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Review

Sustainable bio-processing: Solid-state fermentation and agricultural waste

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Agricultural and agro-food industries produce vast quantities of byproducts, which when not effectively managed, contribute to environmental degradation and resource wastage. This review critically examines the potential of Solid-State Fermentation (SSF) as a transformative biotechnology for valorizing Agro-Food Industrial Residues (AFIRs), such as fruit peels, husks, and pomace. These residues are rich in polysaccharides, proteins, fibers, and bioactive compounds, and their conversion into value-added products through SSF presents opportunities in pharmaceuticals, food, cosmetics, and animal nutrition. The review aims to highlight the role of SSF in sustainable bioprocessing, particularly in converting waste into feed, bioactive metabolites, and biopolymers. It explores microbial systems used in SSF, key factors influencing fermentation efficiency, and advances in process optimization and scalability. Specific case studies, including the production of enzymes from cassava peels and fermented oilseed cakes as animal feed, are discussed to illustrate real-world applications. The review concludes that SSF not only mitigates environmental impacts by reducing organic waste and emissions but also supports food security and rural bioeconomy development. For maximum benefit, it recommends targeted research on strain selection, substrate pretreatment, and techno-economic analyses. Emphasizing integrated strategies, this review positions SSF as a cornerstone technology for circular bioresource management and sustainable development.

Key words: Agricultural byproducts, solid-state fermentation, value-added products, bioconversion, microorganisms.

INTRODUCTION

Agricultural practices, spanning from crop cultivation to food processing and livestock farming, yield substantial quantities of byproducts and residues. These include crop stems, leaves, husks, peels, shells, and animal manure—organic materials that do not directly contribute to human food chains (Koul et al., 2022). The increasing global population and intensification of agricultural operations have led to a significant rise in the generation

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of these materials (Varghese et al., 2023). Historically considered as waste, these residues have contributed to environmental pollution and posed major disposal challenges. However, growing emphasis on sustainability and circular economy practices has shifted attention toward their untapped potential as renewable resources (Zubair et al., 2021).

Among these residues, Agro-Food Industrial Residues (AFIRs)—such as pomace, peels, cereal bran, and post-extraction biomass—represent a substantial portion of agricultural waste streams. They are rich in polysaccharides, proteins, fibers, and bioactive compounds, making them suitable candidates for use in pharmaceuticals, cosmetics, animal feed, and functional foods (Polat et al., 2021). Although the term “residue” denotes non-intentionally generated byproducts, their increasing volumes, particularly in wine and grain processing (up to 30% of raw material mass), require effective valorization strategies (Papaioannou et al., 2022; Jacobs et al., 2022). Improper disposal of these materials leads to environmental degradation, such as greenhouse gas emissions and water pollution (Margallo et al., 2019).

Despite the recognition of agricultural residues as a problem and an opportunity, limited integration exists between solid-state fermentation (SSF) technologies and specific waste streams, microbial innovations, and scalable applications. Most waste continues to go underutilized due to knowledge gaps in process optimization, substrate-microbe compatibility, and economic viability at industrial scales. Addressing this gap requires a deeper understanding of how SSF can transform agricultural residues into high-value products while supporting sustainability goals.

SSF presents a compelling biotechnological pathway that utilizes solid substrates with low moisture content for microbial growth and product formation (Egbune et al., 2023a; Srivastava et al., 2019; Egbune et al., 2024c). Unlike submerged fermentation, SSF allows for the efficient use of lignocellulosic materials without extensive pretreatment or high water and energy input. It supports the production of valuable metabolites including enzymes, organic acids, and nutraceuticals (Russo et al., 2021; Ughe et al., 2024). Furthermore, SSF is suitable for low-cost implementation in resource-limited environments, making it relevant for both developed and developing economies.

The SSF process typically involves three core stages: substrate pre-treatment to enhance porosity and nutrient availability, microbial inoculation using targeted fungal or bacterial species, and controlled fermentation to yield desired bioproducts (Chilakamarry et al., 2022; Šelo et al., 2021; Tonukari et al., 2024). Through SSF, the nutritional quality of agricultural byproducts can be improved, enhancing their value as animal feed or functional food ingredients (Chebaibi et al., 2019). Moreover, by reducing landfill waste and associated emissions, SSF contributes meaningfully to environmental conservation and circular bioeconomy goals (Aidoo et al., 2023).

Given these challenges and opportunities, this review aims to evaluate the potential of SSF as a sustainable strategy for valorizing agricultural waste. Emphasis is placed on the microbial systems involved, optimization parameters, and industrial applications, with the goal of identifying opportunities for scalable and eco-friendly bioprocessing solutions.

AGRICULTURAL BYPRODUCTS AND THEIR POTENTIAL

Types of agricultural byproducts

Agricultural byproducts encompass a diverse range of materials generated from various agricultural processes. These byproducts can be broadly categorized into several types based on their origin and characteristics (Table 1).

