Food Science and Engineering
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UNIVERSAL WISER PUBLISHER

Research Article

The Value of Indigenous *Saccharomyces cerevisiae* Strains as Useful Enzymes Producers: A Systematic Review

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Received: 20 October 2023; **Revised:** 20 March 2024; **Accepted:** 10 April 2024

Abstract: This systematic review has focused on the selection and characterization of indigenous *Saccharomyces cerevisiae* strains for enzymes' production obtained from the fermentation process. The primary studies assessed have demonstrated that indigenous *S. cerevisiae* strains produce a wide range of enzymes during fermentation. These strains have shown different characteristics and were isolated from various locations, including those belonging to the main components of the wine production chain. The research methodology applied to find primary studies about the optimal conditions for enzyme production was effective and identified a wide range of enzyme classes. Cultivation media amended with natural or synthetic inducer substrates were found to be suitable carbon and/or nitrogen sources for producing enzymes of interest in plate-based screening. In submerged fermentation studies, the use of agro-industrial residues has been identified as a relevant carbon source for microbe development and metabolism. For the indigenous *S. cerevisiae* strains, the majority of the enzymes found belong to the glucosidases and hydrolases classes. Due to the activity of these enzymes, yeasts have been traditionally used in classic biotechnological applications, particularly in the process of alcoholic fermentations. Those enzymes are responsible for producing metabolites (such as aromatic compounds) that contribute to the desirable aroma and/or taste during the fermentation of wine, as well as other fermented or distilled beverages. The methods used for enzyme screening were of quantitative and/or qualitative nature and were carried out under acidic pH conditions (3.5-6.5) and at temperatures of 28-35 °C. The results of this systematic review have shown that the enzymes from indigenous *S. cerevisiae* are highly relevant in various biotechnological applications, particularly in the food industry. Conclusions and future perspectives of our findings were discussed in terms of potential developments of novel application methods of the indigenous yeasts and their enzymes in agriculture and industry.

Keywords: fermentation, enzyme, yeast, beverage production

1. Introduction

The phenotypic and metabolic diversity of microorganisms has long been investigated as sources of activities

DOI: https://doi.org/10.37256/fse.5120243808

and molecules that can be extracted and have been applied in an array of industrial needs. For many centuries, the *Saccharomyces cerevisiae* yeast was exclusively used in the production of fermented foods and beverages; nowadays, it has also shown an industrial and commercially significant role in the processes of synthesis of daily use products [1]. The wide biotechnological applications of *S. cerevisiae* are a result of its suitable properties that favor fermentation processes. These interesting properties include resistance to adverse pH conditions, osmotic stress and temperature, low pathogenic activity, and the ability to secrete proteins into the extracellular fluid [2-3]. In this context, indigenous yeast strains represent an interesting industrial alternative for the development of new products [4], as corresponding studies tend to seek and select indigenous strains that adequately produce stable enzymes to be applied in diverse industrial sectors [5-9].

Among the various applications of indigenous *S. cerevisiae* strains, their ability to produce and secrete enzymes for the extracellular fluid and its fermentation aspects stand out, which have been described in detail in the scientific literature [10-11]. According to a set of primary studies, those strains produce pectinases and *β*-glucosidases [9, 12-14], invertase [15], protease, amylase and xylanase activities, as well as other enzymes involved in the degradation of cellulose and hemicellulose [10, 16]. These publications also describe relevant aspects involved in the processes of enzyme production by indigenous *S. cerevisiae* strains. The importance of bioprospecting for those indigenous strains lies in that they are most likely adapted to their niche, thus increasing the potential for appropriate application in contexts that are similar to those original yeast niches.

The study of new isolates of *S. cerevisiae* and their enzymatic production, mainly extracellular enzymes, allowed advancement and improvements in fermentation processes, as well as in biotechnological applications of their products [17-20]. Due to the importance of enzymes in microbial metabolic processes, and the prominence of *S. cerevisiae* as high-performance yeast for fermentative processes, the present systematic review of literature (SRL) study was carried out seeking to understand the current state-of-the-art of knowledge related to the production of enzymes by indigenous yeast strains [21-22]. In this context, the literature included in this study reports the selection, characterization and application of indigenous strains of *S. cerevisiae* that were isolated from different environments and substrates; the results are suggesting that the exploration of natural microbial biodiversity can lead to the discovery of microorganisms capable of a diversified enzyme production, suitable for an array of applications [5, 23-24]. Therefore, the quantitative and qualitative data collected during our research have provided the basis for an assessment on the potential of indigenous *S. cerevisiae* strains for the production of intra- and extracellular enzymes of broad biotechnological interests.

2. Assessment of the primary literature (search/selection methods)

The systematic review followed the PRISMA-P guidelines (Preferred Reporting Items for Systematic Reviews and Meta-analysis) [25]. The study was performed in three stages according to the established protocol (Table 1), which included the planning, execution, and summarization steps [26]. The quantitative data collection during the study was based on the main question: Are there studies related to the production of enzymes by indigenous *Saccharomyces cerevisiae* strains? To answer this question, our research followed the scanning of documents in Science Direct, NCBI/PUBMED and Web of Science databases. The terms used for the systematic search were "*Saccharomyces cerevisiae*", "Enzymatic production", and "Indigenous yeast". These terms were used in specific strings, according to the syntax of each database consulted; in addition, inclusion and exclusion criteria were applied in both selection stages of the retrieved literature.

Inclusion and exclusion criteria-published studies with relevant objectives, data and results for indigenous yeast enzymes production were searched through the strings and assessed based only upon the titles and abstracts available in the databases. The related studies identified in this phase underwent a specific first-stage selection process, considering the following inclusion criteria: (a) the study had to be relevant to the theme of indigenous yeasts strains used for enzymes production, (b) it has to be published until 2023, (c) to be available in English language, and (d) to be a research article reporting a study based on primary empirical data. The exclusion criteria were: (a) studies not fully available (and unfit for downloading) in the databases surveyed, (b) studies without hypotheses proven by the experiments, (c) publications not in articles format, i.e., simple or expanded abstracts, dissertations, theses, and book

chapters, and (d) articles published in languages other than English.

Table 1. Systematic review protocol for the study of fermentation conditions and enzyme production by indigenous *S. cerevisiae* strains

