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CERRADO FRUIT RESIDUES DURING FERMENTATION WITH PROBIOTIC STRAINS: PREBIOTIC PROPERTIES AND POLYAMINE PRODUCTION

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ABSTRACT

Background. Limited information exists on the chemical composition and prebiotic properties of cajuzinho-do-cerrado (*Anacardium humile*) and marmelo-do-cerrado (*Alibertia sessilis*) residues, which are typically discarded during fruit processing. This study characterizes these residues and investigates their prebiotic potential.
Material and methods. The antioxidant capacity, phenolic compounds, functional properties, and prebiotic potential of the residues were evaluated. Methanolic extracts were analyzed using spectrophotometric methods (DPPH, Folin-Ciocalteu) and HPLC. Water and oil holding capacities were measured by centrifugation. Three probiotic strains and two *E. coli* strains were cultivated in modified media using the residues as carbon sources. Cell viability was assessed by agar plate counts. Metabolic activity was monitored by measuring pH, sugar and organic acid concentrations, and bioactive amine production using HPLC. These analyses were designed to evaluate functional characteristics of the residues, including antioxidant capacity, water and oil holding abilities, and their ability to support probiotic growth and metabolism, thereby assessing prebiotic potential.
Results. CR and MR showed high levels of total dietary fiber and protein. Considerable concentrations of total phenolic compounds were detected; gallic acid and coniferaldehyde were quantified in CR, while *p*-coumaric acid and luteolin were quantified in MR. Cultivation of *Lactobacillus acidophilus* LA-05, *Lacticaseibacillus casei* L-26, and *Bifidobacterium animalis* subsp. *lactis* BB-12 in media containing CR and MR promoted their growth – especially *L. casei* – along with a decrease in pH and significant production of organic acids, such as lactic and acetic acids. Fermentation of these residues also led to polyamine production, including spermidine, indicating intense fermentative metabolic activity by these microorganisms.
Conclusion. The residues display characteristics indicative of prebiotic potential and may confer human health benefits. They could also be considered as functional ingredients for the formulation of new food products.

Keywords: cerrado biome, dietary fibers, functional food, phenolic compounds, spermidine, *Bifidobacterium*

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INTRODUCTION

Brazil hosts several underexploited fruit species with potential for agroindustry and as a source of income for local populations (Silva et al., 2014). Among these are *Anacardium humile* (cajuzinho-do-cerrado) and *Alibertia sessilis* (marmelo-do-cerrado), both native to the Cerrado biome. Fruits from this biome are rich in bioactive compounds, which can provide health benefits when consumed regularly (Bailão et al., 2015).

Cajuzinho-do-cerrado contains high levels of bioactive compounds, including flavonoids and vitamin C (Lima Júnior et al., 2021). Few studies have examined the nutritional properties of marmelo-do-cerrado, and most are regional. Its blue-black color suggests the presence of phenolic compounds, which are responsible for color in many fruits and vegetables. Cerrado fruits can be consumed fresh or processed into products such as juices, ice creams, jellies and liqueurs (Santos et al., 2022).

The industrial processing of fruits generates large amounts of residues, which are often discarded despite being rich in nutrients and bioactive compounds (Andrade et al., 2020). Because of their high carbohydrate content, particularly fiber, these fruits and their by-products may have prebiotic potential (Barbosa et al., 2022). Prebiotics are defined as substrates selectively utilized by host microorganisms, conferring health benefits, such as intestinal and immune function, reduced cardiovascular risk, and enhanced satiety (Gibson et al., 2017).

Commonly recognized prebiotics include oligosaccharides, such as fructooligosaccharides (FOS), galactooligosaccharides (GOS), inulin, xylooligosaccharides (XOS), and resistant starch (Ashaolu, 2020). Other compounds, including flavonoids, proteins, unsaturated fatty acids, and micronutrients, have also shown prebiotic activity (Ashaolu, 2020).

Studies assessing the prebiotic potential of fruits have reported promising results, such as enhanced bacterial metabolic activity and production of short-chain fatty acids (SCFAs) (Andrade et al., 2020). Metabolites produced by probiotics from the metabolism of prebiotic ingredients in the gut offer multiple health benefits. In addition to SCFAs, polyamines such as spermidine are important bacterial metabolites, often produced by a balanced gut microbiota. High intestinal concentrations of polyamines can promote longevity, inhibit systemic inflammation, and reduce gut mutagenicity (Matsumoto et al., 2019). Therefore, the intake of prebiotic components is essential for the production of these beneficial metabolites.

Despite this potential, studies on the prebiotic activity of Cerrado fruits and their residues remain limited. Research linking prebiotic potential to polyamine production is even scarcer. Thus, this study aims to characterize and evaluate the prebiotic potential of residues from two native Cerrado fruits: cajuzinho-do-cerrado and marmelo-do-cerrado.

MATERIALS AND METHODS

Samples preparation

The cajuzinho-do-cerrado was purchased from producers in the municipality of Jaraguá (Goiás, Brazil), and the marmelo-do-cerrado was harvested at the Agronomy School of the Federal University of Goiás. The fruits were obtained in 2021 at the mature stage suitable for consumption, and were washed and sanitized. First, the nuts of the cajuzinho-do-cerrado were manually removed. The fruits were then processed using an industrial pulping machine 0.25 DF (Bonina®, Itabuna, Brazil) and sieved through a 2.5 mm mesh to separate the pulp from the residue (peel, seed and bagasse). The samples were freeze-dried (Liotop®, L108, Brazil) for 24 h and crushed in an industrial blender (Mallory®, Kalipso, Brazil) until a powder was obtained. The marmelo-do-cerrado residues were sieved, vacuum-packed (Selovac®, Microvac, Brazil) in plastic bags, wrapped in aluminum foil to protect them from light, and stored under refrigeration (−18°C). Finally, freeze-dried cajuzinho-do-cerrado residues (CR) and freeze-dried marmelo-do-cerrado residues (MR) were obtained.

Characterization of cajuzinho-do-cerrado and marmelo-do-cerrado residues

Centesimal composition

The samples were evaluated separately for moisture, ashes, total lipid, and total nitrogen, with conversion to crude protein according to AOAC (2016). Total, insoluble and soluble dietary fibers were determined using an enzymatic-gravimetric method, and the ratio between insoluble and soluble fibers was calculated

(Spiller, 1986). Total carbohydrate content was estimated by difference. The total energy value of the samples was calculated using Atwater conversion factors of 4, 4, and 9 kcal/g for carbohydrate, protein and lipid, respectively. For dietary fibers, an energy value of 2 kcal/g was considered (FAO/WHO, 2002).

