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Review Article

Fulfilling Feed Demands: Industrial Production of *Saccharomyces cerevisiae* as Key Protein Source for Aquaculture, Poultry and Livestock

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ABSTRACT

With the world's population expected to grow, addressing global hunger sustainably requires innovative solutions. Utilizing microorganisms in the form of single-cell protein can play a crucial role in enhancing food security by offering a sustainable, efficient, and nutritionally valuable protein source that complements traditional food and feed sources. Yeasts are commonly used for single-cell protein production, and *Saccharomyces cerevisiae* has a profound role in this industry, drawing from its historical significance in baking and brewing. In the feed industry, *S. cerevisiae*, as an effective feed supplement, enhances feed efficiency, animal health, and pathogen control. This review explores various aspects of single-cell protein production, emphasizing *S. cerevisiae*'s nutritional benefits for animal feed as a source of proteins, vitamins, minerals, and fatty acids. Future research should optimize industrial production processes for *S. cerevisiae* to maximize yield and minimize costs.

Keywords: Feed industry, food security, protein production, *Saccharomyces cerevisiae*, single-cell protein

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INTRODUCTION

According to the Global Operational Response Plan 2022 of the World Food Program (WFP) and the Global Hunger Index (GHI) 2023, evidence and statistics

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of hunger levels worldwide indicate that food shortages in 2023 were higher than ever before noting that as many as 783 million people were experiencing chronic hunger with the situation expected to worsen in the year 2024 (https://openknowledge.fao.org/items/c0239a36-7f34-4170-87f7-2fcc179ef064; https://www.fao.org/4/y5019e/y5019e00.htm#Contents; https://www.fao.org/fishery/en/publication/295155; von Grebmer et al., 2023). Since 2019, COVID-19 has combined with previous crises across the world, such as conflict, the menace of global recession and climate changes, causing the number of people dealing with acute food insecurity to precipitously rise from 135 million to 345 million (WFP, 2022).

In the definition, food security is the unrestricted access of everyone to food in such a way that it grants them their basic needs. Therefore, taking quick action is needed to prevent an imminent food crisis. In the first place, food insecurity affects diet quality, including the quality of women's and children's diets. Accordingly, it contributes to increasing the risk of child malnutrition as a threat worldwide (https://openknowledge.fao.org/items/c0239a36-7f34-4170-87f7-2fcc179ef064). Many studies have reiterated the magnitude of proteins in food security (Pencharz et al., 2016; Allen, 2017; Bai et al., 2021). According to Jach et al. (2022), the global average meat consumption of a person is 43 kg in a year, and about half of the African population suffers from protein deficiency, with meat in their diets only about 10 kg per person annually. It has been predicted that diet-related health costs linked to mortality and non-communicable diseases under current food consumption patterns will exceed USD 1.3 trillion per year by 2030 (https://openknowledge.fao.org/items/c0239a36-7f34-4170-87f7-2fcc179ef064).

The production of easily available protein products without adverse effects on human life has been one of the most critical global challenges for many years (Jach et al., 2022). The global population of impoverished individuals and the scarcity of protein-rich food have prompted governments to seek alternatives to traditional costly protein sources like soy meal and fishmeal (Anupama & Ravindra, 2000). In the current situation, single-cell protein (SCP) is one of the most attractive choices as a desirable alternative to the conventional protein components of the diet (Haddish, 2015). Humans have been eating products linked to microbes (bread, cheese, and yogurt) for many years; hence, consuming microbial protein is acceptable and familiar (Kieliszek et al., 2017; Bajić et al., 2022). Microbial proteins are derived from microorganisms, including algae, yeasts (single-celled fungi), filamentous fungi, and bacteria, while yeasts are the most broadly accepted among all (Haddish, 2015). The convenience of using fungi, especially yeasts, for SCP production, in comparison with other microorganisms, is due to their easy propagation using cheap raw materials and simple harvesting, as they have bigger cell sizes and flocculation abilities (Bekatorou et al., 2006). From a sustainability viewpoint, exploiting novel biotechnological solutions, i.e., SCP, is indispensable.

Since waste disposal is financially burdensome, producing microorganisms' biomass, such as yeasts, is commercially viable while effectively contributing to waste management practices (Kieliszek et al., 2020). Yeast also provides other benefits, including higher nitrogen content than algae, more ash content compared to bacteria, rapid biomass production because of shorter growth time, and the capacity to grow in acidic pH conditions (Mohammadi et al., 2016)). These impressive advantages of yeasts for microbial protein production are well-known among world-famous manufacturers (Bekatorou et al., 2006). Bajić et al. (2022) in their paper reported that according to a GFI (Good Food Institute) company database where 88 fermentation companies were entirely focused on alternative proteins, the contribution of such companies rose to ~US$1.69 B from 2020 to 2021, which is up 285%, representing 60% of the all-time investment. The Transparency Market Research Report (2020) predicted that the SCP market will reach ~US$ 24.5 M at a CAGR of 9.7% by the end of 2030. The value of the worldwide market for SCP reached US$13.1 B in 2022 (Koukoumaki et al., 2023; Ye et al., 2024).

In 2020, Vietnam's income from the SCP market was over US$ 26.7 M, while economic experts estimate that this number will surpass US$ 69.4 M by 2030 (Transparency Market Research Report, 2020). Pursuing the goal of developing efficient feed formulations for aquaculture, a recent practice in this industry has been the exploration of alternative proteins that promote sustainable further growth. As announced by FAO, the successful Asian countries in the aquaculture industry, such as China, Indonesia, India, Bangladesh, and Vietnam, produce around 50–60% of the total aquaculture production and use SCP as a nutritive and more cost-effective alternative to fishmeal (https://www.fao.org/fishery/en/publication/295155). Thus, it is anticipated that these producers will expand the aquaculture industry in the near future, causing a great rise in the SCP market (Transparency Market Research Report, 2020).

A balanced diet is necessary for livestock animals to give them proper nutrients and energy for growth, reproduction, and immunity against infections, leading to a more sustainable and profitable farming system. Therefore, due to its vital attributes, such as containing different micronutrients, SCP has garnered particular interest in the feed industry. The microorganisms applied for SCP production affect the food values and nutritiousness of the products (Bratosin et al., 2021). *Saccharomyces cerevisiae* is a yeast species widely known for being nutritious and edible by humans. It also has a diverse array of uses in multiple industries, including beverage and food production, biofuel manufacturing, and biotechnological products such as enzymes and probiotics (Bekatorou et al., 2006). One of the advantageous characteristics of *S. cerevisiae* is its ability to use plenty of organic compounds, such as agricultural residues and industrial waste, for growth.

This property is substantial because it creates value-added products and establishes a novel pathway for a circular economy (Nyyssölä et al., 2022). One further recent aspect regarding *S. cerevisiae* that has garnered the attention of researchers and community health participants is the prominent role it can take in the “One Health” concept, from controlling pathogenic microorganisms (in both humans and animals) to leveraging food quality and preserving the environment, due to its unique features. The One Health approach is a collaborative strategy that addresses health issues sustainably through joint efforts of experts across multiple disciplines (animal, human health, and environmental) (Ballet et al., 2023). This review focuses on the single-cell protein as a way out of worldwide protein shortage and its production processes. It also aims to bring up *S. cerevisiae* as one of the most prevalent yeasts in the SCP industry while discussing some critical research demonstrating its unique role in the feed industry.