General information	
Title	The value of indigenous *Saccharomyces cerevisiae* strains as useful enzymes producers: a systematic review.
Researchers	Bárbara Teodora Andrade Koelher; Lorena Brito Pimentel Rodrigues dos Santos; Valter Cruz Magalhães; Ana Paula Trovatti Uetanabaro; Leandro Lopes Loguercio; Antônio Fábio Figueiredo; Andréa Miura da Costa.
Goal	Identify studies in the scientific literature that investigate, demonstrate and evaluate the performance of wild-type (indigenous) yeast strains in the production of enzymes of biotechnological and industrial interest.
Specific objectives	Find the sources for isolation of indigenous strains; Summarize the best methodologies applied for the fermentation of wild-type *S. cerevisiae* strains; Indicate the best cultivation conditions used for the production of intra and/or extracellular enzymes by indigenous *S. cerevisiae* strains; Highlight the information related to practical applications of indigenous *S. cerevisiae* strains and/or their respective enzymes.
Research questions	
Main Question	Are there studies on fermentation and enzyme production by wild-type (indigenous) *Saccharomyces cerevisiae* yeast strains?
Outcomes	Wild-type *S. cerevisiae* yeasts grow and produce enzymes of biotechnological and industrial interest.
Specific questions	What are the isolation sites for indigenous *S. cerevisiae* strains? What are the best methods for detection and production of intra and/or extracellular enzymes by yeasts? What are the best cultivation conditions for the fermentation and production of intra and/or extracellular enzymes by yeasts? In which bioprocesses are yeast strains and their enzymes applied?
Type of studies	Primary empirical studies in the form of scientific articles that have been peer-reviewed
Identification of studies	
Keywords	*Saccharomyces cerevisiae*; enzymatic production; indigenous yeast
Selection criteria for search sources	• Database with peer-reviewed publications • Available on the internet
List of searching sources	• Science Direct • NCBI/Pubmed • Web of Science
Search strategy	Direct search in the databases, using appropriate key-words and strings assembled with adequate sintax per database.
Selection and evaluation of studies	
Inclusion and exclusion criteria for studies	Inclusion: • Primary studies in indexed databases. • Published up to 2023. • The studies must be relevant to the topic of fermentation and production of intra and extracellular enzymes by wild *S. cerevisiae* yeasts. Exclusion: • Articles that are not fully available (and for download) in the researched databases. • Papers that do not detail practical experiments performed to test their hypotheses. • Review articles, theses and dissertations. • Studies that are not in English. • Articles that do not align with the research topic.
Strategy for initial selection of studies	• Searches with the keywords in the defined sources. • Reading titles and abstracts, • Analysis of inclusion and exclusion criteria, • Full reading of pre-selected articles. • Extraction of data related to look up and table construction

Table 1. (cont.)

Selection and evaluation of studies	
Strategy for final selection of studies	• Having all the inclusion criteria; • Not having any of the exclusion criteria; • Reading the main text.
Assessment of the quality of studies	Failure/inconsistency between methodology and results/conclusions
Data synthesis and presentation of results	
Data extraction strategy	A. Title of article B. Journal of publication C. Main objective of the study D. Strain isolation site E. Strain identification code F. Methodology G. Substrate H. Cultivation conditions (Temperature, pH and cultivation time) I. Inoculum concentration G. Enzymes evaluated K. Enzyme activity
Data summarization strategy	Tables and graphs
Publishing strategy	Scientific journal of relevant impact in the area

Data extraction-on the pre-selected papers based on titles and abstracts (first selection stage above), the assessments of a second selection stage were performed now in the full articles' texts. For the data collection, the corresponding spreadsheets included the following information: (i) sites/locations of *S. cerevisiae* strains isolation; (ii) identification of the strains used as experimental model; (iii) strategy/methodological approach for enzymes production; (iv) substrate and/or culture medium; (v) cultivation conditions-pH, temperature and cultivation time; (vi) inoculum concentration; (vii) enzymes evaluated; and (viii) enzymatic activity. The data values were extracted from graphs, tables, and/or figures present in the articles., and data summaries and analytical productions were performed through images, graphs, and tables.

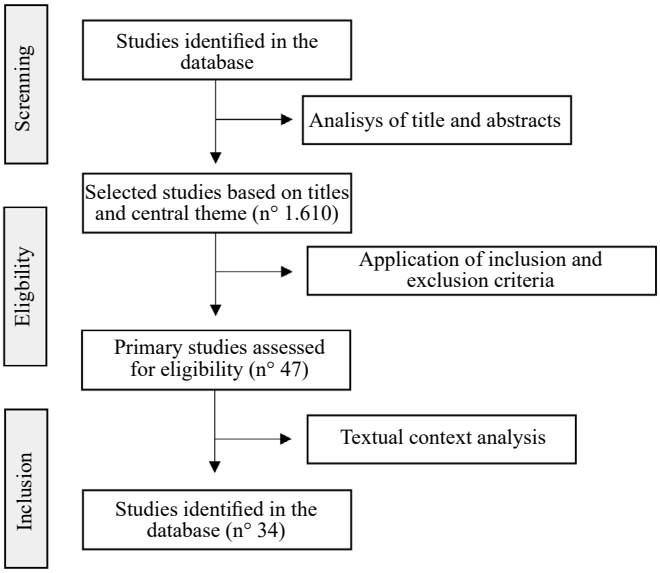

Figure 1. Flow diagram for the research strategy, study selection, and data management procedures on enzymes production by indigenous *Saccharomyces cerevisiae* strains

The overall sequence of steps in this research is shown in the flowchart of Figure 1: the search for papers was performed from July to December 2023 using the predetermined keywords and strings described above, which could be present anywhere in the article's text. Under these conditions, the total amount of publications retrieved was 2,503. Within this number of papers, 1,610 articles specifically related to this research were initially selected by reading titles and abstracts and applying the inclusion and exclusion criteria. Out of these selected studies, 1,566 were excluded due to being abstracts (expanded or simple), book chapters, review articles, dissertations, and theses, as well as those in languages other than English (exclusion criteria). Articles published in English but presenting unclear descriptions of the methodological steps were also excluded. After these selection and exclusion procedures were described, the application of the research protocol led to the selection of 47 primary studies; from these, nine studies were further excluded as they did not meet the criteria of enzyme production by indigenous strains. Hence, a final sample of 35 articles was included in the local database used for this systematic review, with the qualitative and quantitative data being collected and processed based on full articles' texts.

3. Results and discussion

The preliminary evaluation of the final database included a temporal analysis and geographic distribution of publications according to the countries of research. For the temporal aspect, publications on this theme have started to appear in the year 2002, keeping a regular appearance in the literature since then; the period between 2011 and 2016 covered 50% of the finally selected articles (17/34), although the highest frequency of articles related to the research topic was observed specifically for the 2020 year (5/34) (Figure 2a). These results suggest that it was only in the turn of the current century that research on indigenous enzyme-producing *S. cerevisiae* strains started to appear, thus concentrating the respective data, information and knowledge on the last 21 years. This is likely due to an increasing interest from industry (highlighting that of wine production [1-2, 9] in developing novel yeast-based biological products, although the relatively small amount of retrieved/selected papers specifically related to enzyme production from indigenous yeasts point to an open avenue for future research in this theme. Regarding the geographic distribution of those publications, 13 countries were noted, from Europe, Africa, South America, Asia and Oceania. Data indicated that Argentina was the country with the highest amount (20.6%) of publications in the assessed period, followed by China (17.6%) and Italy (14.7%). A significant number of studies was identified for the European continent, with more than one-third of the total articles (35.3%) included in the final database, corresponding to research institutions located in Spain, Greece, Turkey, Italy, and the Czech Republic (Figure 2b). South America represented by Argentina and Brazil has also an important contribution to the field, with 29.4 % of the selected articles. It is interesting to highlight that the countries showing such a higher contribution in this research field of enzyme-producing indigenous yeasts are those with a prominent industry of fermented alcoholic beverages (Table 2).

