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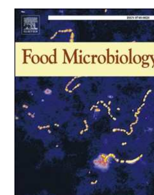

Wet fermentation of *Coffea canephora* by lactic acid bacteria and yeasts using the self-induced anaerobic fermentation (SIAF) method enhances the coffee quality

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A R T I C L E I N F O

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A B S T R A C T

This work aimed to evaluate the impact of inoculation single and co-cultivation of LAB and yeasts during the wet process of *Coffea canephora* using the self-induced anaerobic fermentation method. *Saccharomyces cerevisiae, Totulaspora delbrueckii delbrueckii, Leuconostoc mesenteroides*, and *Lactiplantibacillus plantarum* were monitored during fermentation. *L. mesenteroides* was detected in high concentrations in the coffee fruits (8.54 log10 cells/mL) and remained until the end of fermentation. Lactic and acetic acids were the main acids produced during fermentation. After 36 h of fermentation, 75.39% of malic acid was consumed in the *L. mesenteroides* + *S. cerevisiae* (MC) fermentations. In roasted coffee, the caffeine concentration reached 3.29 higher than the green beans in MC fermentation. Specific volatile compounds were detected in inoculated fermentation and may contribute to the beverage quality. Coffee inoculated with *Leuconostoc mesenteroides* was classified as fine (80.0–89.0), while the other fermentations were classified as premium (70.0–79.0). *L. mesenteroides* inoculation showed the best sensory score, and the beverage was characterized by caramel, fruity, and spices notes. *L. mesenteroides* inoculated alone or in co-culture with *S. cerevisiae* are promising starter cultures to improve Conilon coffee quality and obtain beverages with differentiated sensory profiles.

1. Introduction

Conilon coffee is a *Coffea canephora* variety that stands out for its drought resistance and high commercial value. In Brazil, the average production for 2022 is estimated at 16.96 million bags (CONAB, 2022). The state of Espírito Santo is the largest producer, accounting for more than 60% of the national crop (CONAB, 2022). This species is attractive industrially due to its yield and properties, which can substantially aid in the final composition of blends, with more balanced acidity, body, and thicker cream in espresso coffees (Fonseca et al., 2015).

Coffea canephora beverage has always been characterized as low quality by consumers. However, this concept is changing after developing a specific *Coffea canephora* protocol and introducing new technologies during pre- and post-harvest coffee processing (de Morais et al., 2021; Velásquez and Banchón, 2022). In post-harvest processing, the fermentation method has contributed to the production of coffee with different sensory profiles due to the production of primary and secondary metabolites by microorganisms.

In wet coffee processing, bacteria and yeasts are ubiquitous (Elhalis et al., 2020; Evangelista et al., 2015; Ribeiro et al., 2018). The metabolic activity of these specific microbial groups is related to their intra- and interspecies interaction, resulting in the production of extracellular enzymes, volatile and non-volatile metabolites, and pH changes that contribute to the formation of the sensory profile of coffee beverages (da Silva et al., 2021; Elhalis et al., 2021, 2020).

The use of starter culture has been shown to contribute to the balance

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of volatiles and non-volatiles, improving the sensory attributes of roasted coffee (da Silva et al., 2021; Prakash et al., 2022). In da Silva et al. (2021), the starter *Meyerozyma caribbica* increased the beverage quality and minimized the filamentous fungal population during the fermentation of *Coffea canephora*. In another study, volatile compounds generated by fermentation of conilon coffee inoculated with *Saccharomyces cerevisiae* contributed positively to the beverage sensory profile (Prakash et al., 2022). *Bacillus licheniformis* inoculated in wet-processed conilon coffee increased coffee scores and produced volatile compounds that provided a favorable sensory profile to the beverage (Bravim et al., 2023). Nevertheless, the fermentative performance of lactic acid bacteria as a starter culture in conilon coffee has not yet been investigated.

Lactic acid bacteria (LAB) and yeasts are known to co-exist and cooperate in several fermented foods and beverages such as coffee, cocoa, kefir, kombucha, sourdough, and wine (Andreson et al., 2022; Chen et al., 2021; Minnaar et al., 2019; Viesser et al., 2021; Yang et al., 2021). Consequently, *Leuconostoc* and *Lactiplantibacillus* were detected during the fermentation of C*offea canephora* (Pereira et al., 2020; Prakash et al., 2022). However, the fermentative performance of LAB as a starter culture has not yet been investigated in Conilon coffee, and few studies with yeast inoculation have been described. In Cassimiro et al. (2022), inoculation of bacteria and yeast during wet processing in *Coffea arabica* using whole fruits and induced anaerobiosis influenced the formation of different sensory descriptors. Thus, the co-cultivation between bacteria and yeast can be a strategy to improve the microbiological and sensory qualities of the final product.

The amount of oxygen (O_2) varies depending on the method used and impacts the quality of the beverage. In anaerobic conditions, lactic acid production is intensified, contributing to the perception of acidity and body of coffee beverages (Pereira et al., 2016). On the other hand, self-induced anaerobic fermentation (SIAF) is a fermentation method in which the anaerobic condition is gradually formed by microbial metabolism that uses the remaining O_2 for its metabolic reactions, releasing CO_2, volatile and non-volatile compounds (Pereira et al., 2022; da Mota et al., 2020). Besides, the SIAF method positively impacts the fermentative performance of LAB and yeasts during the processing of natural and pulped coffee (da Mota et al., 2020; Martins et al., 2020).

This study aimed to evaluate the impact of inoculation single and co-cultivation of LAB and yeasts during the wet process with whole fruit using the SIAF method on coffee's chemical and sensory quality. Moreover, the dynamic behavior of the starter cultures was evaluated by real-time PCR.