SINGLE-CELL PROTEIN AS A SUSTAINABLE SOLUTION FOR GLOBAL FOOD INSECURITY

The predicament of world hunger, measured in various indices such as “undernourishment” and “food insecurity,” among other terms, has unfortunately reached a new level of severity. According to the statistics provided by FAO in its 2022 report, between 702 and 828 million people lived in hunger during 2021. Above and beyond, according to this statistic, an increase of 150 million people living in hunger has been observed since the COVID-19 pandemic in 2019 (https://openknowledge.fao.org/items/c0239a36-7f34-4170-87f7-2fcc179ef064). Adding to that, according to WFP (2022), a United Nations Sustainable Development Group (UNSDG) member, in 49 countries, as many as 49 million people are staggering on the edge of starvation. The aforementioned statistics reflect the cruciality of addressing world hunger as it affects human life and future generations. Analytical data on adequate nourishment indicates that proteins are the most significant part of the diet, highlighted in a combined study undertaken by WHO, FAO and United Nations University (UNU) referring to proteins as necessary for growth (WHO, 2007). With reference to the expected growth of the world’s population to approximately 9 billion people by 2050, the food demand will increase by 60%, while the predicted value for protein is 40% (Ye et al., 2024). The International Feed Industry Federation has estimated that the production of different animal proteins like beef, dairy, and poultry will double and that fish production will nearly triple this year (IFIF, 2023). Animal protein in all its forms, such as meat, milk, and eggs, has a substantial place in providing macro and micronutrient deficiencies in a healthy human diet worldwide. Whereas the most expensive and essential component in an animal raising system is feed, the animal feed industry is considered a leading player in achieving sustainable food security.

Novel protein sources like SCP, insects and underused plants are among the most important sources that are anticipated to contribute to the future protein nutrition of humans and animals. Anti-nutritional components of many plant species and allergenicity and biosecurity risks of insect protein, besides questions relating to their digestibility level, are considered the main obstacles before they can become desirable substitutes in human food or as an animal feed ingredient (Salter & Lopez-Viso, 2021). Though SCP is known as a notable source of protein as well as many other vital nutrients, there has been an outstanding rising interest in the consumption of microbial protein in feeding in recent decades. Superiorities such as not being influenced by seasons or climate conditions and being cost-effective and environmentally safe are the most dominant benefits of microbial protein compared with animal and plant proteins (Onyeaka et al., 2022).

SINGLE-CELL PROTEIN

As previously stated, the world's growing population and their increasing requirements for vital nutritional elements, particularly protein sources, represent a critical issue in the coming decades (Raziq et al., 2020). Food security and meat consumption are closely connected as meat remains a primary source of crucial nutrients for a significant proportion of the global population. According to Salazar-López et al. (2022), the preferred source of protein for most consumers is meat products. On the other hand, the dependency of industrial livestock production on human-edible crops makes it fundamentally inefficient. While the land directly utilized for animal housing may not be extensive, a vast amount of arable land is exploited for cultivating the crops that will later serve as animal feed (Stevenson, 2015). To achieve the goal of sustainable food production, competitively priced protein sources, such as microbial protein, can be exploited (Raziq et al., 2020; Salter & Lopez-Viso, 2021). SCP protein sources exhibit remarkable advantages, including significant protein content, a short period of microorganism proliferation, and the capability to be genetically manipulated for desirable content or the degradation of specific raw materials (Kieliszek et al., 2017).

Although the idea of consumption of microbes as a food source for humans and animals may appear to be unacceptable, humans have been using them, either unintentionally or intentionally, as these microscopic organisms are present in bread, fermentative beverages, yogurt, cheese, and soya sauce for thousands of years (Anupama & Ravindra, 2000). Germany in World War I used SCP extracted from *S. cerevisiae* as a replacement for more than half of its important protein sources (Ukaegbu-Obi, 2016; Ye et al., 2024). *Candida utilis* is another yeast species comprising a high amount of exogenous amino acids, which has been applied as a protein source (Kieliszek et al., 2017). In 1968, for the first time, the term single cell protein (SCP) as an alternative to terminologies like microbial protein was introduced by scientists (Sharif et al., 2021). SCP biomass possesses the special attribute of being entirely edible without generating any biowaste like stems, roots or leaves. Since the process of SCP production occurs in a bioreactor with no leakage to the environment and no need for pesticides, the technology has no ecological impact (Bogdahn, 2015). SCP has been reported to be a good source of protein (30%–80%) and also essential amino acids (threonine, lysine and methionine), minerals, vitamins, lipids, and carbohydrates (Salazar-López et al., 2022).

Microbial protein is employed in many food areas, such as ready-to-serve meals, diet recipes, emulsifying aids, vitamins, and aroma carriers (Suman et al., 2015; Ukaegbu-Obi, 2016). Nowadays, SCP is perceived as part of a healthy diet with respect to their appreciable content of bioactive peptides, proteins, amino acids, fatty acids and pigments, which this complex of valuable biological compounds engages in the process of preventing diet-induced obesity (Patias et al., 2018). Furthermore, many other industries like industrial animal feed, wastewater treatment, paper and leather processing, biofuel, and foam stabilizers benefit from SCP in various ways (Suman et al., 2015; Raziq et al., 2020; Bratosin et al., 2021).

MICROORGANISMS FOR SINGLE-CELL PROTEIN PRODUCTION

SCP is produced from many microorganisms, including algae, yeast, filamentous fungi, and bacteria (Anupama & Ravindra, 2000; Mohammadi et al., 2016; Sharif et al., 2021). The microbial communities should exhibit specific traits like rapid as well as stable growth, high biological value, non-toxicity, non-pathogenicity, and minimal nucleic acid content to be appropriate for SCP production (Zhou et al., 2019). The growth rates of microorganisms exploited in SCP production are as follows: bacteria with 30 min to 2 h, yeast with 40 min to 3 h and algae with 3–6 h. It is apparent that yeast and bacteria can multiply in a very short period of time as it has been reported that in only 5–15 min, they double their population, while this duration for algae and filamentous fungi is 2–4 h (Sharif et al., 2021). More examples of each microbial group are given below.

Algae

Algae have been regarded as an important dietary component for people in central Africa and East Asia (Nyyssölä et al., 2022). For example, thousands of years ago, *Spirulina* was harvested from the water by people of the Aztecs near Lake Texcoco in Mexico and near Lake Chad in Africa to be consumed after drying (Costa et al., 2004). Algae species are the source of many vitamins (A, B, C, D and E), proteins and fats. The protein content of algae is 40%–60%, while bile pigments, chlorophyll, mineral salts and fiber are its other biomass contents. In a study, *Pelvetia* was used in cow feed ingredients, which enhanced the milk-yielding capacity (Anupama & Ravindra, 2000). As algae have valuable nutrient contents and can capture solar energy, many algae species (*Soenedesmus*, *Chlorella*, *Coelastrum*, and *Spirulina*) have been exploited for mass cultivation desirably (Raziq et al., 2020). As stated, *Spirulina* has been successfully produced in large quantities and used in dietary supplements and food products. Besides, its usage in the feed industry brings advantageous features such as giving rise to healthy yolk composition for poultry and coloring fish flesh in aquaculture. Both *Chlorella* and *Spirulina*, with a high protein content of up to 50%–70%, are now marketed as functional foods. These species also increase the food and feed values with their other desirable components, i.e., small peptides, lipids, vitamins, and pigments (Nyyssölä et al., 2022).