Agricultural residues

Agricultural residues encompass materials left post-harvest and those resulting from raw material processing, such as pods, stubble, stems, leaves, shells, and more. These hold potential for substantial energy generation. Prominent examples of utilization include cereal straw (wheat, barley, oats), barley hulls, soybean stalks, corn cobs, sunflower stalks, and seed hulls. Table 2 provides comprehensive chemical composition details. Globally, cereal grain diversity and residues, averaging 2.435 million tonnes annually (2008-2017), are influenced by water availability and temperature (Šelo et al., 2021).

Food industry residues

Residual substances are generated in various food sectors, like fruit, beer, oil, and cereal processing, following the processing of raw materials. Examples include oil cake, oil pomace, brewer's grains, bran, and germ. Notable instances from the food industry include wheat bran, rye bran, rice bran, and hull-less pumpkin oil cake. These copious remnants hold promising potential as versatile energy reservoirs and contributors to the formation of valuable compounds. Elaborated details concerning the precise chemical composition of these prevalent food industry byproducts can be found in Table 3. Manufacturers within the European Union (EU) processed food sector are required to adhere to EU environmental policies for recycling or proper disposal of generated residues. The conversion of industrial food residues into value-added products is exemplified by grape pomace, a wine production by-product, and cereal residues from grain processing (Kokkinomagoulos and Kandylis, 2023).

Table 1. Types of agricultural byproducts and their potential application.

No.	Type of agricultural byproduct	Examples	Potential applications	References
1	Crop Residues and Byproducts	Stems, leaves, husks	Bioenergy production, biodegradable materials	Koul et al. (2022)
2	Fruit and Vegetable Waste	Peels, seeds, cores	Natural antioxidants, dietary fiber supplements	Kainat et al. (2022)
3	Animal Byproducts and Manure	Bones, blood, feathers	Animal feed, biofuels, gelatin, collagen	Limeneh et al. (2022)
4	Forestry Residues and Biomass	Branches, bark, sawdust	Bioenergy, wood-based composites, bioactive compounds	Verkasalo et al. (2022)
5	Aquaculture Byproducts	Fish scales, shells, trimmings	Collagen, chitosan, fishmeal	Ozogul et al. (2021)
6	Cereal Processing Byproducts	Bran, husks, spent grains	Enzymes, dietary fiber, bioactive compounds	Fărcaș et al. (2022a)

Table 2. Composition of chemical elements in commonly found agricultural residues.

Agricultural residues	Lignin, % (Dry solids)	Cellulose, % (Dry solids)	Hemicellulose, % (Dry solids)	Ash, % (Dry solids)	Source
Barley straw	9.6-13.8	33.8-46.8	21.9-30.0	4.4	Lallement et al. (2023)
Corn cob	6.1	33.7	31.9	8.5	Lallement et al. (2023)
Corn stalks	7.0-7.3	35.0-39.0	16.8-42.0	24.9	Taghipour et al. (2019)
Oat straw	4.1-23.6	31.7-39.4	23.3-28.2	3.2	Šelo et al. (2021)
Rice straw	8.3-9.9	19.6-36.2	19.0-50.4	14.7	Nabila et al. (2023)
Rye straw	19.0-30.8	37.4-37.6	30.5	5.7	Lallement et al. (2023)
Soybean stalks	19.8	34.5	24.8	5.7	Kumar et al. (2020)
Sunflower stalks	13.4-17.5	38.5-42.1	29.7-33.5	8.6-9.2	Šelo et al. (2021)
Wheat straw	8.9-22.1	32.9-49.8	23.7-25.0	3.6-4.7	Šelo et al. (2021)

Vitis vinifera, commonly known as grapevine, is a significant crop with an annual production of approximately 71 million tons (D’Eusanio et al., 2023). About 80% of grapes are used for wine production, while the remaining 20–30% becomes grape pomace or grape marc. Notably, approximately 30% of phenolic compounds find their way into the wine, leaving a significant 70% of bioactive phenolic compounds within the grape pomace (Singh et al., 2023). This phenomenon is ascribed to the interaction of polymeric proanthocyanidins and phenolic compounds with proteins, fibers, and polysaccharides, necessitating pre-treatment methods such as acid, alkali, or biological treatments to facilitate extraction.

Grape pomace is comprised of seeds, skin, and occasionally stems. The grape seed-to-pomace ratio ranges from 15 to 52% (db), while grape skin content can reach 65% (db) (Aguilar et al., 2016). Due to its composition, grape pomace is suitable for SSF, offering opportunities for enhancing its attributes. Research highlights its abundance in polyphenolic compounds, enzyme production and biofuel extraction.

The category of "cereals" encompasses nine distinct species, including wheat, rye, barley, oats, rice, millet, corn, sorghum, and triticale. Through the process of cereal processing, approximately 30% of residues are produced, predominantly in the form of hulls and bran, which emerge during grain milling (Fărcaș et al., 2022b). Strikingly, wheat and oat whole grains gain recognition for their opulent phenolic compound content, distinguished by noteworthy antioxidant activity. Among these compounds, phenolic acids and flavonoids take center stage, with the bran fraction exhibiting the highest concentrations. Nevertheless, it is pertinent to acknowledge that their bioavailability remains constrained.

