Trends in Food Science & Technology 138 (2023) 628–644

Contents lists available at ScienceDirect

Trends in Food Science & Technology

journal homepage: www.elsevier.com/locate/tifs

Fungal solid-state fermentation of crops and their by-products to obtain protein resources: The next frontier of food industry

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ARTICLE INFO

Keywords:
Solid-state fermentation
Fungi
Crops and by-products
Process variable
Protein profile

ABSTRACT

Background: Over the past three decades, solid-state fermentation (SSF) has gained much attention in biotechnology, allowing efficient production of feed, fuels, industrial enzymes, etc., accompanied by less wastewater and less risk of contamination than submerged fermentation (SmF). Meanwhile, mycoproteins obtained using plant biomass to culture fungi have good nutritional values and interesting functional properties. As the environmental burden of producing high-quality protein grows, there is an ongoing discussion about alternatives to conventional animal proteins; mycoprotein production via SSF may offer a potential solution.

Scope and approach: This review conducted a visualization analysis on related studies, demonstrating research hotspots and trends in the development of fungal SSF, and compared fermentation conditions under different circumstances. We further discussed the protein profile of crops and their by-products, and the effects of fungal SSF on protein content, amino acid composition, bioaccessibility, etc. Lately, the technical feasibility and extant limitations of this design are summarized.

Key findings and conclusions: SSF promotes the conversion of residual biomass into edible ingredients or enzymes, alleviating the environmental impact of the food industry with the development of this technology. The fermentation substrate is diversifying from mainly agro-industrial waste. Most crops and their by-products contain significant amounts of plant proteins, existing studies confirm that fungal SSF can further improve the nutritional profile and bioaccessibility. Such solutions accelerate the decoupling of the food industry from arable land and enable the production of high value-added crops. The protein content and amino acid composition of edible fungi are more desirable than those of general fungi and are expected to contribute to the exploration of meat analogs.

1. Introduction

As is well documented, rapid population growth has reduced the quality of life, exacerbated poverty and starvation (Crist et al., 2017). As the major contributor to human nutrition, the food protein supply has garnered widespread attention (Aschemann-Witzel et al., 2021; Kinnunen et al., 2020). Proteins consumed in the daily human diet are predominantly of animal and plant origin, among which the former chiefly comprises conventional animal proteins from farm animals. Despite the potentially higher risk of metabolic syndrome, traditional animal proteins are typically considered superior in terms of nutritional value and functional properties (Chalvon-Demersay et al., 2017; Day et al., 2021; Kim et al., 2020). Nevertheless, the adverse effects of their production must be addressed, including high greenhouse gas emissions, low land use, generation of large amounts of manure and waste, etc. (Leip et al., 2015; Sun-Waterhouse et al., 2014). According to Pimentel and

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https://doi.org/10.1016/j.tifs.2023.06.020
Received 19 March 2023; Received in revised form 25 May 2023; Accepted 12 June 2023
Available online 23 June 2023

Pimentel (2003), it takes an average of 6 kg of plant protein to obtain 1 kg of animal protein. Such inefficient conversion puts a massive strain on both the environment and society, spawning a debate about identifying new alternatives (Aiking & de Boer, 2020). Future foods are generally defined as novel foods that can be manufactured at higher volumes or lower production costs, while possessing the potential for large-scale manufacturing (Parodi et al., 2018; Tzachor et al., 2021). Unlike conventional protein foods, future foods exhibit a similar or higher dry matter protein content, and require less land to obtain the essential nutrients (Parodi et al., 2018). Undeniably, plant protein remains the most practical and viable protein supplement, as evidenced by its outstanding and well-studied nutritional composition and functional properties (Kim et al., 2020; Sá et al., 2020). Yet, the protein content of dry matter and essential amino acid content of future food (Fig. 1A) are not inferior to the aforementioned proteins. However, its feasibility needs to be discussed (Parodi et al., 2018). For instance, the primary resistance of insect protein stems from regulatory barriers, cultivation technology, and consumer perception (Gasco et al., 2020; Rumpold & Schlüter, 2013). Algal protein production is highly variable, with protein content and amino acid composition variability depending on environmental factors. Moreover, precise control of environmental conditions can be disadvantageous in terms of energy and cost (Bleakley & Hayes, 2017; Mišurcová et al., 2010). Microorganisms have a broader scope for the selection of culture substrates and transformation of waste biomass, while the resulting biomass can be easily recycled as biofertilizers, facilitating the design of an economical and sustainable protein acquisition pathway (Souza Filho et al., 2019).

Solid-state fermentation (SSF) is defined as any microbial fermentation process carried out on insoluble materials in the near absence of free-flowing liquid, and continues to build credibility in the production of food, feed, fuel, pharmaceutical products, etc. Such materials serve as both a source of nutrients and physical support (Couto & Sanromán, 2006). Although submerged fermentation (SmF) is more common in bioprocesses, SSF is emerging as an attractive alternative owing to benefits such as higher productivity, less wastewater contamination, reduced risk of substrate contamination, and lower energy requirements (Chilakamarry et al., 2022; Javourez et al., 2022). The water activity (a_w) required for fungal growth (around 0.5–0.6) is lower compared to that of bacteria (around 0.8–0.9), making it easier for SSF to impersonate the natural environment in which it grows (Chilakamarry et al., 2022; Lenovich, 2017; Thomas et al., 2013). There has been a trend to apply SSF to produce nutritious foods utilizing solid agro-food industrial by-products as substrates. The processed substrates include a considerably lower content of lignin and cellulose (Fig. 1B and C). Mycoprotein's nutritional composition and functional qualities have been extensively acknowledged as a sustainable food source generated from fungi (Souza Filho et al., 2019). Since mycoprotein was considered as Generally Recognized As Safe (GRAS) by the Food and Drug Administration (FDA) in 2002, some international companies (e.g. Quorn and MycoTechnology) have successfully commercialized it (Clark et al., 2022; Denny et al., 2008). More importantly, studies have consistently demonstrated that mycoproteins can be used to compensate for plant protein

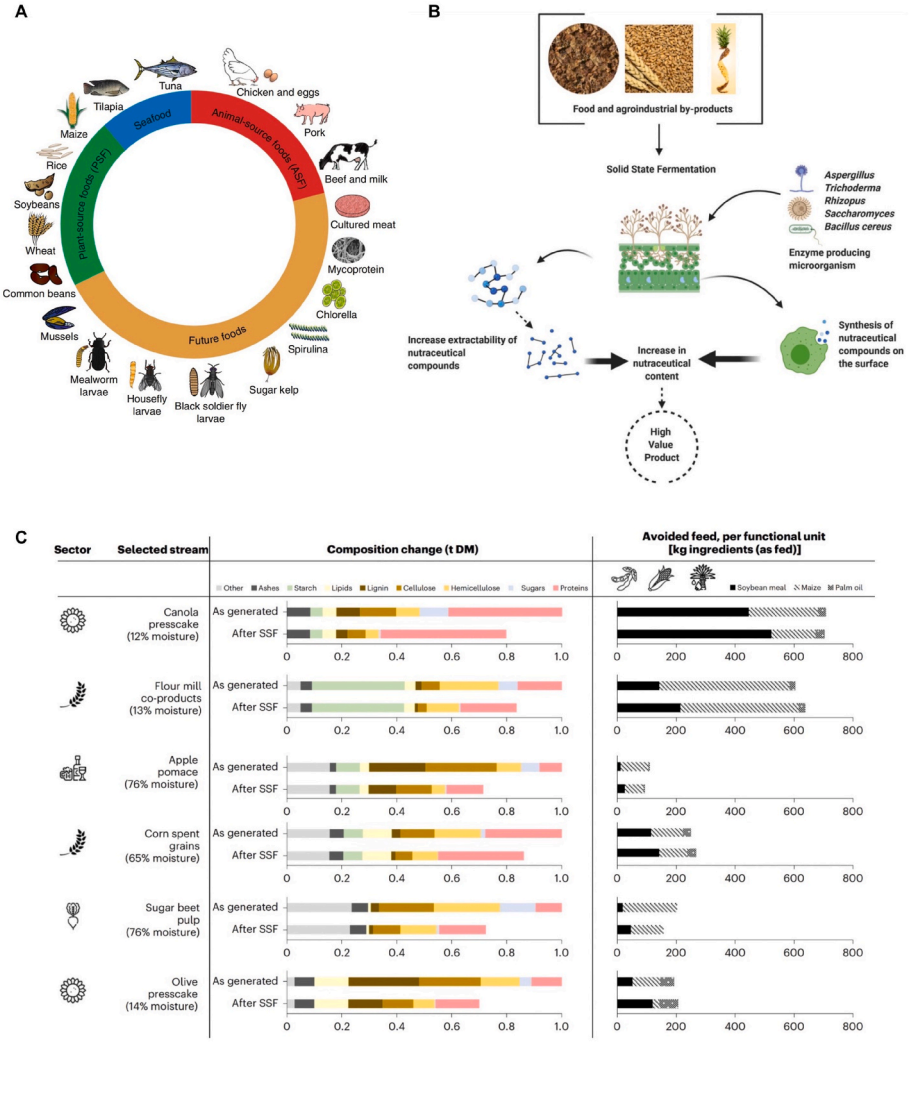

Fig. 1. (A) Traditional and future protein foods from Parodi et al. (2018), copyright (2021), SpringerNature; (B) Schematic representation of a SSF process by using foods and agro-industrial by-products to enhance the nutraceutical content from y Postigo et al. (2021), copyright (2021), Elsevier; (C) SSF changes to agricultural waste composition and avoided soybean meal, corn and palm oil equivalent calculation streams (with or without SSF) from Javourez et al. (2022), copyright (2022), SpringerNature.

deficiencies. In this context, Nosworthy et al. (2017) pointed out that foods based on plant and microbial proteins can be broadly equivalent or even superior to animal-based foods regarding nutritional value, digestibility and processing characteristics. In fact, plant nutrients are coated by cell walls, and as their main content, cellulose significantly affects the human body's digestive ability (Colosimo et al., 2020). SSF can trigger the release of nutrients through the degradation of fibers and lignocellulose, and the derived mycoprotein possesses higher protein digestibility-corrected amino acid score (PDAAS) than beef and chicken proteins, compensating for the absence of essential amino acids in plant proteins (Kim & Kim, 2012; Shrestha et al., 2008). Initially, the SSF substrate was concentrated on agricultural waste, but cultures began to diversify as researchers discovered that the nutrient content of starchy crops was enhanced by fermentation with specific fungi (Zhai et al., 2015). The fungal SSF of crops and their by-products to produce protein biomass is an attractive and up-and-coming area of the food industry.