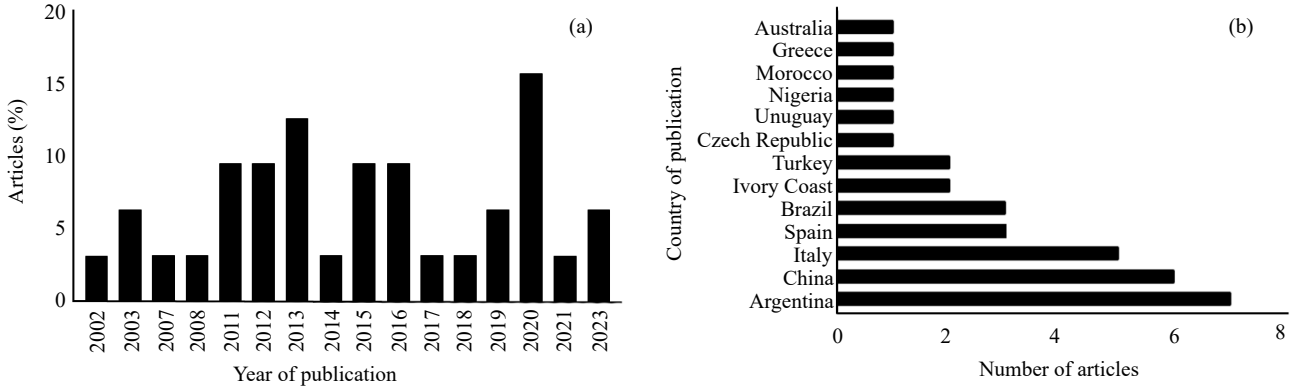

Figure 2. Temporal and geographic distribution of selected articles related to enzymes production by indigenous *S. cerevisiae*. (a) Percentage analysis of a total of 34 selected articles published over the years. (b) Geographic distribution of these publications

Table 2. Conditions for growth and enzyme production by indigenous *S. cerevisiae* yeasts. All articles were selected according to pre-established criteria, being part of the final database of the systematic review

Isolation Location	Strain ID Code	Methodology	Substrate	Cultivation Conditions	Inoculum	Evaluated Enzymes	Enzymatic Activity	Reference
Palm Wines	Sc ADP10-4 Sc ADR2-1 Sc ALR8-5 Sc TR1-6	API-ZYM Testing System	ND	5 hours 37 °C	MCF-arland Scale: Turbidity 5-6	Alkaline Phosphatase, Acid Phosphatase, Naphthol-AS-BI Phosphohydrolase, Cystine Arylamidase, *α*-glucosidase, *β*-glucosidase, *α*-chymotrypsin, Esterase Lipase, Leucine Arylamidase, Valine Arylamidase, Lipase, Esterase	Alkaline phosphatase, acid phosphatase, naphtol-AS-BI-phosphohydrolase, esterase lipase; leucine arylamidase, valine arylamidase, cystine arylamidase, *α*-glucosidase.	[19]
Winery	Sc B-17	Sub-merged Fermentation	Medium broth (containing per liter): 50 mmol of citric citrate buffer, 2 g of yeast extract, 20 g of peptone, 20 g of glucose, 1 g of K2HPO4)	5 days 12 °C pH 3.5	10^5 UFC/mL	Xylanase, *β*-glucosidase, cellulase	Xylanase: 0.062 U/mL. *β*-glucosidase: 0.010 U/mL.	[27]
Olives	Sc UCDFST 09-448	Plate Screening:	YM agar with 1.5% pectin	24 hours 30 °C	ND	Polygalacturonase	Presence of a degradation halo for polygalacturonase.	[14]
Dried grapes and wine	Sc 24 Sc 77	Submerged Fermentation	YDP medium	ND	ND	β-glucosidase, esterase, protease, laccase	Sc 24 *β*-glucosidase: 24 nmole h^{-1} g^{-1} 1.3 nmole h^{-1} g^{-1} Esterase: 24 nmole h^{-1} g^{-1} Protease: 1,074 nmole h^{-1} g^{-1}. Sc 77 *β*-glucosidase: 0.4 nmole h^{-1} g^{-1} 0.7 nmole h^{-1} g^{-1} Esterase: 0.4 nmole h^{-1} g^{-1} Protease: 538.2 nmole h^{-1} g^{-1}.	[28]
Cocoa beans	20 unencoded strains of Sc	Plate Screening	YDP agar	3 days 25 °C	10^5 UFC/mL	*β*-glucosidase, pectinase, xylanase, laccase, cellulase	Presence of a degradation halo for *β*-glucosidase, laccase and xylanase.	[29]
ND	Sc 121 Sc 131 Sc 132 Sc 135 Sc 136 Sc F13	Plate Screening	YDP agar	3 days 25 °C pH 5.5	ND	*β*-glucosidase, esterase	Presence of a degradation halo for *β*-glucosidase and esterase.	[30]
Grape pomace	Sc gm2 Sc gm3	Plate Screening	YDP agar, YNB agar and Nutrient agar with: xylan, polygalacturonic acid starch, carboxymethyl-cellulose, skim milk, tributyrin	6 days 30 °C pH 6.0, 6.5, 7.0, 7.5	10^4 cells/mL	Xylanase, lipase, cellulase, pectinase, protease, amylase	Presence of a degradation halo for lipase, amylase, pectinase, protease.	[13]
	Sc: Fp4, Fp7, Fp13, Fp35, Fp36, Fp38, Fp84, Fp85, Fp87, Fp88, Fp89, s1, s2, s3, s4, s5	Submerged Fermentation	YDP broth	7 days 30 °C 120 rpm pH 4.5, 6.0, 7.5	ND	*α*-amylase, pectinase	Presence of activities for *α*-amylase and pectinase.	

Table 2. (cont.)