Table 3. Composition of chemical elements in commonly found food industry residues.

Food industry residues	Lignin, % (Dry solids)	Cellulose, % (Dry solids)	Hemicellulose, % (Dry solids)	Protein, % (Dry solids)	Ash, % (Dry solids)	Reference
Rice bran	24.8	34.0	28.2	5.8-8.3	-	Šelo et al. (2021)
Rye bran	3.5-4.4	5.0-6.0	-	14.4-18	2.8-6.2	Šelo et al. (2021)
Sugarcane bagasse	18.9-26.1	36.9-45.7	25.60-29.58	2.18	2.84	Šelo et al. (2021)
Wheat bran	3.0-5.0	9.0-12.0	38.9	9.6-18.7	0.04-8.1	Šelo et al. (2021)

CHEMICAL COMPOSITION OF AGRO-FOOD INDUSTRIAL RESIDUES

In Bhardwaj et al.'s (2019) study, substrates for SSF are categorized into three groups based on their main carbon source: starch substrates, lignocellulosic substrates, and soluble sugar-rich substrates. Agro-Food Industrial Residues (AFIRs) often align with lignocellulosic biomass, containing cellulose, hemicellulose, lignin, along with nutrients like proteins, lipids, pectin, and polyphenols. Tables 2 and 3 provide a comprehensive information regarding the chemical composition of AFIRs derived from diverse sources.

The intricate and diverse nature of this material becomes apparent through its chemical constitution. An amalgamation of factors, including cultivation practices, atmospheric conditions, plant varietals, harvesting methodologies, storage circumstances, and the analytical techniques applied to evaluate individual constituents, collectively contribute to shaping the material's chemical makeup.

The inherent lignocellulosic architecture of AFIRs can be perturbed through the biocatalytic operations of diverse microorganisms. Prior to determining the most suitable approach (including microorganism selection, cultivation strategies, process conditions, etc.) for the reutilization of these residues, an essential first step entails an all-encompassing chemical characterization of these materials.

SSF PROCESS

Definition and Principles of SSF

SSF is a bioprocessing method that involves the growth of microorganisms on solid substrates in the absence or near-absence of free-flowing water (Egbune et al., 2022a; Egbune et al., 2023a). In SSF, the substrate serves as both the nutrient source and support for microbial growth, offering a unique environment that differs from submerged liquid fermentation (Kumar et al., 2021).

Principles of SSF

Substrate-microorganism interactions

In SSF, the microorganisms come into direct contact with the solid substrate, leading to intimate interactions between the two (Kumar et al., 2021). The microorganisms secrete enzymes that act on the substrate, breaking down complex molecules into simpler forms that can be absorbed and utilized for their growth and metabolism. These enzymatic reactions are crucial for the conversion of the substrate's components into desired products.

Moisture content and water activity

SSF relies on the controlled moisture content of the solid substrate, which typically ranges from 40% to 80% (wet basis). The water activity (aw) in SSF is crucial for microbial growth and enzyme activity, as it affects the availability of water for microorganisms (Srivastava et al., 2019). The optimal moisture content and water activity need to be maintained to ensure efficient microbial growth and metabolic activities.

Heat generation and temperature control

During SSF, microbial metabolic activities generate heat, which can influence the process kinetics and temperature profiles within the solid substrate. Proper temperature control is essential to prevent excessive heat buildup, which could lead to thermal stress and decreased microbial activity (Mitra et al., 2021). Additionally, temperature affects the rates of enzymatic reactions and microbial growth, making it a critical parameter in SSF.

Nutrient and oxygen availability

SSF relies on the initial nutrient content of the solid substrate to support microbial growth and metabolism (Vandenberghe et al., 2021). Unlike submerged fermentation, where nutrients are dissolved in the liquid medium, SSF relies on the inherent nutrient content and compositional characteristics of the solid substrate. Adequate nutrient availability is essential for sustained microbial growth and desired product formation. Oxygen availability in SSF is limited due to the lack of free-flowing water, and it becomes a limiting factor in the process (Kumar et al., 2021).

Table 4. Key factors influencing SSF.

Key factors	Solid-state fermentation (SSF)	Submerged fermentation (SF)	Liquid-state fermentation (LSF)	References
Substrate utilization	Utilizes solid substrates (agricultural byproducts)	Utilizes liquid media	Utilizes liquid media	Souza et al. (2022)
Water and energy consumption	Lower consumption	Higher consumption	Higher consumption	-
Microbial immobilization	Provides solid support matrix for microbial growth	Microorganisms freely suspended in liquid medium	Microorganisms freely suspended in liquid medium	Behera et al. (2019)
Product yield and composition	Higher product yields and desired compositions	Lower product yields and variations in composition	Lower product yields and variations in composition	Wang et al. (2023)
Nutrient and oxygen distribution within substrate	Heterogeneous distribution of nutrients and oxygen	Homogeneous distribution of nutrients and oxygen	Homogeneous distribution of nutrients and oxygen	Wang et al. (2019) and Kumar et al. (2021)
Scale-up challenges	Complex due to solid nature of substrates	Relatively straightforward scaling up	Relatively straightforward scaling up	Chilakamarry et al. (2022); El Sheikha and Ray (2022)
Fermentation time	Longer fermentation times	Shorter fermentation times	Shorter fermentation times	Ghanavati et al. (2022)
Enzyme production	Advantageous for enzyme production with solid substrates serving as inducers	Can also produce enzymes, but might have higher costs for liquid inducers	Can also produce enzymes, but might have higher costs for liquid inducers	An et al. (2022)