This critical review aimed to investigate the effect of fungal SSF on the nutritional profile and bioaccessibility of proteins in specific crops and their processing by-products, as well as other proteins involved in the food industry that were also discussed. This article provides a reference for high-quality protein sources while mitigating the population crisis and environmental pressure. All crops discussed herein were limited to high-yielding food crops or cash crops, such as pulses, cereals, pseudocereals, and oilseeds. By-products were defined as multi-stage streams generated along the crop transformation process, such as hulls (primary), breadcrumbs (secondary), etc.

2. Trends in fungal SSF research

Agriculture is an essential lifeline for the development of human society and a critical source of raw materials for the food industry. However, a vast amount of agro-food industrial by-products are generated during harvesting, processing, and consumption (López-Gómez et al., 2020). As illustrated in Fig. 2, SSF can bioconvert lignocellulose-rich substrates (straws, bean meal, oil cakes, bagasse, husks and brans of cereals, breadcrumbs, etc.) into a diverse range of industrial products (Chilakamarry et al., 2022; Thomas et al., 2013). The final product of the majority of fermented microorganisms, especially filamentous fungi, *Saccharomycetes*, and edible fungi, are toxin-free and thus safe for animal and human consumption (Novelli et al., 2016). Considering that the previous substrates mostly consisted of agricultural waste, white-rot fungi, brown-rot fungi and soft-rot fungi that can degrade lignin, cellulose and hemicellulose would be preferable (Soccol et al., 2017). With the development of SSF, this technology has been proposed to be potentially available to produce fungal-plant protein biomass with higher nutritional and functional value. The substrates are also diversified into crops such as cereals and legumes, extracts such as plant proteins and starches, or concentrates like flour (Asensio-Grau et al., 2020; Sánchez-García et al., 2022; Zhai et al., 2015). Meanwhile, edible and medicinal fungi have unique advantages in nutrition, taste and physiological functions, and their utilization for SSF has become a novel approach to the development of functional foods (Wu et al., 2021).

With the express development of fungal SSF research, it is critical to identify the primary contributors to the productivity and migration of research hotspots. The visualization analysis strategy was as follows: The data was obtained from the Web of Science Core Collection (WoSCC) database. TS (term search) = ("solid state fermentation" or "solid substrate fermentation") and ("fungi" or "fungal" or "fungus") and ("protein"). We collected 591 original articles and 67 reviews published from January 1, 2002 to December 31, 2022 in total. CiteSpace software (6.1. R6) and Microsoft Charticulator (https://charticulator.com) were employed to visualize the knowledge domain, the parameters were set to 1 year per slice.

2.1. International cooperation network and main distribution institutions

The visualization map of country or institution cooperation (Fig. 3A and B) consists of nodes and lines. Each node represents a country or institution. Its size reflects the number of publications, while the lines between nodes reflect the closeness of cooperation. In the last two decades, India topped the list with 110 publications (16.72% of the total), followed by China (101, 15.35%), Brazil (70, 10.64%), United States (44, 6.69%) and Mexico (44, 6.69%). Among the various issuing institutions, the University of Sao Paulo (also known as Universidade Estadual Paulista, 28, Brazil) and the University of Boras (15, Sweden) yielded the highest productivity, yet the collaborating institutions are

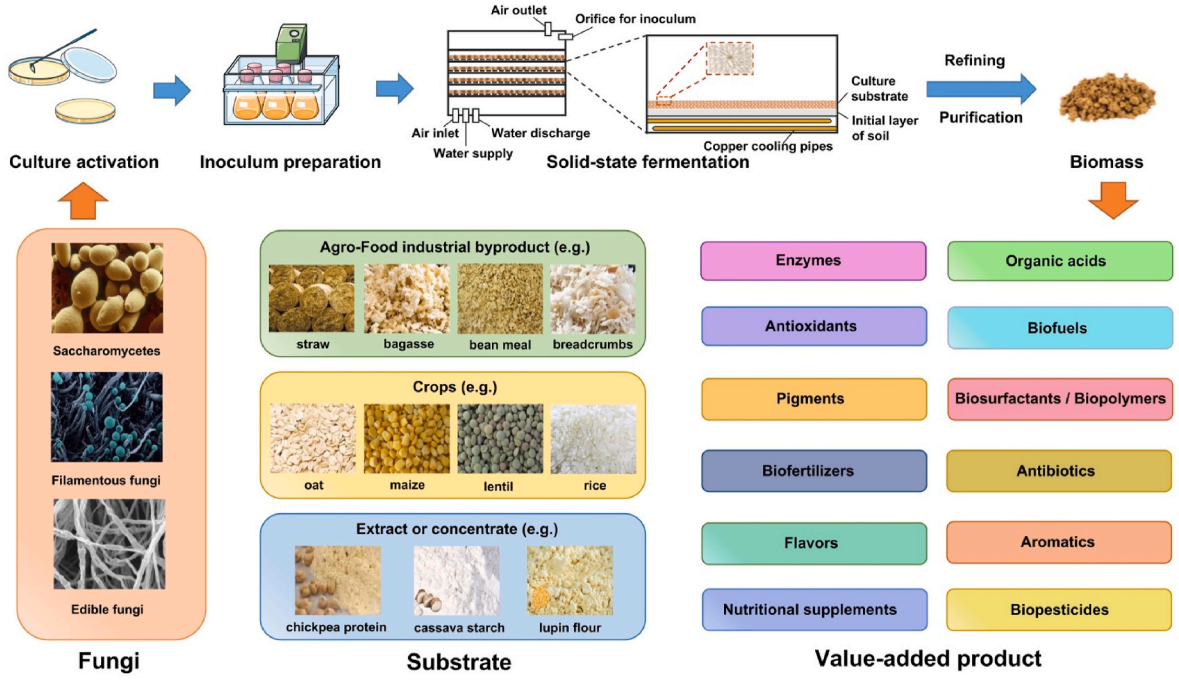

Fig. 2. Fungi, substrates, products and process of solid-state fermentation.

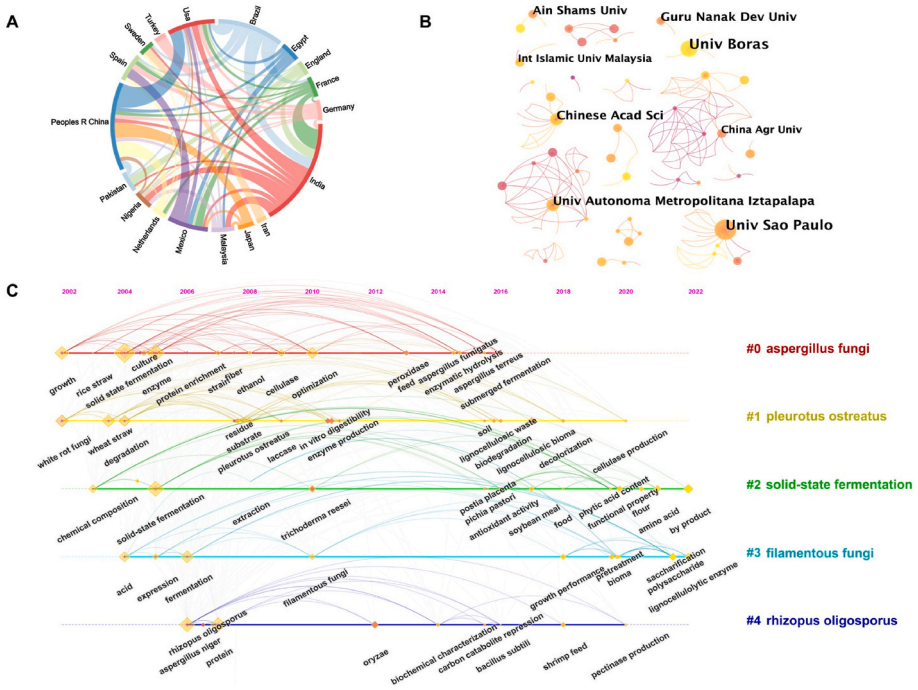

Fig. 3. The knowledge domain of protein production by fungal SSF. (A) Map of international cooperation network; (B) Map of institutions cooperation network; (C) Timelines of keywords evolution trend. Major clusters are labeled on the right from #0 to #4.

relatively homogeneous. While the Universidad Autónoma Metropolitana (12, Mexico), which ranked third, showed a significantly more comprehensive collaborating network. Chinese researchers are also enthusiastic in this field, with five of the top 20 institutions in China, namely the Chinese Academy of Sciences (9), Nanjing Agricultural University (8), Jiangnan University (7), Zhejiang University (7) and China Agricultural University (6).