Determination of antioxidant capacity and phenolic compounds

The residue samples were homogenized with methanol in an ultrasound bath (Unique®, USC-2800A) for 1 h at maximum power and 25ºC, with manual shaking every 15 min. The samples were then centrifuged (Sigma®, 2-3) for 10 min to obtain the extracts. The antioxidant capacity was determined using the DPPH radical spectrophotometric method (2,2-diphenyl--1-picrylhydrazyl – 60 µmol/L) following Brand--Williams et al. (1995). Briefly, 3.9 mL of the DPPH solution was mixed with 0.1 mL of each sample extract, and the mixtures were allowed to stand for 120 min at room temperature under controlled light conditions. Absorbance was measured at 517 nm using a UV/Vis spectrophotometer (Jasco®, V-630). Antioxidant activity was calculated using a Trolox standard curve and expressed as µmol of Trolox equivalents per g of sample (µmol TE/g).

Total phenolic content was determined according to Singleton and Rossi (1965). 0.25 mL aliquot of each extract was mixed with 2.75 mL of the 3% Folin-Ciocalteu solution and left at rest for 5 min. Then, 0.25mL of 10% calcium carbonate solution was added, and the mixture was left to stand for 60 min at room temperature in the absence of light. Absorbance was measured at 765 nm using a UV/Vis spectrophotometer (Jasco®, V-630), and total phenolic content was calculated from a gallic acid standard curve. Results were expressed as mg of gallic acid equivalents per 100 g of sample (mg AGE/100 g).

Phenolic compounds were further analyzed using extracts prepared via the QuEChERS method (Silva et al., 2019) and quantified by high-performance liquid chromatography (HPLC). Analyses were conducted on an Agilent 1260 Infinity LC system (Agilent Technologies®, Santa Clara, USA) equipped with a ventilation pump (quaternary model, G1311C) with degasser, a thermostatic column compartment (G1316A), an automatic injector (G1329B), and a diode array detector (DAD, G1315D). The column used was a Zorbax Poroshel 120 C18 (50 × 4.6 mm, 2.7 µm) with an injection volume of 3 µL. Quantification of phenolic compounds was based on the average peak areas.

Determination of water and oil holding capacity

The water-holding capacity (WHC) and oil-holding capacity (OHC) of CR and MR were determined according to the method described by Zahid et al. (2021). Briefly, 30 mL of ultrapure water or 30 mL of commercial soybean oil (Liza®) were added to 1 g of the samples, vortexed for 1 min, and kept at room temperature for 24 h. The tubes were then centrifuged (3000 g × 20 min), the supernatant was decanted, and the weight of the residues was measured and compared with the initial weight. Results were expressed as grams of water or oil absorbed per gram of dried sample.

Evaluation of prebiotic potential

Microorganisms and inoculum preparation

Probiotics strains used in the assays included *Lactobacillus acidophilus* LA-05, *Lacticaseibacillus casei* L-26, and *Bifidobacterium animalis* subsp. *lactis* BB-12. Stock cultures were maintained in Mann, Rogosa, and Sharpe (MRS) broth (Kasvi®, Spain) with glycerol at −80ºC. To determine prebiotic activity, culture and cell counting procedures were performed according to Albuquerque et al. (2020), with adaptations.

Before the assays, *L. acidophilus* and *L. casei* were cultured for two consecutive days in MRS broth at 37ºC for 24 h under aerobic conditions. *B. animalis* was grown in MRS broth supplemented with 0.5 g/L l-cysteine-HCl (Exodo®, São Paulo, Brazil), at 37ºC for 24 h under anaerobic conditions. The optical density (OD) of each probiotic was standardized to approximately 0.8 at 655 using a spectrophotometer (Jasco®, V-630). *Escherichia coli* strains (*E. coli* ATCC 25922 and *E. coli* ATCC 8739) were used as pathogen controls. They were grown separately in Brain Heart Infusion (BHI) broth (Kasvi®, Spain) at 37ºC for 20 h under aerobic conditions and then combined in a 1:1 ratio to form an enteric mixture. Their OD was standardized at approximately 0.1. The cultures were then diluted to 10^{-8} and plated on MRS agar for probiotic bacteria and on Eosin Methylene Blue (EMB) agar (Kasvi®, Spain) for enteric bacteria using the microdroplet technique to verify viable cell counts of approximately 8 log CFU/mL.

Probiotics strains were supplied by the College of Biotechnology, Portuguese Catholic University (Porto, Portugal), and *E. coli* cultures were supplied by the Faculty of Nutrition at the Federal University of Goiás and the Faculty of Pharmacy at the Federal University of Goiás (Goiania, Brazil).

Modified bacterial cultivation media

MRS broth with a modified carbon source was prepared and used as a basic culture medium to evaluate the prebiotic effects of the fruit residues (Albuquerque et al., 2020). The composition of the different culture media was: tryptone (Kasvi®, Spain) 10 g/L, meat extract (Kasvi®, Spain) 8 g/L, yeast extract (Kasvi, Spain) 4 g/L, dipotassium hydrogen phosphate (Neon®, Brazil) 2 g/L, tween 80 (Neon®, Brazil) 1 g/L, sodium acetate (Neon®, Brazil) 5 g/L, tribasic ammonium citrate (Sigma-Aldrich®) 2 g/L, magnesium sulfate (Neon®, Brazil) 0.2 g/L, manganese sulfate (Neon®, Brazil) 0.04 g/L and its respective carbon source (CR or MR) 20 g/L.

For monitoring strain growth, five different media were prepared: MRS without added carbon source (WCS), MRS with glucose (Neon®, Brazil) 20 g/L, MRS with fructooligosaccharides (Orafti®, Belgium) (FOS) 20 g/L, MRS with cajuzinho-do-cerrado 20 g/L, and MRS with marmelo-do-cerrado 20 g/L.