Bacteria

The rapid growth, short generation time and high protein content (50–80%) of bacteria make them suitable cases for SCP production. Hence, many bacterial species have been investigated for such applications (Raziq et al., 2020). They also can grow on many types of raw materials and edible substrates like sugars and starches (Sharif et al., 2021). *Alcaligenes* and *Cellulomonas* are the most widely used bacterial species in SCP production (Ukaegbu-Obi, 2016). Two bacterial species with good protein compositions applied in animal feed are *Methylophilus methylotrophus* and *Methylotrophic bacterium*, which have about 2 hours of generation time (Raziq et al., 2020). Photosynthetic Purple Non-Sulphur Bacteria (PNSB) are among the beneficial microorganisms in fish feed with 70%–72% protein content and highly resistant to toxicants. It is noteworthy that its essential amino acids profile is similar to soybean protein (Raziq et al., 2020). The limitations of using bacteria as food include public acceptance, high content of nucleic acid on a dried mass basis and difficulty of harvesting due to its small size (Ukaegbu-Obi, 2016).

Filamentous Fungi

Trichoderma album, *White rot fungi* and *Paecilomyces variolii* are examples of filamentous fungi which serve as SCP sources (Anupama & Ravindra, 2000). In general, the nutritional composition of fungi makes them desirable to use as SCP products. They have mainly 30%–50% protein as well as essential amino acids, vitamins and lipids (Anupama & Ravindra, 2000; Nasseri et al., 2011; Onyeaka et al., 2022). Exploiting fungal species in bioconversion of lignocellulosic waste is one of the recent trends in SCP production (Anupama & Ravindra, 2000). One of the oldest providers of commercial fungus is Quorn, which Marlow Foods (GB) launched in 1985. Quorn products are an example of successful protein production from filamentous fungi (*Fusarium venenatum*) for human consumption (Nyyssölä et al., 2022; Graham & Ledesma-Amaro, 2023).

Yeast

Yeasts are microscopic fungi that metabolize organic substances to harness their required nutrients and energy for reproduction and growth (Walker & Stewart, 2016). The non-pathogenic character of many types of yeasts resulted in their significant role in human life since antiquity. Yeasts have superior nutritional qualities like high lysine and malic acid contents (Raziq et al., 2020). Another remarkable advantage of yeasts over other microorganisms is their ability to withstand acidic environments (Bogdahn, 2015). They have been used in the feed as supplements since the olden days. It is noteworthy that a considerable portion of the SCP from yeast and other fungi that are used in the feed industry comprises by-products from food and beverage plants as well as biorefineries. In addition, a large number of studies utilize by-products of industrial processes for producing yeast biomass, mostly for investigating their application as feed supplements. These include culturing various yeast species on brewer's spent grain, dairy waste, orange pulp, potato starch processing waste, and many more (Nyyssölä et al., 2022).

In a study by Onyeaka et al. (2022), food waste and vegetable products used to culture *S. cerevisiae* and the protein content of the biomass were successfully boosted up to 39.8%. They concluded that the use of these types of waste in SCP production by *S. cerevisiae* reduces expenses linked to waste management while producing beneficial food and feed ingredients. Arous et al. (2016) studied the potential capacity of two discovered yeast species, *Candida pararugosa* BM24 and *Schwanniomyces etchellsii* M2, for degradation of olive mill wastewater for SCP production and reported 35.9% protein content as the maximum yield. In this experiment, the concentration of olive mill wastewater was 75% (v/v), followed by an incubation period of 96-h with an inoculum volume of 5% (v/v) at 30^{o}C. As an instance of problematic industrial by-products, potato wastewater and glycerol were successfully applied by Kurcz et al. (2018) as nutrient sources in *Candida utilis* production, and the protein content of produced SCP was 42%. This yeast is validated as a safe species and has contributed to feed and food supplements for decades (Bekatorou et al., 2006; Bzducha-Wróbel et al., 2018a). Apart from protein, some yeast species have the capability to accumulate lipids in their cells, which has been called Single Cell Oil (SCO), with fatty acid profiles that are similar to those of vegetable oils (Gientka et al., 2017). Gientka et al. (2017) applied a similar industrial waste (deproteinated potato wastewater enhanced by carbon sources, i.e., glycerol) to produce SCO and successfully reached lipid accumulation above 20% in the yeast cells. Another noteworthy feature of yeast is its capability to absorb critical microelements in their cell structure and create stable binding with proteins (bioplexes). These complexes are enriched with metal ions (i.e., selenium), which have medical and veterinary applications (Kieliszek et al., 2017). The versatile yeast *S. cerevisiae* is able to easily ferment available sugar in various types of wastes, i.e., glucose, sucrose, fructose, maltose, galactose, maltotriose, and mannose, into carbon dioxide and ethanol (Walker & Stewart, 2016). Furthermore, it has probiotic properties and is regarded as an effective feed supplement that ameliorates feed utilization, reduces the number of pathogens, and improves animal performance and health (Elghandour et al., 2020).

Saccharomyces cerevisiae

In 1838, for the first time, Meyen named the fermentation yeasts *Saccharomyces* (Boynton & Greig, 2014; Stewart, 2014). Subsequently, another researcher named Hansen pinpointed the specific characteristics of *S. cerevisiae* in 1888 (Boynton & Greig, 2014). The application of fermentation for producing food and beverages can be traced back to as early as 7000 BC in China and 6000 BC and 3000 BC in Iran and Egypt, respectively. Therefore, it is concluded that such fermenting techniques developed from Mesopotamia across the world (Legras et al., 2007). It is remarkable that according to the new genomic confirmations, the canonical bread yeast, *S. cerevisiae*, originated in China before moving west 16–14 tya via the Silk Road (Lahue et al., 2020). One of the recognized capacities of yeasts is producing alcohols with intricate and extended chemical structures along with their derived esters that represent intriguing flavor profiles.

De Almeida Silva Vilela et al. (2020), in their experiments, identified phenylethyl alcohol in selected *S. cerevisiae* strains, which is a highly important alcohol in terms of aroma with a rose-like fragrance. *S. cerevisiae* demonstrates resilience to elevated sugar levels, a quality that is pivotal in its industrial uses (Parapouli et al., 2020). Furthermore, the glycoproteins and polysaccharides of *S. cerevisiae* cell walls provide functional qualities for human and animal bodies (Kieliszek et al., 2017). The European Food Safety Authority acknowledged the Qualified Presumption of Safety (QPS) status of this distinguished yeast, the most widely employed food sector (Moslehi-Jenabian et al., 2010). Except for the fermented products, i.e., bread, cider, and beer, *S. cerevisiae* has species that have been isolated from other sources like soil, fruits and trees. *S. cerevisiae* needs to adapt to unique selection pressures to survive in each of these environments. For over a century, companies such as Cenovis R (Gustav Gerig AG), Marmite R (Unilever and Sanitarium Health Food), and Vegemite R (Bega Cheese Ltd.) have been selling *S. cerevisiae* in the form of yeast extract due to its high protein content and its provision of five essential B vitamins. Among some industrial establishments that employ *Saccharomyces* as the main microorganism in their SCP products, Bega Cheese Ltd., Flint Hills Resources, Shanghai Tramy Green Food Co., and Tangshan Top Bio-Technology Co. can be mentioned (Ritala et al., 2017).