2.2. Keywords evolution and hotspot migration

Keywords tend to reflect the main content and research direction of the article and are indispensable guides for the understanding protein of production involving fungal SSF. A timeline view can depict the shift in research trends, and the position of a keyword on the timeline represents an estimate of the time when the keyword first received certain attention. The clustering results of #0, #1, #3, and #4 reflect several fungi commonly used in SSF, the most frequently occurring one was *Aspergillus* fungi. Combining Fig. 3C with the extensive literature analysis revealed that research around 2010 was focused on the bioconversion of agricultural waste. Substrates such as rice straw and wheat straw are often used to produce enzymes, organic acids, bioethanol, etc. to reduce the environmental burden (Darwish et al., 2012; Liu et al., 2011; Yu & Tan, 2008). Furthermore, they can provide the nutrients necessary for fungal production in most scenarios and may sometimes require the addition of specific inorganic salts and growth factors (Soccol et al., 2017). The keywords "*in vitro* digestibility" and "feed" both appeared around 2012, whereas "food" appeared in 2018, the edible trend can mainly be seen in this interval. Lastly, the key words "functional property", "amino acid", "phytic acid content" and "polysaccharide" began to appear during the 2020–2022 period, which confirms the initiation of the exploration of fungal SSF in food development.

3. Fungi

The selection of microorganisms is pivotal for SSF development because it can have a significant impact on the productivity, efficiency, and quality of the fermented product. Filamentous fungi are particularly well-suited for SSF, as this technique highly restores their natural habitat (Gmoser et al., 2019; Pérez-Rodríguez et al., 2014). In addition, *Saccharomycetes* and edible fungi along with a few bacteria (e.g. *Lactobacillus* sp. and *Bacillus subtilis*) can adapt to low water activity environments. However, the range of products that can be developed is limited when using bacteria to produce enzymes (Sadh, Duhan et al., 2018). This can be attributed to the fact that the biochemical composition of bacteria makes them more likely to pose a safety risk when designing edible resources and is therefore beyond the scope of this review (Sillman et al., 2019).

3.1. Saccharomycetes

Saccharomycetes has a long history in the fermentation industry and its nutritional quality is globally recognized. Cases of protein enrichment by *Saccharomyces cerevisiae* to improve the nutritional value of feed have been reported (Aruna et al., 2017; Godoy et al., 2018; Hassaan et al., 2015; Sharawy et al., 2016). Inulinase is a type of fructose hydrolase produced by *Saccharomycetes* isolated from fermented sugarcane that plays an essential role in the manufacturing of high fructose syrup (Onilude et al., 2012). Single-cell protein (SCP) is the total protein extracted from microbial cells that can be produced on agro-food waste (Gervasi et al., 2018). More specifically, SCP obtained from *Saccharomycetes* is proposed as space food, and the amino acid score, antioxidant activity, and functional properties of the product are excellent (Razzaq et al., 2020). The genome engineering of *Saccharomycetes* allows for the specific and efficient production of a particular protein resource. A substantial number of markers are available, which is an advantage that other fungi do not possess (Jakočiūnas et al., 2015).

3.2. Filamentous fungi

Filamentous fungi, especially *Aspergillus* spp. such as *Aspergillus ricinus* and *Aspergillus niger*, are the principal contributors to enzyme production. Xylanase and cellulase-associated studies were the most frequently conducted, followed by protease, laccase, lipase and amylase (Soccol et al., 2017). Glucoamylase and alpha-amylase produced by the

filamentous fungal SSF effectively degrade starch during the production of Chinses *Moutai*-flavor liquor, and the fungal species are decreased during SSF, with *Paecilomyces variotii* and *Aspergillus oryzae* being the predominant species (Chen et al., 2014). As for the acquisition of edible protein, *Fusarium venenatum* A3/5 is a typical type of filamentous fungi that was employed for mycoprotein production by Quorn™. Jacobson and DePorter (2018) collected self-reports of adverse reactions to mycoprotein produced by Quorn™ through a web-based questionnaire, and the results uncovered that allergic reactions and gastrointestinal symptoms were the most frequently encountered adverse events. For safety concerns, filamentous fungi always require additional evaluation when manufacturing food products.

3.3. Edible fungi

Edible fungi are the most acceptable source of fungal protein for consumers, usually combining lignocellulosic degradation and heavy metal enrichment capability (Kim, 2021; Kumla et al., 2020). The protein dry weight of edible fungi is typically 19–37%, similar to or even higher than livestock products such as pork and chicken (González et al., 2020). Their amino acid profile is complete, containing all essential amino acids with essential histidine for infants (Table 1). According to prior reports, the high content of amino acids and glutamic acid in meat analogs produced using the mycelium of *Agaricus bisporus* mimics the umami characteristics of meat (Kim et al., 2011). *Pleurotus ostreatus* and *Ganoderma lucidum* belong to the category of white-rot fungi, which are known to be most effective in secreting laccase, which can effectively improve the stability of wine (Melanouri et al., 2022; Minussi et al., 2007). Additionally, health active ingredients (functional polysaccharides, terpenoids, adenosine, etc.) in edible fungi have received increasing attention and are therefore more suitable for functional food development. These ingredients can improve the antioxidant activity of fermented substrates and enrich proteins while reducing the amount of antinutrients through bioconversion (Asensio-Grau et al., 2020).

4. Process variables

Regulating process variables in SSF is crucial because it affects the growth and metabolism of the fungi, which in turn, affects the yield and quality of the final product. These factors can be classified into physicochemical, biochemical and environmental factors according to their characteristics.

4.1. Substrate

A suitable substrate for SSF should offer all the necessary nutrients for the growth and metabolism of the fungi, as well as an appropriate physical environment for the fermentation process. Some examples of substrates used in SSF with fungi include agricultural waste, food waste, and cellulose-based materials. A combination of different substrates can also be used to improve nutritional balance and optimize the process (Erkan et al., 2020; Machado et al., 2016). An adequate carbon source is necessary. However, an excessively high concentration may inhibit protein secretion (Irfan et al., 2014).

4.1.1. Substrate pretreatment

When a substrate for SSF is being prepared, pretreatment is a critical step that could significantly enhance the efficiency of the process. This can be achieved through various methods, including physical, chemical, and biological methods, as well as moisture and sterilization. The surface area increases by physically grinding or milling the substrate, providing greater access to the microorganisms. Furthermore, by using chemical agents such as acids or enzymes, complex carbohydrates and proteins can be broken down, making them more readily available for fungi. Another approach to preparing the substrate is to utilize other microorganisms to break it down prior to fermentation. Pretreatment can also assist in mitigating the risk of contamination by unwanted microorganisms, which can negatively impact fermentation. This can be attained by using sterilization techniques such as heat treatment, ultraviolet radiation, or chemical treatment (Chilakamarry et al., 2022).

4.1.2. Substrate particle size

Smaller particle sizes can increase the surface area-to-volume ratio of the substrate, thereby improving the fermentation rate by increasing the availability of nutrients and oxygen to the fungi. Consequently, faster growth and higher yields of the desired fermentation products (Singhania et al., 2015). However, smaller particle sizes can also elevate the risk of clogging and compaction, reducing the efficiency of the fermentation process (Kumar et al., 2021). On the other hand, larger particle sizes can decrease the surface area-to-volume ratio and reduce the fermentation rate, but can also increase the stability and longevity of the fermentation process. The optimal particle size for SSF depends on the specific strains and substrates being used, as well as the desired fermentation products. Zhai et al. (2015) and Cai et al. (2012) pre-crushed or ground grains before fermentation, and the particle size was generally controlled to about 2 mm. In another instance, Xiao et al. (2014) used shelled chickpeas directly for SSF and still achieved favorable results, signifying that particle size is not required to be tightly controlled in most cases, especially in the laboratory.

4.2. Inoculum size

The amount of inoculation refers to the quantity of fungal spores or mycelium that are added to the substrate, and can affect the growth rate and biomass production of the fungi (Thomas et al., 2013). Research has established that increasing inoculum size can lead to a faster and more efficient fermentation process. However, it is worthwhile emphasizing that increasing the size of the inoculum can also result in decreased oxygen availability and increased competition for nutrients among microorganisms, which can negatively impact the efficiency of the fermentation process. Nema et al. (2019) tested suspensions containing 5.4, 10.8, 16.2, and 21.6 million *Aspergillus niger* spores per mL and found that the highest lipase activity was produced at 10.8 million per mL. Furthermore, the physical properties of the substrate can also impact the optimal inoculum size for a given SSF process. For example, if the substrate is highly porous, a larger inoculum size may be necessary to ensure that all parts of the substrate are colonized by the fungi. However, if the substrate is less porous, a smaller inoculum size may be sufficient. By monitoring the progress of the size of the fermentation, the size of the inoculum can be increased or decreased as necessary to optimize the yield and quality of the final product.

4.3. pH

The pH of the medium can be affected by a multitude of factors, including the type of fungus employed, the composition of the substrate, and the conditions of the fermentation process. During fungal SSF, the pH of the substrate typically decreases as a result of the production of organic acids by the fungi upon the break down of the substrate for energy and nutrients. Previous studies have evinced that various species of fungi, such as *Aspergillus niger* and *Rhizopus oryzae* can significantly lower the pH of the substrate during fermentation (Das et al., 2015; Dessie et al., 2018; Dhillon et al., 2013). Edible fungi and *Saccharomycetes* generally require a slightly acidic environment, while an above neutrality pH is preferable for filamentous fungi (Kumar et al., 2021).