The 20 g/L concentration for all carbon sources (glucose, FOS, and fruit residues) was chosen to maintain a consistent energetic input across treatments, ensuring that differences in bacterial growth and metabolism could be attributed to the substrate type rather than quantity. This concentration aligns with standard MRS broth composition, which includes 20 g/L glucose as the sole carbohydrate source (De Man et al., 1960), and reflects common practice in in vitro prebiotic assays, where 1–2% (w/v) is typically used (Albuquerque et al., 2020; Alves-Santos et al., 2023). Additionally, it corresponds to concentrations used in industrial applications, such as dairy and fruit-based beverages enriched with prebiotics.

Evaluation of bacterial cell viability

The viable cell count procedure was used to determine the cell viability of *Lactobacillus*, *Bifidobacterium*, and the enteric mixture in each culture medium (Albuquerque et al., 2020). For tests with *E. coli*, M9 broth (Sigma-Aldrich®) was used as basal medium, supplemented with CR, MR, glucose and FOS (20 g/L). For each assay, 200 µL of the culture with known OD was added to 10 mL of the respective modified medium. The tubes were vortexed for 10 s, and 100 µL of culture was serially diluted in sterile saline (8.5 g/L). Then, 20 µL aliquots of each dilution were inoculated onto MRS agar (probiotics) or on EMB agar (for the enteric mixture) using the microdrop technique at different time points: 0 (immediately after inoculation and homogenization), 18, 24, and 48 h after incubation. Plates were incubated at 37°C for 48 h, and results were expressed as log CFU/mL.

Evaluation of bacterial metabolic activity

The metabolic activity of the strains was evaluated by measuring pH and the concentrations of sugars and organic acids in the cultivation media at different incubation intervals (0, 18, 24 and 48 h). The pH was monitored using a digital pH meter (Adwa®, AD1000, Hungary), following standard procedures (AOAC, 2016). For sugar and organic acid quantification, extracts were prepared and analyzed using an HPLC system equipped with a pulsed amperometric detector (Dionex, Sunnyvale, USA) and a CarboPac PA1 (4 × 250 mm) (Purgatto et al., 2002).

To explore the potential mechanisms by which CR and MR stimulate probiotic metabolic activity, analyses were performed on media containing the carbon sources and the respective probiotics to identify the production of bioactive amine-related metabolites, including putrescine, cadaverine, tyramine, histamine, serotonin, agmatine, spermidine, phenylethylamine, spermine, and tryptamine. Media samples were treated with 5% TCA, vortexed, centrifuged, and filtered. The combined supernatants were adjusted to 25 mL and filtered through a 0.45 µm membrane. Extracts were analyzed by HPLC using a Shimadzu LC-10 AD system with a µBondapack C18 column and a sodium acetate/acetonitrile mobile phase (Dala-Paula et al., 2021).

Detection was performed after post-column derivatization with o-phthaldialdehyde. The derivatization solution (1.5 mL of Brij-35 + 1.5 mL of mercaptoethanol + 0.32 g of o-phthalaldehyde in 500 mL of solution containing 25 g of boric acid and 22 g of KOH, pH adjusted to 10.5) was delivered at a flow rate of 0.4 mL/min. The column was maintained at 23 ±1°C. Amines were identified by comparison with standard chromatograms, and quantification was performed using a standard curve constructed from external standards for each of the ten investigated amines (Dala-Paula et al., 2021). Media without a carbon source was used as a negative control.

Statistical analysis

Chemical analyses were performed in triplicate, and results were expressed as mean ±standard deviation. Assays evaluating prebiotic potential were conducted in two replicates across three independent experiments. Data were submitted to analysis of variance (ANOVA) followed by Tukey's test, with differences considered significant at $p \leq 0.05$. Statistical analyses were performed using RStudio version 4.1. (R Core Team, Vienna, Austria).

RESULTS AND DISCUSSION

Characterization of cajuzinho-do-cerrado and marmelo-do-cerrado residues

CR and MR exhibited high content of protein, total dietary fiber – primarily insoluble fiber – and total phenolic compounds (Table 1). It is important to emphasize that the centesimal composition of residues from the *Alibertia sessilis* fruit (MR) has not yet been reported in the literature. MR displayed a high moisture content, which may be related to the large amount of seeds in this residue.

CR had a higher total dietary fiber content compared to other Cerrado fruits, such as pequi almond (5 g/100 g of dry sample), murici seed (27.5 g/100 g of dry sample), and sweet passion fruit seed (41.3 g/100 g of dry sample), as well as in flours made from residues like mango peel (35.41%) (Pérez-Chabela et al., 2022).

The dietary fiber content of both CR and MR exceeds the daily intake recommended by the World Health Organization (FAO/WHO, 2002), which is at least 25 g/day. Fiber consumption is associated with multiple health benefits, including reducing the risk of chronic non-communicable diseases, such as cardiovascular disease and cancer. Additionally, dietary fiber can lower blood cholesterol and glucose, increase satiety, and influence the composition and metabolic activity of intestinal microbiota (Rezende et al., 2021). Therefore, the high total dietary fiber content in these residues is a relevant finding, as it may contribute to prebiotic effects.

Table 1. Chemical composition and antioxidant capacity of freeze-dried cajuzinho-do-cerrado and marmelo-do-cerrado residues

Parameters	CR	MR
Proximate composition (g/100 g)		
Moisture	9.01 ±0.42	34.68 ±0.32
Ash	1.63 ±0.06	2.50 ±0.06
Protein	9.51 ±0.20	6.14 ±0.76
Lipid	3.10 ±0.74	1.25 ±0.11
Total dietary fiber	43.51 ±0.07	25.97 ±0.02
Soluble dietary fiber	4.59 ±0.12	4.08 ±0.31
Insoluble dietary fiber	38.69 ±0.21	21.43 ±0.16
Carbohydrate	76.75 ±0.73	55.43 ±0.29
Available carbohydrate	33.24 ±0.73	29.46 ±0.29
Energy value (kcal/100 g)	285.92 ±4.19	205.59 ±1.74
Phenolic compounds (mg/L)		
Gallic acid	4.37 ±0.02	<LOD
3,4-dihydroxybenzoic acid	1.44 ±0.13	1.27 ±0.06
Syringic acid	1.13 ±0.03	1.34 ±0.06
Caffeic acid	ND	<LOD
p-coumaric acid	ND	10.66 ±0.74
Ferulic acid	ND	1.71 ±0.02
Coniferaldehyde	10.86 ±0.31	ND
Rutin	<LOD	<LOD
Salicylic acid	ND	1.54 ±0.15
Hesperidin	3.76 ±0.41	ND
Luteolin	ND	13.18 ±1.36
Naringenin	4.21 ±0.58	<LOD
Abscisic acid	<LOD	<LOD
Total phenolics (mg GAE/100 g)	372.50 ±0.03	135.39 ±0.05
Antioxidant capacity (µmol TE/g)	46.82 ±2.18	3.29 ±2.36

Values are expressed as mean ±standard deviation. Abbreviations: CR, freeze-dried cajuzinho-do-cerrado residues; MR, freeze-dried marmelo-do-cerrado residues; GAE, gallic acid equivalents; TE, trolox equivalents; NF, not detected; LOD, limit of detection.