Isolation Location	Strain ID Code	Methodology	Substrate	Cultivation Conditions	Inoculum	Evaluated Enzymes	Enzymatic Activity	Reference
Wine and fermentation tanks	Sc A11-9, Sc UBA-21, Sc MaE-1C, Sc Bo-1C	Plate Screening	YNB agar with amino acids 6.7 g/L, arbutine 5 g/L, 10 g/L ferric ammonium citrate solution	7-15 days 25 °C pH 4.0	ND	*β*-glucosidase	Presence of a degradation halo for *β*-glucosidase.	[6]
Grapes, musts from vineyards and wineries	Sc M00/12F, Sc M00/13F, Sc M00/14F, Sc M00/30F, Sc M00/35F, Sc M00/05G, Sc T00/15F, Sc T00/16F, Sc T00/17F.	Plate Screening	Esculin Glycerol Agar: esculin 1 g/L, ferric chloride 0.3 g/L, casein hydrolyzate 1 g/L, yeast extract 25 g/L, glycerol 8 ml/L	2-8 days 25 °C pH 6.0	ND	*β*-glucosidase	Presence of a degradation halo for *β*-glucosidase.	[31]
Environmental samples	Sc MK-157	Submerged Fermentation	MSM medium (mineral salt), 1% orange peel, yeast extract	2 days 30º C 150 rpm For immobilization, the yeasts were cultured in the presence of two pieces of pre-treated corn on the cob	Optical density (OD 600 nm) = 1.0	Pectinase	Three cycles with agitation (IU/mL): 11.40/13.92/10.04 Three cycles without agitation (IU/mL): 13.45/13.08/10.46.	[32]
ND	Sc AS11, Sc AS15, Sc BV12, Sc BV14.	Submerged Fermentation	YDP medium with arbutin and esculin	ND	ND	*β*-glucosidase	AS11: 70.04 nmol pNPha/mL, AS15: 50.43 nmol pNPha/mL, BV12: 25.26 nmol pNPha/mL, BV14: 47.87 nmol pNPha/mL.	[33]
Grape berries	Sc F27	Submerged Fermentation	YDP medium	3 days 28 °C 200 rpm	5% (v/v)	*β*-glucosidase	0.0155 U/mL	[5]
Grape berries	Sc F27 Sc F30	Submerged Fermentation	YDP medium	3 days 28 °C 200 rpm	5% (v/v)	*β*-glucosidase	F27: 0.190 U/mL F30: 0.0181 U/mL	[34]
Coffee fermentation	Sc UFLA CN727, Sc UFLA CN724.	Submerged Fermentation	Culture media with synthetic pectin and medium with coffee pulp	4 days 28 °C 120 rpm	104 UFC/mL	Pectate Lyase (PL), Pectin Methyl Esterase (PME)	CN727 (PL) Coffee Pulp: 2,637.00/ Pectin: 4,961.07 (PME) Coffee Pulp: 1,712.83/Pectin: 2,532.30 CN724 (PL) Coffee Pulp: 2,557.51/ Pectin: 5,256.12 (PME) Coffee Pulp: 2,600.20/Pectin: 2,443.14	[17]
	Sc UFLA-CN727, Sc UFLA-CN724.	Plate Screening	Polygalacturonase: MP5 media with polygalacturonic acid; Pectin lyase: MP7 media with pectin	ND	ND	Pectin lyase, polygalacturonase	Presence of a degradation halo for pectin lyase	

Table 2. (cont.)

Isolation Location	Strain ID Code	Methodology	Substrate	Cultivation Conditions	Inoculum	Evaluated Enzymes	Enzymatic Activity	Reference
Tannery effluent	Sc 122	Submerged Fermentation	YPS medium: 1% yeast, 2% peptone, 2% sucrose, 0.1% chromium	25 °C pH 5.5 150 rpm	100 µl ≅ 200 cells	Invertase, catalase	Catalase (with chromium): 13.75 SA/mL, (without chromium): 16.93 SA/mL. Invertase (with chromium): 230 SA/mL, (without chromium): 155 SA/mL.	[35]
Sorghum beer, palm oil	30 strains	API-ZYM Testing System	ND	1 day 30 °C	ND	Alkaline Phosphatase, Acid Phosphatase, Naphthol-AS-BI Phosphohydrolase, Cystine Arylamidase, *α*-glucosidase, *β*-glucosidase, ***α***-chymotrypsin, Esterase Lipase, Leucine Arylamidase, Valine Arylamidase, Lipase, Esterase	Esterase, esterase lipase, lipase, alkaline phosphatase, acid phosphatase, naphtol-AS-BI-phosphohydrolase, leucine arylamidase, valine arylamidase, cystine arylamidase, *α*-chymotrypsin, ***α***-glucosidase.	[36]
Artisan cheeses	3 unencoded strains of Sc	Plate Screening	Skim milk agar 10% (v/v); Calcium caseinate agar; Tween 80 agar 1% (w/v); Tributyrin agar 1% (w/v) with gum arabic 1%	3 days 30 °C pH 6.0	106 UFC/mL	Lipase, protease	Presence of a degradation halo for lipase.	[18]
Grape berries	Sc NM1 to NM3; Sc NP1 to NP13; Sc AR1 to AR20; Sc TV1 to TV21	Submerged Fermentation	Synthetic medium with cellobiose	7 days 25 °C-42 °C pH 3.5, 5.5	ND	*β*-glucosidase	ND	[37]
Brewer's malt waste	Sc LMQA-CSC1; Sc LMQA-CSC6; Sc LMQA-CSC48; Sc LMQA-CSC76	Plate Screening	YNB agar (6.7 g/L) with 10 g/L of substrate: xylan, citrus pectin, starch, carboxymethyl-cellulose	4 days 30 °C	106 UFC/mL	Amylase, pectinase, cellulase, xylanase	Presence of a degradation halo for xylanase and cellulase.	[10]
	Sc LMQA-CSC1; Sc LMQA-CSC6; Sc LMQA-CSC48; Sc LMQA-CSC76	Submerged Fermentation	YNB broth with 10 g /L (xylan and carboxymethyl-cellulose, citrus pectin, starch) and peptone 7 g/ L	5 days 30 °C	106 UFC/mL	Amylase, pectinase, cellulase, xylanase	Sc LMQACSC6 Xylanase: 37.71 U/L Sc LMQACSC48 Xylanase: 18.42 U/L; Cellulase: 2.74 U/L.	
Raw wheat	Sc JY5	Submerged Fermentation	Crushed raw wheat (3-4 pieces) with 40% (w/w) water	82 hours 26-40 °C	5% of cell culture	Amylase, protease	Amylase: 2.03 g/g·h Protease: 18.6 µg/g·min.	[16]

Table 2. (cont.)

Isolation Location	Strain ID Code	Methodology	Substrate	Cultivation Conditions	Inoculum	Evaluated Enzymes	Enzymatic Activity	Reference
Wyne	Sc Kalecik II; Sc T1; Sc Narince 3; Sc CA; Sc Kalecik I; Sc Narince 4; Sc J33; Sc CH; Sc Hasandede	API-ZYM Testing System	ND	ND	ND	Alkaline phosphatase, acid phosphatase, naphthol-AS-BI phosphohydrolase, cystine arylamidase, α-glucosidase, β-glucosidase, α-chymotrypsin, esterase lipase, leucine arylamidase, valine arylamidase, lipase, esterase	Presence of activities for esterase, esterase lipase, lipase leucine arylamidase, valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, acid phosphatase, β-glucosidase, naphthol-AS-BI-phosphohydrolase.	[38]
Apple cider	Sc 3	Plate Screening	5 g/L of arbutin, 1 g/L of yeast extract, 20 g/L of agar and 0.1 mL of iron chloride (1%)	15 days 28 °C	ND	β-glucosidase, β-xylosidase	Presence of a degradation halo for β-glucosidase.	[39]
Wine fermentation must	Sc BSc-562	Submerged Fermentation	Fresh must: the grape skins remained in contact with the juice during the alcoholic fermentation	35 days 20 °C pH 4.25	3.106 UFC/mL	Pectinase, protease, β-glucosidase	Pectinase: 862.8 U/mL Protease: 324.8 U/mL β-glucosidase: 43531.5 U/mL.	[40]
	Sc ERS1; Sc ERS2; Sc ERS3; Sc EYS4; Sc EYS5; Sc EYS6; Sc L2056	Submerged Fermentation	YP media (1% yeast extract; 2% peptone) supplemented with 0,05% or 2% glucose	2 hours 30 °C	2.107 cells/mL 1.106 cells/mL	Invertase	Presence of invertase activity. Values ND.	
Chicha	Sc ERS1; Sc ERS2; Sc ERS3; Sc EYS4; Sc EYS5; Sc EYS6; Sc L2056	Plate Screening	YPS agar with starch 5 g/L, peptone 5 g/L, yeast extract 5 g/L, MgSO4 · 7H2O 0.5 g/L, FeSO4 · 7H2O 0.01 g/L, NaCl 0.01 g/L YPS agar with 1% (w/v) yeast extract, 2% (w/v) peptone, 0.002% (w/v) histidine and 1% (w/v) starch, pH 5.2	3 days 30 °C pH 5.0, 5.2	OD 0.1: 5 µl	Xylanase Cellulase Amylase	Presence of a degradation halo for xylanase and cellulase.	[11]
ND	Sc IOC 18-2007	Submerged Fermentation	Wine must	18 days 8º-25°C	105-106 UFC/mL	Pectinase	6.69 U/mg-protein.	[27]
Winery	Sc BSc49; Sc BSc56; Sc BSc61	Plate Screening	Phospholipase: 1.7 g of NaCl, 0.1 g of CaCl2 and sterile egg yolk at 10% (v/v) Protease: 0.04 g MgSO4 · 7H2O, 0.5 g K2HPO4, 1 g NaCl, 0.2 g yeast extract, 4 g glucose and 0.5 g BSA	Phospholipase: 7-10 days 30 °C Protease: 7 days 37 °C	106 UFC/mL	Phospholipase, protease	Presence of a degradation halo for phospholipase and protease.	[23]
Grape berries and fermented musts	45 strains	Plate Screening	B-glucosidase: 0.67% yeast nitrogen base (YNB), 0.5% arbutin, 2% agar Glycosidase: 0.67% yeast nitrogen base, 0.2% rutin, 2% agar	3-5 days 26 °C	ND	β-glucosidase, Glycosidase	None of the strains showed enzymatic activities.	[7]