Microbial diversity and synergistic interactions

SSF often involves multiple microorganisms, including bacteria and fungi, which can interact synergistically during the fermentation process. Some microorganisms may produce enzymes that facilitate the breakdown of complex substrates, creating simpler compounds that support the growth and activities of other microorganisms (Christensen et al., 2022). This microbial diversity can lead to more efficient substrate utilization and the synthesis of a broader range of products.

Substrate structure and physical properties

The physical structure and properties of the solid substrate play a significant role in SSF (Kumar et al., 2021). The porosity and surface area of the substrate influence the accessibility of microorganisms to nutrients and water, affecting the overall process efficiency. Substrate particle size, shape, and surface chemistry can also impact the adhesion and growth of microorganisms on the substrate surface.

Process monitoring and control in SSF

SSF requires careful monitoring and precise control of various physicochemical parameters to ensure optimal microbial growth, metabolic activity, and product yield (Kumar et al., 2021). Parameters such as moisture content, temperature, pH, oxygen availability, and substrate porosity are particularly critical due to the limited mobility of nutrients and gases in the solid matrix.

Real-time control of these parameters is challenging, especially on an industrial scale, because of the heterogeneous nature of the substrate and limitations in sensor placement. Nevertheless, recent technological advances have significantly enhanced process control strategies.

Modern monitoring tools such as biosensors, fiber-optic probes, and infrared thermography have been integrated into pilot and industrial-scale SSF operations to track key variables in real-time. These devices help detect localized temperature spikes (hot spots), oxygen gradients, or moisture fluctuations, which can negatively impact microbial activity and process consistency (Gargalo et al., 2022).

Additionally, Internet of Things (IoT)-based systems and cloud-connected platforms are now being adopted for SSF bioreactor control. These systems allow remote monitoring, data logging, and predictive maintenance through machine learning algorithms. For example, a smart SSF setup using IoT sensors was implemented in a cocoa pod husk fermentation process to maintain uniform moisture and temperature levels, resulting in a 28% increase in enzyme yield compared to manual control systems (Adeleke et al., 2023).

Case studies from industrial enzyme production (e.g., amylase, protease from *Aspergillus* species) have demonstrated the effectiveness of automated SSF systems incorporating feedback loops for air humidity, temperature regulation, and moisture spraying units. These innovations ensure uniform microbial performance and reduce product variability, which is a critical factor in scaling SSF technologies (Filer, 2000; Rudakiya, 2019).

While implementation costs remain a constraint, the integration of intelligent monitoring systems is increasingly viewed as essential for optimizing SSF bioprocesses, especially in the context of large-scale agricultural residue valorization.

KEY FACTORS INFLUENCING SSF

SSF is influenced by various factors that play crucial roles in determining the success and efficiency of the process. Understanding and controlling these factors are essential for optimizing microbial growth, enzyme production, and product formation in SSF (Egbune et al., 2023a; Egbune et al., 2023c).

SSF offers several distinct advantages over conventional fermentation methods, such as lower water and energy consumption, utilization of low-cost solid substrates, and improved enzyme production. Understanding these differences is crucial for choosing the most appropriate fermentation method based on specific application requirements.

SSF offers unique advantages over submerged fermentation (SF) and liquid-state fermentation (LSF), including the utilization of low-cost solid substrates, reduced water and energy consumption, and improved enzyme production. However, SSF faces challenges in scaling up and longer fermentation times due to the solid nature of substrates and heterogeneous nutrient and oxygen distribution. Understanding these differences is crucial in choosing the most suitable fermentation method for specific applications.

Enhancement of agricultural byproducts through SSF

Several success stories highlight the effectiveness of SSF in enhancing various agricultural byproducts. These studies demonstrate SSF's potential in converting crop residues, fruit and vegetable waste, dairy byproducts, and forestry residues into valuable bioproducts, such as enzymes, nutraceuticals, biogas, and biodegradable materials. The success achieved in these applications underscores SSF's significant role in sustainable waste utilization and value addition. Table 5 summarizes the case studies and success stories of SSF in enhancing various agricultural byproducts.

REDUCTION OF ANTI-NUTRITIONAL FACTORS AND TOXINS

SSF stands as a potent strategy for mitigating the presence of anti-nutritional factors (ANFs) and toxins in diverse agricultural byproducts. By subjecting these materials to controlled microbial activity, SSF contributes to the degradation and elimination of ANFs and toxins, thereby improving the overall nutritional quality and safety of the resulting products (Egbune et al., 2022a; Egbune et al., 2023b) (Table 6).