Due to their high protein content, these residues have potential for use in developing food products with added protein value. Both CR and MR also contain significant amounts of phenolic compounds, which may aid in disease prevention, act as prebiotics, and modulate the human intestinal microbiota (Sadef et al., 2022).

Phenolic compounds were quantified in both residues. In CR, gallic acid and coniferaldehyde were the most prominent, while MR contained higher levels of *p*-coumaric acid and luteolin. Gallic acid, found in both CR and MR, has been associated with several biological activities, including antioxidant, anti-inflammatory, antimicrobial, anticarcinogenic, cardioprotective, and neuroprotective effects, as well as a possible role in modulating the intestinal microbiota (Yang et al., 2020). Coniferaldehyde, identified in CR, is a derivative of ferulic acid and also exhibits antioxidant and anti-inflammatory properties (Karamac et al., 2017).

In MR, *p*-coumaric acid was found in considerable amounts. This compound, common in fruits and vegetables, is known for its antioxidant, anti-inflammatory, antimicrobial, antihypertensive, and antidiabetic effects (Malik and Dhiman, 2022). MR also contained a notable amount of luteolin, a flavone abundant in plant foods, with antioxidant, anti-inflammatory, antiproliferative, and antiviral activities (Caporali et al., 2022).

Although rutin was detected below the quantification limit, its presence is noteworthy. Flavonoids such as rutin can positively influence intestinal microbiota by promoting the growth of beneficial bacteria like *Lactobacillus* and *Bifidobacterium*, while inhibiting pathogenic microorganisms (Martín and Ramos, 2021).

The water holding and oil holding capacities (g water/g sample) of CR and MR were 6.39 ±0.10 and 3.46 ±0.06, 2.04 ±0.20 and 1.93 ±0.18, respectively. These technological properties indicate that products developed from these residues will have limited ability to retain large amounts of water or oil. Understanding these properties is important for food processing and new product development, as they can affect texture, viscosity, caloric content, and help prevent degradation during storage (Zahid et al., 2021).

Evaluation of prebiotic potential

In vitro assays were conducted to evaluate the prebiotic potential of CR and MR by monitoring microbial growth and pH changes in probiotic strains and the enteric mixture. Based on the experimental model proposed by this study, these residues can be considered potential prebiotic ingredients.

The growth curves of the probiotic microorganisms demonstrated microbial activity in the different substrates (Fig. 1). Glucose was used as a positive control, as it is a simple, readily metabolizable carbohydrate, while fructooligosaccharide (FOS), which is commonly used to enhance the growth of beneficial bacteria in the colon, served as a comparative prebiotic. Media without a carbon source served as a negative control (Ibrahim, 2021).

Overall, microbial growth (log CFU/mL) occurred in all strains. Higher viable cell counts were observed for *Lactobacillus acidophilus* (LA-05) and *B. animalis* (BB-12) in MR-containing media at 18 h and CR-containing media at 24 h, whereas *Lacticaseibacillus casei* (L-26) showed higher counts in both CR and MR media at 48 h.

The media containing CR and MR showed similar behavior ($p > 0.05$) to the media containing FOS and glucose at all times for all probiotic strains. For the LA-05 strain, there was a significant difference ($p < 0.05$) between the 0 h and 18 h, 24 h and 48 h in the media containing glucose, FOS and CR, whereas for the media with MR, a significant difference ($p < 0.05$) was observed only between 0 h and 48 h.

For the L-26 strain, a significant difference ($p < 0.05$) was observed in the CR-containing media between 0 h and 18 h, 24 h and 48 h, while in the MR-containing media, the difference was significant ($p < 0.05$) between 0h and 18 h and 48 h. For the BB-12 strain, no significant differences ($p > 0.05$) were observed across time points in the CR and MR media.

The viable cell counts of the probiotic strains in the different media were ≥ 6.7 log CFU/mL initially and ≥ 8.2 log CFU/mL at the end of incubation. Growth was comparable ($p > 0.05$) across all strains at 0 h, 18 h, and 48 h, whereas L-26 showed a significant difference ($p > 0.05$) in microbial growth at 24 h compared with LA-05 and BB-12.

These findings demonstrate that these substrates can serve as a carbon source for 48 h, suggesting a high content of fermentable carbohydrates, and that the growth of these probiotic microorganisms is linked to their potential to survive using fruit residues (Albuquerque et