Table 2. (cont.)

Isolation Location	Strain ID Code	Methodology	Substrate	Cultivation Conditions	Inoculum	Evaluated Enzymes	Enzymatic Activity	Reference
Rice noodle	57 strains	API-ZYM Testing System	ND	4 hours 37 °C	MCF-arland Scale: Turbidity 6	Esterase, esterase lipase, protease, cystine arylamidase, trypsin, α-chymotrypsin, naphthol-AS-BI-phosphohydrolase, β-galactosidase, β-galactosidase, β-glucosidase, β-glucuronidase, α-glucosidase, n-acetyl-b-glucosaminidase, α-mannosidase, α-fucosidase	Presence of activity for esterase, esterase lipase, protease, β-glucuronidase, β-glucosidase, β-galactosidase, α-glucosidase, n-acetil-b-glucosaminidase, α-manosidase, α-fucosidase.	[41]
Fruit pulp	3 un-encoded strains of Sc	Plate Screening	Casein agar, Mineral pectin, medium agar, Arbutin agar	2-7 days 22-25 °C pH 5.0, 7.0	ND	Protease, pectinase, β-glucosidase	Presence of a degradation halo for β-glucosidase	[42]
Grape and wine must	Sc A102	Plate Screening	YNB agar 6.7 g, 5 g arbutin	3 days 25 °C pH 5.0	ND	β-glucosidase	Presence of a degradation halo for β-glucosidase	[43]
Cocoa fermenter	Uniden-tified strains	Plate Screening	Basal medium containing: pectin, cellulose, gelatin, casein, skin milk, starch, tributyrin	2-7 days 25-30 °C pH 5.0, 6.0, 7.0	ND	Pectate lyase, polygalacturonase, cellulase, amylase, protease, lipase	Presence of a degradation halo for lipase	[44]
Dried grains of white corn	77 strains	Plate Screening	Basal medium containing: amylopectin, starch, tween 80, tributyrin	2-5 days 25 °C pH 6.0, 6.8	106 UFC/mL	Amylase, esterase, lipase, phytase	2.6% of the strains were positive for amylase; 50.65% for lipase; 70.12% for esterase; 6.49% for phytase.	[45]
Grape	Sc 20 g	API-ZYM Testing System	ND	ND	ND	Esterase, esterase lipase, cystine arylamidase, α-chymotrypsin, naphthol-AS-BI-phosphohydrolase, β-glucosidase, α-glucosidase,α-mannosidase, α-fucosidase, valine arylamidase, alkaline phosphatase, leucine arylamidase, acid phosphatase	Presence of activity for esterase, esterase lipase, cystine arylamidase, naphthol-AS-BI-phosphohydrolase, β-glucosidase, α-glucosidase, α-mannosidase, valine arylamidase, alkaline phosphatase, leucine arylamidase, acid phosphatase.	[46]
Grape epidermis Winery	FM53; JCT3; Z-2-1; H-1-1; H-2-1	Plate Screening	Sulphite reductase: BIGGY agar medium. β-Glucosidase: 0.05% ammonium, 0.3% esculin, 0.2% NaCl, 0.05% MgSO4·7H2O, 0.01% KH2PO, 2% agar. Protease: 0.3% malt extract, 0.3% yeast extract, 0.5% peptone, 1% glucose, 0.5% NaCl, 2% agar, 10% skimmed milk	Sulphite reductase : 3 days 28 °C β-glucosi-dase: 1 day 28 °C Protease: 3 days 28 °C	ND	Sulphite reductase, β-glucosidase, protease	Presence of a degradation halo for: FM53: sulphite reductase, protease. JCT3: sulphite reductase, β-glucosidase, protease. Z-2-1: sulphite reductase. H-1-1: sulphite reductase, protease. H-2-1: sulphite reductase, β-glucosidase, protease.	[47]

*ND = Not Described; *ID = Identification; *Sc = *Saccharomyces cerevisiae*

3.1 *Yeast isolation sources*

To understand where the indigenous *S. cerevisiae* strains have been collected from, the selected articles were

assessed with regard to the types of sources for these yeast isolates. A total of 22 distinct sources for the *S. cerevisiae* yeast strains isolation were identified, which comprised a total of 396 strains/isolates under study. Among those sources, three frequency groups could be identified: the first group was comprised of a single source type, i.e., grape berries, which was the most frequent source found (nine appearances in the selected articles-23%). The second group was comprised of three sources, all related to wine production: wine itself, wine must and winery, with four appearances (10.2%) each. Finally, the third frequency group is composed of 18 sources (81.8%), each with a single appearance (2.5%) in the articles: wine fermentation tank, cocoa beans, grape pomace, apple cider, olives, environmental samples, coffee fermentation, sorghum beer, palm oil, tannery effluent, artisan cheese, brewer's malt residue, raw wheat, rice noodles, fruit pulp, chicha, corn grains, and palm tree sap. Among these 18 sources, we highlight the fruit pulp (tropical 'acerola' and 'mangaba' fruits), alcoholic beverages such as chicha, cider, and sorghum beer, olives and fermented sap from palm trees exploited in different localities of Côte d'Ivoire. These results clearly showed a wide variety of natural origins with the potential to serve as relevant yeast sources for fermentation and enzyme production in classic biotechnological industries, either involving fermented beverages or an array of other alternative applications (see corresponding enzymes and potential applications in Table 2 and Table 3). From this information, one can clearly realize a large number of different opportunities to research novel strains from yet unexplored sources, thus expanding the biotechnological potential of indigenous yeasts.