Moreover, the use of *S. cerevisiae* as a model organism in various fields of research ranging from molecular biology to basic genetics is frequently preferable due to a number of its pivotal (Mohammadi et al., 2016). As Stewart (2014) mentions, among eukaryotes, the inner cell structure of *S. cerevisiae* is very close to animals and plants. In addition, there are several other justifications that make this species a valuable tool in a wide range of investigations, including ease of genomic manipulation, which is beneficial in various biotechnological areas from human genetics investigations to testing new drugs and much more (Stewart, 2014; Parapouli et al., 2020). Including a simple unicellular character while demonstrating most of the metabolic pathways and essential cellular activities that appeared in higher eukaryotes, simplicity of culturing and maintaining in the lab, the possibility of storing viably at -80°C that provides researchers with the feasibility of cross-generational studies, its special economic importance among all other microorganisms, and its application in contagious illnesses studies, specifically prions, ssRNA viruses and dsRNA viruses through explanation of the interactions between them and cellular components (Stewart, 2014; Parapouli et al., 2020). In addition, multiple studies have proven that *S. cerevisiae* exhibits a great tolerance to high sugar levels in the medium, which has an impressive role in its industrial usage (Parapouli et al., 2020). The cellular response system triggered by such conditions contributes to yeast survival by maintaining the robustness and integrity of the cell wall (Bzducha-Wróbel et al., 2018b).

In recent years, significant efforts have been made to modify yeast species in order to enhance the generation of desirable compounds (Kieliszek et al., 2020). Regarding *S. cerevisia*e species, genetic engineering for utilizing targeted substrates, producing high-value chemicals, and boosting stress resistance are among the most attentive studies. A vast area of this research concerns the development of the capability of utilizing lignocellulosic biomass in *S. cerevisiae* production as a cheap and problematic raw material. Lignocellulosic wastes are one of the most abundant agricultural residues, and acid treatments are the common method for their hydrolyzation (Çakar et al., 2012). This approach is not considered attractive due to its high cost and not being in accordance with the environment. Currently, recombinant *S. cerevisiae* strains have been produced for later commercial usage. Production of organic acids such as lactic acid, succinic acid, and 3-hydroxypropionic acid by this genetically engineered *S. cerevisiae* are noteworthy case studies. One of the carbohydrates with a considerable volume in the market is sorbitol, a common sweetener widely applicable in food industries. It has been successfully produced by a mutant of *S. cerevisiae* yeast (Baptista et al., 2021).

As mentioned, demonstrating adequate tolerance to agitated conditions during industrial processes plays an important role in most *S. cerevisiae* applications. Researchers introduced a mutant strain of *S. cerevisiae* that possesses more resistance to such conditions, e.g., higher freeze tolerance (Teunissen et al., 2002). Another aspect that needs to be addressed for sustainable and meaningful yeast production is conducting comprehensive life cycle assessments (LCA) of procedures to perceive their environmental impact compared to traditional protein sources. Life-cycle assessment (LCA) is a useful assessment of a process or product throughout its entire life cycle to analyze its environmental impacts (Ye et al., 2024). As stated by McAuliffe et al. (2023), multiple recent research on life cycle assessment (LCA) has come to the conclusion that animal proteins (especially those from ruminants) have a significant environmental footprint and should be highly limited. Ye et al. (2024) reviewed the latest life-cycle assessments and techno-economic analyses of SCP production by various microorganisms. The raw material used, cultivation methods, and downstream processing are some of the critical factors that must be confronted for yeast production. At the same time, feedstock upstream treatment seems to be the major obstacle to filamentous fungi and yeast production. The main strategies to overcome this hurdle are co-cultivation and pretreatment, which have been reported to improve process productivity.

In a report prepared by the Norwegian Institute for Sustainability Research (NORSUS), the Life Cycle Assessment (LCA) for yeast production has been documented. According to the data, sugar source, the major proportion of raw material production, had the most significant environmental impact across different groups, followed by ammonia and other materials. They declared that consequences from yeast processing only contributed to a small percentage of climate change, and it was negligible in all other categories. In addition, yeast production had lower environmental impacts when nitrogen source was derived from an organic source, such as wastes from the livestock slaughter process (Møller & Modahl, 2020).

S. cerevisiae in Feed Industry

The industrial application of amino acids in the feed industry dates back to the late 1950s and 1960s, when DL-Methionine was synthesized chemically and used in poultry feed. During the 1960s, L-Lysine was produced through fermentation in Japan (https://www.fao.org/4/y5019e/y5019e00.htm#Contents). Apart from these products, in the late 1980s, L-Tryptophan, HCl and L-Threonine were introduced. Decreasing the production costs of each amino acid due to biotechnological advancements has led to the growth of using amino acids in animal feed. It is important to note that amino acids are a key factor in improving feed efficiency. With this respect, there is a notable interest in the expansion of the use of SCP as a natural source of essential and nonessential amino acids among owners of livestock industries. Kieliszek et al. (2017) stated that the well-balanced amino acid profile of SCP yeasts led to outstanding interest in their application.

The obtained SCP from yeast has a relatively low proportion of methionine, but its lysine and threonine contents meet FAO guidelines (Nyyssölä et al., 2022). In their experimental study, Bertasini et al. (2022) discovered that in the single-cell protein produced by *S. cerevisiae*, nearly all amino acid concentrations exceeded those found in the commercial monogastric feed (Table 1). It could be concluded that SCP from *S. cerevisiae* source can be utilized to enhance growth performance and general animal health as well as improve the nutritional quality of the feed.

Another study mentioned that the amino acid profile of SCP from *S. cerevisiae* is similar to that of soya protein. It also contains vitamins such as riboflavin, nicotinic acid, biotin, thiamine, ascorbic acid, pyridoxine, β-carotene, cyanocobalamin, pantothenic acid, αtocopherol and folic acid, which maintain a pivotal function in metabolism and health (Bratosin et al., 2021). What makes using yeast (i.e., *S. cerevisiae*) as animal feed superior is their nutritional quality, together with their history of long-term use without adverse effects (Nasseri et al., 2011). The composition of fresh *S. cerevisiae*, depending on the growth condition and strains are as follows: around 40.6%–58.0% of proteins, 31.55%–45.0% of carbohydrates, 6.5%–9.3% of nitrogen, 5.0%–7.98% of minerals, 4.0%–6.0% of lipids, and different vitamin contents (Bekatorou et al., 2006; Onofre et al., 2017). β-glucans is another advantageous compound identified in *S. cerevisiae* with diverse applications in biotechnology. These polysaccharides are applied as novel nutritional ingredients but are also utilized in the role of antimicrobial and anticancer agents, immunomodulators, oral vaccine carriers, and cosmetics components (Bzducha-Wróbel et al., 2018a). In summary, the most significant effects of *S. cerevisiae* are associated with the above-mentioned valuable nutrients, which ultimately lead to overall animal health by inducing positive effects on gut microbiota and the immune system and acting as a natural antibiotic.