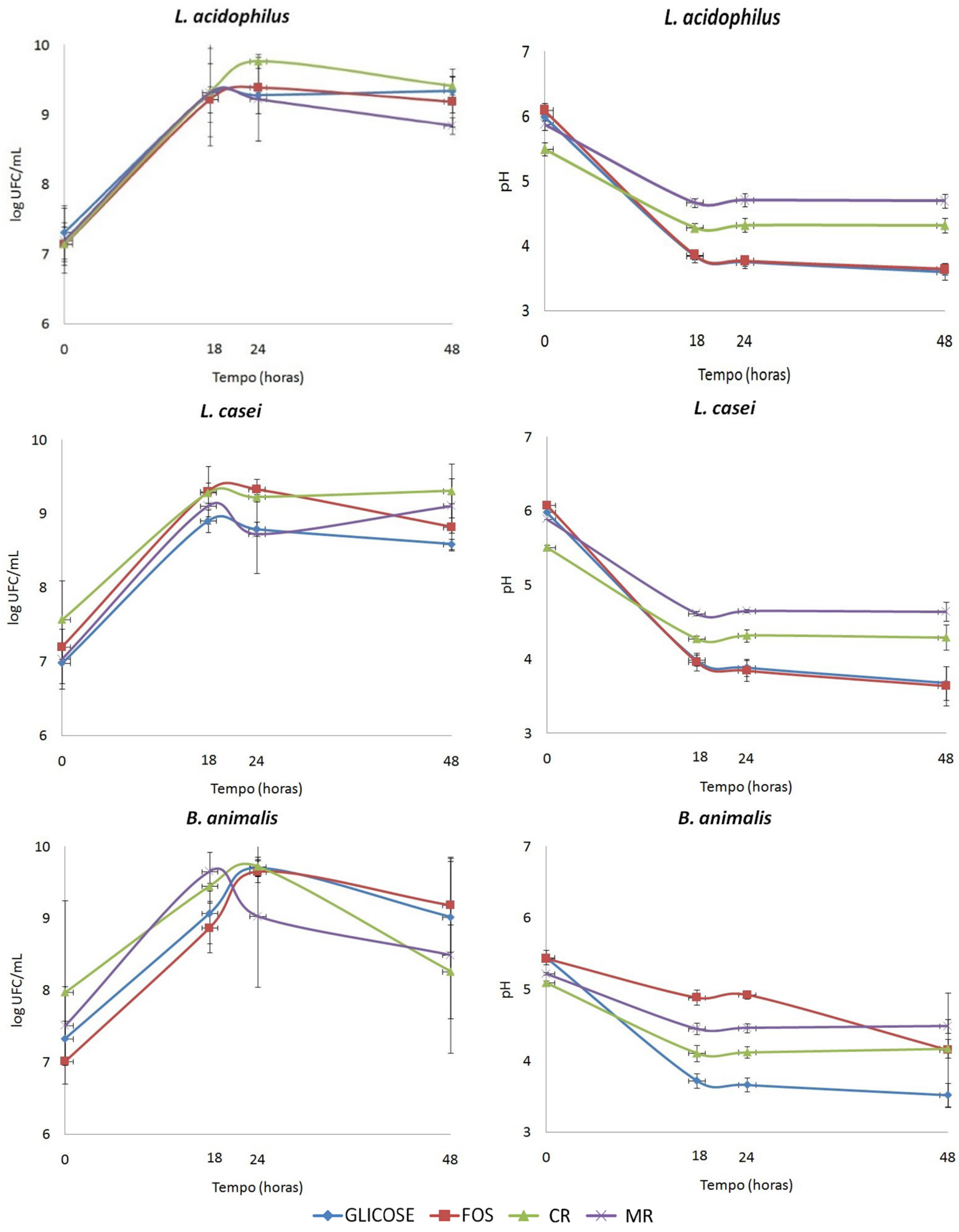


Fig. 1. Viable cell counts (log CFU/mL) and pH values of *Lactobacillus acidophilus* LA-05, *Lacticaseibacillus casei* L-26 and *Bifidobacterium animalis* subsp. *lactis* BB-12 in media containing glucose (GLU), fructooligosaccharides (FOS), freeze-dried cajuzinho-do-cerrado residues (CR) and freeze-dried marmelo-do-cerrado residues (MR) during 48 h of incubation

al., 2020). Probiotics provide several beneficial effects on human health, acting through mechanisms such as strengthening epithelial barriers, preventing pathogen adhesion and competitive exclusion, and regulating the immune system, with the intestinal barrier serving as the primary defense (Akter and Rabeta, 2021).

To further confirm the metabolic activity of these bacteria, pH assays were performed. Cultivation of the probiotic strains in media with different carbon sources resulted in a gradual decrease in pH over time (Fig. 1), as expected, and consistent with other studies investigating the prebiotic potential of fruits and vegetables (Barbosa et al., 2022). The observed reduction in initial pH, alongside the growth of the probiotic populations in the different media, indicates the intense fermentative metabolic activity of these microorganisms in the tested substrates (Menezes et al., 2021).

Considerable decreases in pH were observed in media containing glucose, FOS, CR and MR, whereas media without a carbon source showed only a slight decrease, remaining relatively stable. The pH dropped to ~ pH 3.5 in media with glucose and FOS, and to pH 4.1 in media with CR and MR. For all probiotic strains, there was a significant difference ($p < 0.05$) in the pH between 0 h and 18 h, 24 h and 48 h in media containing CR and MR.

During fermentation, prebiotics generate short-chain fatty acids (SCFA) such as butyric acid, propionic acid and lactic acid. These compounds are highly digestible by bacteria, help maintain a low pH, and inhibit the proliferation of pathogens, providing benefits to the host (Akter and Rabeta, 2021). SCFAs also benefit human health through their metabolic and signaling properties; at appropriate concentrations, they can contribute to the prevention and treatment of diseases such as diabetes, obesity, neuropathologies and cancer (Cong et al., 2022).

In general, the concentrations of sugars (fructose and glucose) in the cultivation media decreased, while the levels of acetic and lactic acids increased at 18 h of fermentation compared with the initial values ($p < 0.05$) (Table 2). Acetic acid was produced in higher concentrations than lactic acid in all cultivation media. The observed reduction in pH is likely associated with the production of these organic acids by probiotics during fermentation.

Various anaerobic bacteria produce lactic acid during carbohydrate fermentation, with *Lactobacillus* and *Bifidobacterium* using it as a primary metabolic byproduct (Markowiak-Kopeć and Śliżewska, 2020). Glycolysis is the main pathway for converting monosaccharides such as glucose and fructose into lactic acid. Lactic acid production is associated with the inhibition of potentially harmful bacteria, including *E. coli*. Acetic acid, another short-chain fatty acid (SCFA), also serves as an important gut microbiota metabolite and has been linked to body weight regulation and improved insulin sensitivity (Hernández et al., 2019).

E. coli can utilize prebiotics as a carbon source (Andrade et al., 2020). Growth curve analysis of the enteric mixture confirmed that these strains were able to use CR and MR (Fig. 2). The residues showed similar behavior ($p > 0.05$) during microbial growth, and no significant difference ($p > 0.05$) in pH was observed between the media at 18 h. Overall, pH values remained largely stable. However, significant differences ($p < 0.05$) were observed between 0 h and 18 h, 24 h and 48 h for both viable cell counts and pH in the media containing CR and MR.

Based on the growth curves and pH values, CR and MR residues appear capable of supporting the growth of probiotic microorganisms relative to *E. coli* strains. Overall, CR and MR served as effective carbon sources in the in vitro fermentation, promoting the growth of probiotic strains and a corresponding reduction in pH. Further studies are recommended to fully evaluate the prebiotic potential of these residues, including experiments using human colonic fermentation models *in vitro*.