Progress has been made towards the feasibility of applying indigenous *S. cerevisiae* isolates as a suitable microorganism for fermentation processes [2, 48-49]. The studies considered in this review have explored these opportunities, emphasizing morphological, physiological and metabolic properties of these cultures in pure or mixed states (Table 2). As stated above, the most frequently found sources of *S. cerevisiae* isolates came from the wine production chain, being consistent with the number of articles published in the two continents with well-established winery industries. First, the European continent is a worldwide reference for grape planting and diverse categories of wine production. According to the *World Atlas of Wine*, traditional wine-producing countries are located in the Mediterranean region (Portugal, France, Italy, Germany, Greece, Hungary, and Austria) [50]. Historically, the wine-making field is divided into the '*old world*', a territory with more than 23 centuries of tradition and culture of wine production and consumption, established in Europe since the Roman Empire; and the '*new world*', emerging from the introduction of winemaking technologies by the Spanish-British colonizers in Americas (Argentina, USA, and Chile), South Africa, New Zealand, and Australia, between the 17th and 19th centuries [51-52]. In Brazil, the winery industry has developed after the European immigration fostered at the turn of the 20th century.

Studies on indigenous strains have revealed a great diversity of environments in which *S. cerevisiae* can be found. Although most studies report that Saccharomyces strains are mostly found in fermentation environments, mainly in wine production [53-57], recent reports have described the isolation of indigenous yeasts from an array of different niches, such as the natural environment and tannery effluent (Table 2). The search for Saccharomyces isolates in different sources allows the selection and evaluation of strains with unique physiological and biochemical phenotypes, which can improve a number of processes for applications in different industrial sectors [16, 35, 55, 58]. Grape berries appeared in this review as a frequent source of indigenous yeast, since the research on the characterization of grape berries' microbiota has revealed a diversity of yeast species, including some contaminants that may lead to wine deterioration [53-55]. Strains of *S. cerevisiae* are known to be found on the surface of berries because of their predominance in the fermentation stumps, which undergo the process of sugars' conversion into ethanol, CO_2, and other compounds, including volatiles that provide the unique organoleptic and sensory characteristics of wine [1, 9, 56].

3.2 *Enzyme production systems*

Microorganisms such as *S. cerevisiae* are responsible for the use and metabolization of organic matter distributed in the environment, as a form of energy supply for their own cell growth. They also comprise microbial lineages applied in industry for the production of proteins, chemical (mainly aromatic) compounds, biosurfactants, among other metabolites obtained through microbe-related bioprocesses [56, 59]. The study and understanding of the enzymatic profiles of wild/indigenous microorganisms enable us to explore and test their activities, selecting those enzyme-producing strains with potential to be applied in the production and/or improvement of alcoholic fermentation and their derived processes and products [19, 22, 32, 34]. The selected database includes 34 articles that report practical experiments aiming at gauging appropriate culturing conditions for enzyme production and activity. These experiments include the cultivation

method and/or fermentation category used in the enzymatic prospection of the strains. Results in Table 2 showed that plate screening (53.1%) was by far the most commonly used methodology in the studies, followed by submerged fermentation (SmF-46.8%) and the API ZYM® testing system (12.5%). Some studies have applied two methodologies (plate screening and SmF) in the same research. As discussed further below, Solid-State Fermentation (SSF) was not cited as a method for enzyme production, likely because the growth pattern of these microorganisms is different and they do not properly yield hyphae to grow into the residues substrates like it does filamentous fungi.

3.3 *Plate-based screening*

To identify possible enzymatic activities of isolated strains, some studies have applied the plate screening methodology in which the positive activity is measured by the presence of a clearer halo (substrate degradation region) around the fungal colony [39]. According to the technique, agar-based solid media with different carbon and nitrogen sources have been used, namely, Yeast Malt (YM), Yeast extract, Dextrose and Peptone (YDP), Malt extract, Yeast, Glucose, and Peptone (MYGP), Yeast Nitrogen Base (YNB), Yeast Peptone Starch (YPS), or Yeast Extract and Peptone (YEP). Depending on the investigated enzyme, these media were also added to synthetic or natural inductive substrates. This same activity-inducing protocol has been found for the other enzymes in Table 3. It was noticed that all 18 plate-based studies relied on one or more inducers that could stimulate yeast cellular metabolism. The results revealed that almost half of these studies (8) assessed the production of *β*-glucosidase, which showed positive activity in 71.4% of the tests, followed by amylase, protease and lipase enzymes, which showed halo degradation in more than 50% of the plate-based tests performed (Table 3). In a screening study with this method and using two substrates with different starch concentrations (1 and 5%), no statistical significance was observed in the amylase activity among the strains evaluated [11].

The surveyed strains appeared to have grown within a temperature range of 22 to 42 ℃ [37, 42] (Table 2). However, most of the articles assessed have considered ideal temperatures as being in the range between 25 and 30 ℃ (78%) [35, 30, 44, 47]. For the pH conditions, most of the enzymes studied were produced at a more acidic pH, ranging between 4.0 and 6.0 (Table 3), which is compatible with the optimal pH for the growth of *S. cerevisiae* strains. The incubation time for the plate-based tests varied greatly, ranging from 24 hours to 15 days for enzyme activity production and development, with an average of 3 to 7 days [16, 29, 39]. The production of various extracellular enzymes detected by the qualitative plate-based method was shown to be dependent on the availability of specific inducing compounds (Table 3).

The plate-based screening appeared to be the technique mostly applied in the production of enzymes, as it tends to offer a safe exploratory methodology for better detection of possible enzymatic activities from yet untested strains. This type of screening can be conceived as a primary qualitative and first-tier selective approach for the study of indigenous yeasts, as it provides quick and comparable results, thus paving the way for application of further methods to fully explore the biotechnological potential of selected microorganisms [11, 13, 60]. It should be noted that the degradation halos formed in plate-based screening techniques do not always reflect the actual enzymatic activity/production of the evaluated microorganisms. Several interfering factors are important for growth, substrate metabolism, and enzyme production, such as medium thickness and pH, inoculum and oxygen concentrations, temperature, premature assessment end, and error in the measurement of degradation halos [61-62]. As indicated above, pH and temperature play key roles in the enzymatic activity of *S. cerevisiae* cultures [7, 12, 42]. Due to being easily executable, prone to short-time results, and enabling the use of natural and synthetic inducing substrates (e.g., glucose, starch, cellulose, pectin, xylan, polygalacturonic acid, potato starch, etc., added to the growing media), the plate-based screening methodology continues to be researchers' first choice for identification of enzyme-productive indigenous yeast [10, 14, 43].

