Metchnikoff observed the higher longevity of Bulgarian farmers who consumed fermented dairy food (Mackowiak, 2013). The term “probiotics” was later coined by Werner Kollath in 1953 to refer to “essential active substances for the healthy development of life” (Gasbarrini et al., 2016). In 2001, the Food and Agriculture Organization (FAO) and the World Health Organization (WHO) officially defined probiotics as “live microorganisms that, when administered in adequate amounts, confer a health benefit on the host.” The definition was further confirmed by the International Scientific Association for Probiotics and Prebiotics (ISAPP) in 2014 (Hill et al., 2014). The microorganisms commonly used as probiotics belong to various bacterial species, with *Bifidobacterium*, *Lactobacillus*, *Streptococcus*, *Bacillus*, and *Enterococcus* the most commonly used (Kim et al., 2020). Over the years, numerous scientific studies have demonstrated the high potential of probiotics to provide health benefits on livestock, leading to a significant increase in research on probiotics in animal feeding (Di Gioia and Biavati, 2018).

The positive effects of prebiotics on health are associated to their capability to modify the gut microflora by selectively stimulating the growth and/or activity of beneficial bacteria, such as Firmicutes, and Bacteroidetes, which produce beneficial metabolites (Uyeno et al., 2015; Yin et al., 2018). Other phyla have specific niches that differ based on the animal species. This can help to control pathogenic bacteria in livestock species, promoting overall health (Azad et al., 2020). Studies have shown that prebiotics, when employed as feed additives in animal nutrition, can lead to significant population proliferation of probiotic bacteria like *Bifidobacterium* and *Lactobacillus*. Supplementing generally healthy calves with a prebiotic has revealed to have a positive but not significant effect on the microbial community that is relatively stable in these animals

(Heinrichs et al., 2009). Recent findings have shown the potential use of prebiotics as alternatives to antibiotics to enhance animal growth and health without eventual risks to human wellness and the ecosystem (Chiesa et al., 2017; Pan et al., 2019). Studies examining the effects of prebiotics on animal health frequently yield inconsistent results due to the high specificity of individual compounds, variations in dosages, and differences in the timing of the application.

The agriculture industry produces diverse types of wastes, including stems, stalks, leaves, seeds, straws, husks, peels, sugar cane bagasse, and pulp from fruits, cereals, or legumes, among others (Sadh et al., 2018). Various nutrients derived from these wastes, including pectins, cellulose, hemicellulose, and xylans, can support the development of different intestinal microorganisms. In this regard, this review highlights recent findings of prebiotics derived from agro-industrial waste and their effects on animal health.

2. Types of prebiotics

Prebiotics can be classified into several categories based on their development and regulatory status. Inulin, fructo-oligosaccharides (FOS), galacto-oligosaccharides (GOS) and lactulose are generally classified as well-established prebiotics. Xylo-oligosaccharides (XOS), isomalto-oligosaccharides (IMO) among others are classified as “emerging” prebiotics (Cardoso et al., 2021) (Fig. 1). Inulin, XOS, cereal fibre, lacticol, FOS, and GOS are among the most common prebiotics used in animal nutrition (Crittenden and Playne, 2008).

2.1. Inulin

Inulin is a linear polymer with β -glycosidic bonds (2 $\rightarrow$ 1) derived from D-fructose, having usually terminal glucose units with β (2 $\rightarrow$ 1) linkage. Inulin has degree of polymerization of up to 60. It is classified as a fructan and is synthesized by a range of plants. Inulin is a storage carbohydrate present in many plant species (Davani-Davari et al., 2019).

2.2. Fructo-oligosaccharides

Fructo-oligosaccharides are categorized as a type of inulin-derived oligosaccharides, specifically fructans, consisting of 2 to 60 D-fructose units connected by β -(2,1) linkages. They are naturally existing short-chain carbohydrates with a D glucosyl ending (Apolinário et al., 2014). There are three types of FOS with variant polymerization degrees, and also of different origin and structure: 1) linear long-chain fructan, 2) oligomeric fructan (degree of polymerization from 3 to 9); oligofructose consists of fructosyl chains ending with fructose or glucose monomers and 3) short-chain FOS consisting of different fructosyl chains with a terminal glucose monomer (Csernus and Czeplédi, 2020). Fructo-oligosaccharides at an administration dose of 4 g/kg feed (Xu et al., 2003) have been found to promote the growth of probiotic bacteria in male broilers. However, FOS administered at concentrations of 0.5%, 1% and 2% had no effect on growth and productivity of turkey (Juśkiewicz et al., 2006).

2.3. Galacto-oligosaccharides

Galacto-oligosaccharides are galactose-containing oligosaccharides that exhibit diverse variations in chain length, branching, and glycosyl linkages in their chemical structures. Based on the source of β -galactosidase, when lactose acts as the sole substrate, the galactose released during the enzymatic hydrolysis of lactose can

be transferred to another lactose molecule via $\beta(1 \rightarrow 6)$, $\beta(1 \rightarrow 4)$ or $\beta(1 \rightarrow 3)$ glycosidic linkage to the galactose moiety (Mei et al., 2022). A novel GOS mixture (Tzortzis et al., 2005) has been shown to promote the growth of *Bifidobacterium* and *Lactobacillus* in pigs.

2.4. Lactulose

Lactulose is an artificial disaccharide produced from lactose through the action of β -galactosidase or epimerase. It is composed of fructose and galactose. Lactulose has low absorption rates in the gastrointestinal tract, and the cells lining the intestinal tract lack digestive enzymes for its hydrolysis (Chu et al., 2022).

2.5. Xylo-oligosaccharides

Xylo-oligosaccharides are oligomers of sugar consisting of β -D-xylopyranosyl (xylose) units connected via $\beta(1 \rightarrow 4)$ -xylosidic linkages (Santibáñez et al., 2021). Xylo-oligosaccharides are isolated from xylan-containing lignocellulosic materials, such as crop residues, wood, and herbaceous biomass, known to have prebiotic effects. Xylo-oligosaccharides can also be generated by the addition of exogenous enzymes, such as xylanase, to the lignocellulosic residues (Baker et al., 2021).

2.6. Isomalto-oligosaccharides

Isomalto-oligosaccharides are glucose oligomers that exhibit α -D-(1,6)-linkages, occurring as isomaltose, isomaltotriose, isomaltotetraose, isomaltopentaose, and other oligosaccharides with higher branching. IMO are derived from starch through the

action of enzymes belonging to various glycosyl hydrolase families. The enzymes involved in the production of IMO exhibit transferase, hydrolytic or branching activity, leading to a mixture of α -linked gluco-oligomers with varying types of glycosidic linkages and degrees of polymerization (2 to 10) (Logtenberg et al., 2021).

2.7. Polydextrose

Polydextrose is a highly branched glucose polymer with random linkages, characterized by an average polymerization degree of 12, with a range from 2 to 120. The molecule encompasses all possible combinations of α - and β -linked $1 \rightarrow 2$, $1 \rightarrow 3$, $1 \rightarrow 4$, and $1 \rightarrow 6$ glycosidic linkages, although the $1 \rightarrow 6$ (both α and β) linkages are the most common. Polydextrose undergoes partial fermentation in the large intestine, favoring increases in the amount of fecal volume, reduction in transit time, and the softening of fecal material, along with a decrease in fecal pH (do Carmo et al., 2016).