4.4. Moisture content and water activity

Insufficient moisture content can limit the growth and metabolism of the microorganisms, resulting in low biomass and enzyme production. This is attributed to fungi requiring enough water to maintain their

Table 1
Nutritional and amino acid composition of different edible fungi.

	A. bisporus	*A. brasiliensis*	*F. velutipes*	*L. edodes*	*P. djamor*	*P. eryngii*	*P. ostreatus*	*P. djamor*	*P. ferulae*	*P. nebrodensis*	*P. sapidus*	*A. chaxingu*
General nutritional composition (g/100 g DW)												
Total protein	26.99 ± 0.46	33.39 ± 0.15	19.01 ± 0.71	18.87 ± 0.39	22.54 ± 0.19	16.47 ± 0.42	22.54 ± 0.20	15.6 ± 1.52	30.3 ± 1.45	27.7 ± 1.71	20.4 ± 1.09	/
Lipids	2.08 ± 0.14	1.43 ± 0.27	1.97 ± 0.18	1.40 ± 0.07	1.40 ± 0.17	1.74 ± 0.13	1.40 ± 0.07	1.65 ± 0.32	5.71 ± 0.61	7.35 ± 0.93	4.85 ± 0.24	/
Ash	11.85 ± 0.04	9.34 ± 0.26	8.52 ± 0.14	8.82 ± 0.12	8.17 ± 0.27	6.93 ± 0.16	6.99 ± 0.17	5.83 ± 1.06	4.96 ± 0.36	3.84 ± 0.48	5.32 ± 0.88	/
Total dietary	29.43 ± 0.77	33.97 ± 1.29	32.14 ± 1.06	41.89 ± 0.57	35.30 ± 1.44	29.04 ± 1.73	46.62 ± 0.92	17.2 ± 0.72	11.2 ± 0.19	15.7 ± 1.18	12.3 ± 0.22	/
Amino acid composition (g/100 g DW)												
(i) Essential												
Histidine (His)	0.69 ± 0.02	0.91 ± 0.09	0.58 ± 0.02	0.52 ± 0.01	0.59 ± 0.00	0.41 ± 0.01	0.69 ± 0.01	0.18	0.45	0.32	0.33	0.30 ± 0.02
Isoleucine (Ile)	1.26 ± 0.05	0.94 ± 0.02	0.77 ± 0.03	0.88 ± 0.01	0.88 ± 0.01	0.61 ± 0.03	0.85 ± 0.01	0.43	1.14	0.58	0.56	0.39 ± 0.07
Leucine (Leu)	1.87 ± 0.02	2.37 ± 0.08	1.10 ± 0.08	1.28 ± 0.04	1.46 ± 0.02	0.87 ± 0.04	1.41 ± 0.01	0.41	0.22	0.90	0.96	0.61 ± 0.11
Lysine (Lys)	1.52 ± 0.03	1.92 ± 0.18	1.43 ± 0.00	1.14 ± 0.02	1.22 ± 0.01	0.87 ± 0.04	1.23 ± 0.01	0.37	1.30	0.68	0.78	0.29 ± 0.07
Methionine (Met)	0.59 ± 0.03	0.50 ± 0.01	0.34 ± 0.03	0.37 ± 0.02	0.45 ± 0.02	0.29 ± 0.01	0.37 ± 0.01	0.12	0.36	0.26	0.62	0.08 ± 0.01
Phenylalanine (Phe)	1.21 ± 0.02	1.21 ± 0.05	1.02 ± 0.01	0.91 ± 0.00	0.94 ± 0.00	0.73 ± 0.01	1.05 ± 0.01	0.27	0.87	0.45	0.56	0.29 ± 0.02
Threonine (Thr)	1.50 ± 0.00	1.46 ± 0.10	1.01 ± 0.01	1.11 ± 0.02	1.14 ± 0.01	0.84 ± 0.02	1.29 ± 0.04	0.37	0.81	0.47	0.62	0.53 ± 0.06
Tryptophan (Trp)	0.50 ± 0.03	0.55 ± 0.01	0.26 ± 0.01	0.30 ± 0.01	0.30 ± 0.01	0.19 ± 0.00	0.24 ± 0.01	0.32	/	/	/	/
Valine (Val)	1.58 ± 0.05	1.09 ± 0.05	1.08 ± 0.01	1.20 ± 0.01	1.21 ± 0.02	0.87 ± 0.01	1.36 ± 0.01	0.56	0.12	0.68	0.65	0.51 ± 0.08
(ii) Non-essential												
Alanine (Ala)	3.28 ± 0.02	2.10 ± 0.13	1.47 ± 0.04	1.40 ± 0.02	1.89 ± 0.02	1.22 ± 0.05	2.27 ± 0.04	0.55	1.29	0.57	0.79	1.03 ± 0.06
Arginine (Arg)	1.41 ± 0.00	2.04 ± 0.06	1.17 ± 0.03	1.38 ± 0.01	1.64 ± 0.02	1.95 ± 0.01	1.41 ± 0.03	0.74	1.26	1.01	0.81	0.50 ± 0.05
Aspartic acid (Asp)	2.59 ± 0.06	2.65 ± 0.07	1.56 ± 0.12	1.73 ± 0.02	2.04 ± 0.07	1.35 ± 0.01	2.52 ± 0.09	0.86	2.11	1.18	1.24	0.56 ± 0.02
Cysteine (Cys)	0.90 ± 0.01	0.45 ± 0.06	0.80 ± 0.00	1.21 ± 0.11	1.03 ± 0.04	0.63 ± 0.01	0.95 ± 0.03	0.59	0.25	0.05	0.07	/
Glutamic acid (Glu)	4.50 ± 0.02	5.73 ± 0.13	3.49 ± 0.08	2.93 ± 0.02	3.86 ± 0.04	2.21 ± 0.03	5.98 ± 0.18	0.71	0.33	0.22	0.21	1.20 ± 0.12
Glycine (Gly)	1.96 ± 0.02	2.70 ± 0.02	1.30 ± 0.07	1.53 ± 0.01	1.65 ± 0.01	1.22 ± 0.01	1.55 ± 0.00	0.55	0.95	0.56	0.56	0.47 ± 0.05
Proline (Pro)	1.45 ± 0.03	1.87 ± 0.04	0.73 ± 0.02	0.98 ± 0.01	1.06 ± 0.01	0.61 ± 0.01	0.97 ± 0.01	0.47	0.57	0.71	0.25	0.48 ± 0.05
Serine (Ser)	1.33 ± 0.02	1.46 ± 0.10	0.94 ± 0.01	1.08 ± 0.01	1.35 ± 0.01	0.84 ± 0.00	1.38 ± 0.01	0.60	0.86	0.46	0.67	0.58 ± 0.08
Tyrosine (Tyr)	1.01 ± 0.01	0.77 ± 0.07	0.98 ± 0.03	0.81 ± 0.01	0.71 ± 0.00	0.63 ± 0.01	0.92 ± 0.01	0.34	0.33	0.25	0.36	0.19 ± 0.01
Total sulfur amino acids (Met + Cys)	1.49	0.95	1.14	1.58	1.48	0.92	1.32	0.71	0.61	0.31	0.69	0.08
Total aromatic amino acids (Phe + Tyr)	2.22	1.98	2.00	1.72	1.65	1.36	1.97	0.61	1.20	0.70	0.92	0.48
Essential (EAA)	10.72	10.95	7.59	7.71	8.19	5.68	8.49	2.48	7.15	3.65	4.43	3.00
Total Amino acid (TAA)	29.15	30.72	19.99	20.78	23.42	16.36	26.44	8.44	19.2	11.3	11.9	8.01
EAA/TAA (%)	36.78	35.64	37.97	37.10	34.97	34.72	32.11	29.38	37.24	32.30	37.23	37.45
Reference	Bach et al. (2017)	Bach et al. (2017)	Bach et al. (2017)	Bach et al. (2017)	Bach et al. (2017)	Bach et al. (2017)	Bach et al. (2017)	Guo et al. (2007)	Guo et al. (2007)	Guo et al. (2007)	Guo et al. (2007)	Lee et al. (2011)

Note: data not found in some of the literature.

turgor pressure, which is key for their growth and metabolism. Fungal SSF processes perform best at a moisture level of 50–60% (Table 3), since a substrate with low moisture content can cause an increase in viscosity. Contrastingly, high moisture content can cause substrate collapse, leading to poor aeration and the formation of micro-clusters of microorganisms (Deswal et al., 2011; Kumar et al., 2011). Water activity and water content are strongly correlated because water activity corresponds to the amount of water available to fungi since some of the bound water is not available to cells (Sala et al., 2020). Agarwal et al. (2020) quantified the water condensate on the surface of the substrate to estimate water activity with digital image processing techniques in MATLAB, which takes SSF further towards automation.

4.5. Temperature

Most fungi are known to grow well at temperatures between 20 and 30 °C. It is well established that an increase or decrease in temperature outside of the optimal range can harm the fermentation process (Farinas, 2015). For example, if the temperature is too low, fungal growth may slow or stop, resulting in a decrease in substrate utilization and in the production of enzymes and metabolites. On the other hand, if the temperature is excessively high, the fungi may be killed or may produce toxins, resulting in an unsafe and undesirable fermentation product. However, it is worth noting that the optimal temperature for efficient production of a specific product is not necessarily the optimal temperature for fungal growth. Naturally, the ideal fermentation temperature should be a compromise between these two temperatures (Yoon et al., 2014).