Table 3. Cultivation conditions used for plate-based screening applied in studies of extracellular enzyme production by indigenous *Saccharomyces cerevisiae* strains

Enzyme	Culture Medium	pH	Substrate	Halo reveal/type	Reference
Amylase	Nutrient agar with yeast extract and inorganic salts YPS agar with peptone and edinburgh minimal medium (EMM) YNB agar	5.2 6.0	Starch Potato starch Amylopectin	Iodine solution Iodine-Potassium Iodide Solution Translucent Halo	[13] [11] [10] [45]
Polygalacturonase	YM agar Mineral medium	ND	Polygalacturonic Acid	Ruthenium red Cetyl trimethyl ammonium bromide	[14] [17]
Pectinase	YNB agar with glucose YNB agar	7.0	Polygalacturonic acid Citric pectin	Solution of 6N HCl Iodine-potassium iodide solution	[10] [13]
Esterase	NaCl, CaCl2, Peptone and Agar	6.8	Tween 80	Opaque halo	[45]
Xylanase	Modified hankin and anagnostakis medium YNB agar with	6.7	Xylan from Oat-Spelt Xylan	Congo red	[13] [10]
β-glucosidase	YNB agar with ferric ammonium citrate solution Esculin Glycerol Agar (EGA) Yeast extract agar with iron chloride YNB agar	4.0 6.0 5.0	Arbutin Esculin	Dark brown halo	[6] [31] [39] [43]
Protease	Skim milk agar Calcium caseinate agar	6.0	Skimmed milk powder	Translucent halo	[30] [18]
Lipase	YDP agar Yeast extract agar	6.5 6.0	Tributyrin Tween 80 Arabic gum	Copper sulfate solution	[13] [18]
Celulase	Hankin and anagnostakis medium YNB agar	ND	Carboxymethyl-cellulose	Congo red	[13] [10]
Pectate lyase	Mineral medium	ND	Pectin	Cetyl trimethyl ammonium bromide	[17]
B-Xylosidase	YNB agar with ammonium sulfate	5.5	Xylose	4-methylumbelliferyl-b-Dxyloside: UV illumination as fluorescent halos	[39]
Phytase	Phytate Screening Medium (PSM)	ND	Calcium phytate	Translucent halo	[45]

3.4 *API ZYM® testing system®*

Five out of the 34 articles used in this work (14.7%) have used the methodology of the miniaturized test kit API ZYM® (BioMérieux, France), with the pure cultures being pre-activated on agar DRBC (Dicloran Rose-Bengal Cloranfenicol Agar), or broth YDP (Yeast extract, Dextrose and Peptone) at 30 °C for 24 hours. Out of the 101 evaluated strains in this system, 47 (46.5%) exhibited similar extracellular enzymatic profiles. All yeasts have demonstrated Naphthol-AS-BI-phosphohydrolase activity but none showed *α*-galactosidase activity. The highest activities were obtained for phosphatases, esterases and aminopeptidases classes, as shown in Figure 3. On the other hand, the lipases have been less represented (10.85%), similarly to the enzymes of the protease group. Acid phosphatase and esterase activities were present in 97.65% of the isolates, followed by leucine (43/46), esterase (42/46) and valine (39/46) Arylamidases. The protease and glycosyl hydrolase enzymes showed varying activities expressed by a lower number of strains, especially *α*-glucosidase (19.53%) and *α*-chymotrypsin (15.19%); other enzymes such as trypsin, b-galactosidase, b-glucuronidase, b-glucosidase, N-acetyl-b-glucosaminidase, *α*-mannosidase and *α*-fucosidase showed a reported activity in less than 7% of the isolates (Figure 3) [19, 36, 41, 43, 46, 63].

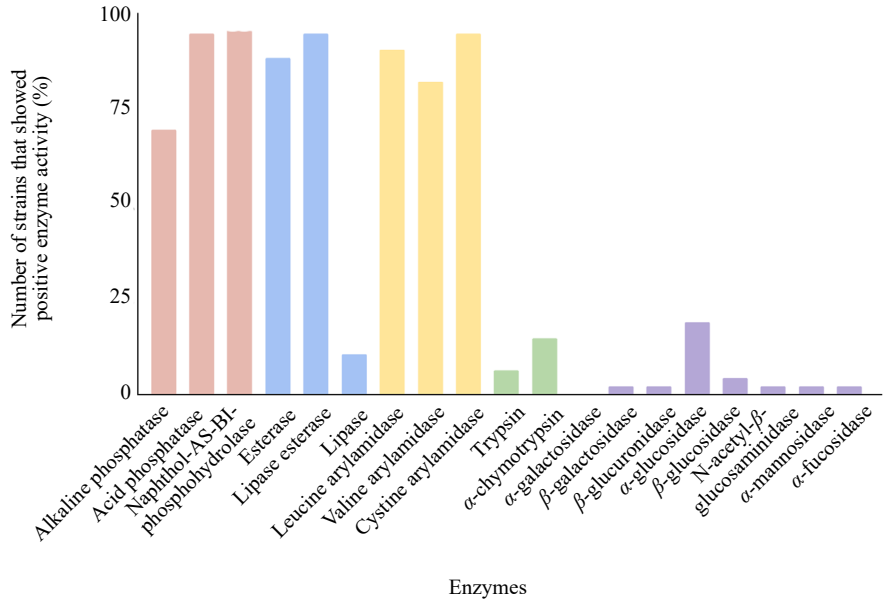

Figure 3. Enzymatic activities of wild (indigenous) yeast isolates tested by API ZYM. The bars were plotted according to the class belonging-Phosphatase (EC 3.1.3-pink); esterase (EC 3.1.1.1-blue); amino peptidase (EC 3.4.11-yellow); protease (EC 3.4.21-green) (EC 3.2.1-lilac) (BRENDA Enzymes)

It is worth mentioning that although several *S. cerevisiae* isolates produce useful enzymes, this production is not always considered to be high enough for direct application purposes [Table 2]. The alkaline phosphatase, leucine arylamidase and naphthol-AS-BI-phosphohydrolase enzymes showed intense collors upon the substrate degradation (30 and 50 nmol/L). These results differed from esterase, lipase, alkaline phosphatase and cystine arylamidase, which were found in more than a third of the isolates evaluated, being characterized by weaker staining reactions that account for a less intense substrate degradation (10 and 20 nmol/L). The other enzymes described in a reduced number of strains also showed low or no hydrolytic activity (only up to 10 nmol/L) [19].

3.5 *Submerged fermentation (SmF)*

In different fermentation processes, the assimilation of distinct carbon and nitrogen sources, as well as cell growth across a wide range of temperatures and pH levels are factors assessed with the aim of establishing the best conditions for enzymes production and activity. Adequate and sufficient enzyme production by yeasts to fulfill practical purposes is typically achieved through Submerged Fermentation (SmF) methods. The selected studies in this systematic research showed that SmF has been performed in liquid media, with or without specific inducible nutrient sources, to favor the production of xylanase, *β*-glucosidase, esterase, protease, pectinase, catalase, invertase and amylase enzymes (Table 2). Cultures supplemented with glucose, peptone and esculin have shown improved activities for *β*-glucosidase, ranging from 0.010 U/mL to 0.190 U/mL [27-28, 34]. In relation to cellulase enzymes, the inclusion of carboxymethylcellulose to the culture media resulted in an increase in enzymatic production to 2.74 U/L, whereas in the absence of that compound, no activity was detected [10]. However, in some cases, it has been observed that enzymes such as proteases (1,074 nmol/h/ml) and esterases (24 nmol/h/g) can be sufficiently produced, even without a specific inducing compound in the substrate [28]. Concerning the culturing times, a wide range of variation was observed, with the fermentation processes ranging from 48 hours to 35 days, with the longest culturing time being used for simultaneous enzyme production and micro-vinification. In terms of temperature, a wide range from 8 to 42 ℃ was verified, with most studies indicating temperatures of 25 or 28 ℃ [7, 16, 27, 37, 47] which likely encompasses the range of ideal temperature for productive fermentation. Enzymatic activities were found to lie within the pH range of 3.5-7.5, with better activities observed when strains were inoculated in fermentation media with an acidic pH between 4.25 and 6.5 [13, 31, 35, 40]. The studies assessed only three agitation patterns of the culturing procedures: 120, 150 and 200 rpm [5, 13, 32, 34], thus suggesting that no specific experiment was set to test a wider range of agitation speed.