2. Material and methods

2.1. Coffee harvesting and processing

Ripe coffee fruits (cherry coffee) of *Coffea canephora* variety Conilon LB1 were harvested mechanically at Fazenda Venturim, located in the municipality of São Domingos do Norte (19°06′22″S 40°35′32″W), Espírito Santo, Brazil where the experiment was performed. The whole coffee fruits were processed by the wet method. Fermentations were carried out using the SIAF method, without (spontaneous fermentation - control) and with starter culture (*Leuconostoc mesenteroides* CCMA 1105; *Lactiplantibacillus plantarum* CCMA 1065, *Torulaspora delbrueckii* CCMA 0684, and *Saccharomyces cerevisiae* CCMA 0543). In the SIAF method, 32 L of coffee fruits and 16 L of freshwater were placed in high-density polyethylene bioreactors (50 L capacity), hermetically sealed, and kept at room temperature for 72 h.

After fermentation, the coffee was washed, mechanically pulped (Ecoflex, Pinhalense, São Paulo, Brazil), and taken to suspended terraces for the drying stage (until the moisture content was 11–12%). The pH (PHmeter - KASVI, model K39-0014 PA), temperature, and soluble solids (Refractometer - DFV, model RM-M3) were measured during the fermentation. Samples (150 g) were collected every 36 h and stored at −20 °C for analysis (chemical and microbiological). High barrier packaging (double kraft paper and internally coated with a plastic film impermeable to oxygen) were used to store the coffee beans for further sensory analysis. All fermentations were performed in triplicate.

2.2. Culture conditions and inoculum preparation

The starter cultures used in this study were previously isolated from different processing methods and coffee varieties (*Saccharomyces cerevisiae* CCMA 0543, *Torulaspora delbrueckii* CCMA 0684 (Silva et al., 2000), *Leuconostoc mesenteroides* CCMA 1105, and *Lactiplantibacillus plantarum* CCMA 1065 (former *Lactobacillus plantarum* CCMA 1065) (Ribeiro et al., 2018) and were deposited at the Agricultural Microbiology Culture Collection of the Federal University of Lavras.

Yeast and lactic acid bacteria were grown separately in YEPG broth [10 g/L yeast extract (Merck); Peptone 20 g/L (HiMedia); 20 g/L dextrose (Merck)] at 30 °C and MRS broth (MRS) at 35 °C (De Man Rogosa Sharpe, Merck, Darmstadt, Germany), respectively, and replicated every 24 h until reach a final concentration of 10^9 cells/mL. The cells were recovered by centrifugation (7000 RCF, 10 min) and resuspended in 500 ml distilled water. The solution was added inside the bioreactor (coffee + water) to a concentration of approximately 10^7 cells/g of total volume.

The inoculated fermentations were identified as **M**: *Leuconostoc mesenteroides*; **P**: *Lactiplantibacillus plantarum*; **MP**: *Leuconostoc mesenteroides* + *Lactiplantibacillus plantarum;* **MD**: *Leuconostoc mesenteroides* + *Torulaspora delbrueckii;* **MC**: *Leuconostoc mesenteroides* + *Saccharomyces cerevisiae;* **PD**: *Lactiplantibacillus plantarum* + *Torulaspora delbrueckii* and **PC**: *Lactiplantibacillus plantarum* + *Saccharomyces cerevisiae* (Supplementary Material Fig. S1).

2.3. Real-time PCR (qPCR)

The population of *Saccharomyces cerevisiae*, *Torulaspora delbrueckii*, *Leuconostoc mesenteroides,* and *Lactiplantibacillus plantarum* was monitored during fermentation (0, 36, and 72 h) by qPCR. Samples of coffee cherries (10 g) were mixed with 10 ml of ultrapure water for 10 min. The liquid phase was separated in a falcon tube, and the extraction was repeated. The liquid phase (20 ml) was centrifuged at (7000 RCF, 4 °C for 10 min) and the pellet was used for total DNA extraction using a QIAamp DNA Mini Kit (Qiagen, Hilden Germany) according to the "DNA Purification from Tissues" protocol.

The standard curve was performed by extracting DNA from yeast and bacterial strains used as starter cultures. Yeasts and bacteria were grown separately in YEPG broth (30 °C/24 h) and MRS (35 °C/24 h). Yeast populations were measured by counting in a Neubauer chamber, and LAB populations by plating on MRS agar (Merck, Darmstadt, Germany), and 1 ml was taken for DNA extraction using a QIAamp DNA Mini Kit (Qiagen, Hilden Germany) according to the "DNA Purification from Tissues" protocol. Serial dilution (1:10) of each strain was performed from 10^3 to 10^8 cells/mL. Each point on the curve and coffee samples were analyzed in triplicate.

A Rotor-Gene Q system (Qiagen, Hombrechtikon, ZH, Switzerland) was used for qPCR analysis. Each reaction had a final volume of 25 μL: 12.5 μL of Rotor-Gene SYBR Green master mix (Qiagen, Stockach, Konstanz, Germany), 2.5 μL (10 μM) of each primer (Invitrogen, São Paulo, SP, Brazil), 1 μL of DNA and 6.5 μL of ultrapure water. The mixture was heated at 95 °C for 10 min, followed by 40 cycles of denaturation at 95 °C for 10 s and annealing/extension at 60 °C for 15 s. The cycling temperature was increased by 1 °C every 5 s from 50 °C to 99 °C to obtain the melting curve (Batista et al., 2015). Specific primers were used (Supplementary material: Table S1). The nucleotide sequences specificity of each primer set was assessed via GenBank BLAST modules, including BLASTn and BLASTx (http://www.ncbi.nlm.nih.gov/BLAST/).