2.8. Pectic oligosaccharides

Pectic oligosaccharides are derived from the depolymerization of pectin. Pectins are branched heteropolymers made up of a linear backbone consisting of $\alpha(1-4)$ -linked D-galacturonic acid (GalA) units, which can undergo random acetylation and/or methylation. These linear structures constitute the “smooth region” of pectins, occasionally interrupted by the “hairy regions” characterized by branches composed of neutral sugars. Pectic oligosaccharides have been suggested as a novel category of prebiotics capable of providing several health-promoting effects, such as the promotion

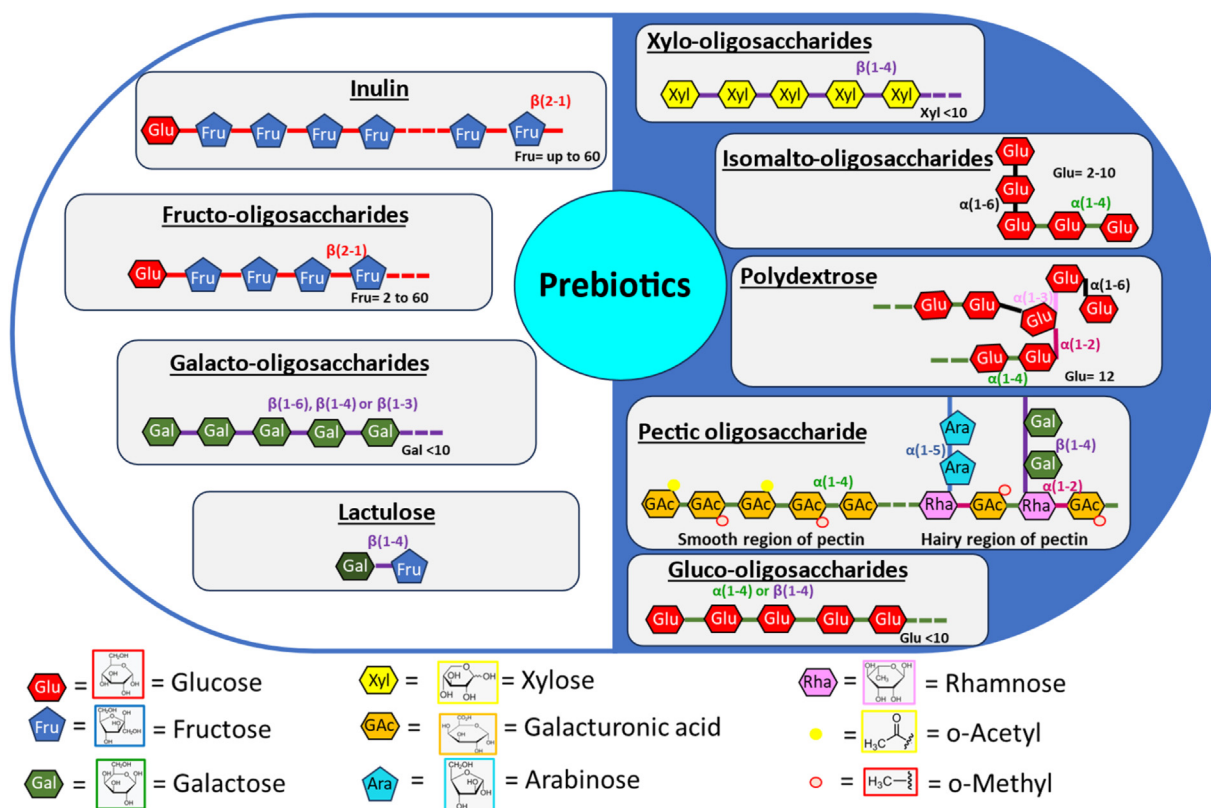


Fig. 1. Chemical and bonding structures of prebiotics. Different types of prebiotics, including both well-established and emerging prebiotics. The well-established prebiotics include inulin, fructo-oligosaccharides (FOS), galacto-oligosaccharides (GOS), and lactulose. The emerging prebiotics consist of xylo-oligosaccharides (XOS), isomalto-oligosaccharides (IMO), polydextrose, pectic oligosaccharide, and gluco-oligosaccharide.

of bifidogenic flora, and antioxidant activity (Wongkaew et al., 2022).

2.9. Gluco-oligosaccharides (GlcOS)

Gluco-oligosaccharides refer to the oligosaccharides consisting of exclusively D-glucose units, exhibiting diverse degree of polymerization and glycosidic linkages. The α -gluco-oligosaccharides (α -GlcOS) are hydrolysates of starch (α -[1 $\rightarrow$ 4] glucan), while β -gluco-oligosaccharides (β -GlcOS) are hydrolysates of (1,3) (1,4)- β -D-glucan. Both provide a valuable prebiotic source that promote the selective proliferation of probiotic bacteria (Zeng et al., 2023).

3. Effects of prebiotics on gut health

The gastrointestinal tract (GIT) harbors a vast array of live microorganisms collectively referred to as gut microbiota, which play crucial roles in both health and disease (Ursell et al., 2012). Nowadays, the prohibition of the utilization of antibiotics as growth promoters has posed a challenge in animal nutrition, resulting in the search for alternative strategies to manage and prevent the colonization of pathogenic bacteria. The alteration of the gut microbiota using novel feed additives (e.g., probiotics and prebiotics) with host-protective functions to promote animal health is a buzzword in the fields of animal feeding (Gaggia et al., 2010; Markowiak and Śliżewska, 2018). A healthy gut microbiota has numerous important functions in animal health, including aiding in modulating the gastrointestinal environment, strengthening the immune system, and inhibiting the proliferation of pathogenic bacteria (Anadón et al., 2019; Markowiak and Śliżewska, 2018).

3.1. Proposed mechanisms of action

Prebiotics and probiotics are beneficial for gut health as they help establish a balanced gut microbiota in animals (Arsène et al., 2021; Flickinger and Fahey, 2002; Verdonk et al., 2005). They achieve this through several mechanisms, which can be categorized into two main groups: combating pathogenic bacteria and modulating immune cells in the gut.

Prebiotics and probiotics have been observed to exhibit antagonistic activity against pathogenic bacteria (Arsène et al., 2021; Śliżewska and Chlebicz-Wójcik, 2020). In a study by Śliżewska, the population of several *Listeria* and *Salmonella* strains decreased significantly after the addition of a synbiotic mix consisting of *Lactobacillus* strains and inulin. This suggests that synbiotics possess antimicrobial properties towards pathogenic and harmful bacteria in the gut. Further studies have explored this characteristic and identified multiple mechanisms of action against pathogenic bacteria.

Probiotics possess binding sites for adhesion to glycolipid and glycoprotein receptors, such as toll-like receptors in the host, which can block and compete for adhesion sites with various pathogens (Arsène et al., 2021; Pandey et al., 2015). This reduces the likelihood of harmful bacteria entering the bloodstream through adhesion. Some probiotic strains also boost mucus-binding abilities in the gut by having binding protein molecules on their cell surfaces, which enhances their attachment to the mucosal layer. This provides probiotic bacteria a higher chance of competing for nutrients with pathogenic bacteria as they colonize the gut and are less likely to be carried away by the chyme in the intestinal tract (Arsène et al., 2021; Peng et al., 2019). Prebiotics and probiotics can also induce mucin production in the gut, further enhancing their mucus-binding properties. Probiotics are shown to upregulate mucin production from goblet cells in the gut through inflammatory pathways, while prebiotics encourage mucin production to aid the

colonization of probiotic bacteria (La Fata et al., 2018; Markowiak and Śliżewska, 2017). The thickening of mucin strengthens the gut barrier function, protecting intestinal cells against the invasion of pathogenic bacteria and regulating the homeostasis of water, antimicrobial, and immune molecules.