POTENTIAL BENEFITS OF SSF

SSF provides diverse benefits. It transforms byproducts into valuable products like enzymes, bioactive compounds, and biofuels (Chilakamarry et al., 2022). It enhances byproduct nutrition while reducing anti-nutritional factors (Egbune et al., 2023c). SSF aids waste reduction through organic waste utilization, aligning with sustainable agriculture by enhancing soil (Ndego et al., 2023). It supports resource efficiency, environmental impact reduction and cost-effectiveness, particularly with low-cost substrates (Egbune et al., 2023c). SSF shows potential for bioremediation, bioactive compound synthesis and suits local, small-scale applications (Chilakamarry et al., 2022). SSF offers a multitude of advantages for the utilization of agricultural byproducts, making it an innovative and sustainable approach in various fields. These benefits are well-documented in recent research studies: Egbune et al. (2022b) have reported that SSF plays a role in enhancing the nutritional profile of byproducts, while simultaneously reducing anti-nutritional factors. This is particularly beneficial in the food and nutrition industries. The research by Šelo et al. (2021) underscores the ability of SSF to valorize waste streams, thereby addressing the issue of waste disposal and promoting sustainable resource utilization. Chilakamarry et al. (2022) discuss the versatility of SSF in terms of product applications, offering a wide range of possibilities for different industries, including bioremediation, bioactive compound synthesis, and local, small-scale applications. Both Wang et al. (2019) and Tonukari et al. (2023) have highlighted the potential of SSF in reducing production costs, especially when utilizing low-cost substrates. This makes it an

Table 5. Case studies of Solid-State Fermentation (SSF) applications with agricultural byproducts and their benefits.

No.	Case study/Success story	Type of agricultural byproduct	SSF application	Outcome and benefit	Source
1	Enrichment of proteins and amino acids	Soybean meal	Enhanced protein content for livestock feed	Increased protein content for more nutritious feed	Barnharst et al. (2021)
2	Production of bioactive compounds	Grape pomace	Extraction of antioxidant-rich bioactive compounds	Potent antioxidant extracts for functional foods	Kainat et al. (2022)
3	Enzyme production for digestibility enhancement	Rice bran	Carbohydrase enzyme production	Improved digestibility and nutritional value	Gallardo et al. (2020)
4	Synthesis of bioactive peptides	Whey proteins	Bioactive peptide production	Health benefits in functional foods and nutraceuticals	Yiğit et al. (2023)
5	Conversion of lignocellulosic materials to fermentable sugars	Corn stover	Fermentable sugar production for ethanol	Feedstock for biofuel production	Gong et al. (2020)
6	Enhanced vitamin and mineral content	Fruit and vegetable waste	Vitamin-enriched products	Reduced food waste, enhanced nutritional value	Laranjeira et al. (2022)
7	Bioconversion of antinutritional compounds	Cassava byproducts	Detoxification of antinutritional compounds	Safer animal consumption, improved feed safety	Egbune et al. (2023b)
8	SSF for biogas production from fruit waste	Fruit and vegetable waste	Biogas production	Conversion of fruit waste into biogas for energy	El Sheikha and Ray (2022)
9	SSF for lactic acid production from whey	Dairy byproducts	Lactic acid production	Conversion of whey into lactic acid for various uses	David et al. (2022)
10	SSF for bioethanol production from sawdust	Forestry residues	Bioethanol production	Conversion of sawdust into bioethanol for fuel	El Sheikha and Ray (2022)

economically viable option for industries seeking cost-effective solutions.

MICROORGANISMS IN SSF

In SSF, a diverse array of microorganisms—including filamentous fungi, yeasts, and bacteria—are employed to convert agricultural byproducts into value-added products such as enzymes, organic acids, amino acids, biofuels, and biopreservatives. Filamentous fungi are the most commonly used due to their natural adaptation to low-moisture environments and their ability to secrete large quantities of extracellular enzymes. Common genera include *Aspergillus*, *Rhizopus*, *Penicillium*, and *Trichoderma*. Yeasts (*Saccharomyces*, *Candida*) and bacteria (*Bacillus*, *Lactobacillus*, *Corynebacterium*) are also utilized depending on the target metabolite (Egbune et al., 2024a; Egbune et al., 2024b).

Table 6. Reduction of anti-nutritional factors and toxins.

Degradation process	ANF/Toxin	Microbial action during SSF	Outcome and benefit	Reference
Phytic acid reduction	Phytic acid (ANF)	Production of phytase enzymes	Improved mineral bioavailability and nutrition	Garrido-Galand et al. (2021)
Tannin decomposition	Tannins (ANF)	Microbial enzymatic breakdown	Enhanced nutrient absorption and value	Yasar et al. (2020)
Toxin detoxification	Mycotoxins (Toxins)	Microbial enzymatic degradation	Reduced health risks from harmful compounds	Xu et al. (2022)
Reduced levels of cyanogenic glycosides	Cyanogenic glycosides	Microbial enzymatic breakdown	Minimized toxic potential in byproducts	Egbune et al. (2023a)
Enhanced nutritional safety	ANFs and toxins	Reduction of harmful compounds	Improved safety and bioavailability of nutrients	Ali et al. (2022)
Economic and environmental benefits	ANF and toxin reduction	Sustainable practices and resource utilization	Waste reduction and efficient byproduct utilization	Chojnacka et al. (2021)
Innovative applications	Glucosinolates (ANF)	SSF for detoxifying agricultural materials	Expanded potential of byproducts in livestock feed	Vandenberghe et al. (2021)