2.4. Determination of organic acids, caffeine, chlorogenic acid, and trigonelline

Organic acids (acetic, butyric, citric, lactic, malic, and succinic) and bioactive compounds (chlorogenic acid, caffeine, and trigonelline) were evaluated by high-performance liquid chromatography (LC-10Ai, Shimadzu Corp., Japan). A UV–VIS detection system (SPD-10Ai) was used for organic acids (Shim-pack SCR 101-H; 7.9 mm × 30 cm column) and bioactive compounds (C18 reversed-phase column AG-120; 150 × 4.6 mm, 5 μm).

The organic acids were extracted (0, 36, and 72 h of fermentation) according to Ribeiro et al. (2017), and the operating conditions were performed as described by da Mota et al. (2020).

The bioactive compounds were extracted and analyzed from coffee fruit and roasted coffee, following the protocol proposed by Malta and Chagas (2009). The concentration of each sample was determined through an external calibration method, injecting different concentrations of the standard. The analysis was performed in triplicate.

2.5. Determination of volatile compounds

Volatile compounds were extracted by headspace solid-phase microextraction (HS-SPME). A Green and roasted coffee sample (2 g) was macerated with liquid nitrogen and placed in a 15 ml hermetically sealed vial. The samples were heated in a water bath (15 min/60 °C) until the system reached equilibrium. A divinylbenzene/carboxen/polydimethylsiloxane (DVB/CAR/PDMS) 50/30 μm SPME fiber (Supelco Co., Bellefonte, PA, USA) was used (30 min/60 °C) for the absorption of volatile compounds. Volatile compounds were analyzed in a gas chromatograph coupled to a mass spectrometer (Shimadzu GCMS-QP2010) using a Carbowax column (30 m × 0.25 mm x 0.25 mm). The operating conditions were the same as those described by Ribeiro et al. (2017). Alkane standards (C10-C40) were used to identify and calculate each compound's linear retention index (LRI). The mass spectra generated for each compound were compared with those of the NIST 11 library.

2.6. Sensory analysis - cup test

Six trained tasters with Q-Grader coffee certification evaluated the coffee beverage samples corresponding to each treatment according to the Fine Robusta Cupping protocol (ICO, 2010). Each coffee beverage was evaluated five times by the same taster. The attributes evaluated fragrance/aroma, flavor, aftertaste, salinity/acidity, bitterness/sweetness, and mouthfeel received scores that ranged from 6 to 10 points. Descriptive analysis of the samples was also performed, in which the tasters reported on the notes perceived in the coffee beverage.

2.7. Statistical analysis

The experiment was conducted in a completely randomized design and consisted of one process (wet process) and eight fermentations (with and without inoculation) performed in triplicate, totaling 24 experimental units. Microbial density, organic acids, and sensorial analysis data were analyzed statistically using variance analysis (ANOVA) followed by the Scott-Knott test ($p < 0.05$) to determine significant differences among treatments. Statistical analysis was carried out using the statistical program RStudio, version 3.3.3.

3. Results

3.1. Physicochemical parameters measure during fermentation

The initial temperature of the coffee mass ranged from 22 to 26 °C. The temperature of the coffee mass during fermentation varied by up to 2 °C depending on the treatment (Table 1). The soluble solid concentration in coffee fruit ranged from 7 to 16 °Brix, decreasing during fermentation. The PD fermentation had a more noticeable reduction in the soluble solids concentration (16–8 °Brix) than the other fermentations. For all fermentation, the initial pH was approximately 4.6–5.5 and decreased gradually during the fermentation of 72 h reaching approximately 3.5–3.9. The MC fermentation was characterized by higher acidity (pH 3.5).

Table 1
Physicochemical parameters during fermentation.

Fermentations	Time (h)	Temperature (°C)	Soluble solid (°Brix)	pH
Control	0	24.0	14.0	5.5
	36	22.0	11.0	4.1
	72	23.0	8.5	3.9
M	0	24.5	13.0	4.8
	36	22.0	11.0	4.0
	72	24.0	7.0	3.7
P	0	24.0	13.5	4.9
	36	22.0	9.0	3.9
	72	24.0	8.5	3.8
MD	0	23.0	13.5	5.3
	36	22.0	11.5	4.0
	72	23.0	11.0	3.8
PD	0	22.0	16.0	5.4
	36	24.0	11.0	4.1
	72	24.0	8.0	3.9
MP	0	24.0	13.9	4.6
	36	22.0	11.2	3.9
	72	23.0	7.8	3.7
MC	0	26.0	16.0	4.8
	36	22.0	11.0	4.1
	72	23.0	9.0	3.5
PC	0	22.0	15.5	5.0
	36	23.0	12.0	4.1
	72	24.0	8.5	3.6

Control: Spontaneous fermentation; **M**: *Leuconostoc mesenteroides*; **P**: *Lactiplantibacillus plantarum*; **MP**: *Leuconostoc mesenteroides* + *Lactiplantibacillus plantarum;* **MD**: *Leuconostoc mesenteroides* + *Torulaspora delbrueckii;* **MC**: *Leuconostoc mesenteroides* + *Saccharomyces cerevisiae;* **PD**: *Lactiplantibacillus plantarum* + *Torulaspora delbrueckii*; **PC**: *Lactiplantibacillus plantarum* + *Saccharomyces cerevisiae*.

3.2. Microbial density of starter cultures

The microbial density of *L. mesenteroides, L. plantarum, S. cerevisiae,* and *T. delbrueckii* was monitored during coffee fermentation (Fig. 1). The *Leuconostoc mesenteroides* population showed no significant difference between fermentations. Among the strains evaluated, *L. mesenteroide* was the microorganism that predominates in the fruit, and the MP fermentation showed the highest microbial density, 9.63 $\log_{10}$ cells/mL (Fig. 1A).