Probiotics also produce antibacterial substances, such as short-chain fatty acids (SCFAs) and lactic acid, which help maintain a low pH environment in the gut that inhibits the survival of pathogenic bacteria (Markowiak and Śliżewska, 2018; Peng et al., 2019; Qamar et al., 2016). Some probiotic species produce antibacterial peptides, including bacteriocins and antibiotics, which are effective in inhibiting the proliferation of many harmful bacteria, such as nisin, lactacin, pediocin, and enterocin (Peng et al., 2019). Butyric acid, a type of SCFA, can promote the production of antimicrobial peptides (Chibbar et al., 2017). Probiotics can also disintegrate bacterial toxins and block toxin receptors, metabolize certain toxins, and bind to them, preventing them from coming into contact with intestinal cells and disrupting the gut microbiota (Arsène et al., 2021; Markowiak and Śliżewska, 2017).

Short-chain fatty acids, particularly butyrate, have been shown to inhibit inflammatory pathways. Butyrate uptake into intestinal cells inhibits the ERK/MAPK pathway and downregulates NF- κ B dependent gene expression, which reduces the expression of proinflammatory cytokines like TNF- α and IL-6, while increasing the expression of anti-inflammatory IL-10. Butyrate also inhibits HDAC, mediating and reducing inflammation responses in the gut through inhibition of the above two signalling pathways (Nawaz et al., 2018; Parada Venegas et al., 2019). Short-chain fatty acids have also been found to stimulate the expression of anti-inflammatory PGE2 (Cox et al., 2009). Pectin, a mixture of plant polysaccharides, inhibits pro-inflammatory signals in dendritic cells by impeding the TLR signalling pathways, which helps regulate and control inflammation in the gut (Nawaz et al., 2018; Sahasrabudhe et al., 2018).

3.2. Interaction of prebiotics with the host gut microbiota

Prebiotics are short-chain carbohydrates that are resistant to digestion by enzymatic methods but selectively enhance the activity of certain probiotic bacteria in the gut (Anadón et al., 2019; Sarkar, 2007). These carbohydrates include disaccharides, oligosaccharides, polysaccharides, resistant starch, and some sugar polyols, and have a low level of polymerization and a linear shape (Al-Sheraji et al., 2013). They are non-digestible as they have glycosidic bonds that are resistant to digestion, allowing them to be selectively fermented by bacteria in the gut. Mechanistically, as presented in Fig. 2, prebiotics have a promising effect on gut health in both polygastric and monogastric animals (Azad et al., 2020; Zapata et al., 2021). Polygastric animals, such as ruminants, possess a unique digestive system characterized by a specialized fermentation chamber called the rumen. Prebiotics exert their effects in polygastric animals by modulating the microbial population and activity within the rumen. When prebiotics are introduced into the diet of ruminants, they serve as a substrate for specific beneficial microorganisms, promoting their growth and activity. These microorganisms, including fibrolytic bacteria and protozoa, possess the ability to ferment complex carbohydrates and fiber into SCFAs, such as acetate, propionate, and butyrate. During fermentation, combustible gases, lactate, and beneficial SCFAs including acetic, propionic, and butyric acids are produced (Gibson et al., 2017; Sarkar, 2007). Short-chain fatty acids are important for the growth of beneficial bacteria in the gut, preventing dysbiosis, and exerting immunomodulatory effects in the host (Al-Sheraji et al., 2013; Gibson et al., 2017). This modulation of the rumen microbiota by prebiotics enhances the efficiency of nutrient utilization, improves

gut health, and reduces the production of methane, a potent greenhouse gas emitted by ruminants (Michalak et al., 2021). In monogastric animals, prebiotics primarily act on the gastrointestinal tract by selectively stimulating the growth and activity of beneficial bacteria. Upon consumption, prebiotics resist digestion in the upper gastrointestinal tract and reach the colon, where they serve as a substrate for specific groups of bacteria, such as *Bifidobacteria* and *Lactobacilli* (Gaggia et al., 2010). These bacteria ferment prebiotics, producing SCFAs. Furthermore, SCFAs have been found to influence the secretion of gut hormones, such as peptide YY (PYY) (Browne and Horgan, 2024; Tellez et al., 2020) and glucagon-like peptide-1 (GLP-1) (Azad et al., 2020; Bachmann et al., 2021), which regulate appetite, satiety, and glucose homeostasis. The fermentation of prebiotics also leads to a decrease in the luminal pH, creating an environment unfavourable for the growth of pathogenic bacteria (Jha et al., 2019). Additionally, prebiotics can enhance the production of mucins, which are protective substances that form a physical barrier in the gut, and stimulate the immune system, contributing to improved gut health and overall well-being in monogastric animals (Azad et al., 2020). Sources of prebiotics typically come from breast milk, plants, microbiological, and enzymatic activities (Sarkar, 2007). Common examples of prebiotics include lactulose, GOS, FOS, inulin, and its hydrolysates, and mannan-oligosaccharides (MOS). In the following paragraphs, three of these prebiotics as examples will be discussed.

The beta glycosidic bonds in FOS render them indigestible until they reach the small intestine (Chen et al., 2016). Fructo-oligosaccharides include 1-ketose, nystose, and 1-fructofuranosyl-nystose, and belong to the same family of carbohydrates with varying degrees of polymerization and chain length (Martins et al., 2019). Fructo-oligosaccharides were recognized as prebiotic components in the 1990s due to their gut-promoting and selective fermentation properties, evidenced through their ability to stimulate the growth of bifidobacterial strains in the gut (Anadón et al., 2019; Sarkar, 2007). Fructo-oligosaccharides and oligo-fructose are produced through partial enzymatic hydrolysis of inulin and exhibit similar physical and physiological effects. Like FOS, inulin due to the beta glycosidic bonds also remains undigested in the upper digestive tract, providing physical benefits. In terms of physiological effects, inulin has been shown to improve gut health by altering the composition of fecal metabolites and exerting immunomodulatory and therapeutic effects on the gut in animal (Anadón et al., 2019; Flickinger and Fahey, 2002; Markowiak and Śliżewska, 2018; Meyer and Stasse-Wolthuis, 2009). Like FOS and inulin, both types of GOS, as α -GOS, found in plant sources and β -GOS from lactose (Martins et al., 2019), have galactosidic bonds that render them non-digestible in the upper digestive tract, promoting their fermentation in the colon (Verdonk et al., 2005).

4. Effects of prebiotics on animal health

Nutritional feed additives encourage the establishment of beneficial bacteria. They have been found to strongly influence the progression of the intestinal epithelium while modulating the physiological functions needed to maintain immunity, the digestion of nutrients and the fortitude of the intestinal barrier which favourably affects the growth performance of animals (Al-Baadani et al., 2021). Given that there is a ban on antimicrobial growth promoters, it is necessary to employ different methods to prevent and control the colonization of pathogenic bacteria in animals (Anadón et al., 2019). Using antimicrobial growth promoters in animal feed have aided in the increase of multidrug-resistant microorganisms in livestock and poultry; resulting in animal products that contain antibiotic residues (Bosco, 2019; Forgetta et al., 2012; Mazhar et al., 2021; Mohammadigheisar et al., 2019). The existence

of this ban has propelled the scientific community to find alternative products such as prebiotics, not only because of the above mentioned reasons, but also for the well-being of the animals as it is crucial to achieve and maintain good gut health (Al-Baadani et al., 2021; Angwech et al., 2019; Vasanthakumari et al., 2023).