4.6. Aeration

Aeration helps dissipate the heat generated during SSF, removes excess water to prevent ponding, and inhibits excess carbon dioxide from promoting the growth of other anaerobic microorganisms. The rate of metabolic heat production requires real-time monitoring and appropriate reduction in inlet air temperature during the peak (Finkler et al., 2021). Besides, the oxygen content is the most concerning factor. The presence of pores in the aerial mycelium layer allows for swift diffusion of oxygen, which is of great significance for improving yields. *Aspergillus oryzae* usually forms abundant aerial mycelium to overcome oxygen limitation in deeper positions (Barrios-González, 2012). The larger the bioreactor, the greater the possibility of uneven airflow, while the temperature distribution inside the bioreactor serves to determine the occurrence of trench flow (Mitchell et al., 2006). Agitation enables more efficient transfer at the interface between gas and liquid, but is particularly damaging to filamentous fungi. Therefore, its applications are limited. The uniformity of aeration is necessary for efficient SSF regulation, which can also be modified by the inclusion of bed porosity regulators and by designing structured filled beds (Pitol et al., 2017). In relatively narrow fermentation environments, there is also a need to involve the wall effect, which refers to the lower density of accumulation near the wall, that is relatively intensified when long fibers (such as bagasse, straw and other agricultural waste) are added, and can be used as inert materials to ensure the porosity of the substrate (Casciatori & Thoméo, 2018).

4.7. Bioreactor

The role of a bioreactor in SSF is to provide a controlled environment for the growth and metabolism of microorganisms, as well as to facilitate the transfer of nutrients and oxygen to the substrate and the removal of waste products. Bioreactors can also be used to mix, agitate, and control the temperature and humidity of the substrate, thereby enhancing the efficiency and yield of the fermentation process. Certainly, most laboratory studies are conducted in conical flasks, reagent bottles, plastic bags, and Roux bottles. In addition, when the process is scaled up, the selection of a suitable bioreactor and operating conditions are instrumental in optimizing the production. As conducted in Table 2, there are various types of SSF bioreactors which can be mainly divided into static (fixed bed, perforated tray, etc.) and dynamic (koji bioreactor, drum, mixing bioreactor, etc.) types, basically designed to address heterogeneity in heat and mass transfers (Arora et al., 2018; Spier et al., 2011). From the point of view of economic feasibility, the tray bioreactor is the most scalable and the easiest to maintain. Despite the disadvantages in heat transfer capability, aseptic operation and *in situ* product recovery capability, commercial companies still prefer tray bioreactor. Moreover, shearing of the upper layer does not damage the mycelium, and growth is not impaired if it is exclusively used to harvest aerial mycelium (Vaseghi et al., 2013). Drum bioreactors provide unique advantages in temperature and moisture control, but inadequate aeration may still lead to agglomeration (Alam et al., 2009; Ge et al., 2017; Lopez-Ramirez et al., 2018). Gas-solid fluidized bioreactor, despite its excellent heat transfer capacity, provides too much shear for mycelium and is not suitable for most filamentous fungal SSF (Zhang et al., 2021).

4.8. Co-culture

In pure culture, the utilization of biomass by fungi is relatively limited (Behera & Ray, 2016). The use of multiple fungi in SSF allows for the utilization of different substrates and the ability to produce a variety of proteins. This is particularly useful in producing food and feed proteins, as well as enzymes and other bioactive compounds (Wongwilaiwalin et al., 2010). For example, when *Aspergillus sojae* and *Aspergillus ficuum* were co-cultured on canola meal, the content of macronutrients and functional properties of proteins were improved. The investigators concluded that the reduction in *in vitro* digestibility was a coincidental phenomenon that was not necessarily universal and required further discussion (Olukomaiya, Fernando et al., 2020). Furthermore, when bacteria and fungi grow together, they can form mutualistic relationships, where they aid each other in growing and producing more protein. For example, bacteria can produce vitamins and amino acids that the fungi can use for growth and protein production, whilst fungi can produce enzymes that break down complex carbohydrates for the bacteria to utilize. In a study conducted by Ding et al. (2020), the highest crude protein content was obtained when *Bacillus subtilis*: *Aspergillus niger*: *Saccharomyces cerevisiae* was used to ferment tea pomace in a 1:1:2 ratio. The strain ratio accelerated the synthesis of biomass, and the period of degradation rate was shorter. Besides, Alhomodi et al. (2021) described that when *Trichoderma reesei* was co-cultured, carbohydrate release and utilization efficiency were higher during canola meal fermentation.

5. Effects of fungal SSF on the protein profile and processing potential of substrate

A huge body of evidence signals that the nutrient composition of the substrate markedly fluctuates during the SSF (Kumitch et al., 2020; Lateef et al., 2008; Sitanggang et al., 2019). The proteins produced via SSF have not been fully studied and may possess health benefits beyond any other functions that need to be unlocked. For instance, Myco-Technology has designed CleatIQ™ bitter taste blocker using edible fungi fermentation, which partially blocks the bitter taste receptors on the tongue.

5.1. Protein content

Variations in total protein content before and after SSF visualized the perspective of a certain substrate-strain combination. The SSF efficiency of different bioreactors varies widely, and its effect on protein content cannot be ignored. Fortunately, bioreactors concerning enzyme production tend to be more complex, whereas research on enhancing nutritional value is mostly limited to laboratory trials. In other words,

Table 2
Overview of SSF bioreactors performance.

	Loading capacity	Heat transfer capability	Damage to fungal mycelia	Main characteristics	Application Scenarios	Reference
No forced aeration						
(i) No mixing						
Tray bioreactor	Operating bed height limits the substrate bed loading	Low thermal conductivity, inefficient heat dissipation	No damage	The substrate is spread onto each tray and maintained in a chamber at constant temperature. Tray surface is covered with heat transfer media (e.g. linen) and nutrients are uniformly sprayed by peristaltic pumps	Relatively loose substrates, such as bagasse, bran, etc. Sufficient production space (requires a large number of trays with large volume chambers)	Vaseghi et al. (2013)
(ii) Continuous or frequent mixing						
Rotating drum bioreactor	Low substrate bed loading, around 30%	At high substrate bed loading temperature control is off limits	Shear forces come into play	Consists of three subsystems: the drum wall, the headspace and the substrate. May come with different sizes and shapes of internal threaded baffles or lifters	Relatively small substrate particle size. Mostly applied to produce cellulase and hemicellulase	Arora et al. (2018), Farinas (2015)
Stirred drum bioreactor	Loading is also around 30%	Superior to rotating drum bioreactor	More damage than rotating drum bioreactor. Related to the agitation strength and the shape of the agitation device	Stirring devices (e.g. paddles and baffles) are installed inside the drum. Fungal biomass and enzyme productivity are significantly higher than conical flasks	Smaller substrate particle size than rotating drum bioreactor. Conditions of high humidity and easy caking	Alam et al. (2009), Lopez-Ramirez et al. (2018)
Forced aeration						
(i) No mixing						
Packed bed bioreactor	Low substrate loading coefficients due to bed compaction	Multiple heat transfer modes, but bed compaction and air channeling at large scale production	No damage	The entire system consists of columns with solid substrate supported on a perforated base, from which air is forced through the bed	Produce xylanase, endoglucanase and other enzymes that require high temperature stability. Also commonly used in the manufacture of commercial wine batches	Couto and Sanromán (2006), Farinas (2015)
Intermittently stirred packed-bed	Substrate bed loading generally higher than tray bioreactor, rotating drum bioreactor and packed bed bioreactor	Improvement in the occurrence of bed compaction and air channeling	Potential damage, prior mixing optimization required	Reduces the gradient distribution of temperature and moisture content. Similar to drum bioreactor, intermittent agitation allows the mycelium to form the particles into appropriately sized agglomerates, which enhances SSF efficiency	Similar to stirred drum bioreactor	Finkler et al. (2017)
(ii) Continuous or frequent mixing						
Rocking drum bioreactor	High loading coefficient	High degree of convection	Circulation velocity affects mycelial integrity	Consists of three drums - inner drum, middle drum and outer drum. Air and water enter the bioreactor through the inner drum, while the other two drums provide mixing. Stronger oxygen transfer and weaker shear than stirred bioreactors. Moderate surface area to volume ratio compared to other bioreactors	Expanded production volume than other drum bioreactors	Ge et al. (2017)
Gas-solid fluidized bioreactor	Low bed loading	Efficient heat transfer, fluidized state by the action of upward flow of fluid	Intensive, not suited for aseptate fungi	Consists of two main parts, the lower part (containing the liquid/gas inlet and distribution plate) and the upper part (mainly the bed post).	Few or no aerial mycelium, not suitable for most filamentous fungi	Zhang et al. (2021)

Note: Referenced the classification in y Postigo et al. (2021); Some parameters in Loading capacity, Heat transfer capability, and Damage to fungal mycelia are collated from Arora et al. (2018).

containers of SSF are mostly conical flasks, reagent bottles, plastic bags, etc., which helps to compare yields (Table 3). Although it is challenging to accurately control the proportion of wet base by prior soaking, the moisture is evenly distributed, and the fungi promptly proliferate. The increase in protein content is higher in high fiber substrates, but this is not absolute. The most significant increase occurred in a study conducted by Darwish et al. (2012), in which the protein content of maize stalks increased by 127.8–227.8% following the fermentation of *Saccharomyces cerevisiae*. Baldwin et al. (2019) compared the ability of *Aureobasidium pullulans* to convert soybean meal to high-protein feeds during submerged fermentation versus solid-state fermentation separately. They found that the most efficient conversion of carbohydrates to protein occurred when the solid loading rate was 40% (solid-state). The timing for halting fermentation is also a significant factor in determining protein content. As the fungus grows and produces protein, harvesting at the right time plays a decisive role in achieving optimal protein yields.