The first 36 h of fermentation were favorable for the *L. plantarum* growth in the samples inoculated by CCMA 1065 strain, which showed a population ranging from 5.62 $\log_{10}$ cells/mL (MP) to 6.29 $\log_{10}$ cells/mL (P), in addition to all cell counts were higher than the control treatment. In contrast, after 72 h, the lowest *L. plantarum* population (4.71 $\log_{10}$ cells/mL) was observed in PD fermentation (Fig. 1B).

In co-cultivation fermentation, the inoculated LAB influenced the growth of starter yeast. Thus, the *T. delbrueckii* growth was favored mainly in co-inoculated with *L. mesenteroides*, reaching a population of 7.89 $\log_{10}$ cells/mL at the process end (Fig. 1C). However, *S. cerevisiae* was favored in co-inoculated with *L. plantarum*, but only in the first 36 h of fermentation, reaching 6.89 $\log_{10}$ cells/mL. However, the population of the yeast species in the co-inoculated treatments was always higher than in the control treatment (Fig. 1D).

3.3. Organic acids

Acetic, citric, lactic, malic, and succinic acids were identified in all

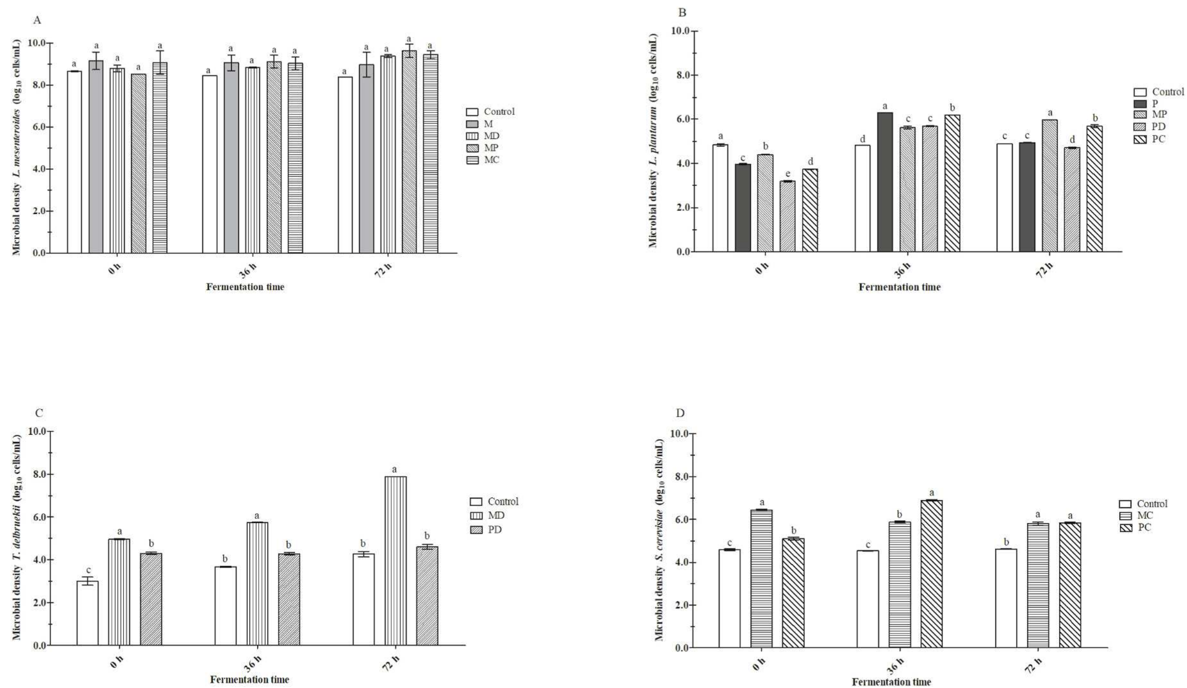

Fig. 1. Microbial density in spontaneous and inoculated coffee fermentations: (A) *L. mesenteroides* CCMA 1105, (B) *L. plantarum* CCMA 1065, (C) *T. delbrueckii* CCMA 0684, (D) *S. cerevisiae* CCMA 0543. **Control**: Spontaneous fermentation; **M**: *Leuconostoc mesenteroides*; **P**: *Lactiplantibacillus plantarum*; **MP**: *Leuconostoc mesenteroides + Lactiplantibacillus plantarum;* **MD**: *Leuconostoc mesenteroides + Torulaspora delbrueckii;* **MC**: *Leuconostoc mesenteroides + Saccharomyces cerevisiae;* **PD**: *Lactiplantibacillus plantarum + Torulaspora delbrueckii*; **PC**: *Lactiplantibacillus plantarum + Saccharomyces cerevisiae*.
Mean values followed by the same letter do not differ significantly by the Scott-Knott test ($p > 0.05$).

treatments (Table 2). At the beginning of the fermentation process, high concentrations of malic acid (2.38–5.05 g/kg) were detected, followed by citric (0.88–2.03 g/kg) and succinic acid (0.05–0.10 g/kg).

After 36 h of fermentation, the malic acid consumption in the fermentations with *S. cerevisiae* was 75.39% (MC) and 63.34% (PC). On the other hand, acetic acid production was more intense at the end of the fermentation process, except for PD fermentation. P fermentation showed high production (0.25 g/kg) of this acid, but there was no significant difference between treatments.

Lactic acid was produced after 36 h of fermentation, reaching maximum production within 72 h of fermentation. The highest lactic acid concentration was obtained for MP (1.43 g/kg) and MD (1.35 g/kg). The succinic acid concentration increased during fermentation, more evident in the fermented P (0.05–0.12 g/kg) and MP (0.05–0.12 g/kg).