Prebiotics are able to protect the epithelial cells from harmful microorganisms by acting as receptors that assist with the modulation of the host's immune system; controlling inflammation (Ahmadifar et al., 2019; Mohammadi et al., 2022). Insoluble fibres that are isolated from legumes, plants, grains, fruits and cruciferous vegetables are the usual sources of prebiotics; while they may not always be of nutritive value, they carry out functions such as stimulation of the intestine and selection of the microbiota composition (Leone and Ferrante, 2023). The most frequently used prebiotics are non-starch polysaccharides (NSP) or oligosaccharides such as alginate oligosaccharide (AOS), arabinoxylo oligosaccharides (AXOS), FOS, galacto-oligosaccharides (GOS), isomalto-oligosaccharides (IMO), inulin, MOS and xylo-oligosaccharides (XOS) (Azad et al., 2020; Jahan et al., 2022).

According to Azad et al. (2020), inulin, FOS, GOS, tragalacto-oligosaccharides, and lactulose are the prebiotics primarily studied in animal health promotions, used as feed additives given that they are easily fermented in the colon and result in decreased luminal pH and increased SCFA production.

Furthermore, as stated by Patel and Goyal (2012), most prebiotics stimulate bifidogenic and lactic acid bacteria in animals. Prebiotics serve as substrates for fermentation and attach themselves to pathogens. They can increase osmosis in the lumen of the intestine, stimulate the macrophages' response and the production of SCFAs indirectly, while modulating the immune system. Whenever evaluating the effects prebiotics have on animal health, the following should be taken into consideration: the anatomy and physiology of the animal, how much they rely on the gut microbiota as an energy source, their living environment and dietary composition (Gibson et al., 2017).

4.1. Effects of prebiotics on growth performance and nutrient digestion

Gastrointestinal health is one of the primary objectives to enhance production performance, given its role in crucial biological processes. Sustaining gastrointestinal functionality is indispensable for promoting optimal growth, normal and stable microbiota, effective immune status, and nutrient utilization efficiency (Vasanthakumari et al., 2023). A healthy intestine is necessary to allow proper nutrient digestion and absorption in the host, leading to reduced excretion of metabolites (Peng et al., 2020). The maintenance of intestinal health is attributed to the microbiota that reside within the gastrointestinal tract (Celi et al., 2019).

Beneficial effects of prebiotics on growth performance likely result from the interplay and interaction of several mechanisms, including decreased pathogen colonization, increased SCFA production, alterations in lipid metabolism, and improved mineral absorption (Solís-Cruz et al., 2019). While prebiotics hold the potential to enhance overall intestinal health, their effects on growth performance may be dependent on the broader husbandry management practices employed (Anadón et al., 2019). Nonetheless, nutritional interventions targeting the modulation of gastrointestinal health hold promise as a means to boost a variety of farm animal production parameters, such as growth rates, meat and egg quality, and milk yield.

4.1.1. Monogastric animals

Monogastric animals have one simple, single-chambered stomach of which horses, poultry and pigs are the most popular

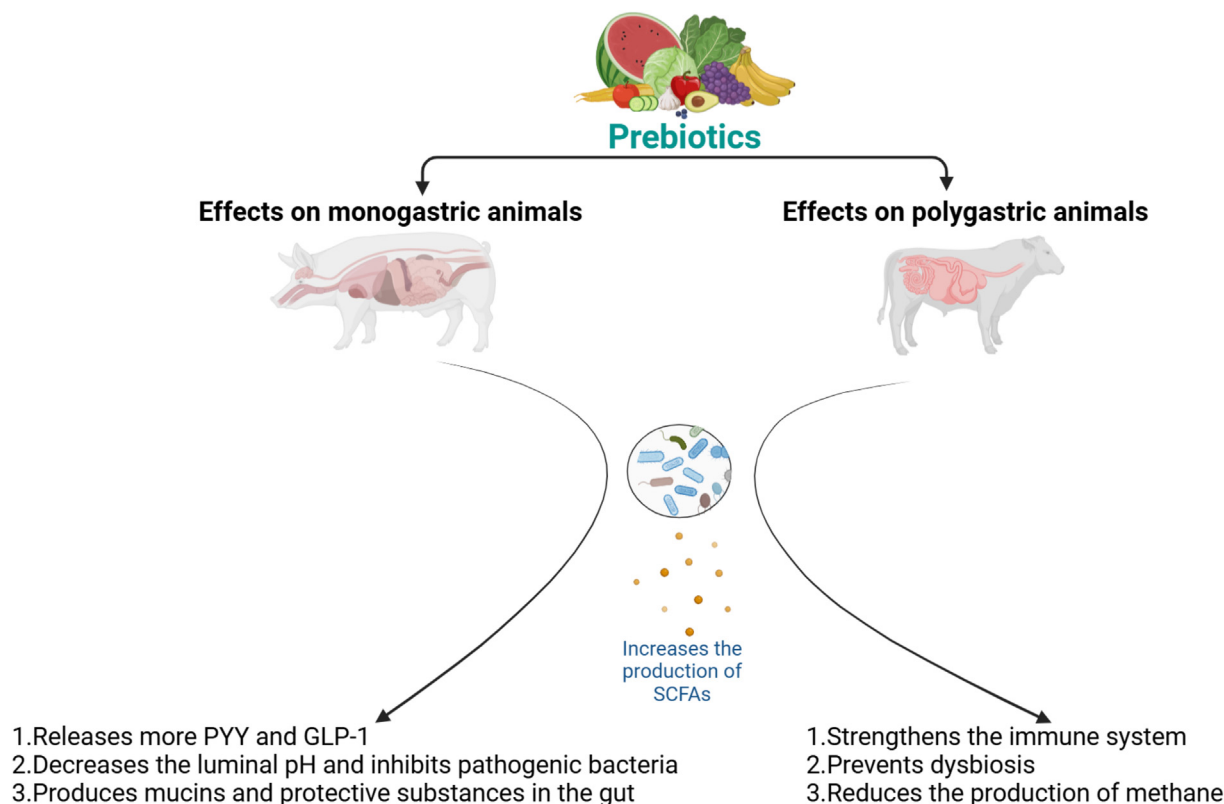


Fig. 2. Health benefits and mechanisms of prebiotics in polygastric and monogastric animals. SCFAs = short-chain fatty acids; PYY = peptide YY; GLP-1 = glucagon-like peptide-1.

agricultural species (Ojha et al., 2019). Scientific evidence shows that prebiotics have been used in animal feed for poultry and pigs since the 1990s; with the majority of such research being in poultry (Di Gioia and Biavati, 2018). The prebiotics most commonly used in monogastric animals are FOS, MOS, GOS and inulin; with FOS being more widely investigated than GOS (Park et al., 2013; Rehman et al., 2009).

According to Solís-Cruz et al. (2019), bacteria such as *Lactobacillus* spp. and *Bifidobacterium* spp. that form a part of the intestinal microbiota in poultry, confer positive effects on the intestinal physiology and are beneficial to their health. These beneficial bacteria have reportedly increased when chickens were fed diets supplemented with prebiotics—they fermented and metabolized the prebiotics and thus increasing their activity.