Although *E. coli* strains were able to metabolize the CR and MR substrates, the probiotic strains exhibited a more efficient fermentation profile, as evidenced by higher cell viability, greater pH reduction, and increased production of organic acids such as lactic and acetic acids. These findings suggest that the bioactive and fermentable compounds present in the residues, including dietary fibers and phenolic compounds, selectively stimulated beneficial bacteria over potentially pathogenic strains (Loo et al., 2020). This selective stimulation is a hallmark of prebiotic substrates and supports the hypothesis that CR and MR can favorably modulate gut microbiota composition by promoting the growth and metabolic activity of probiotic microorganisms while limiting the proliferation of pathogenic enteric bacteria (Azad et al., 2018).

Table 2. Organic acid and sugar content (g/L) in media containing GLU (20 g/L), FOS (20 g/L), MR (20 g/L), and CR (20 g/L) inoculated with *L. acidophilus*, *L. casei*, and *B. animalis* during 18 h of incubation

Organic acids	Carbon source	Strains					
		LA-05		L-26		BB-12	
		0 h	18 h	0 h	18 h	0 h	18 h
Lactic	GLU	1.61 ±0.33^{Ab}	12.85 ±0.66^{Bb}	1.74 ±0.03^{Ab}	14.39 ±0.99^{Bab}	1.54 ±0.07^{Aa}	14.27 ±0.14^{Ba}
	FOS	1.87 ±0.23^{Aab}	15.37 ±0.89^{Ba}	1.78 ±0.04^{Ab}	18.60 ±3.05^{Ba}	1.56 ±0.06^{Aa}	2.74 ±0.21^{Bc}
	MR	1.90 ±0.11^{Aab}	7.15 ±0.21^{bc}	1.93 ±0.00^{Ab}	7.14 ±0.18^{Bc}	1.57 ±0.10^{Aa}	9.62 ±0.10^{Bb}
	CR	5.40 ±2.72^{Aa}	14.79 ±0.24^{Aa}	6.84 ±0.19^{Aa}	13.58 ±1.03^{Bb}	1.63 ±0.06^{Aa}	10.02 ±2.81^{Bb}
Acetic	GLU	29.50 ±0.64^{Aab}	26.56 ±0.81^{Bc}	28.82 ±1.00^{Ab}	29.11 ±1.43^{Ab}	30.21 ±1.27^{Aa}	31.21 ±0.45^{Ab}
	FOS	28.55 ±0.10^{Aab}	28.53 ±1.09^{Abc}	29.75 ±0.64^{Aab}	29.18 ±1.02^{Ab}	31.39 ±1.31^{Aa}	37.52 ±2.64^{Ba}
	MR	28.12 ±1.21^{Ab}	37.89 ±1.47^{Ba}	30.59 ±0.33^{Aa}	38.00 ±1.77^{Ba}	28.87 ±1.58^{Aa}	37.37 ±1.16^{Ba}
	CR	30.26 ±0.58^{Aa}	31.62 ±1.30^{Ab}	30.85 ±0.46^{Aa}	31.09 ±2.08^{Ab}	29.32 ±1.85^{Aa}	28.26 ±0.43^{Ab}

Sugars	Carbon source	Strains					
		LA-05		L-26		BB-12	
		0 h	18 h	0 h	18 h	0 h	18 h
Glucose	GLU	2.29 ±13.18^{Aa}	0.92 ±0.06^{Ba}	2.18 ±3.53^{Aa}	0.89 ±0.27^{Ba}	2.24 ±6.48^{Aa}	1.08 ±8.85^{Ba}
	FOS	0.05 ±2.77^{Ab}	0.03 ±1.09^{Ab}	0.04 ±0.49^{Ab}	0.02 ±0.49^{Ab}	0.05 ±1.36^{Ab}	0.00 ±0.32^{Ab}
	MR	0.24 ±3.33^{Ac}	ND	0.24 ±0.91^{Ac}	0.00 ±0.02^{Bb}	0.26 ±1.60^{Ac}	ND
	CR	0.46 ±0.91^{Ac}	ND	0.44 ±3.55^{Ac}	ND	ND	0.44 ±0.85^{Aa}
Fructose	GLU	0.09 ±1.64^{Aa}	ND	0.07 ±0.45^{Aa}	ND	0.07 ±0.63^{Aa}	ND
	FOS	0.10 ±0.96^{Aa}	0.93 ±2.27^{Ba}	0.07 ±1.18^{Aa}	0.62 ±2.94^{Ba}	0.14 ±0.24^{Aa}	ND
	MR	0.18 ±2.46^{Aa}	ND	0.16 ±0.64^{Aab}	ND	0.24 ±3.78^{Ab}	ND
	CR	0.38 ±0.56^{Ab}	ND	0.34 ±2.42^{Ac}	ND	0.55 ±2.54^{Ac}	ND
Sacarose	GLU	0.11 ±0.71^{Aa}	0.12 ±0.70^{Aa}	0.10 ±0.20^{Aa}	0.11 ±0.51^{Aa}	0.10 ±0.97^{Aa}	0.15 ±0.53^{Aa}
	FOS	0.12 ±0.78^{Aa}	0.28 ±1.97^{Bb}	0.10 ±0.13^{Aa}	0.12 ±0.77^{Aa}	0.19 ±2.12^{Ac}	0.17 ±2.48^{Aa}
	MR	0.09 ±0.44^{Aa}	0.13 ±0.75^{Aa}	0.08 ±1.05^{Aa}	0.12 ±1.57^{Ba}	0.10 ±1.50^{Aa}	0.16 ±1.88^{Ba}
	CR	0.09 ±0.45^{Aa}	0.12 ±1.73^{Aa}	0.08 ±0.57^{Aa}	0.13 ±1.90^{Ba}	0.15 ±2.52^{Aab}	0.14 ±3.42^{Aa}

a–c: different superscript small capital letters in the same column for the same sugar/organic acid at different cultivation times for each tested isolate denote differences ($p \leq 0.05$) based on Tukey's test; A–C: different superscript capital letters in the same row and different measured sugar/organic acids for each isolate among media with GLU, FOS, PR, and GR denote difference based on Tukey's test ($p \leq 0.05$). ND: not detected; GLU: glucose; FOS: fructooligosaccharides; freeze-dried cajuzinho-do-cerrado residues (CR) and freeze-dried marmelo-do-cerrado residues (MR).