3.4. Caffeine, trigonelline, and chlorogenic acid

Chlorogenic acid, trigonelline, and caffeine showed different concentrations between green and roasted coffee samples (Fig. 2). There were changes in chlorogenic acid and trigonelline levels in all roasted coffee samples. In green coffee, chlorogenic acid levels were more evident in Control (12.68 g/kg), and in roasted coffee, the reduction of this compound reached up to 8.61 times (MC). The reduction of trigonelline reached 7.2-fold in the fermented PC. On the other hand, the caffeine content was more evident in the samples of all roasted coffees. In green coffee, the concentration was more expressive in the fermented M (8.09 g/kg). After roasting, it was observed that the concentration of caffeine reached higher levels, such as the MC fermentation, which presented caffeine levels 3.29 higher than the green beans. Furthermore, the fermented products in which *S. cerevisiae* was inoculated in co-culture showed more evident levels of this compound.

3.5. Profile of volatile compounds

In the samples of green and roasted coffee were identified 137 volatile compounds belonging to 16 chemical classes (Supplementary Material Table S2), such as acids (21), esters (18), pyrazines (15), ketones (12), alcohols (10), furans (14), hydrocarbons (7), phenols (8), aldehydes (6), pyrroles (6), lactone (3), formate (2), furanones (2), pyridines (2), thiophenes (2) and thiazole (1) and others (8). The peak areas corresponding to each compound in the different fermented products can also be observed in the Supplementary material (Table S2).

The starter culture modified the profile of volatile compounds when compared to the control in green coffee beans. Octadecanoic acid, benzene acetic acid, ethyl ester, benzoic acid, 2-hydroxy-, and ethyl ester were detected in the inoculated fermentations. Tridecanal was detected in co-cultures of LAB with *T. delbrueckii*. Specific compounds were produced by P (decanol; 2-undecanone; Phenol, 2-methyl-), PC (glycerol; benzoic acid, ethyl ester), PD (hexadecanal), MP (geraniol; 9,12-octadecadienoic acid, methyl ester; benzyl benzoate; tetradecane) and MC (ethyl 9-hexadecenoate) fermentations.

In the roasted coffee, 2-butanone,1-(acetyloxy) was detected in the co-cultivation between *L. mesenteroides + L. plantarum* (MP) and *L. mesenteroides + S. cerevisiae* (MC). 2-furancarboxaldehyde, 5-methyl-; 1H-pyrrole-2-carboxaldehyde, 1-methyl-; 2-ethyl-6-methyl-pyrazine; and 2,5-dimethyl-4-hydroxy-3(2H)-furanone were detected in all fermentations inoculated. Pantolactone and 2-thiophenemethanol were detected in the co-culture of lactic acid bacteria and *S. cerevisiae*. 1-Nonadecanol; 3-hexen-2-one, 5-methyl-; 4-hydroxy-2-methylacetophenone; furan, 2,2′-methylenebis-; 4-methyl-5H-furan-2-one; 2-hydroxy-gamma-butyrolactone was detected in PC fermentation. Furfuryl formate and 2-furanmethanol, propanoate was detected in P fermentation. 1,2-Cyclopentanedione,3-methyl; 2-cyclopenten-1-one, 3-ethyl-2-hydroxy- and 2(5H)-furanone were detected in MC fermentation. 2,6-dimethylpyrazine and 1H-indole, 3-methyl- were detected in MD fermentations. Phenol, 4-ethyl-; 1H-pyrrole, 1-butyl- and 1-hexanone, 1-(2-thienyl)- were

Table 2
Organic acids detected during coffee fermentation.

Fermented	Time (h)	Organic acids (g/kg)				
		Acetic	Citric	Lactic	Malic	Succinic
Control	0	n.d	0.89 ± 0.00^{e}	n.d	2.51 ± 0.13^{d}	0.06 ± 0.0^{b}
M	0	n.d	1.60 ± 0.01^{b}	n.d	3.62 ± 0.24^{c}	0.05 ± 0.00^{c}
P	0	n.d	0.88 ± 0.01^{e}	n.d	3.39 ± 0.13^{c}	0.05 ± 0.00^{c}
MD	0	n.d	1.30 ± 0.05^{c}	n.d	3.45 ± 0.19^{c}	0.10 ± 0.00^{a}
PD	0	n.d	1.28 ± 0.00^{c}	n.d	3.48 ± 0.19^{c}	0.05 ± 0.00^{c}
MP	0	n.d	1.11 ± 0.01^{d}	n.d	2.38 ± 0.16^{d}	0.05 ± 0.00^{c}
MC	0	n.d	1.79 ± 0.01^{a}	n.d	3.82 ± 0.26^{c}	0.05 ± 0.00^{c}
PC	0	n.d	2.03 ± 0.00^{a}	n.d	5.05 ± 0.30^{b}	0.06 ± 0.00^{b}
Control	36	0.08 ± 0.01^{b}	0.97 ± 0.00^{d}	0.17 ± 0.00^{a}	2.33 ± 0.14^{b}	0.07 ± 0.00^{b}
M	36	0.16 ± 0.00^{a}	1.10 ± 0.00^{c}	0.29 ± 0.00^{a}	3.19 ± 0.16^{a}	0.07 ± 0.00^{b}
P	36	n.d	1.42 ± 0.00^{b}	0.28 ± 0.00^{a}	2.39 ± 0.21^{b}	0.07 ± 0.00^{b}
MD	36	n.d	1.77 ± 0.00^{a}	0.31 ± 0.00^{a}	2.52 ± 0.26^{b}	0.08 ± 0.00^{a}
PD	36	0.16 ± 0.00^{a}	1.10 ± 0.00^{c}	0.31 ± 0.00^{a}	2.53 ± 0.16^{b}	0.06 ± 0.00^{c}
MP	36	n.d	1.10 ± 0.00^{c}	0.27 ± 0.00^{a}	2.20 ± 0.15^{b}	0.05 ± 0.00^{d}
MC	36	n.d	0.91 ± 0.01^{d}	0.27 ± 0.00^{a}	0.93 ± 0.13^{d}	0.06 ± 0.0^{c}
PC	36	0.17 ± 0.00^{a}	1.01 ± 0.00^{d}	0.41 ± 0.00^{a}	1.85 ± 0.15^{c}	0.07 ± 0.0^{b}
Control	72	0.18 ± 0.00^{a}	0.78 ± 0.02^{c}	1.05 ± 0.00^{b}	0.81 ± 0.11^{b}	0.07 ± 0.00^{d}
M	72	0.19 ± 0.00^{a}	1.01 ± 0.00^{b}	1.11 ± 0.00^{b}	1.41 ± 0.15^{a}	0.09 ± 0.00^{c}
P	72	0.25 ± 0.00^{a}	0.94 ± 0.00^{b}	1.11 ± 0.00^{b}	1.58 ± 0.14^{a}	0.12 ± 0.00^{a}
MD	72	0.17 ± 0.00^{a}	0.55 ± 0,00^{c}	1.35 ± 0.05^{a}	0.59 ± 0.08^{b}	0.08 ± 0.00^{c}
PD	72	n.d	0.90 ± 0.00^{b}	0.87 ± 0.00^{c}	0.34 ± 0.13^{c}	0.07 ± 0.00^{d}
MP	72	0.20 ± 0.00^{a}	1.41 ± 0.00^{a}	1.43 ± 0.00^{a}	0.88 ± 0.11^{b}	0.12 ± 0.00^{a}
MC	72	0.17 ± 0.00^{a}	0.94 ± 0.00^{b}	0.68 ± 0.00^{c}	0.67 ± 0.10^{b}	0.10 ± 0.00^{b}
PC	72	0.18 ± 0.00^{a}	1.24 ± 0.00^{a}	0.50 ± 0.00^{d}	0.76 ± 0.11^{b}	0.10 ± 0.00^{b}