Studies by Totton et al. (2012) and Park et al. (2013) found that prebiotics regulated the intestinal microbiota of chickens by selectively stimulating the beneficial bacteria and inhibiting the unwanted bacteria like *Salmonella* which resulted in an increase of their stool volume. Prebiotics, including FOS and MOS, were found to increase body weight in poultry along with the quantities of beneficial bacteria such as *Lactobacillus* and *Bifidobacterium* spp. while decreasing the quantities of pathogenic bacteria like *Escherichia coli*, *Salmonella* and *Clostridium perfringens* (Chambers and Gong, 2011; Lee et al., 2012; Stanley et al., 2014). Angwech et al. (2019) reported that in ovo delivered prebiotics (3.5 mg/embryo on the 12th d of incubation) diminished the severity of intestinal lesions and oocyst excretion-induced infections by *Eimeria* (parasites capable of causing the disease coccidiosis) in Kuroiler chickens. The chickens were protected from coccidia for the first 56 d of their lives which worked in synergy with an anticoccidial drug to manage the disease post-infection. This resulted in positive effects on the performance of the birds and the quality of their meat.

On the other hand, Wan et al. (2018) found that pigs supplemented with AIOS at 100 mg/kg for 2 weeks exhibited increased villus height, villus height-to-crypt depth ratio and goblet cell counts. Similar examples are cited in Table 1.

Recently, novel precision biotics (PB) have been actively researched for their ability to improve growth performance and control nitrogen emissions (Jacquier et al., 2022; Walsh et al., 2021). This novel class of nutritional feed ingredients function as microbiome metabolic modulators (Jacquier et al., 2022; Walsh et al., 2021). The mechanism of action of PB is through the modulation of metabolic pathway abundance, rather than the modulation of bacterial taxa or overall gut microbial profiles, which differentiates them from existing microbiome-targeting technologies (Bortoluzzi et al., 2023). This targeted modulation promotes beneficial outcomes for both the animal and the environment. Several studies have focused on the impact of a glycan-based PB in the poultry industry. Walsh et al. (2021) and Jacquier et al. (2022) have reported the effects of supplementation of this mixture in broiler chickens. Walsh et al. (2021) evaluated, through meta-analysis, the effects of two structurally distinct, precision glycan microbiome metabolic modulators (MMMs) on the performance of broiler chickens. Microbiome metabolic modulator 1 and MMM2 increased final body weight compared to the negative control by 43 and 48 g/bird, respectively. The different structure of MMMs had an impact on size and performance effects in broiler chickens. Meta-genomic analysis confirmed an increase in the abundance of genes belonging to the acrylate pathway, involved in propionate production (fatty acid biosynthesis) in response to both MMMs. Arginine-N-succinyl transferase genes, involved in arginine catabolism, were also upregulated in response to MMM2 (Walsh et al., 2021). Jacquier et al. (2022) conducted a two-part experiment to examine the effects of PB. In the first trial, they tested the main

Table 1

The effects of feeding prebiotics on animal nutrition and health in monogastric animals.

Prebiotics	Animal	Dosage	Duration	Effects of prebiotics on gut microbes and immune responses	References
TOS	Pigs	35 g/kg	42 d	Increased the count of stool <i>Bifidobacterium</i> and <i>Lactobacillus</i> .	Smiricky-Tjardes et al. (2003)
FOS	Broiler chickens	4 g/kg	49 d	Increased daily growth and growth of <i>Bifidobacterium</i> and <i>Lactobacillus</i> . Inhibited the growth of <i>Escherichia coli</i> in gastrointestinal tract.	Xu et al. (2003)
FOS	Male turkeys	2%	56 d	A reduction of the intestinal pH.	Juśkiewicz et al. (2006)
FOS	Weaned piglets	0.6%	7 d	Increased intestinal microbes, <i>Bifidobacteria</i> and <i>Lactobacillus</i> in the middle jejunum, along increased IFN- γ levels. Decreased abundance proteobacteria in posterior jejunum and ileum. Decreased levels of IL-4 and IL-10.	Chang et al. (2018)
scFOS	Adult pigs	10 g/d	28 d	Increased abundance of Bacteroidetes and <i>Prevotella</i> , and decreased abundance of <i>Ruminococcaceae</i> .	Le Bourgot et al. (2019)
AOS	Pigs	100 mg/kg	14 d	Increased villus height, villus height-to-crypt depth ratio and goblet cells.	Wan et al. (2018)
FOS	<i>Salmonella</i> challenged laying hens	0.5% and 1.0%	3 wk	Increased the gene expression of TLR-4 and IFN- γ , along with IgA+ cells in the ileal lamina propria. Decreased ceca <i>Salmonella</i> in mature hens.	Adhikari et al. (2018)
GOS	Kuroiler chickens	3.5 mg/embryo	12th d of incubation until hatched	Reduced severity of intestinal lesions and oocyst excretion induced by natural infection with <i>Eimeria</i> , with positive effects on the chicken's productive traits.	Angwech et al. (2019)
MOS + MP	Broiler chickens (Ross 308)	100 g/t of diet	35 d	Longer jejunal villus length, positive changes in microbial population and higher level of calcium in blood. Increased serum concentration of calcium.	Karimian and Rezaei-pour (2020)
<i>Saccharomyces</i> -derived prebiotics	Broiler chickens	50 and 100 g/t	42 d	Decreased the prevalence of <i>Camphylobacter</i> .	Froebel et al. (2019)
XOS	Pigs	100 to 500 g/t	70 d	Decreased relative abundance of Proteobacteria, <i>Citrobacter</i> , along with increased relative abundance of <i>Firmicutes</i> , <i>Lactobacillus</i> during the growing and fattening period. Also, increased SCFAs concentrations in the intestine.	Pan et al. (2019)
XOS	Weaned piglets	0.01%	Weaned	Increased relative abundance of <i>Streptococcus</i> and <i>Turicibacter</i> , along decreased relative abundance of <i>Lactobacillus</i> . Reduced IFN- γ concentration and higher expression of ZO-1 in the ileum.	Yin et al. (2019)

TOS = trans-galactooligosaccharides; FOS = fructo-oligosaccharides; scFOS = short-chain fructo-oligosaccharides; AOS = alginate oligosaccharide; GOS = galacto-oligosaccharides; MOS = mannan-oligosaccharides; MP = microbial phytase; XOS = xylo-oligosaccharides; IFN = interferon; IL = interleukin; SCFAs = short-chain fatty acids; ZO = zonula occludens; Ig = immunoglobulin.

effects of PB dose (0, 250 and 500 g/t) and xylanase supplementation (0 or 100 g/t) in boiler chickens. No significant interaction was detected between PB and xylanase on performance. However, supplementation with PB at 250 and 500 g/t improved feed conversion ratio by 7 and 11 points compared to diets without glycans. The glycan effect was observed to depend on the age of the birds. At 35 d, PB reduced the pH and ammonia concentration in diets with xylanase. The second experiment explored the effect of a single PB dose (500 g/t) compared to a control diet on broiler performance. In both trials, the inclusion of 500 g of glycan PB per tonne feed resulted in a greater proportion of birds without foot pad lesions or defective gaits. The glycan supplement, by targeting the modulation of microbial metabolic pathways related to SCFAs and amino acid metabolism, may have facilitated improved nitrogen utilization in the broilers, thereby reducing ammonia emissions and enhancing litter quality (Jacquier et al., 2022). Additionally, Bortoluzzi et al. (2023) tested the mixture of glycan-based PB to modulate the utilization of proteins and improve the growth performance of broiler chickens. It was observed that supplementation with 3% of PB in the diets had a positive impact on performance, with improved body weight gain and the corrected feed conversion ratio (cFCR). The functional microbiome analysis revealed that PB shifted the microbiome pathways toward a beneficial increase in protein utilization, and desirable pathways related to nitrogen utilization, resulting in improved growth performance (Bortoluzzi et al., 2023).