During 18 h and 48 h of fermentation by the different microorganisms, media containing CR and MR significantly increased polyamine-related metabolites, such as spermidine and phenylethylamine, compared with media supplemented with FOS and glucose ($p < 0.05$) (Fig. 3). Polyamines have been reported to

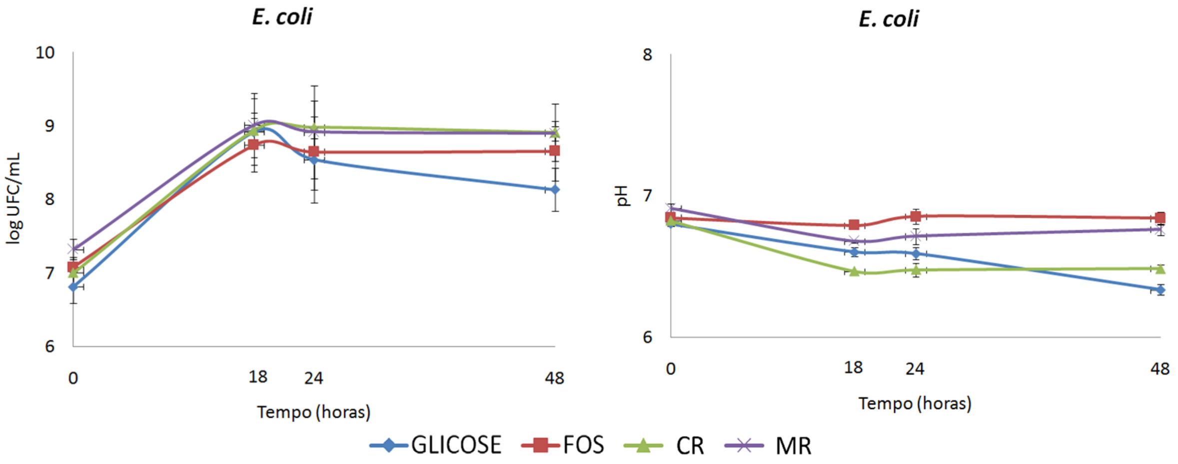


Fig. 2. Viable cell counts (log CFU/mL) and pH values of enteric mixture in media containing glucose (GLU), fructooligosaccharides (FOS), freeze-dried cajuzinho-do-cerrado residues (CR) and freeze-dried marmelo-do-cerrado residues (MR) during 48 h of incubation

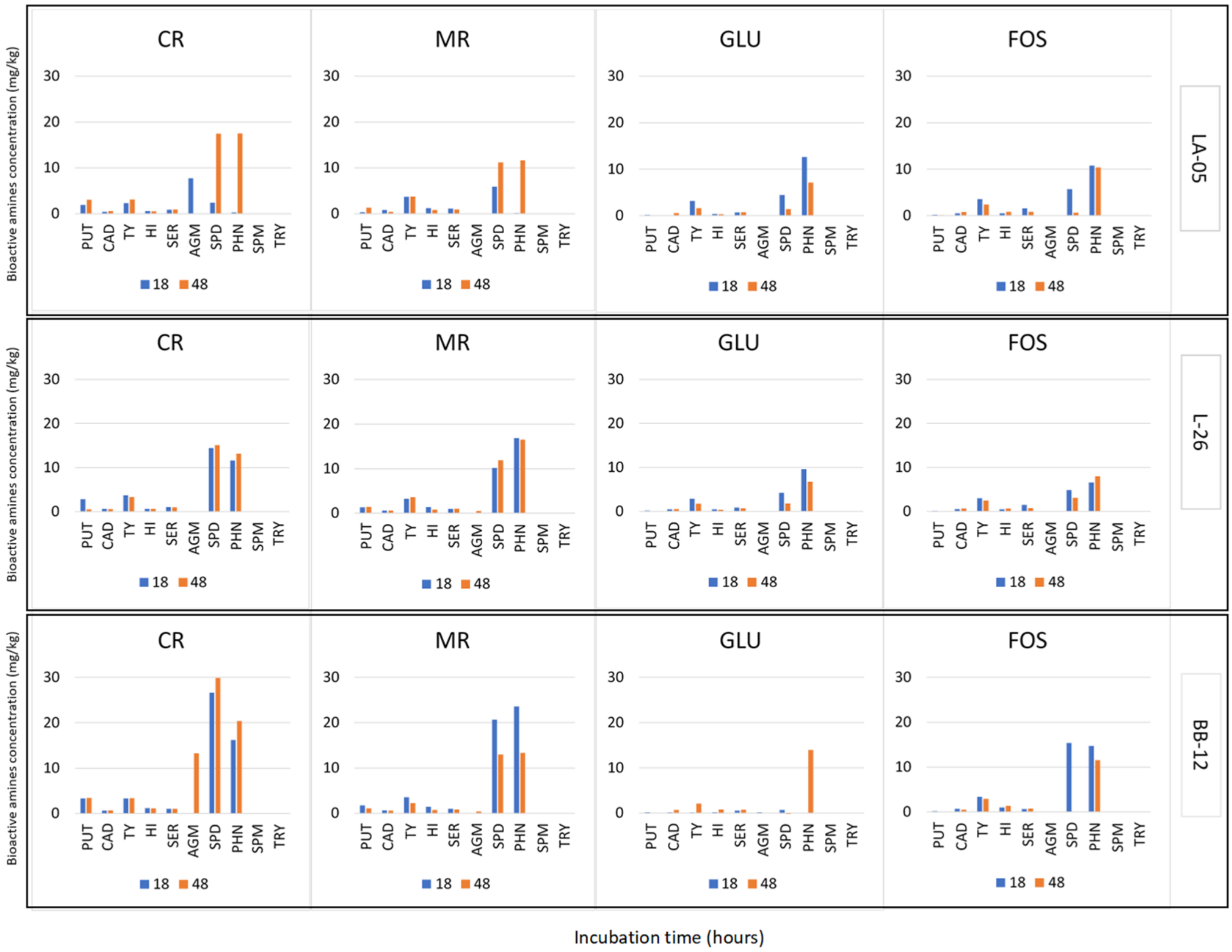
promote colonic mucosal growth, maintain intestinal epithelial cell and intestinal barrier integrity, and their production has been linked to the presence of prebiotic ingredients (Dong et al., 2021).