Table 1
Aminoacidic profile of the SCPs (S. cerevisiae) *and of monogasteric animals (Bertasini et al., 2022)*

	Monogasteric feed (NRC, 1998)	**SCPs**
Arginine	34	53
Cysteine	31	23
Hstidine	32	41
Isoleosine	55	70
Leosine	100	87
Lysine	100	100
Methionine	29	26
Phenylanaline + Tyrosine	94	106
Thronine	65	82
Tryptophan	16	18
Valine	65	65

The obvious relationship between animal gut microbiome and their immune status and health has been reported in numerous studies (El-Bab et al., 2022). Thus, understanding the yeast's impact on the animal microbiota could positively contribute to optimizing and enhancing animal health. Wang et al. (2022), in their study on the effects of *S. cerevisiae* supplementation in fatting sheep diet, observed better growth and animal performance in comparison with the controlled groups, particularly well-developed rumen epithelium and microbial flora of rumen. Another investigation on grass carp with %12 *S. cerevisiae* dietary supplementation improved the host's gut microbiota and biochemical parameters (Liu et al., 2018). Overall, the findings of studies on gut microbiome in various animals demonstrate promising effects of *S. cerevisiae* on gut microbiota profile in various hosts.

Table 2 represents the pivotal effects of *S. cerevisiae* supplementation in the diets of different animal species.

Table 2
Effects of S. cerevisiae *supplementation in diets of different animal species*

S. cerevisiae **Doses**	**Animal Species**	**Effects**	**References**
(2 kg/ton feed)	Broiler	Increase in the number of gut yeast and lactic acid-fermenting bacteria while causing a reduction of *Escherichia coli* Enhancement of feed intake and weight gain	(Koç et al., 2010)
0.2%–0.4% diet	Broiler	Modulating the intestinal immune system and microbiology boosts production metrics and enhances feed efficiency	Bortoluzzi et al. (2018)
1–5 g/d	Dairy calves	Regulates both mucosal immune and systemic responses, diminishing clinical disease, occurrence of secondary bacterial infection, and lung pathology	Mahmoud et al. (2020)
28 g/calf/day	Fattening calves	Improvement of body weight reduces feed intake and average feed conversion rate (FCR)	Maamouri and Salem (2022)
5 g/day	Goats	Betterment of intestinal microecology, protein, lactose and fat content enhancement of the milk	Ma et al. (2020)
0.60% of the dry matter (DM) weight of the basal diet	Heat-stressed goats	Higher rumen fermentation, improvement in digestibility factors, increased growth performance	Xue et al. (2020)
0.8 g/kg diet	Fattening lambs	Increase in dry and organic matter, acid detergent fiber digestibility, enhancement of daily gain	Sun et al. (2022)
0.1% (w/w)	New Zealand white (NZW) Rabbit	Higher feed conversion efficiency and body weight, increase in nitrogen utilization	El-Badawi (2017)
11 g/head/day	Horse	Enhancement in intake and digestibility of dry matter, organic matter, neutral detergent fiber and acid detergent fiber	Salem et al. (2016)
4 mg/g of feed dry matter	Horse	Higher fiber digestibility and fermentation	Elghandour et al. (2016)

S. cerevisiae in Poultry Feed

As a cheap and affordable animal protein source, chicken is economically valuable for most societies. Many poultry producers use antibiotics as medicine to prevent diseases or as a growth enhancer, which has recently caused concerns among chicken consumers about antibiotic residues. In this situation, probiotic or live microbes and spores that develop in the intestine provide their hosts with beneficial properties of their metabolites directly or indirectly, encouraging nutritionists to use them as an alternative to antibiotics (Wulandari & Syahniar, 2018). In poultry nutrition, *S. cerevisiae* attains the position of the most popular probiotic or prebiotic among all yeast species. As in healthy broiler chicken, *S. cerevisiae* improves gut health by balancing the gut microbiome (increasing the multiplication of useful microbes, producing short-chain fatty acids, decreasing intestinal pH, and thus preventing pathogenic proliferation). This is in addition to possessing positive effects on histomorphological parameters and helping to maintain the homeostasis of epithelial cells (Ahiwe et al., 2021). Fanelli et al. (2015) in their study evaluated the effect of live *S. cerevisiae* on *Campylobacter jejuni* and *Salmonella enteritidis* content in broiler chicken and observed a remarkable control of *C. jejuni* as well as preventive effects on *S. enteritidis*. They concluded that *S. cerevisiae* in chicken feed could decrease the contamination of carcasses and prevent human foodborne illnesses.

In addition, *S. cerevisiae* can result in boosting the synthesis and release of pro-inflammatory cytokines from macrophages (Elghandour et al., 2020). Gheisari and Kholeghipour (2006) studied the *S. cerevisiae* effects on blood parameters, growth performance and immune response on 3-days-old male broilers by dietary inclusion of 01, 02 and 03% (w/w) of live *S. cerevisiae* powder and observed daily and final body weight, feed intake, serum high-density lipoprotein level, and antibody titer against influenza disease virus increased. Faria-Oliveira et al. (2013) mentioned the favorable effects of baker's yeast for laying chicken and breeder turkeys. They relate the effects to the rich folic acid content in *S. cerevisiae*, an important vitamin for turkeys and other poultry. As previously noted, *S. cerevisiae* is an excellent source of various vitamins, including biotin. A deficiency in biotin can result in poor hatchability, low egg production and reduced feed conversion. In fact, reproductive improvements in chickens fed by *S. cerevisiae* are connected to the high level of biotin and selenium in yeast, which is more effective than inorganic selenium, which is usually added to their diets. Chollom et al. (2017) declared the nutritional value of *S. cerevisiae*, which could be replaced with soybean in poultry feed as a protein source. They evaluated the amino acid profile of *S. cerevisiae* and identified the presence of essential amino acids, including lysine, threonine, histidine, valine, phenylalanine, leucine, isoleucine, tyrosine, and arginine. In addition, they found nonessential amino acids in the following order: aspartic acid, serine, glycine, glutamic acid, alanine, and proline. Interestingly, it was comparable to the amino acid profile of soybeans. Although tryptophan, cystic acid and methionine were not reported, the content levels were even higher than that of soybean. Izah et al. (2019) evaluated the vitamin content of *S. cerevisiae* cultured in cassava wastewater, and the results (Table 3) showed desirable vitamin content (A, E, D, C, B1, B3 and B12) of *S. cerevisiae* to be used in animal feed.

Table 3
Vitamin content in S. cerevisiae biomass cultured in cassava mill effluents (Izah et al., 2019)

Vitamins	Mean ± Standard deviation
Vitamin A, µg/100 g	2280.37 ± 105.85
Vitamin D, mg/100 g	40.73 ± 7.94
Vitamin E, µg/100 g	132.54 ± 14.00
Vitamin C, µg/100 g	6.88 ± 1.62
Vitamin B12, µg/100 g	0.58 ± 0.10
Vitamin B3, mg/100 g	2.62 ± 0.92
Vitamin B1, mg/100 g	1.05 ± 0.21

S. cerevisiae in Aquaculture (Fish Feed)

For both humans and animals, amino acids play a crucial role as intermediates in many metabolic pathways while serving as protein building blocks (Kasozi et al., 2019). Although fishmeal's essential amino acid profile is satisfactory for most species, the growing price has made producers use unbalanced ingredients as alternatives. Therefore, finding a substitute that meets the standard criteria for proteinous feed ingredients seems necessary. On the other hand, the pressure of increasing demand for marine resources doubles the necessity for finding novel protein sources with lower costs, like SCP (Ahmed et al., 2019). *S. cerevisiae* is the most used species in fish farming, demonstrating health-boosting effects (Agboola et al., 2021). Currently, most feeding trials tend to work on shrimp and salmon. In a study, the replacement of soybean meals (up to 24%) and fish meal (from 15% to 24%, depending on the product) with *S. cerevisiae*, *Kluyveromyces marxianus*, and *C. utilis* exhibits satisfactory results for shrimp (Jones et al., 2020). Bertasini et al. (2022) observed that the concentration of almost all amino acids was higher than the required levels for monogastric animals in producing SCP from *S. cerevisiae* using the effluent of the candy production process mixed with agricultural digestate. The only exceptions were leucine and cysteine levels, which were slightly lower. Furthermore, according to the review of literature conducted by Agboola et al. (2021) on selected yeast species of commercial importance for aquafeeds, based on several studies on *S. cerevisiae* from 1997 to 2016, they concluded that the total essential amino acid contents of *S. cerevisiae* are in similar concentration of the requirements for rainbow trout and Atlantic salmon.