n.d: not detected.
Control: Spontaneous fermentation; M: *Leuconostoc mesenteroides*; P: *Lactiplantibacillus plantarum*; MP: *Leuconostoc mesenteroides* + *Lactiplantibacillus plantarum*; MD: *Leuconostoc mesenteroides* +*Torulaspora delbrueckii*; MC: *Leuconostoc mesenteroides* + *Saccharomyces cerevisiae*; PD: *Lactiplantibacillus plantarum* + *Torulaspora delbrueckii*; PC: *Lactiplantibacillus plantarum* +*Saccharomyces cerevisiae*.
Mean values followed by the same letter in a column do not differ significantly by the Scott-Knott test ($p > 0.05$).

detected in PD fermentation. 4-Methylpyrrolo[1,2-a]pyrazine was detected in MP fermentation.

2-Cyclopenten-1-one, 3-ethyl-2-hydroxy-4-methyl (roasted coffee), and benzothiazole (green coffee) were detected in fermentations with lactic acid bacteria (M and P) (Supplementary material: Table S2).

3.6. Analysis of sensory characteristics

The attributes of fragrance/aroma, flavor, aftertaste, salinity/acidity, bitterness/sweetness, and mouthfeel were evaluated (Supplementary Material Table S3). Coffees M, MD, MP, and MC, were classified as fine (80.0–89.0), while control, P, PD, and PC were classified as premium (70.0–79.0). The inoculation of *L. mesenteroides* single and co-cultivation with *S. cerevisiae* and *L. plantarum* achieved the best sensory scores (M: 81, MC: 81.33, and MP: 80.33 pts).

Caramel, fruity, and spices were the sensory characteristics detected in these coffees (Fig. 3). Chocolate, caramel, almond, nutty, and spices were described as P coffee. Chocolate, dark Chocolate, nutty, fruity, and spices characterize PD coffee. Dark Chocolate, caramel, nutty, and spices characterize PC coffee. M (7.75 pts) and MC (7.83 pts) stood out in the fragrance attribute. P, PD, and PC had similar sensory scores (79 pts) but different sensory profiles. Salinity/acidity showed no significant difference between the fermented coffees. The control obtained the lowest score for all attributes. Furthermore, control and P coffee showed no significant difference in bitterness/sweetness and mouthfeel.

4. Discussion

Coffee fruits fermented by SIAF favored the development of *L. mesenteroides* CCMA 1105 and *L. plantarum* CCMA 1067. Species belonging to the LAB group can develop in an environment with low oxygen concentrations and ferment available carbohydrates without oxygen. Therefore, some metabolites, such as lactic and acetic acids, contribute to coffee's quality and sensory profile, providing acidity, a desirable attribute by coffee connoisseurs and consumers (Pereira et al., 2020). Furthermore, the additional growth of these strains may be associated with adaptability to the medium and stress factors such as competition with other microorganisms, pH variation, and carbohydrate availability (Lahtinen et al., 2012; Pereira et al., 2020). Moreover, *L. mesenteroides* is one of the epiphytic microbiota of coffee that seems to dominate the entire coffee fermentative process from wet processing (Cruz-O'Byrne et al., 2021; Elhalis et al., 2020; Ribeiro et al., 2018).

Yeasts play an important role in coffee fermentation, impacting the flavor and aroma profile (Elhalis et al., 2020). LAB and yeast are known to co-exist and cooperate in various fermented foods and beverages such as coffee, cocoa, kefir, kombucha, natural yeast, and wine (Andreson et al., 2022; Chen et al., 2021; Minnaar et al., 2019; Viesser et al., 2021; Yang et al., 2021). The fact that one group contributes to the growth of the other encourages us to use co-cultivation between LAB and yeasts as a strategy to improve the microbiological and sensory quality of coffee. Yeasts contribute to the development of LAB through cellular autolysis; they provide essential amino acids and vitamins for their development. On the other hand, organic acids (such as lactic acid) produced by the LAB decrease the pH, contributing to the growth of yeasts, which reached (in this study) their maximum population after 72 h of fermentation. These extrinsic factors of fermented foods provide an unfavorable environment for the growth of pathogenic bacteria and filamentous fungi, providing food safety (Chikindas et al., 2018).