Table 3
Substrates, fungi, fermentation condition and the protein content change of SSF.

Substrate	Fungi	Fermentation conditions	The increase in protein content (%)	Reference
Agro-food industrial by-products				
(i) single substrate				
canola meal	*Pleurotus ostreatus*	65% moisture content, 28 °C, 4–20 d	11.0–18.0	Heidari et al. (2022)
canola meal	*Trichoderma reesei*	50% moisture content, 30 °C, 7 d	23.0	Croat et al. (2016)
	Aureobasidium pullulans		15.4–16.9	
canola meal	*Aspergillus sojae*	45% moisture content, 30 °C, 7 d	0.8–4.6	Olukomaiya, Fernando et al. (2020)
	Aspergillus ficuum			
soy meal	*Aspergillus oryzae*	50% moisture content, 30 °C, 36 h	16.8	Chen et al. (2013)
soybean meal	*Saccharomyces cerevisiae*	50% moisture content, 40 °C, 2 d	13.7	Hassaan et al. (2015)
soybean meal	*Rhizopus oligosporus*	50% moisture content, 30 °C, 5 d	6.0–18.5	Sitanggang et al. (2019)
	Aspergillus oryzae			
rapeseed cake	*Aspergillus niger*	50% moisture content, 30 °C, 3 d	23.0	Shi et al. (2015)
olive cake	*Beauveria bassiana*	60% moisture content, 25 °C, 14 d	25.5	Chebaibi et al. (2019)
	Fusarium flocciferum		51.9	
	Rhizodiscina cf. *lignyota*		49.2	
	Aspergillus niger		35.0	
peanut oil cake	*Aspergillus oryzae*	47.6% moisture content, 30 °C, 6 d	/	Sadh, Chawla et al. (2018)
maize stalk	*Pleurotus ostreatus*	70% moisture content, 28 °C, 7 d	75.0–126.4	Darwish et al. (2012)
	Saccharomyces cerevisiae		127.8–227.8	
grape stalk	*Lentinula edodes*	85% moisture content, 28 °C, 28–42 d	70.8–77.1	Costa-Silva et al. (2022)
	Pleurotus eryngii		31.3–39.6	
	Pleurotus citrinopileatus		83.3–106.3	
wheat bran	Commercial baker's yeast	50% moisture content, 37 °C, 1 d	6.2	Zhao et al. (2017)
stale bread	*Neurospora intermedia*	semi-continuous fermentation	/	Wang et al. (2021)
waste bread	*Neurospora intermedia*	60% moisture content, 35 °C, 4 d	161.0	Gmoser et al. (2019)
(ii) multiple substrates				
palm kernel cake	*Rhizopus stolonifer*	65–72% moisture content, 30 °C, 5 d	33.3	Lateef et al. (2008)
cassava peel			55.4	
cocoa pod husk			94.8	
Oat bran	*Pleurotus ostreatus*	60% moisture content, 25 °C, 21 d	31.8–57.2	Eliopoulos et al. (2022)
Olive mill stone waste				
rice bran	*Lentinus citrinus*	80–90% moisture content, 25 °C	/	Machado et al. (2016)
nutshell				
Crops				
chia seed	*Pleurotus ostreatus*	42.9% moisture content, 28 °C, 14 d	14.2	Calvo-Lerma et al. (2022)
sesame seed			3.8	
soybean	*Tricholoma matsutake*	full soaking in advance, 30 °C, 12 d	/	Lee et al. (2019)
red kidney bean	*Rhizopus oligosporus*	appropriate amount of sterile saline, 37 °C, 35 h	/	Sun et al. (2022)
mung bean	*Cordyceps militaris*	full soaking in advance, 25 °C, 7 d	/	Xiao, Zhang et al. (2015)
black bean	*Pleurotus ostreatus*	50–57.4% moisture content, dark, 14 d	8.0–36.3	Espinosa-Páez et al. (2021)
kidney bean				
oat				
black bean	*Pleurotus ostreatus*	indoor temperature, 14 d	−3.6	Espinosa-Páez et al. (2017)
kidney bean			13.0	
oat			6.6	
wheat	*Agaricus blazei*	culture in the dark, 25 °C, 30 d	32.0	Zhai et al. (2015)
corn			29.0	
rice			30.0	
millet			22.4	
millet broomcorn millet			22.0	
oat			19.0	
sorghum			20.0	
Extract or concentrate				
lentil flour	*Pleurotus ostreatus*	42.5% moisture content, 28 °C, 14 d	23.0	Asensio-Grau et al. (2020)
chickpea flour	*Cordyceps militaris*	full soaking in advance, 25 °C, 7 d	19.4–19.9	Xiao, Xing, et al. (2015)
lupin flour	*Aspergillus sojae*	45% moisture content, 30 °C, 7 d	0.6–1.8	Olukomaiya, Adiamo et al. (2020)
	Aspergillus ficuum			
balck-eyed pea seed flour	*Aspergillus oryzae*	full soaking in advance, 30 °C, 4 d	/	Chawla et al. (2017)
cassava starch	*Saccharomycopsis fibuligera*	61% moisture content, 28 °C	/	Chen et al. (2010)
pea protein	*Aspergillus oryzae*	40 °C, 6 h	5.1	Kumitch et al. (2020)
	Aspergillus niger		14.6	

Note: accurate total protein content is not available in some literature.

5.2. Peptides

SSF has also been a central biochemical method for releasing antioxidant peptides in the last decades (He et al., 2012; Wu et al., 2014). Protein degradation during SSF caused by proteases and peptidases is obvious to all, which can be confirmed by SDS-PAGE and peptide molecular weight distribution (Arte et al., 2015). In a SSF study, bran proteins with molecular weights 15,000–10,000 Da and <180 Da accounted for 45.08% and 19.89% of the total, respectively, while this value declined to 18.31% and 41.37% after commercial baker's yeast

fermentation (Zhao et al., 2017). Zhao et al. (2018) noted that defatted soybean meal already had more than 70% of soluble peptides with a molecular weight of less than 3000 Da after 24 h of fermentation by *Aspergillus oryzae*. The peptide chain subsequently breaks, thereby exposing more active fragments to trap free radicals and inhibiting lipid peroxidation in the substrate (Elias et al., 2008). Regarding *Rhizopus oligosporus* fermented red kidney beans, the content of soluble protein was significantly decreased in the first 11 days, but the peptide content remained essentially unaltered (Fig. 4A and B). In the early stages of SSF, the fungus consumes protein as a nitrogen source, so we speculate that some of the individual cases with short fermentation times in Table 3 cannot comprehensively illustrate the potential of this combined protein yield (Erkan et al., 2020).

Bacteria such as *Bacillus subtilis* and *Lactobacillus* spp. are commonly involved in producing peptides with antioxidant activity, and a similar approach can be applied to fungi (Lorenzo et al., 2018). The short-term fermentation of soybean flour by *Aspergillus oryzae* produced considerable antioxidative peptides (Lee et al., 2013). However, peptides formed by microbial action from waste proteins with dietary value partially inhibit cell viability in a concentration-dependent manner (Sun et al., 2015). Most scholars speculate that fungi have less potential than bacteria for active peptides, but using genetic engineering to modify *Saccharomyces* spp. for specific expression could also be a promising area. Sun et al. (2022) collected cotyledon cells from different stages of SSF and performed microscopic analysis. Around the 17th day of fermentation, the cell surface became smooth and thin, after which fissures appeared on the surface of the cell wall (Fig. 4C). SEM results revealed that on day 29, the cells were fragmented owing to mycelial action. The location of the protein matrix was further determined by confocal laser scanning microscopy (CLSM), and the results exposed that the protein content inside was drastically reduced after the disruption of the cell integrity. Cellulase stimulates cell wall disintegration and protein efflux, thereby fully interacting with other enzymes produced by fungi (Krakowska-Sieprawska et al., 2022).

5.3. Amino acid composition

The effect of fungal SSF on free amino acids is normally more pronounced than that of total protein. Again, there are differences in the representative amino acids of various fungi that can be targeted to compensate for the amino acid deficiencies of the substrate. The protein of soybean residue after *Yarrowia lipolytica* SSF decreased by 10.38%, but the total free amino acid content increased by about 4-fold. The content of Glu, which can impart fresh flavor, increased by approximately 20-fold, and the amino acid content of Ser, Asn, Gly and Ala were all increased substantially (Vong et al., 2016). *Tricholoma matsutake*, an edible fungus with medicinal value, markedly boosts for the free amino acids in soybean (Lee et al., 2019). During the 12-day SSF, Glu and Lys were most notably elevated from 1.69 mg/g and 0.35 mg/g to 16.11 mg/g and 6.33 mg/g, respectively. There was also a significant difference in the content of Gly (0.13–3.17 mg/g), Asp (0.8–4.83 mg/g), Ala (0.63–5.87 mg/g), Tyr (0.15–3.33 mg/g), and Orn (0.02–3.27 mg/g). Moreover, among the seven crops that Zhai et al. (2015) used *Agaricus blazei* to ferment with wheat, rice, and grain could reach more than ten times the amino acid nitrogen content compared to the control group. In most cases, the optimization of free amino acids by fungal SSF is very prominent.