In vitro fecal fermentation with *Bifidobacterium* (probiotic) and lactulose (prebiotic) led to significant spermidine production, demonstrating that prebiotic compounds play an important role in intestinal polyamine production and human health (Hashikura et al., 2023). *In vivo* studies have also linked polyamine production to the presence of recognized prebiotic ingredients. For example, Manzoni et al. (2017) showed that the consumption of symbiotic beverages containing *Bifidobacterium animalis* ssp. *lactis* BB-12 and functional ingredients (soy and yacon as natural prebiotic sources) increased polyamine levels – particularly spermidine – in the intestines of elderly individuals (Manzoni et al., 2017).

Elevated levels of polyamines in the intestine, notably spermidine, have been shown to enhance longevity in mice, and *Bifidobacterium* plays a role in suppressing the production of inflammatory cytokines, likely through mechanisms involving polyamines (Matsumoto et al., 2019).

While polyamines such as spermidine and putrescine are generally associated with beneficial physiological effects, some biogenic amines, including tyramine and histamine, can pose health risks at high concentrations. Toxicity thresholds have been established, particularly for sensitive individuals. According to EFSA (2011), adverse effects may occur when histamine concentrations exceed 50 mg/kg in food, particularly in fermented products. Similarly, tyramine levels above 100–800 mg/kg can trigger hypertensive crises in individuals taking monoamine oxidase inhibitors (MAOIs). In the present study, neither histamine nor tyramine was detected at concentrations considered toxic. Moreover, this *in vitro* model does not simulate host absorption or metabolism. Nonetheless, monitoring these amines in future *in vivo* studies is essential to ensure the safety of potential food applications of these residues.

After 48 h of fermentation by BB-12, greater production of phenylethylamine was observed in the medium containing CR ($p < 0.05$). This amine has been associated with improved digestive process in animals by stimulating the intestine and enhancing gastrointestinal circulation (Broadley et al., 2009). The genus *Bifidobacterium* appears to be particularly effective as a probiotic for metabolizing prebiotic ingredients to produce polyamines. This capacity was also observed by Sugiyama et al. (2018), who demonstrated that some indigenous human *Bifidobacterium* species possess spermidine biosynthetic ability. Thus, probiotics and prebiotics can modulate polyamine balance, and CR and MR have proven to be significant substrates for polyamine production, especially when metabolized by BB-12.



PUT – putrescine; CAD – cadaverine; TY – tyramine; HI – histamine; SER – serotonin; AGM – agmatine; SPD: spermidine; PHN – phenylethylamine; SPM – spermine; TRY – tryptamine.

Fig. 3. Bioactive amines concentration (mg/kg) production in media containing glucose (GLU), fructooligosaccharides (FOS), freeze-dried cajuzinho-do-cerrado residues (CR) and freeze-dried marmelo-do-cerrado residues (MR) during 18 h and 48 h of fermentation

Phenylethylamine is a trace amine naturally present in the human body and certain foods. It has been associated with neuromodulatory effects, including potential roles in mood regulation and gastrointestinal stimulation. However, its role in humans is complex and not fully understood. Unlike in animal models, where phenylethylamine may exert pronounced physiological effects, in humans it is rapidly degraded by monoamine oxidase-B (MAO-B), limiting its systemic bioavailability (Narang et al., 2011). Therefore, although the increased phenylethylamine levels observed in this study indicate microbial metabolic activity, caution is warranted in attributing functional benefits. Further research is needed to determine whether microbial production of phenylethylamine from dietary substrates can elicit meaningful effects in the human gastrointestinal tract or systemically.

The observed metabolic effects, including reduced pH, increased production of lactic and acetic acids, and elevated levels of spermidine and phenylethylamine, may be mechanistically linked to the biochemical composition of CR and MR. These residues are rich in dietary fiber and phenolic compounds, such as gallic acid, *p*-coumaric acid, and flavonoids, which are known to modulate microbial metabolism (Tomás-Barberán et al., 2016). The fiber fraction likely provides fermentable substrates that stimulate saccharolytic fermentation pathways in probiotic strains, leading to the generation of short-chain fatty acids and acidification of the medium (Slavin, 2013). At the same time, specific polyphenols may influence microbial gene expression related to amino acid decarboxylation and polyamine biosynthesis (Barbosa et al., 2024). Moreover, the antioxidant environment created by these compounds may help maintain microbial viability and metabolic activity (Brglez Mojzer et al., 2016). Together, these interactions suggest a synergistic effect between fermentable fibers and bioactive phenolics in CR and MR, supporting a model in which these components co-modulate probiotic metabolism toward beneficial end products. Further targeted studies are needed to confirm these mechanisms and assess their *in vivo* relevance.

This study is the first to characterize and evaluate the prebiotic potential of residues from cajuzinho-do-cerrado and marmelo-do-cerrado. To the best of our knowledge, no previous study has reported the effects of these potential prebiotic Cerrado residues on polyamine production. Therefore, these findings contribute to a better understanding and valorization of these residues, supporting the conservation and sustainable use of the Cerrado biome. Additionally, they highlight a nutritionally valuable product with applications in the food industry.

CONCLUSION

The freeze-dried residues of cajuzinho-do-cerrado and marmelo-do-cerrado are rich in dietary fiber, protein, and phenolic compounds, with bioactive substances relevant to human health. Coniferaldehyde was the most abundant phenolic compound identified in cajuzinho-do-cerrado residues, while luteolin predominated in marmelo-do-cerrado residues. These residues appear to serve as metabolizable substrates, promoting the growth of probiotic strains. The observed pH decrease, alongside microbial proliferation, indicates active bacterial metabolism and increased production of organic acids, especially acetic acid. Additionally, the residues served as substrates for polyamine production, including spermidine, by probiotic bacteria. Therefore, these residues hold potential as prebiotic ingredients for functional food applications. While the results demonstrate promising *in vitro* functional and prebiotic effects, further *in vivo* studies are required to confirm the health-related benefits of CR and MR.

DECLARATIONS

Data statement

All data supporting this study has been included in this manuscript.

Ethical Approval

Not applicable.

Competing Interests

The authors declare that they have no conflicts of interest.

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