4.1.2. Polygastric animals

The stomachs of ruminants consists of four compartments: the rumen, reticulum, omasum and the abomasum; with each

chamber performing different processes (Stover et al., 2016). Prebiotics effectively alter the activity and composition of the microbiome in the ruminant's gastrointestinal tract because they are substrates that enhance the presence of certain beneficial ruminal microorganisms. However, because ruminants are capable of catabolizing most of the common prebiotic compounds, using prebiotics to promote growth in the ruminant industry has been limited (Bakowski and Kiczorowska, 2020). Additionally, several nondigestible oligosaccharides naturally found in cell walls of plants are included in ruminant feeds, possibly making the implementation of prebiotics in ruminants unnecessary (Anadón et al., 2019; Di Gioia and Biavati, 2018). Nonetheless, using prebiotics in pre-weaned ruminants (given that they are fed a low-roughage diet) have been found to increase their growth, diminish the chances and severity of diarrhoea and respiratory diseases while aiding in the formation of a desirable intestinal flora, which can improve their performance as they age (Ghosh and Mehla, 2012; Roodposhti and Dabiri, 2012; Uyeno et al., 2015).

Prebiotics such as galactosyl lactose, cello-oligosaccharides, MOS and yeast cell wall extracts are used in pre-weaned calves. It is believed that MOS block the colonization of pathogens in the digestive tract, while FOS along with spray-dried bovine serum reduced the occurrence of enteric disease in calves due to the ability of this sugar to block the adhesion of *E. coli* and *Salmonella* to the intestinal epithelium. It was reported that adding galactosyl-lactose (GL) to milk replacer positively impacted the growth and general health of dairy calves. While further investigation is necessary, research has shown that supplementation with MOS, FOS and GL may serve to improve the growth performance of calves

Table 2

The effects of feeding prebiotics on animal nutrition and health in polygastric animals.

Prebiotics	Animal	Dosage	Duration	Effects of prebiotics on gut microbes and immune responses	References
MOS	Holstein calves	4 g/d in milk replacer	42 d	Improved feed intake and fecal scores.	Heinrichs et al. (2003)
MOS (Bio-MOS)	Young calves	4 g/d in milk replacer	42 d	Stimulated calf starter intake. Decreased presence of <i>Cl. Perfringens</i> , <i>E. coli</i> and <i>Salmonella</i> spp.	Terré et al. (2007)
MOS	Holstein cross calves	4 g/d	56 d	Average body weight gain, feed intake and feed conversion efficiency increased. Significant decrease in severity of scours as measured by fecal score and fecal coliform count.	Ghosh and Mehla (2012)
scFOS	Veal calves	3 or 6 g in milk replacer	168 d	Increased growth performance, carcass quality, faecal concentration of SCFAs and microbial fermentation.	Grand et al. (2013)
GOS	Holstein calves	33.5 mg/g	56 d	Increased <i>Lactobacillus</i> and <i>Bifidobacterium</i> bacteria.	Castro et al. (2016)
MOS	Surti buffalo calves	10 g/d per calf		Increased colon crypt depth and jejunal villus length.	Patel et al. (2019)
MOS	Calves	5 g/d	56 d	Increased body weight, average daily gain, feed conversion ratio.	Alves Costa et al. (2019)
CWS	Calves	50 g/d	84 d	Significant increases in jejunal villus height and rumen papillae.	Senevirathne et al. (2019)
Y-MOS	Male Zell lambs	1.5 g/d in milk replacer	70 d	Overall improvement in starter intake, postweaning body weight, β -hydroxybutyrate, maintained frame growth and fecal scores.	Chashnidel et al. (2020)
Inulin	Female calves	12 g/d in milk replacer	63 d	Caused feed intake and daily weight gain improvements. Improved immune function (specifically an elevation in serum IgG).	Tóth et al. (2020)
MOS and β -glucans	Pelibuey $\times$ Katahdin crossbred male lambs	3 g/d per lamb	93 d	Significantly increased faecal concentration of total anaerobic bacteria and <i>Lactobacillus</i> . Increased total aerobic bacteria count in faeces.	Zapata et al. (2021)
<i>Alhagi camelorum</i> fisch polysaccharides from Shanshan county, Xinjiang Uyghur Autonomous region, China	Sheep lambs	1.5 g/kg	28 d	Resulted in enhanced feed efficiency by 6.9% and dietary net energy by 5.9%. Increased levels of GH, INS, IgA and IgM, and cytokines IL-4, IL-10, IL-17, TNF- α and IFN- γ . Various metabolic pathways were modulated; growth was promoted; immunity improved; the risk of gastrointestinal disease was reduced; improved composition of gastrointestinal microbiota observed.	Manafu et al. (2024)

MOS = mannan-oligosaccharides; scFOS = short-chain fructo-oligosaccharides; GOS = galacto-oligosaccharides; CWS = condensed whey solubles-product containing proprietary prebiotics derived from milk; Y-MOS = mannan oligosaccharides and β -glucans, extracted from cell wall of the yeast (*Saccharomyces cerevisiae*); SCFAs = short-chain fatty acids; GH = growth hormone; INS = insulin; Ig = immunoglobulin; IFN = interferon; IL = interleukin; TNF = tumor necrosis factor.

in both pre- and post-weaning stages (Bhat and Shaheen, 2017; Uyeno et al., 2015).

In Table 2, Patel et al. (2019) found that Surti buffalo calves who received MOS (10 g/d) experienced increased body weight, average daily gain and feed conversion ratio. While, Alves Costa et al. (2019) found that calves who received MOS (5 g/d for 56 d) experienced significant increases in jejunal villus height and rumen papillae. Similar examples are cited in Table 2.

5. Agro-industrial residues and processing as sources of prebiotics

Agro-industrial residues are produced in large volumes on an annual basis and represent both an environmental burden and a potential source of value creation. Despite being considered a source of environmental pollution (Das et al., 2018), these organic residues have high nutritional content and bioactive compounds, making them valuable resources for application in animal feed, bioenergy production, and biorefinery processes (Yaashikaa et al., 2022).

Agro-industrial residues are categorized as agricultural (e.g. leaves, stems, seeds) and industrial residues (e.g. food processing waste) (Sadh et al., 2018). Agro-industrial residues are mainly formed of lignocellulosic biomass. Lignocellulose is a source of functional oligosaccharides that can promote the proliferation of probiotic microorganisms, including XOS, arabino-oligosaccharide (AOS), and MOS.

Given their rich nutrient content, agricultural residues provide a valuable source of raw material for prebiotic production.

5.1. Agro-industrial residues as sources of prebiotics

Table 3 summarizes agro-industrial wastes used to obtain prebiotics. These residues come primarily from food processing industries. A list of agro-industrial wastes used in prebiotic production is further discussed.

5.1.1. Sugarcane by-products

Sugarcane bagasse, major by-product of sugarcane industry, reaches 513 million tonnes annually (Toscano Miranda et al., 2021). Sugarcane bagasse is composed of 35% to 50% cellulose, 20% to 25% hemicellulose, 15% to 25% lignin, moisture, and 4% to 6% ash content (Kolawole et al., 2021). Studies have extracted xylan from bagasse and enzymatically hydrolyzed it to generate XOS with prebiotic potential (Kathiresan et al., 2021). Xylo-oligosaccharides from sugarcane bagasse have shown to promote the growth of probiotic bacteria like *Lactiplantibacillus plantarum*, *Lactobacillus brevis*, *Lactobacillus acidophilus* and *Lactobacillus viridescens*, and exhibit antioxidant and antibacterial activities (Gupta et al., 2022; Kaur et al., 2019). The prebiotic effect of XOS was attributed to their degree of polymerization and the presence of xylobiose and xylo-triose (Kaur et al., 2019). Sugarcane bagasse has also been utilized as biomass for the production of fructosyltransferase (Ganaie et al., 2017), an enzyme used to commercially produce FOS.