For the efficient creation of functional foods, selecting substrates with direct edible potential in conjunction with the amino acid properties of edible fungi (Table 1) can simplify the safety inspection process. However, since the environment produced by fermentation is relatively acidic, the content of alkaline amino acids like Lys and Arg may not fluctuate or may even decrease (Espinosa-Páez et al., 2017). To acquire a better amino acid profile, strain selection requires two main considerations, one is the suitability of the protease produced to the substrate and the other is the formation of a complementary pattern by the amino acid composition of the mycelium of the strain.

5.4. In vitro digestion

The bioaccessibility of protein can be characterized by indicators (i.

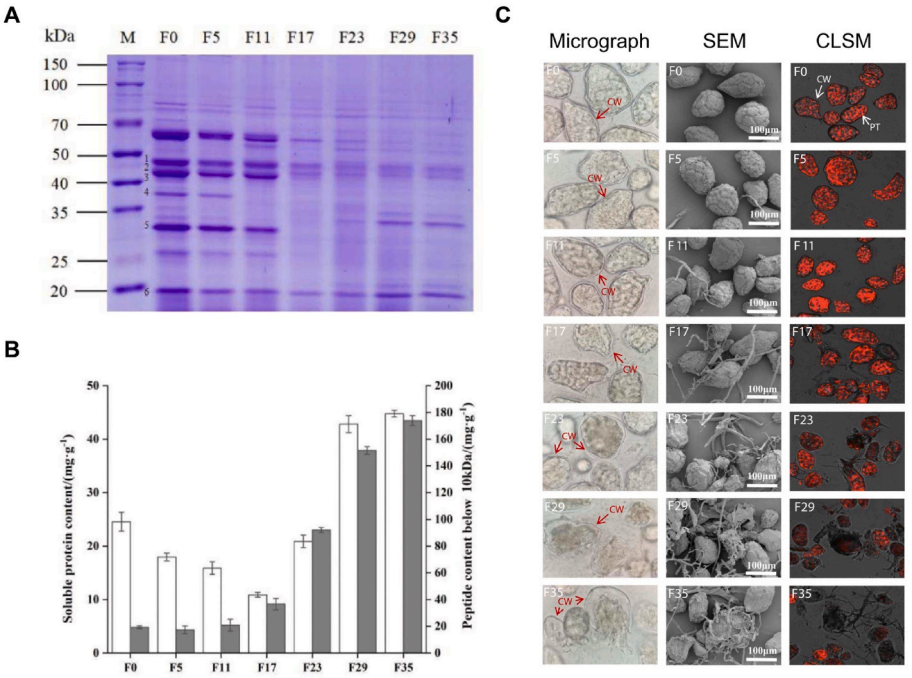

Fig. 4. Protein molecular weight (A), Soluble protein and peptide (<10 kDa) content (B), Optical micrographs, SEM images and CLSM images (C) of red kidney bean during different SSF stage adapted from Sun et al. (2022), copyright (2022), Elsevier. Abbreviations: F-fermentation time, M-marker, CW-cell wall, PT-protein. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

e. *in vitro* digestion), but the health benefits of protein in humans go far beyond that. In general, the increased bioaccessibility caused by fungal SSF is predominantly attributed to the digestion of antinutritional factors and macromolecules into small molecules of proteins, peptides and free amino acids (Rayaprolu et al., 2013). One of the main drawbacks of plant legumes such as peas is the low digestibility of proteins, and some bioactive compounds (e.g. protease inhibitors) exerts a considerable impact (Nosworthy et al., 2018). According to a previous study, the *in vitro* enzyme protein digestion (IVPD) of pea proteins fermented by *Aspergillus oryzae* and *Aspergillus niger* was increased, which was also validated in another study on desi chickpea (Chandra-Hioe et al., 2016; Kumitch et al., 2020). The robust performance of *Pleurotus ostreatus* as an edible mushroom in improving IVPD is probably one of the reasons for which it was involved in the most relevant studies. At the same time, antinutrients are eliminated during the SSF process, which is achievable by most fungi (Espinosa-Páez et al., 2021). In contrast, there are also a few reports that indicate that the IVPD of flour decreased after SSF (Olukomaiya, Adiamo et al., 2020). This could be explained by the fact that the proteins were locked in the fibrous matrix, making it difficult for the enzyme to function. In turn, autoclaving and final drying treatment at the SSF preparation stage may cause partial protein inactivation, resulting in loss of dispersibility and solubility.

By combining rapeseed cake and *Aspergillus niger*, *in vitro* AA and EAA digestibility increased by 5.87% and 6.69%, respectively (Shi et al., 2015). The activities of endoglucanase, xylanase, acid protease and phytase were significantly increased with increasing fermentation time, which may be the chief reason for the improved *in vitro* digestibility. Darwish et al. (2012) reported that the maximum organic matter digestibility rose from 29.25% to 53.50% when using only *Pleurotus ostreatus* for fermentation, and from 28.25% to 72.50% when using both *Pleurotus ostreatus* and *Saccharomyces cerevisiae*. In addition, *Pleurotus ostreatus* is known for its high glutamate content. After SSF, the digestibility of the protein of lentil flour increased from 20% to 28% after the gastric digestion phase and from 40% to 57% following intestinal digestion (Asensio-Grau et al., 2020). *Rhizopus oryzae* decreased the trypsin inhibitor content by 24.8%, but it's IVPD was instead reduced by 16.5%, thus it was not recommended for the SSF of de-oiled rice bran (Ranjan et al., 2019).

5.5. Processing potential

The SSF product is generally prepared as flour, the bulk density of which decreases rapidly with fermentation time, and the texture and mouthfeel are improved (Chawla et al., 2017). Substrates that have undergone SSF typically exhibit a higher water absorption capacity (WAC), which may be attributed to the increase in small molecular weight proteins with polar groups (Ghumman et al., 2016). The improved WAC, swelling index (SI) and swelling capacity (SC) of SSF canola meal enable more straightforward incorporation into aqueous food formulations, especially baked foods (Olukomaiya, Fernando et al., 2020b). According to Sadh, Chawla et al. (2018), emulsifying properties, bulk density and foaming capacity of peanut oil cakes were improved by SSF with *Aspergillus oryzae*. Indeed, SSF causes the unfolding and modification of macromolecules, exposing the hydrophilic structural domains, while the resulting low molecular weight peptides easily migrate to the oil-water interface to improve emulsification activity (Lim et al., 2010; Oloyede et al., 2016). Fat absorption capacity (FAC) is related to the surface availability of hydrophobic amino acids, and the FAC of chickpea flour increased by 18.9% after *Cordyceps militaris* SSF (Abd Elmoneim & Bernhardt, 2010; Xiao, Xing, et al., 2015). Scanning electron microscopy (SEM) studies showed that the microstructure of fermented pearl millet flour changed from an irregular dense structure to a regular fluffy structure (Adebiyi et al., 2016). The change in processing potential after fungal SSF is highly consistent and favors the formation of a fine paste (Olukomaiya, Adiamo et al., 2020). This performance is advantageous whether the ferments are processed directly into food products or further isolated for extraction of single components. At the same time, the SSF with *Fomitopsis pinicola* improved the dense structure of wheat bran, producing bread that reduces the incidence of obesity and diabetes (Tu et al., 2020). The enhanced SC compensated for the destruction of the gluten protein network by the wheat bran, and the reconstituted bread had superior firmness and chewiness.

6. Applications and future perspectives

As the concept of sustainable agro-food industry continues to gain popularity, the industrial applications of SSF are facing various challenges. In this way, it's imminent to find precise and efficient manufacturing approaches. Therefore, future research requires more efforts on the integration of SSF with emerging technologies.

6.1. Industrial applications

During the upgrading of byproducts with SSF, a portion of the biomass is not suitable to produce edible ingredients. However, other resources developed by SSF are also valuable for industrial production. Considering that products in cell factories tend to be diverse, a rational design allows for a circular replenishment of materials-energy-products in a production system, thus reducing the environmental burden of climate change, water depletion and land use.

6.1.1. Enzyme

Enzymes produced by fungal SSF are widely used in food, feed, detergent and pharmaceutical industries, while participating in various biotransformation processes (Rantasalo et al., 2018). As a class of proteins with specific activities, industrial enzymes are among the most commercialized products of SSF. They serve an instrumental auxiliary role in food production. The yield of enzymes is increasing annually and filamentous fungi are more suitable for commercial manufacturing. The main SSF enzyme products have been summarized in detail in Chilakamarry et al. (2022), including α-amylase, amylase, lipases, β-galactosidase, protease, etc. Enzymes are also involved in the production of non-protein active substances. In SSF of oat with *Monascus anka*, there was a good correlation between enzymes activities and phenolic release (Bei et al., 2018). α-amylase played a key role in driving carbohydrate metabolism towards phenolic mobilization, xylanase and cellulase were mainly responsible for the breakdown of cellular structure. Moreover, the target enzymes are usually not unique, simultaneous production of multiple enzymes or enzyme complexes is a common strategy. Guillaume et al. (2019) cultured *Aspergillus tubingensis* and obtained a biocatalyst containing more than 130 different enzymes, demonstrating better catalysis than a combination of seven purified enzymes. This will provide new insights into the optimal manufacturing of enzymes.