S. cerevisiae in Livestock Feed

Alongside increasing interest in the use of *S. cerevisiae* in animal feed, related techniques and technologies need to be examined. In their research, Song et al. (2021) examined the effects of *S. cerevisiae* supplemented into pelleted total mixed rations (TMR) at two proportions of corn in the diet on fatting lambs. This study aims to determine whether the process of pelleting resulted in *S. cerevisiae* becoming ineffective. The measured parameters were feed digestion, rumen fermentation, animal performance, microbial community, and blood parameters. Their findings indicated that pelleting resulted in dead yeast cells, which improved male lamb growth performance, probably due to improved fiber digestibility regardless of the proportion of corn in the diet. The change in the rumen bacteria and species was also reported. Alugongo et al. (2017) reported that supplementing mature ruminants feed with active live *Saccharomyces* and inactivated cell culture increased the production parameters, altered rumen fermentation and improved nutrient utilization. Interestingly, animals that were exposed to transport stress exhibited better health and growth performance when *S. cerevisiae* was added to their feed. In the process of preparing live *S. cerevisiae* for animal feed, the first step involves introducing live yeast cells into damp cereal grains or grain by-products. The mixture is then partially fermented, followed by a drying process that preserves the enzymes, vitamins and yeast without killing them. Providing a consistent supply of dicarboxylic acids and vitamins while reducing the presence of pathogenic microorganisms such as protozoa and removal of oxygen are among the main benefits of *S. cerevisiae* in ruminants. These effects ultimately result in improved digestion of fibers, increased feed intake and better animal performance (Faria-Oliveira et al., 2013).

According to Alugongo et al. (2017), the weaning process in some animals, such as calves, might be very stressful and even lead to respiratory problems, while supplementing the feed with *S. cerevisiae* can amend the situation as well as help the animal's immune system to reduce the risk of diseases that are intensified in this condition. In particular, it has been reported that *S. cerevisiae* can increase feed efficiency, improve immunity and reduce diarrhea in calves. In field research, the effect of *S. cerevisiae* on lactating Holstein cows and their lactational performance was assessed. All the cows were under heat stress during the experiment. Results of this study indicated that feeding *S. cerevisiae* to cows improved milk yields (1.2 kg/d), with more milk and true protein, and produced solids, not fat (Bruno et al., 2009). Another study by Hiltz et al. (2023) demonstrated that adding *S. cerevisiae* to the feed of dairy cows resulted in an enhancement of milk yield and also an improvement in efficiency at the beginning of lactation.

Substrates for SCP Production by S. cerevisiae

Various substrates have been used for SCP production by cultivating bacteria, algae, filamentous fungi, and yeasts. Some researchers classified them into conventional substrates like fruit and vegetable waste, molasses, whey, straw, starch, distiller's wash and wood and unconventional ones like lignocellulosic biomass, natural gas, methanol, petroleum by-products and ethanol (Bekatorou et al., 2006; Bzducha-Wróbel et al., 2018b). Others categorize the SCP raw materials into different groups, such as various types of waste (fruit waste, molasses, whey, sulfite waste liquor and milk), renewable plant resources (sugar, cellulose and starch), carbon dioxide, and high-energy resources (natural gas, ethanol, gas oil, n-alkanes, acetic acid and methanol) (Bratosin et al., 2021). In addition, SCP is regarded as an economic by-product of biorefinery processes that enhance their profitability while reducing the burden of waste disposal. As a matter of fact, selling residual biomass in the form of SCP for animal feeding is preferable to selling them as fertilizer (Ritala et al., 2017). According to Koukoumaki et al. (2023), who reviewed the latest progress in SCP production, many by-products from industrial sectors and agricultural wastes, such as residues containing high levels of carbohydrates or a variety of effluents, are considered preferable substrates in terms of sustainability matters.

Generally, various agricultural and industrial wastes represent 20 to 30% of the total production cost (Sharif et al., 2021). A high proportion of by-products is generated during fruit and vegetable processing, such as those from apple processing, which are considered a major environmental problem in many countries. The issue could be managed through an environmentally friendly approach by exploiting yeast species (e.g., *S. cerevisiae*) to produce aromatic compounds that have vast applications in the food industry (Kieliszek et al., 2020). In their experiments, Bzducha-Wróbel et al. (2018a) effectively utilized deproteinated potato juice water to produce *S. cerevisiae* cell wall polysaccharides with biotechnology applications in the food industry. They presented a theory regarding the feasibility of yeast biomass production while enhancing the cell wall polysaccharides. Hence, utilizing various types of waste to produce SCP is considered an interesting strategy as it simultaneously produces food-grade protein for human and animal usage and lowers the waste load and environmental pollution (Kieliszek et al., 2020). In this respect, SCP production techniques are often combined with waste processing and bioremediation practices. In China, technologies related to producing SCP from agricultural or food residues are highly favored, and this country holds the record for the highest number of patent submissions and publications related to SCP (Ribeiro et al., 2023). Their share of patent applications from 2001 to 2016 was up to 70% (Ritala et al., 2017). Besides, the ability of microorganisms to decompose hydrocarbon residues as a source of carbon and energy has been widely exploited to produce SCP (Al-Mehmdi & Al-Rawi, 2019).

Nevertheless, there are specific standards that waste materials must meet to be considered a suitable substrate in SCP production. Some of the important ones include abundant, non-toxic, inexpensive and regenerable. The selection of proper substrate is also important since it has a direct impact on the biomass yield and the productivity of fermentation. Microorganisms react differently to various substrates; thus, for each type of substrate, an appropriate fermentation technique needs to be optimized (Reihani & Khosravi-Darani, 2019). Many of the raw materials for producing SCP need to be hydrolyzed through different techniques (physical, chemical and enzymatic) for better fermentation (Suman et al., 2015; Ukaegbu-Obi, 2016). Furthermore, some microorganisms need to be provided with extra minerals and vitamins to obtain maximum productivity (Sharif et al., 2021). The yeast *S. cerevisiae* is mainly cultured on beet or cane molasses, which are the major by-products of the sugar industry. The fermentable sugars in molasses are glucose, galactose, sucrose, fructose, and melibiose, with 45%–55% of the substrate while containing approximately 40% (dry mass) of nonfermentable substances. Molasses in SCP production possess advantages such as the absence of fermentation inhibitors and toxic substances, desirable composition, low cost and abundance (Bekatorou et al., 2006).