Table 3
Examples of prebiotic types, effects and potential substrate sources used for animal health.

Type of prebiotics	Physiological effects	Agro-industrial residues	References
FOS	Increase in growth performance; improvement in gut microbiota composition; positive immunological effects	Sugarcane bagasse Sugarcane molasses Olive pomace powders Apple pomace, wheat bran, banana peels, guava peels, corn straw, cassava peels, and beetroot peels Jerusalem artichoke tubers Flesh of onion bulbs Flesh and peel of red pitaya, white pitaya, and papaya Coffee silverskin, corn cobs, and cork oak	de la Rosa et al. (2019) Khatun et al. (2021) Ribeiro et al. (2021) Ganaie et al. (2017) Khuenpet et al. (2017) Mabrok et al. (2018) Khalili et al. (2014) Mussatto and Teixeira (2010) Abd El-Aziz et al. (2022) Csernus and Czeplédi (2020) Quijada et al. (2020) Tian et al. (2017)
MOS	Improvement of intestinal morphological traits; immune modulator; improvement in gut microbiota composition	Spent coffee grounds brewed coffee Copra meal Soybean meal Sugar palm fruit Palm kernel cake	Chantorn et al. (2018) Pangestu et al. (2019) Purnawan et al. (2017) Duan et al. (2019) Youssef et al. (2023) Yang et al. (2022)
XOS	Improvement in gut microbiota composition; improvement of nutrient digestibility and energy metabolism; growth performance	Sugarcane bagasse Olive pomace Grape pomace	Kathiresan et al. (2021) Freitas et al. (2022) Costa et al. (2019) González-Solé et al. (2022) Rao et al. (2024) Dong et al. (2023)
GOS	Increase in growth performance; improvement in gut microbiota composition and immune response; reduce the incidence of diarrhea	Whey permeate Milk whey Milk whey permeate Spent coffee grounds Brewed coffee	Mano et al. (2019) Yañez-Neco et al. (2021) Hackenhaar et al. (2021) Tian et al. (2017) Chang et al. (2022) Yu et al. (2023) Tian et al. (2022)
Inulin	Increase in growth performance; improvement in gut microbiota composition; enhance immune function	Chicory roots Flesh of onion bulbs	Chikkerur et al. (2020) Mabrok et al. (2018) Tian et al. (2019) Xia et al. (2021)
Polyphenols	Increase in growth and antioxidant performance; enhance immune function	Grape pomace Cranberry pomace Blueberry pomace Apple pomace Mango peels and seed kernels	Meini et al. (2021) Yang et al. (2023) Costa et al. (2022) Nicolás García et al. (2023) Serra et al. (2021) Waqas et al. (2023)
SCFAs	Contribute to energy requirements; pathogen inhibition	Cranberry pomace	Islam et al. (2020) Wong et al. (2006) Hackmann (2023)

FOS = fructo-oligosaccharides; MOS = mannan-oligosaccharides; XOS = xylo-oligosaccharides; GOS = galacto-oligosaccharides; SCFAs = short-chain fatty acids.

Another sugarcane by-product, molasses, has been explored for prebiotic production. Enzymatic synthesis of prebiotic oligosaccharides from molasses has been performed using dextranuclease from *Leuconostoc mesenteroides* MTCC 10508 (Sharma et al., 2016), and whole-cell biocatalyst of *Aspergillus pullulans* have been used to transform molasses into FOS (Khatun et al., 2021). Overall, these studies have demonstrated the potential of sugarcane by-products, including bagasse and molasses, as valuable sources of prebiotics with attractive health properties for a tailored use. Further research is still needed to fully understand the effects of these derived prebiotics on animal health when used as feed.

5.1.2. Pomace

Pomace, a major food industry residue, is a valuable source of bioactive compounds, including polyphenolics, fibre, vitamins, and carbohydrates. Pomace yield varies by fruit, with grape pomace comprising typically 20% to 30% of the fruit weight, orange pomace 45% to 60%, apple pomace 25% to 35%, olive pomace 30%, and berry pomace 30% to 50% (Gowman et al., 2019; Joshi, 2005; O'shea et al., 2015; Rodríguez-Gutiérrez et al., 2012; Struck et al., 2016). Studies show that pomace can potentially enhance beneficial gut bacteria

in monogastric animals like poultry (Mnisi et al., 2022). Olive pomace has been found to promote the production of SCFAs by gut microbiota and exhibits antimicrobial activity (Ribeiro et al., 2021).

Polyphenols with prebiotic activity have also been extracted from grape pomace (Meini et al., 2021). Supplementing broiler chickens' diet with cranberry pomace has been shown a positive effect on the population of probiotic bacteria and reduce the abundance of pathogens (Islam et al., 2020). The addition of cranberry and blueberry pomace to broiler chicken feed has been found to increase the relative population of *Lactobacillus*, a beneficial type of bacteria (Yang et al., 2023). Other studies have shown the potential of various fruit pomaces and agro-residues as a suitable source of polyphenols and prebiotic fibres that can benefit animal health and nutrition (Costa et al., 2022; Ganaie et al., 2017; Vlad et al., 2022).

The use of pomace from various sources is now common as a source of biocompounds, due to research revealing its health-promoting properties. Although relevant and positive effects on animal welfare have been disclosed, the potential use of pomace is still at a basic level requiring more investment in fundamental research.

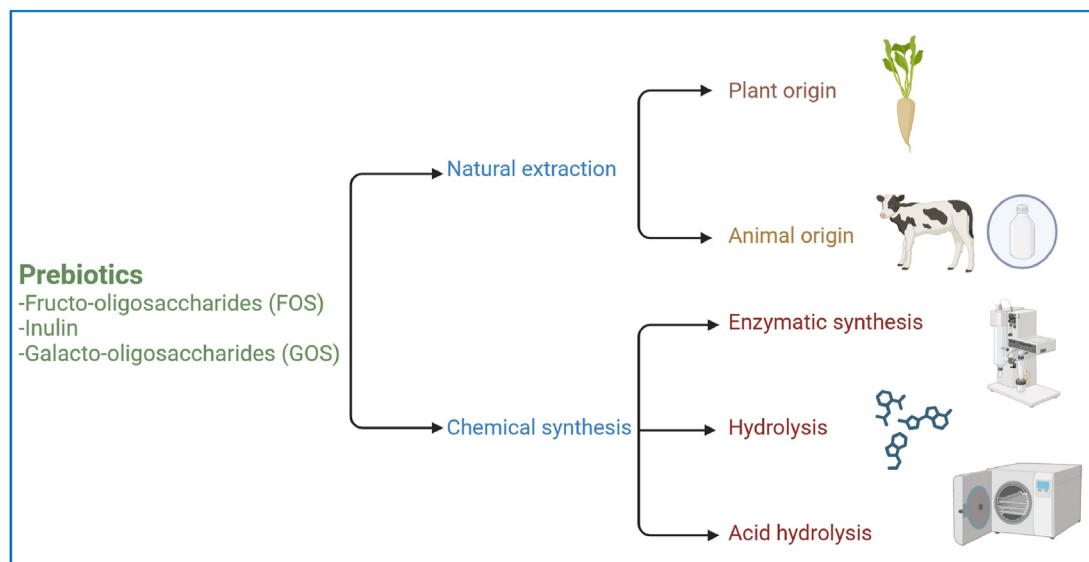


Fig. 3. The pathways of prebiotic production.