The impact of co-inoculation of LAB and yeasts on the sensory profile is probably due to the symbiotic interaction relationship between them and the entire microbial community (Adesulu-Dahunsi et al., 2020; Vale et al., 2019). In the fermentative pathways, ethanol and CO_2 are produced, besides several other by-products, including cell biomass, glycerol, organic acids, and volatile compounds (Faria-Oliveira et al., 2015).

Yeasts are recognized producers of succinic acid, and their metabolism contributes to the culture growth, which can be supported by the high microbial population of the MC fermentation (Fig. 1). In *S. cerevisiae,* four main pathways can form this acid: the glyoxylate cycle by isocitrate oxidation, the reductive pathway of the TCA cycle, the oxidative pathway of the TCA cycle, and from amino acid catabolism (Radler, 1993).

The coffee quality also is influenced by acid composition, which is generally recognized as a flavor precursor for quality descriptors of coffee (Borém et al., 2016). Malic, succinic, and citric acids are part of the fruit composition and contribute to the beverage's acidity (Elhalis et al., 2020; Evangelista et al., 2014). Lactic, acetic, and succinic acid increase during fermentation. Lactic acid bacteria are recognized for producing lactic and acetic acid (Avallone et al., 2002). Species

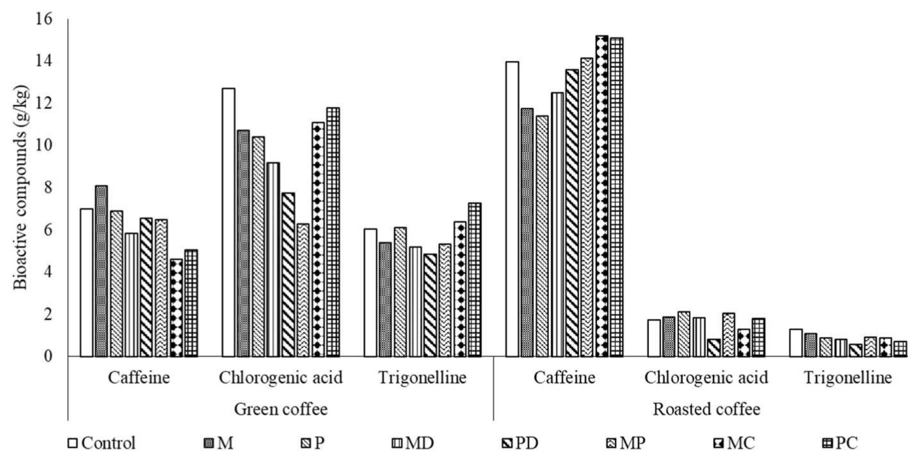

Fig. 2. Caffeine, chlorogenic acid, and trigonelline contents in (A) green coffee and (B) roasted coffee.

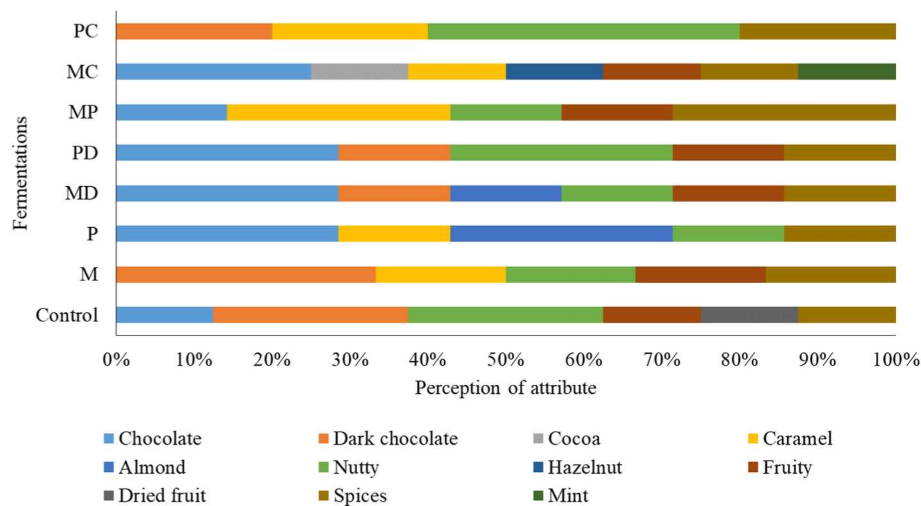

Fig. 3. Sensory descriptors perceived by Q-grader.

belonging to the genus *Leuconostoc* can perform malolactic fermentation, in which malic acid is converted into lactic acid by decarboxylation with the participation of the malolactic enzyme, increasing bacterial survival under environmental stress conditions, such as low pH (Konings et al., 1997). During coffee fermentation, all coffees presented a reduction in malic acid contents. Most of the fermented samples showed an increase in acetic acid concentration. The P and MP fermentation had the highest acetic acid production since this acid can be produced by LAB through citrate metabolism (Gemelas et al., 2014).

Non-volatile compounds are essential for the characterization of the beverage's sensory profile. Bioactive compounds, such as chlorogenic acids, are coffee's most relevant phenolic compounds, contributing to astringency, pigmentation, potential antioxidant activity, and radical scavenging properties (Duarte et al., 2010). Besides, chlorogenic acids are precursors of compounds responsible for bitterness, and during roasting, part of this compost is degraded (Duarte et al., 2010; Frank et al., 2006; Martínez et al., 2017).