The cultivation conditions for the SmF method can typically vary among experimental settings, depending upon the composition of the fermentation medium and the enzyme being evaluated. The best yields in microbial growth are generally achieved under acidic pH, an average temperature of 28 °C (as mentioned above), and gentle stirring of the must. The growth parameters for SmF are well-documented in the literature to produce enzymes and other metabolites by yeast strains, particularly during the alcoholic fermentation process [64-65]. The kinetics of enzymatic production by yeasts can be positively or negatively affected by key factors such as inoculum concentration, fermentation time, pH and temperature. It was observed in the selected articles that a common way to provide inocula for the fermentation processes includes the growth of strains in liquid broth and/or in semisolid media, during 24 to 48 h, with initial concentrations of 10^4, 10^5 or 10^6 cells/mL [10, 17, 23, 45]. To determine such an initial number of cells, most articles (34.3%) use the counting cells/colonies method to achieve the desired cell concentrations for the inoculum; only a few studies (6.2%) have used optical densities (OD) at 600 nm to define the cell concentration for fermentation procedures [11, 32].

In general, the nutritional conditions of the medium influence the production of enzymes, i.e., media containing substrates that induce the production of enzymes were better than the media containing only glucose, yeast extract and mineral salts [5, 34]. In this context, agro-industrial residues appear as excellent alternatives for inducing microbial growth and enzymatic production, likely due to their complex nature. Studies have shown that crushed raw wheat inoculated with 5% of cells at a temperature of 26 to 40 °C for 82 hours exhibited amylase (2.03 g/g.h) and protease (18.6 µg/g.min) activities [16]. When using orange peel substrate (1% in MSM medium) for fermentation studies, the SC MK-157 strain was cultivated with pieces of corn cob and yielded adequate levels of pectinase production (13.92 U/mL) [32].

During alcoholic fermentation processes, *S. cerevisiae* can produce multiple enzymes. This phenomenon was observed in a fermentation medium of fresh must, where grapes with peels were in contact with the juice for approximately one month of fermentation at pH 4.25 and 20 °C. Among the five enzymes evaluated, only three exhibited improved quali- and quantitative results: pectinase (862.8 U/mL), protease (324.8 U/mL) and B-glucosidase (43,531.5 U/mL) [40]. No activity was reported for amylase and xylanase. Taken together, the studies we addressed have shown the importance of testing different types of substrates, such as the agro-industrial residues mentioned above. These residues have shown to be promising nutrient sources for the production of stable enzymes, with compatible profiles of amount and activities for the food, beverage, cosmetics, pharmaceuticals and chemicals industries, among others [10, 17].

It is noteworthy that no article was found using Solid-State Fermentation (SSF) as an alternative to *S. cerevisiae* enzyme production. These circumstances can be explained not only by the way in which yeasts grow, but also due to their nutritional needs. Filamentous fungi tend to colonize the entire substrate and obtain energy through their developing hyphae, whereas yeasts have unicellular structures that prevent easy access and colonization of the solid substrate; when placed in liquid media, yeasts enhance their contact with carbon and nitrogen sources [35, 37, 66-67]. Nevertheless, other natural and synthetic solid substrates were evaluated and compared as adequate sources of nutrients [17, 22]. In these studies, for example, carbon sources like coffee pulp and pectin were used aiming to produce pectinamethylesterase and pectinase; The conclusion was that agro-industrial residues appear as viable options for producing pectinolytic enzymes at lower costs. Qadir et al. [32] achieved satisfactory pectinase activities during SmF, by immobilizing yeasts in a natural corn cob support, using orange peel as the sole source of pectin.

Most of the selected articles in this study have evaluated the enzymatic potential of indigenous *S. cerevisiae* strains in fermented beverages (such as wine), through a single SmF process, without extracting and purifying the raw enzyme extract for subsequent application on the must [52]. In this context, yeasts produce enzymes in the fermentation medium to break up the complex carbohydrates (starch, pectin, cellulose, etc.) present in the must, while simultaneously metabolize the monosaccharides obtained; in this process, they produce ethanol, CO_2, and aromatic compounds such as esters, which are the relevant substances in the sensory context of fermented and/or distilled beverage [27, 68-71]

4. Conclusions and future perspectives

The systematization of the collected data in this review provided current state-of-the-art evidence on the isolation, improved cultivation conditions, and enzyme production by indigenous *Saccharomyces cerevisiae* yeasts. The results

showed that strains with different functional characteristics (phenotypes) were isolated from several locations, with the main components of the wine production chain standing out. The research methodologies applied to determine the optimal conditions for enzyme production were found to be effective. The use of natural or synthetic inducer substrates was deemed suitable for the production of enzymes of interest. Indigenous *S. cerevisiae* strains have mostly produced enzymes belonging to the glucosidases and hydrolases classes. Yeasts have been traditionally used in classic biotechnological applications, particularly in the process of alcoholic fermentation. They have been responsible for producing metabolites that contribute to the desirable aroma and taste of wine, as well as other fermented or distilled beverages.

Considering the vast microbial diversity found in various niches and biomes worldwide, and the relatively small number of primary studies dealing with research on indigenous yeasts, one can conclude that there is an open avenue for further investigation in this topic. This includes exploring current and novel indigenous isolates and strains of *S. cerevisiae*, aiming to obtain alternative and advantageous outcomes for an array of industrial uses and applications, such as alternative flavors in food and beverage industries, novel enzymatic activities, or improvements to current ones. Additionally, in submerged fermentation procedures, the use of agro-industrial residues as carbon/nitrogen sources was highlighted as relevant for microbial metabolism, growth and production of enzymes with industrial applicability. The data indicated that there are plenty of opportunities for developing strategies to process environmentally harmful agro-industrial residues for reuse or recycling as energy sources for yeast growth at attractive costs. Based on the information and trends described in this systematic review study and considering the potential for efficient biological production of ethanol, as well as for innovations in industrial enzyme production, further research and technological development associated with indigenous strains of *S. cerevisiae* are certainly warranted at the primary empirical level.

Acknowledgments

The authors would like to thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) for scholarship support, and Universidade Estadual de Santa Cruz for financial (073.11014.2022.0003271-26) and providing the infrastructure.

Author contributions

All authors contributed to the study conception and design. The literature search was performed by B.T.A.K. and L.B.P.R.S., and data analysis was made by B.T.A.K., L.B.P.R.S., A.M.C., V.C.M., L.L.L., M.P.F.S., A.P.T.U., and A.F.R.F. The first draft of the manuscript was written by B.T.A.K., V.C.M. and A.M.C.; L.L.L and A.M.C. revised and edited the final submission version; and all authors made critical comments on previous versions of the manuscript and read and approved the final manuscript.

Conflicts of interest

All authors of this manuscript declare that none of them have any specific conflict of interest.

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