Unicellular organisms such as bacteria and yeasts typically grow in biofilm mode under SSF conditions, while filamentous fungi develop complex mycelial networks consisting of both aerial and penetrating hyphae. High hyphal density can result in capillary-driven moisture redistribution, often transitioning the microbial layer into a moist biofilm. Mechanical mixing of the substrate bed during fermentation can further enhance biofilm formation by compacting the aerial mycelia onto the substrate surface (Montoya et al., 2021).

Microbial selection is influenced by the substrate type, moisture content, temperature, aeration, nutrient availability, and microbial inoculum characteristics (Kataki et al., 2021). Additionally, microbes can be applied as monocultures, mixed cultures, or engineered microbial consortia to improve metabolic synergy, substrate breakdown, and process efficiency.

Genetically modified strains and engineered consortia

Recent advances in genetic engineering have enabled the development of genetically modified (GM) microbial strains optimized for SSF. These strains are tailored to overproduce desired metabolites, exhibit improved tolerance to substrate inhibitors, or express heterologous enzymes with high catalytic efficiency. For instance, engineered *Aspergillus niger* strains overexpressing cellulases or proteases have been used to enhance biomass degradation and nutrient release. Similarly, CRISPR-based genome editing tools have been applied to modify *Corynebacterium glutamicum* for enhanced amino acid production during SSF (Cho et al., 2018; Wang et al., 2023).

Engineered consortia—artificially assembled microbial communities—are also being explored to mimic natural microbial interactions and promote division of metabolic labor. These consortia may include both aerobic and anaerobic organisms, or primary degraders and secondary metabolizers, working together to improve substrate utilization and product yield. This approach also helps mitigate microbial inhibition and metabolic bottlenecks that may occur in monoculture systems (Cao et al., 2022).

Microbial succession in long-duration SSF

Microbial succession plays a critical role in long-duration SSF processes, especially when using unsterilized or minimally pre-treated substrates. As fermentation progresses, shifts in pH, moisture, nutrient availability, and metabolite accumulation favor the dominance of different microbial populations over time. For example, initial colonization may be dominated by fast-growing bacteria or yeasts that consume simple sugars, followed by the emergence of filamentous fungi that degrade complex polysaccharides such as cellulose and hemicellulose. In some cases, secondary metabolites produced by early colonizers also act as signaling molecules or inhibitors, guiding succession dynamics

(Rangel et al., 2021).

Understanding and managing microbial succession can enhance process stability, product consistency, and microbial synergy. Techniques such as metagenomic profiling and transcriptomic analysis are now being employed to monitor these shifts and inform the rational design of inoculation strategies, including staggered inoculation and sequential microbial introduction (Wani et al., 2022).

Selection of suitable microorganisms

Microorganism selection is a critical factor in the success of SSF, influencing product yield, quality, and overall process efficiency. The choice of microorganisms should align with the specific characteristics of the agricultural byproduct and the desired biotransformation (Egbune and Tonukari, 2023). SSF offers the advantage of utilizing a diverse range of microorganisms, including bacteria, fungi, and yeast, for various applications (Šelo et al., 2021). Each microorganism type brings unique enzymatic capabilities and metabolic pathways that contribute to the desired bioprocess. The screening of microbial strains is essential to identify those with optimal growth and enzyme production characteristics under SSF conditions (Anigboro et al., 2022). High enzyme yield, substrate utilization efficiency, and tolerance to environmental factors are key criteria for strain selection.

Utilizing native microorganisms present in the agricultural byproduct or the processing environment can enhance SSF efficiency (Aganbi et al., 2023; Egbune et al., 2024d). These microorganisms are adapted to the substrate and can exhibit improved performance compared to exogenous strains. Microorganisms with specific functional attributes, such as cellulolytic or ligninolytic activity, are preferred for SSF involving lignocellulosic materials. This ensures effective degradation and conversion of complex substrates. Yeasts are valuable for SSF due to their ability to ferment sugars and produce ethanol. Strains like *Saccharomyces cerevisiae* and *Pichia pastoris* have been utilized for bioethanol and enzyme production through SSF (Bala and Singh, 2019).