In SCP production, a major portion of the cost is attributed to the carbon source, while ammonia contributes only 7%–15%; hence, efforts have been made for *S. cerevisiae* propagation from inexpensive carbon sources such as different fruit waste and cheese whey (Reihani & Khosravi-Darani, 2019; Sharif et al., 2021). For instance, cucumber waste and orange peels have been recommended as useful substrates for producing SCP from this yeast (Suman et al., 2015). Shahzad et al. (2024) studied SCP production from vegetable residues (eggplant, tomato, cucumber, and capsicum) by some yeast species. Their experiments revealed that a co-cultivation of *S. cerevisiae* and *Candida tropicalis* indicated the highest protein yield. Starch will only be usable by *S. cerevisiae* after conversion to fermentable sugars, i.e., glucose and maltose. To maintain the cost of the process, simultaneous culture of *S. cerevisiae* with amylolytic fungi such as *Aspergillus* species are common practices in SCP production from starch (Bekatorou et al., 2006). Molitor et al. (2019) designed a two-stage bioprocessing system under aerobic and anaerobic conditions and caught the ammonia in wastewater as a nitrogen source for edible protein production by *S. cerevisiae*, aligned with the needs of a circular economy. They also applied renewable electric power in their system, referring to a power-to-protein (P2P) scheme to produce SCP (Molitor et al., 2019).

SCP Production Process by S. cerevisiae

Technically, SCP is the production of beneficial biomass cells using microorganisms by culturing them on raw materials or different agricultural and industrial wastes (Anupama & Ravindra, 2000). After choosing a suitable substrate, microorganisms such as algae, bacteria, yeasts, and filamentous fungi can be cultivated on it to increase their cell mass (Bratosin et al., 2021). The industrialization of yeast production began when optimized and standardized manufacturing systems replaced handmade processes of producing fermented food and beverages. Since then, millions of tons of yeast biomass have been produced every year, while optimization of the process is continuously monitored to reduce costs and boost productivity. *S. cerevisiae* is cultured through a two-stage fermentation process: batch fermentation and then fed-batch or aerobic metabolism, designed to propagate the cell numbers. The process occurs in bioreactors where the conditions are controlled, such as temperatures kept between 28–30^{o}C, pH levels between 4.5 and 5.0, and oxygenation rates below 140 mM/L.h. In the initial phase (batch fermentation), high carbon concentration induces hyperosmotic stress in *S. cerevisiae*.

Gradually, the carbon source is consumed along the exponential growth phase, which results in the accumulation of ethanol. This condition exposes the yeast cells to high ethanol concentration as well as nutritional deprivation stress at the end of the process. Under these conditions, *S. cerevisiae* cells switch their metabolism from the fermentative to the oxidative method. If the ethanol concentrations are lower than 0.05%, it is alternatively used as a carbon source (Pereira et al., 2021). Another common method for industrial propagation of *S. cerevisiae* comprises several stages: proliferation through several fermentation processes, harvesting, concentration and/or drying, and packaging (Bekatorou et al., 2006). First, specific *S. cerevisiae* strains from a pure yeast culture are cultivated on an appropriate substrate in the laboratory. Then, the biomass from the laboratory culture is transferred precisely into anaerobic bioreactors. The next stage is *S. cerevisiae* proliferation in fermentation bioreactors operating in anaerobic and fed-batch mode. Using centrifugation, the produced biomass is harvested and utilized for the next steps: fed-batch pitch fermentor and then trade fermentor. The maturation phase includes aerating the contents of the trade bioreactor in the last step. Manufacturers vary in the number of bioreactors, fermentation stages, and sequences. The end product is collected using a rotary vacuum filter or a filter press, with a 27–33% dry cell mass concentration. Appropriate quantities of water, emulsifiers, and cutting oils derived from cottonseed or soybean oil are mixed with *S. cerevisiae* cake to achieve an adequate form for extrusion (Figure 1) (Bekatorou et al., 2006).

A complete setup is required to maintain hygiene and sterile conditions to prevent various types of contamination. This is a recognized occurrence that the SCP process of all types of microorganisms, except algae, requires adequate aeration, which might contain different pathogens (Raziq et al., 2020). The nutritional value of the final SCP product is affected by the methods of harvesting and drying as well as processing techniques (Bratosin et al., 2021). Some researchers have also mentioned further processing stages, such as purification, cell disruption, washing, and protein extraction (Sharif et al., 2021). Generally, the last stage is packaging under a vacuum or nitrogen atmosphere and shipping the product as compressed yeast (Bekatorou et al., 2006).

Regardless of recent promising advancements in SCP production (particularly those from yeast), the primary technologies must be modified for greater improvement in cost efficiency and availability on scale (Ye et al., 2024). In this context, major consideration should focus on optimized utilization of abundant agro-industrial wastes, new process design in line with circular economy principles, exploiting recent innovative automation and control techniques for large-scale production, harnessing genetically manipulated microorganisms for the purpose of degradation of aimed substrates, and novel co-culture cultivation to enhance efficiency and final product yield. In addition, the results of life cycle assessments (LCA) must be factored into a new fermentation scheme and further development of this technology.