6.1.2. Feed

Both plant and fungal proteins are essential ingredients in the food industry while providing elasticity to the livestock industry. Hybrid protein systems tend to complement each other in amino acid profiles, but the design principles are still undefined and there is considerable scope for innovation (Day et al., 2021). For better process and quality control prior to final product formulation, animal feeds are preferably fermented with single substrate. Soybean meals are the most common used substrates, they are converted into high protein feed during SSF process and fed to animals in the form of blends (Baldwin et al., 2019; Hassaan et al., 2015). Other substrates include bagasse, fruit peels, grain hulls, etc. SSF's improvement in the protein profile (especially amino acid composition) of animal feeds is the most concerned. Except for histidine and serine, yeast fermented soybean meal showed significantly higher content of amino acids (Hassaan et al., 2015). The largest increase in growth rate was observed when replacing 37.4% of fish meal with yeast fermented soybean meal. Blood indicators showed a decrease

in liver enzymes alanine aminotransferase (ALT) and aspartate aminotransferase (AST), which can improve liver function and benefit the health of fish. Other improvements provided by SSF for animal feeds include, the reduction of anti-nutrients, improved digestibility of organic matter and the inhibition of pathogenic microorganisms such as *Salmonella* sp. (Vandenberghe et al., 2021). The development concept of the feed and SSF food is analogous, both mainly producing blends, and using GRAS fungi as possible. In integrated production, some SSF foods that do not meet the standards can be fed directly to livestock, reducing resource consumption.

6.1.3. Others

As one of the principal fungal SSF products, fuels are the most dominant source of energy in industrial production. Agro-food waste contains considerable lignocellulosic materials, which are mainly composed of three polymers: cellulose, hemicellulose and lignin. Lignocellulolytic enzymes secreted by fungi serve as an essential link in ethanol production, reducing the binding of nutrients by the cell wall, and contributing to the release of fiber-bound starch (Guillaume et al., 2019). *Saccharomyces cerevisiae* also produced glycerol when assimilating carbohydrates, which has been considered as another source of SSF fuel (Chilakamarry et al., 2022). Biofuels provide energy for food manufacturing, preservation and transportation, reducing the carbon footprint and dependencies on fossil fuels. Other SSF products such as pigments, flavors, aroma, organic acids and biosurfactants also have multiple food industrial applications, and researchers are continuing to enhance production processes with emerging technologies (Thomas et al., 2013).

6.2. Impact of emerging technologies on SSF

Faced with numerous challenges in the current food system, the development of microbial foods can alleviate the health crisis of the environment and society (Mazac et al., 2022; Zurek et al., 2022). Microbial foods have a long history of safe consumption and usually exhibit a lower environmental footprint than conventionally grown crops and livestock products (Leger et al., 2021). Moreover, the solid-state fermentation (SSF) process can match the natural physiology of the fungi and effectively enhance the nutritional profile and bioaccessibility of the protein. The agro-food industry has a wide range of abundant waste streams, and fungal SSF makes creating ideal food from them a reality. In particular, whole crops or isolated ingredients directly as substrates are less resistant to policy and are more likely to establish legitimacy in consumer perceptions. Although limited, the potential of SSF to create novel food protein resources is already visible. Furthermore, emerging technologies contribute to SSF's transformation and upgrading.

6.2.1. Artificial intelligence

With the advent of Industry 4.0, artificial intelligence can be applied to monitor and regulate the fermentation environment (Wainaina & Taherzadeh, 2022). It is relatively challenging to monitor changes in biomass during complex biological processes. Doppler et al. (2020) chose UV chromatograms to monitor various impurities released by fungi during growth as fingerprints, and combined partial least squares (PLS), principal component regression (PCR), principal component analysis (PCA), and other models to predict cell viability, with an accuracy of over 90%. Meanwhile, digital imaging analysis (DIA) is susceptible to subtle changes in color and can be used to quantify colony area and density. However, the data was collected at the SSF surface, and the growth below the substrate surface was difficult to estimate (López-Gómez et al., 2019). A smart bioreactor has a microcomputer at its core and collects real-time data through sensors, image collectors and other hardware. Artificial intelligence tools such as convolutional neural networks (CNN) continue to estimate the growth status, and control the content, and environmental variables through a robot system. de Menezes et al. (2021) combined an artificial neural network (ANN) with a genetic algorithm (GA) to increase the yield of lipase, which is more efficient in optimization than the rotational central composite design (RCCD) model. Other algorithms can also be introduced in ANN modeling to achieve higher accuracy and enhanced predictions after training, validation and testing. Furthermore, artificial intelligence can be used to analyze data from fermentation sensors and identify optimal fermentation conditions for specific products. This can help to improve product quality and consistency while minimizing waste and reducing costs.

6.2.2. Genetic engineering

Genetic engineering e.g. CPRISPR-Cas9 enables the addition of entirely new traits to SSF products (Jahn et al., 2023; Rantasalo et al., 2018). To improve industrial-scale production of fungi, it is necessary to use metabolic and genetic techniques because wild-type strains are incapable of synthesizing the desired proteins at an industrial scale. By identifying the determinants of tolerance, the key genes and environments involved, protein secretion engineering, promoter engineering and genomics are applied to enhance the performance of fungi (Madhavan et al., 2022). Besides, studies have shown that codon optimization and mutagenesis will enhance the secretion of fungal proteins. Under non-inducing conditions, Alazi et al. (2018) enhanced the pectinase production capacity of *Aspergillus niger* by achieving overexpression of the gaaR gene, while the deletion of creA showed synergistic effects. Super-efficient secretion of specific proteins can be achieved by replacing the original signal peptide with a more effective one. The expression of α-galactosidase in *Aspergillus niger* was increased 12-fold with GlaA instead of natural signaling peptide (Xu et al., 2018). Modulating endoplasmic reticulum-associated protein degradation-related genes avoids the degradation of heterologous and semi-folded proteins, thus enhancing protein production (Wang et al., 2020). Meanwhile, disruption of specific protease genes is significant for improving the yield and stability of heterologous enzymes (Zhang et al., 2014). Engineering specific enzymes to degrade antinutrients can improve the bioaccessibility of the final product, and fungi resistance is also improved accordingly.

6.2.3. 3D printing technology

3D printing technology removes SSF from the confines of bioreactors and improves space utilization but requires more stringent rheological properties of the raw materials. In the manufacturing of meat analogs, the metabolic viability of the mycelial network can also provide adjustable textural properties to the product (Gantenbein et al., 2022). In fact, biomass-fungal composites are already being used as sustainable materials in the construction and packaging sectors. Rahman et al. (2022) inoculated a biomass-flour mixture with fungi that belong to the Basidiomycete group and added psyllium husk powder to improve its rheological properties. The prepared material should be printed as soon as possible, otherwise the reduction of storage modulus and loss modulus will eventually lead to the loss of mycelial uniformity and layer height shrinkage. The biological activity of the fungus remains unchanged after printing. According to Gantenbein et al. (2022), as long as the hydrogel containing mycelium has sufficient nutrients, it could self-repair into a more substantial structure despite suffering a certain degree of mechanical damage. The mycelium of *Pleurotus ostreatus* and *Ganoderma lucidum* possess elastic mechanical properties and have been used to imitate human tissue, which offers insights into a new approach to the production of artificial meat (Antinori et al., 2021).

7. Conclusion

Faced with the challenges of fresh water depletion, climate change and biodiversity, a significant portion of the global population still cannot access animal protein at reasonable prices. Among the major sources of plant protein, excluding major crops such as rice and corn, the

future of legumes such as chickpea and lupin is promising. However, the presence of antinutritional components reduces their bioavailability. Fungal SSF not only removes these restrictions to a large extent, but also provides the necessary complement to the protein profile. From a carbon footprint perspective, the environmental burden of this type of production may even be lower than that of the plant-only output, considering that the fermentation substrate may come from different stages of agro-food by-products. This review highlighted the trends in SSF for protein production, the main process variables and the characteristics of the products. The improved amino acid composition proves its potential in human nutrition, and digestibility and bioavailability are also essential aspects to assess the differences with conventional production methods.

The future of protein food innovation is exciting, and commercial companies have explored the production of naturally organized microbial biomass with SSF. However, social and cultural values are also integral to a healthy diet, and consumers continue to have concerns about mycoprotein. Mycoprotein also inevitably encounter policy resistance in the commercialization process, which warrants further discussion. Herein, we recommend the following directions for future research on the acquisition of food proteins by fungal SSF:

1. Screening high-quality strains and substrates for SSF production of food proteins, exploring the nutritional profile and functional properties of proteins.
2. Utilizing emerging technologies such as genetic engineering and 3D printing to make SSF more designable.
3. Further validating the economic, environmental, and policy applicability of SSF thus promoting microbial foods.

CRediT authorship contribution statement

Jian Wang: Conceptualization, Investigation, Writing - Review & Editing, Funding acquisition. Zhenyu Huang: Writing - Original Draft, Conceptualization, Investigation, Visualization. Quanjin Jiang: Investigation, Writing - Review & Editing. Hynek Roubík: Writing - Review & Editing. Qihao Xu: Visualization. Adem Gharsallaoui: Writing - Review & Editing. Ming Cai: Project administration, Supervision, Writing - Review & Editing, Funding acquisition. Kai Yang: Supervision, Funding acquisition. Peilong Sun: Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgments

This work was supported by the Key Research and Development Projects of Zhejiang [grant numbers 2022C04021, 2022C02041]; the Zhejiang Provincial Natural Science Foundation [grant number LQ23C200013]; and the Science & Technology General Project of Longyou [grant number JHXM2022004]. We thank Home for Researchers editorial team (www.home-for-researchers.com) for language editing service.

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