Filamentous fungi like *Aspergillus*, *Penicillium*, and *Trichoderma* are commonly employed in SSF due to their robust growth and broad substrate utilization (Strong et al., 2022). These fungi secrete a variety of enzymes and metabolites beneficial for biotransformation. Filamentous fungi constitute a predominant fungal kingdom, encompassing a diverse array of microorganisms characterized by their filamentous hyphal growth. SSF replicates the inherent environments of these fungi, simulating their flourishing within and on substrate components through hyphal expansion. The expression "filamentous fungi" stands in clear juxtaposition to yeasts, which primarily manifest as unicellular fungi. Leveraging their hyphal growth, filamentous fungi offer substantial potential in SSF for generating enzymes of significant commercial value and a wide spectrum of valuable compounds, driven by their enzymatic activity (Table 7)

Certain bacterial strains, such as *Bacillus* species, are suited for SSF due to their enzyme secretion and ability to produce bioactive compounds. They can enhance nutrient bioavailability and contribute to product quality. SSF can benefit from mixed cultures, where synergistic interactions between microorganisms lead to enhanced enzymatic activities and metabolic pathways. Co-culturing bacteria and fungi can improve substrate degradation and product yield. Advances in genetic engineering allow for the modification of microorganisms to optimize their performance in SSF (Kumar et al., 2021). Engineered strains with enhanced enzyme production or stress tolerance can be designed for specific applications. Microorganism selection should consider process parameters such as temperature, humidity, aeration, and pH, as these factors influence microbial growth and metabolic activities in SSF (Srivastava et al., 2019).

Microbial interactions during the Fermentation Process

Microbial interactions are integral to the complex and dynamic nature of SSF. The coexistence, cooperation, and competition among various microorganisms significantly influence the outcomes of SSF processes, impacting product yield, quality, and overall efficiency (Li et al., 2021). Microbial consortia often display synergistic interactions, where the metabolic activities of one species support the growth and functions of others. For instance, cellulolytic fungi like *Trichoderma* can break down complex substrates into simpler compounds, which can be further metabolized by bacteria such as *Clostridium* (Periyasamy et al., 2023). Different microorganisms may possess complementary metabolic pathways, enabling the utilization of various components of the substrate. Bacteria and yeasts can consume byproducts generated by fungi, promoting the efficient conversion of complex substrates.

Microbial interactions contribute to nutrient cycling within the SSF system. Nutrients released by one microorganism can serve as a nutrient source for others, facilitating the recycling of carbon, nitrogen, and other essential elements (Alam et al., 2022). Certain microorganisms release extracellular enzymes that break down complex polymers into smaller molecules. These breakdown products, such as sugars and amino acids, can serve as substrates for other microorganisms in the community, fostering cross-feeding interactions. Microbial interactions can lead to the exchange of metabolites, including volatile organic compounds, organic acids, and signaling molecules. These compounds can influence

Table 7. Filamentous fungi harnessed in SSF to create enzymes and additional value-added items from diverse food industry residues and by-products.

Microorganisms	**Substrates**	**Products**	**Source**
Aspergillus niger	Citrus peel waste	Pectinase, fruit juice clarification, texture improvement	Nighojkar et al. (2019)
Penicillium species	Dairy by-products (whey)	Lactase, lactose-free dairy products	Mangiagalli and Lotti (2021)
Rhizopus oryzae	Soybean residues	Protease, protein hydrolysis for animal feed, food products	-
Phanerochaete chrysosporium	Brewery residues (spent grains)	Lignin-degrading enzymes, biofuels, Sustainable waste management, value addition	Sodhi et al. (2022)
Neurospora species	Coffee pulp waste	Cellulolytic enzymes, potential biofuel production, cellulose breakdown	Chilakamarry et al. (2022)
Rhizopus oligosporus	Cassava roots and palm kernel cake (PKC)	increased nutritional value, animal feed	Egbune and Tonukari (2023)
Rhizopus oligosporus	Elephant grass	Xylanase, increased phenolic antioxidants, increased nutritional value, animal feed	Egoamaka et al. (2021); Egbune et al. (2022b) Eghagha et al., 2023
Rhizopus oligosporus	Tropical grasses	Xylanase, increased phenolic antioxidants, increased nutritional value	Ezedom et al. (2022)
Rhizopus oligosporus	Maize cob	α-Amylase, phenolic antioxidants, increased nutritional value, animal feed	Ndego et al. (2023)
Rhizopus oligosporus	Cassava stem	α-Amylase, phenolic antioxidants, increased nutritional value, animal feed	Ojo et al. (2022)
Rhizopus oligosporus	Cassava peels	α-Amylase	Anigboro et al. (2023)
Rhizopus oligosporus	Cassava roots	α-Amylase	Egbune et al. (2022a)
Rhizopus oligosporus	Cassava roots	phenolic antioxidants, increased nutritional value, animal feed	Egbune et al. (2023a, c)
Trametes versicolor	tomato pomace	laccase, xylanase, protease	Iandolo et al. (2011)
Trametes versicolor	corn silage	laccase, manganese peroxidase, caffeic acid, vanillic acid, syringic acid	Bucić-Kojić et al. (2017)
Aspergillus niger	Cassava tuber	α-Amylase, increased nutritional value, animal feed	Tonukari et al. (2016)
Aspergillus niger	apricot pomace	neochlorogenic and chlorogenic acids, rutin, quercetine-3(6“acetyl-glucoside)	Šelo et al. (2021)

microbial growth, differentiation, and overall community dynamics (Zhan et al., 2021). Competitive interactions between microorganisms can also occur during SSF. Some microorganisms may inhibit the growth of others through the production of antimicrobial compounds, organic acids, or enzymes that degrade cell walls (Ibrahim et al., 2021).