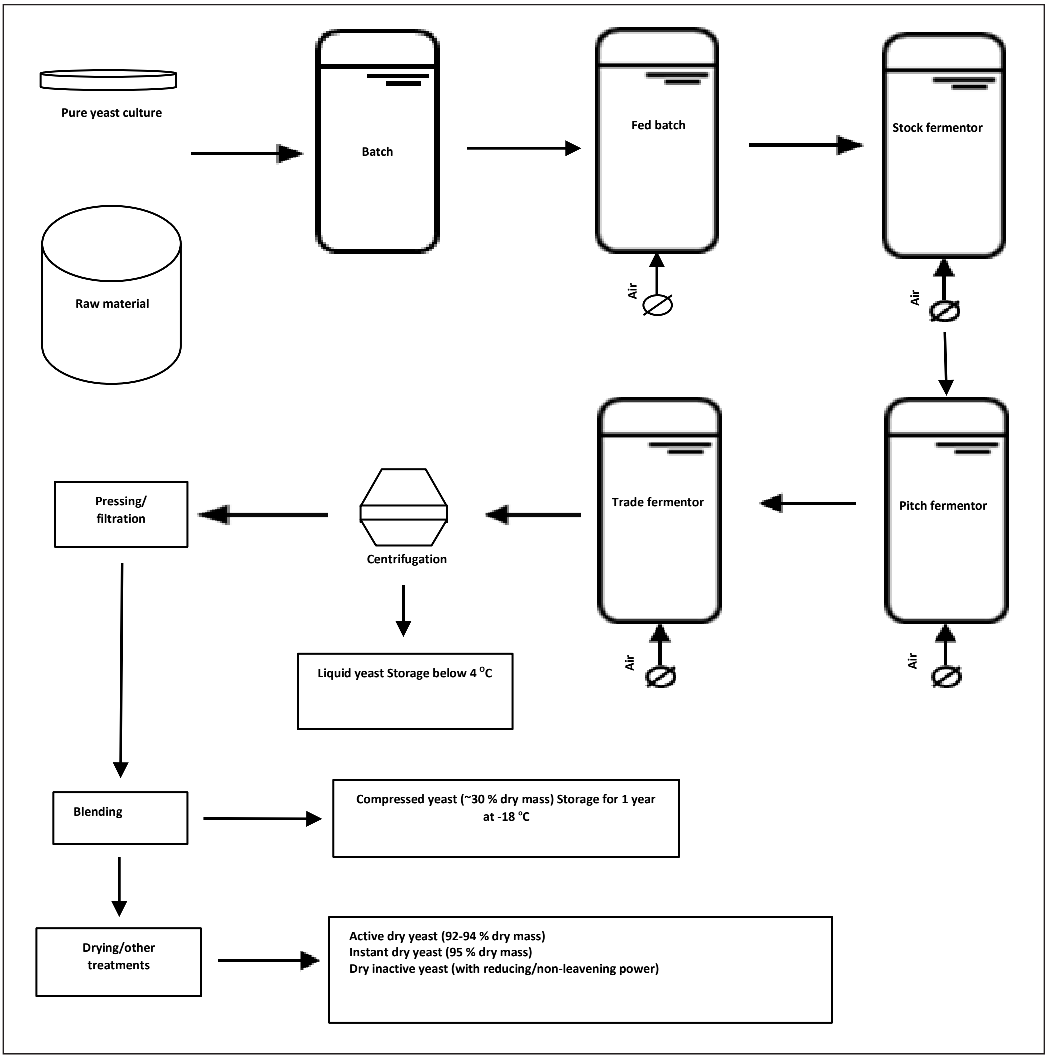

Figure 1. The propagation scheme of a commercial baker's yeast (Bekatorou et al., 2006)

Precision fermentation is one of the newest advances in utilizing recombinant yeast strains to express proteins that have evolved to make particular food-related items accessible (Martin & Chan, 2024). As previously noted, utilizing waste substrates is crucial for any further development of yeast production in the future. One of the main challenges of using lignocellulosic wastes in producing microbial protein is that they need to be hydrolyzed prior to introducing to the main fermentation media (Martin & Chan, 2024). Thanks to the advancement of genetic engineering, a new modified microbial strain with the capability of lignocellulosic waste hydrolyzation could be generated. Another successful example of employing agro-industry by-products is using potato wastewater for yeast cultivation since it is rich in organic carbon, minerals, amino acids and different proteins (Gientka et al., 2017). The high nucleic acid content of yeast cells is a problematic issue addressed through enzyme, alkali, and heat treatments as one of the newest developments in the downstream processing of yeast production (Martin & Chan, 2024).

Microbial protein production via membrane bioreactors is another recent development in the field that could lead to a prominent contribution to efficient manufacturing. In conclusion, the interdisciplinary approach to SCP production involves combining biotechnology and environmental sciences with chemical engineering to reach an efficient and sustainable production system. While biotechnology advancements enable the optimization of culture conditions, instrumental tools of environmental sciences (e.g., life cycle assessment (LCA) and techno-economic analysis (TEA)) evaluate major impacts of the process and present solutions where required for minimizing ecological effects. The integration of chemical engineering and biotechnology offers innovative final products (e.g., environmentally friendly compounds). Moreover, the synergy between the above-mentioned technologies and agricultural systems further supports SCP production.

CULTIVATION METHODS

Based on the physical state of the nutrient medium, SCP production processes (fermentation process) are categorized into three groups (Gupta et al., 2022):

- Submerged fermentation
- Semisolid fermentation
- Solid state fermentation

Submerged Fermentation

Submerged fermentation is known as a more commonly used method in SCP production (Reihani & Khosravi-Darani, 2019). In this type of fermentation process, the used substrates, which contain the nutrients required for microorganisms' growth, are always in liquid forms. The fermenter tank operates continuously, and the biomass yield is harvested continuously through different techniques. The produced SCP is then filtered or centrifuged and subsequently dried. Due to the heat generation during the whole cultivation process, aeration is required, which is done using a cooling device (Ukaegbu-Obi, 2016; Raziq et al., 2020; Sharif et al., 2021). In addition, stirring the fermentation media is required during the submerged fermentation to provide microorganisms with sufficient oxygen (Ukaegbu-Obi, 2016). The methods for harvesting microbial biomass vary, as yeast and bacteria can be recovered through centrifugation, while filtration is usually used for filamentous fungi. Recovery of maximum water content is important, especially prior to the final drying stage. This water has valuable soluble nutrients that can be extracted under clean conditions (Ukaegbu-Obi, 2016; Raziq et al., 2020; Sharif et al., 2021).

Semisolid Fermentation

SCP production by semisolid fermentation involves key operations, including preparing proper media with suitable carbon sources, preventing medium and bioreactor contamination, separating the final product, and processing it accordingly. Effective preparation of substrates plays a crucial role in this type of fermentation. This process takes place in a solid state and requires substantial operating costs and capital investments. Many types of carbon sources, such as carbon oxide, gaseous hydrocarbons, methanol, polysaccharides, ethanol, effluents of various breweries, n-alkenes, molasses and other solid substrates, are usable in semisolid fermentation. The cultivation process itself consists of several steps, including multiphase system mixing, stirring, transport of oxygen from gas bubbles to microorganisms through the liquid phase, and finally, heat transfer to the surroundings (Ukaegbu-Obi, 2016; Raziq et al., 2020; Sharif et al., 2021).

Solid State Fermentation

Solid-state fermentation is implemented via various types of bioreactors, process conditions and many microorganism species to produce a variety of value-added products like SCP, enzymes, feeds, organic acids, flavors, B- complex vitamins, and pigments (Ukaegbu-Obi, 2016; Sharif et al., 2021). The process requires substrates in pure solid form, such as rice and wheat bran. The selected substrate is deposited on the flatbeds subsequent to inoculation with microorganisms, and then the substrate is left in a temperature-controlled room for a few days. The optimal yield can be achieved by ensuring that the moisture level is properly maintained at 60%–65% (Ukaegbu-Obi, 2016; Raziq et al., 2020; Sharif et al., 2021). Although submerged fermentation is the common process for producing SCP from yeast and other fungal species, recently, solid-state fermentation has caught the interest of producers. As previously mentioned, this type of fermentation provides solid nutrients and physical support for the culture, resulting in some advantages over the submerged production process, including lower energy requirements and less wastewater production (Nyyssölä et al., 2022).

CONCLUSION

The yeast *S. cerevisiae*, with unique biological characteristics, is among the most prominent microorganisms used in industrial SCP production, and it is regarded as a promising solution to the feed industry for addressing the challenges of sourcing a safe, sustainable, and competent protein ingredient. Despite the fact that it has been many years since *S. cerevisiae's* introduction to the feed industry, both traditionally and industrially, there are still several challenges that need to be discussed by the scientific research community in the future. The condition that favors *S. cerevisiae* growth and subsequently improves the techno-economics in the related SCP industry is a case in point. Novel bioprocess designs in the industrial production of *S. cerevisiae* require particular consideration in terms of maximizing biomass yields at low costs. The number of research papers investigating the LCA of S. cerevisiae is rather low, while such analyses can lead to an increase in interest in scaling up the related technologies. According to the most recent research under different aerobic and anaerobic conditions, the yeast proteomes and their amino acid profile are not similar. This concept could be more considered in future studies aiming to identify growth conditions focused on targeted results.

In addition to the above-mentioned gaps, some of the key issues to be addressed in future studies are as follows: (1) the effects of *S. cerevisiae* supplementation on growth performance of many non-studied livestock and aquatic animals (2) continuing the use of genetic engineering to enhance the performance of *S. cerevisiae* strains in converting lignocellulosic biomass (3) alleviating the concentration of nucleic acid content of the produced SCP by *S. cerevisiae*. Undeniably, empirical investigations that can assist in providing affordable and feasible solutions for producing protein requirements of feed can eventually help in reducing the burdens of world hunger.

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