Trigonelline is a pyridine alkaloid that contributes to the beverage's flavor, and the levels of this compound are greatly affected by the roasting of the grains (Selmar et al., 2015). During roasting, trigonelline degradation gives rise to pyrroles and pyridines (Flament and Bessière-Thomas, 2001).

Caffeine is a thermostable compound that contributes to the bitterness of coffee, especially in Conilon coffee, where its levels are higher than Arabica coffee (Selmar et al., 2015). The increase in caffeine concentration in fermentations inoculated with *S. cerevisiae* was also obtained by Bressani et al. (2021). However, the mechanism of production of bioactive compound by yeasts is not yet elucidated.

Volatile compounds influence the aromatic profile of coffee, directly impacting the composition of the flavor and fragrance of the beverage. Most of these compounds are derived from precursors formatted in green coffee. During roasting, thermally catalyzed reactions occur, giving rise to these compounds, which can also be originated from chemical and biochemical reactions during processing (Buffo and Cardelli-Freire, 2004).

In green coffee, volatile compounds can be formed from the metabolism of microorganisms or chemical reactions during coffee processing. For example, alcohols class, such as decanol (P fermentation), 1-dodecanol, 1-hexadecanol, octadecanoic (P and MD fermentation), and benzyl alcohol were identified in green coffee, coming primarily from the reduction of aldehydes and methyl ketones corresponding, from glucose degradation or amino acid catabolism by yeasts and bacteria during coffee fermentation (Arora et al., 1995; Cheng et al., 2010). The volatile compound detected may be derived from the metabolism of fatty acids by yeasts and bacteria present during the coffee fermentation. The different volatile compounds, such as hexanoic, heptanoic, octanoic, nonanoic, and decanoic (green and roasted coffee), can contribute to the sensory profile with nutty and fruity notes and acid odor (Swiegers et al., 2005).

Esters are of great relevance in the composition of coffee and are

mainly responsible for the fruity and floral aroma of the beverage. They can be formed by LAB through the esterification of short-chain free fatty acids with an alcohol molecule and by the metabolism of lipids and acetyl-CoA by yeasts (Nogueira et al., 2005; Swiegers et al., 2005). Moreover, some esters were detected only in the inoculated treatments, such as benzene acetic acid, ethyl ester; benzoic acid, 2-hydroxy, ethyl ester-; 2-ethyl hexyl salicylate, and isopropyl myristate inferring that starter cultures produced them. These esters can correlate with trained tasters' sweet and fruity notes. 9,12-Octadecadienoic acid, methyl ester, octadecyl trifluoroacetate, and benzyl benzoate were detected in MP fermentation. Benzyl benzoate may have influenced fruity notes detected in this coffee beverage.

Relevant volatile compounds were formed during roasting, mainly from the Maillard reaction, contributing to the complex composition of coffee. Pyrazines (2,6-dimethylpyrazine, 2-ethyl-3-methyl-pyrazine, and 2-ethyl-2,5-dimethyl-pyrazine) can be correlated with the sweet, hazelnut, nutty, caramel, roasted, and chocolate notes detected in the different coffees. The formation of pyrazines involves condensing carbonyl and amine groups, producing a Schiff base (Caporaso et al., 2018).

Heterocyclic compounds such as pyrroles and furans classes found in roasted coffee are formed during roasting from non-volatile precursors (such as polysaccharides, lipids, proteins, and free amino acids) in green coffee (Lee and Shibamoto, 2002). 1H-pyrrole-2-carboxaldehyde-1-methyl; 1*H*-pyrrole, 1-butyl (PD fermentation); indole and 1H-indole, 3-methyl (MD fermentation) contributed characteristic notes of sweet, green, woody, and floral in the sensory profile this beverage. In the furan class, the furfural can contribute to a sweet, caramel odor that arises from the rearrangement of the compounds of Armadori. The formation of 5-hydroxymethylfurfural probably results from the thermal degradation of glucose or other hexoses and contributes to the sweet notes of coffee (control, M, P, MC, and PC) (da Silva et al., 2008).

The formation of the coffee's aroma is a complex process; however, volatile compounds play a significant role in the sensory characteristics of the final product. The different functional classes detected could correlate with the different sensory notes reported by the tasters during cup testing, giving rise to beverages with specific and unique characteristics. Consumers' search for coffees with differentiated quality is a growing reality, boosting the specialty coffee market (Martinez et al., 2021). Thus, sensory analysis has become a valuable tool for determining the characteristics related to coffee quality.

Leuconostoc mesenteroides impacted both the production of volatile compounds and the sensory quality of the beverage, being caramel, fruity, and spices the sensory notes detected. MP, M, and MC fermentations obtained the best sensory notes. Fruity notes may be associated with esters, acids, ketones, and aldehydes composition. The ability of the starter culture to produce metabolites that positively influence the coffee quality reinforces the importance of starter cultures in developing the sensory profile of the beverage, contributing to the improvement of the quality of the coffee.

5. Conclusions

Yeasts and lactic acid bacteria, inoculated single and co-culture, were essential to improve beverage quality and obtain coffees with differentiated sensory profiles. The strains used benefited from the bioreactors' conditions (self-induced anaerobiosis), resulting in the coffee beverage with differentiated sensory characteristics. *L. mesenteroides* CCMA 1105 inoculated single and co-culture with *S. cerevisiae* CCMA 0543 produced superior quality coffees (fine beverages). Therefore, the wet fermentation of coffee with inoculation of LAB and yeasts by the SIAF methodology becomes a viable alternative for obtaining superior-quality conilon coffee.

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Declaration of competing interest

The authors do not have any conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fm.2022.104161.

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