5.1.3. Other residues

The potential prebiotic effects of phenolic compounds derived from mango peels and seed kernels have been discussed (Nicolás García et al., 2023). These compounds offer health benefits, including prebiotic effects on the gut microbiota. Studies have investigated the potential of Jerusalem artichoke (*Helianthus tuberosus* L.) tubers and chicory roots as sources of prebiotics like inulin and FOS (Chikkerur et al., 2020; Khuenpet et al., 2017). Onions and pitaya fruits are additional sources of FOS and inulin, with the red pitaya showing the highest production of FOS compared to white pitaya and papaya (Khalili et al., 2014; Mabrok et al., 2018).

Studies have evaluated coffee waste materials, like spent coffee grounds and brewed coffee, as sources of oligosaccharides such as GOS and MOS (Nguyen et al., 2019; Tian et al., 2017; Wongsiridetchai et al., 2021). Mannan-oligosaccharides (MOS) derived from spent coffee grounds were found to promote *Lactobacillus* growth, and inhibit pathogens (Wongsiridetchai et al., 2021). Other agricultural wastes, including potato peels, soybean meal, sugarcane bagasse, and palm products, have also been used to produce MOS with potential prebiotic and antimicrobial effects (Chantorn et al., 2018; Pangestu et al., 2019; Purnawan et al., 2017).

5.2. Prebiotic production from agro-industrial residues

Prebiotic can be produced from agro-industrial waste through enzymatic technologies, fermentation, and acid hydrolysis (Bamigbade et al., 2022; Gonçalves et al., 2023; Patel and Shukla, 2017). Enzymatic hydrolysis uses specific enzymes to gently break down carbohydrates into prebiotic like oligosaccharides, preserving functionality (Radenkovs et al., 2018). Fermentation uses microorganisms to metabolize waste carbohydrates into prebiotic like FOS or GOS (Gonçalves et al., 2023; Patel et al., 2020; Patel and Shukla, 2017). Acid hydrolysis employs acids to break down carbohydrates into prebiotics (Bamigbade et al., 2022), breaking glycosidic bonds and releasing monosaccharides or smaller oligosaccharides, but it requires careful handling due to its corrosive nature. The treatment conditions depend on the type of waste being processed.

As shown in Fig. 3, the two main industrial methods used for producing prebiotics are: 1) natural extraction or hydrolysis from

plant or milk sources and 2) chemical synthesis pathways using enzymatic or isomerization reactions (Al-Sheraji et al., 2013). However, natural sources have limited prebiotic content, so most commercial prebiotics are chemically synthesized from raw materials like lactose and sucrose (Davani-Davari et al., 2019). The manufacturing process of FOS and GOS will be discussed in the following paragraphs.

Fructo-oligosaccharides can be produced through enzymatic synthesis or inulin hydrolysis (Martins et al., 2019). Enzymatic synthesis involves the use of fructosyltransferase, such as β -fructofuranosidase from *Aspergillus niger*. This enzyme cleaves glycosidic bonds and transfers fructose from sucrose to form FOS (Davani-Davari et al., 2019). Free enzymes are typically preferred over those within the microorganism, as they simplify extraction and purification. Glucose oxidase may also be added to prevent glucose build-up, which can inhibit the conversion to FOS (Martins et al., 2019).

Inulin hydrolysis is another approach, and can be performed through enzymatic or acid-based methods. Enzymatic hydrolysis, the most common industrial method, uses endo-inulinase and exo-inulinase enzymes from fungal sources to break down inulin into shorter-chain compounds (Martins et al., 2019). Acid hydrolysis is used when enzymatic methods are not feasible, breaking down inulin in a highly acidic environment to produce FOS (Martins et al., 2019).

Galacto-oligosaccharides can be produced through enzymatic synthesis or hydrolysis, with enzymatic synthesis being the more common industrial method. In enzymatic synthesis, α -galactosidase and β -galactosidase enzymes derived from fungi catalyze transgalactosylation reactions and produce α -GOS and β -GOS, respectively (Martins et al., 2019). These enzymes can be used in both free form and within microorganisms, but they are expensive, so recombinant β -galactosidase is often introduced to enhance yield and simplify processing (Davani-Davari et al., 2019). Lactose and glucose are produced as by-products, which can lower GOS yield and inhibit the reaction. Techniques like chromatography, and precipitation are employed to remove these by-products and optimize the process (Martins et al., 2019). Hydrolysis is mainly used for plant-derived α -GOS, where long polymer chains are hydrolysed to break apart the galactosidic bonds and

produce compounds like sucrose, stachyose, and verbascone. Purification and extraction steps are then taken to obtain a higher yield of α -GOS by removing fat, proteins, and fibre (Martins et al., 2019).

Techniques to produce prebiotics from agro-industrial residues are diverse and have been developed on an industrial scale. These methods can secure a production rate compatible with applications in both animal and human nutrition without compromising the need of either. Future work should focus on developing products that integrate or include these prebiotics in applications for animal feeds, fostering animal welfare.

6. Conclusions and future perspectives

In conclusion, with the ban on antimicrobial growth promoters, the utilization of prebiotics derived from agro-industrial residues has emerged as a promising and safe alternative for maintaining animal health and well-being through optimal nutrition. These agro-industrial residues, which may be detrimental to human health and the environment, can be repurposed as valuable resources for prebiotic production.

Prebiotics have been recognised as possessing numerous health-promoting properties that are highly relevant in the management of animal care and well-being through proper nutrition. Prebiotics can be categorized into different groups based on their development and regulatory status, ensuring that their production or extraction from various sources is conducted accordingly. Considering the ban on antimicrobial growth promoters, prebiotics offer an interesting and safe alternative in the treatment of health issues in animal production. Numerous studies have demonstrated the beneficial use of different types of prebiotics in maintaining the health of both polygastric and monogastric animals. Furthermore, research on the interaction between prebiotics and probiotics has proved to be necessary for optimizing animal gut health.

To gain a perspective on the future, it is a prerequisite to bear in mind that the animal gut microbiome and prebiotics have become a prevalent topic in the agriculture and food industry, with intense research in recent years. This research focus is predicted to continue expanding, indicating bright and assured prospects for prebiotics. Current research directions will continue aiming to optimise the harvesting process and benefits of prebiotics, exploring the potential of biofortification, unconventional sources, and discovering new applications for future prebiotics. On the other hand, biofortification that involves editing, eliminating, and inserting specific genetic material into various organisms, will have the potential to greatly enhance the development of prebiotics by simplifying their production process and improving their efficacy. As mentioned earlier, genetically modified yeast currently being used in the production of GOS, will see easier purification and higher yields compared to traditional extraction methods. This technology is expected to be applied in the manufacturing processes of other prebiotic components as well. With biofortification, companies will be able to choose a bacterial strain that requires less stringent growing conditions and will reduce the operational cost of producing prebiotics. Natural bio-resources, such as mushroom polysaccharides and marine seaweed that have been shown to display prebiotic effects, will continue to attract research interests on their feasibility, efficacy, and potential as novel prebiotic sources. Although the extraction methods for the functional components in these natural bio-resources are still relatively immature and underdeveloped, their potential to become the next best source of prebiotics will doubtlessly thrive.

Credit Author Statement

M. Cristina Ravanal: Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Carolina A. Contador:** Writing – review & editing, Writing – original draft. **Wing-Tak Wong:** Writing – original draft. **Qile Zhang:** Writing – original draft. **Analese Roman-Benn:** Writing – original draft. **Kong Shun Ah-Hen:** Writing – original draft. **Pilar E. Ulloa:** Writing – original draft. **Hon-Ming Lam:** Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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