Microbial communities in SSF often undergo dynamic changes over time, with different species dominating at different stages of fermentation. Understanding these succession patterns is crucial for process optimization and product consistency (Cardoso et al., 2021). Environmental factors, such as temperature, pH, and moisture content, influence microbial interactions in SSF. Microorganisms with different physiological and ecological preferences may thrive under specific conditions. Harnessing microbial interactions in SSF can be strategically employed to achieve desired outcomes. By manipulating microbial consortia and optimizing fermentation conditions, it is possible to enhance product yield, quality, and consistency (Chenebault et al., 2022).

CHALLENGES AND FUTURE DIRECTIONS

SSF has emerged as a potent bioprocessing technique with diverse applications; however, its ongoing progress confronts several obstacles and holds promising prospects for future advancements. This section explores the prevailing challenges in SSF implementation, emerging trends and inventive solutions, and potential avenues for forthcoming research. The intricate and inherent variability of agricultural byproducts poses considerable hurdles when seeking consistent outcomes in SSF. Variations in elements like composition, moisture content, and particle size exert a direct influence on both microbial activity and the final product's quality (Jain et al., 2019). Ensuring the reproducibility of results across numerous SSF iterations is complex, owing to the delicate interplay of microbial dynamics within the solid-state environment. Fluctuations in variables like inoculum composition, temperature, and humidity contribute to divergent findings (Domeignoz-Horta et al., 2020).

The process of scaling up SSF from laboratory to industrial scales introduces a host of technical and logistical hurdles. Complexities arise in managing heat and mass transfer limitations, achieving uniform nutrient distribution, and maintaining precise process control (Rahman et al., 2022). Upholding aseptic conditions within solid-state systems poses a notable challenge, elevating the risk of unintended microbial contamination. Such contaminants can significantly impact the safety, yield, and quality of the final product.

The selection of appropriate microorganisms for specific substrates and desired products is a multifaceted undertaking. The intricate considerations of microbial interactions, compatibility, and competition demand careful navigation. Furthermore, the uneven dispersion of nutrients and oxygen within solid substrates results in spatial disparities in microbial growth and the production of metabolites, thereby influencing both process efficiency and product consistency. The real-time monitoring and control of SSF parameters face difficulties due to the limited availability of sensors tailored for solid-state systems and the intricate web of interactions within these systems (Brookwell et al., 2023).

EMERGING TRENDS, INNOVATIONS, AND POTENTIAL FUTURE DEVELOPMENTS IN SSF

These dynamic shifts hold the promise of revolutionizing how agricultural byproducts are transformed into valuable resources. From synthetic biology and metagenomics to advanced monitoring techniques and nanotechnology applications, SSF is on the brink of transformative breakthroughs.

(1) Synthetic Biology and Genetic Engineering: The advancement of synthetic biology allows for the precise engineering of microorganisms, optimizing their metabolic pathways to enhance SSF performance and product specificity. This innovation has the potential to revolutionize SSF processes (Palazzotto et al., 2019).
(2) Nanotechnology Applications: The application of nanomaterials offers benefits such as improved enzyme immobilization, enhanced substrate accessibility, and efficient product separation within SSF systems. Nanotechnology-driven enhancements contribute to heightened process efficiency and superior product quality (Saritha et al., 2022).
(3) Tailored Microbial Consortia: Future developments may involve designing microbial consortia tailored to specific substrates and desired products. This approach holds the potential to elevate SSF efficiency, yield, and product diversity to new heights (Vishwakarma et al., 2022).
(4) Sustainable Resource Management: SSF can play a pivotal role in the valorization of waste materials, aligning with the principles of a circular economy. By harnessing byproducts and reducing waste, SSF contributes to sustainable resource management (Singh et al., 2021).
(5) SSF in Pharmaceuticals: Expanding SSF applications to the pharmaceutical industry for the production of bioactive compounds and secondary metabolites presents exciting opportunities for drug discovery and development (Kumar et al., 2021).
(6) Climate-Resilient Agriculture: Utilizing SSF to transform agricultural byproducts into climate-resilient products like biofuels and bioplastics addresses environmental challenges and supports sustainable agricultural practices (Singh et al., 2021).

The dynamic landscape of SSF is characterized by ongoing challenges, exciting emerging trends, and the vast potential for future developments. Addressing these challenges and capitalizing on innovative approaches will propel SSF toward heightened efficiency, sustainability, and diverse applications across industries.

CONCLUSION

SSF is a promising and adaptable bioprocessing technique that plays a pivotal role in the sustainable utilization of agricultural byproducts. This review has demonstrated that SSF efficiently transforms agro-food industrial residues—such as fruit peels, oilseed cakes, and cereal husks—into value-added products, including enzymes, organic acids, bioactive compounds, animal feed, and biofuels. One notable example is the use of cassava peels and palm kernel cake in SSF to enhance protein content and reduce cyanogenic glycosides, making them safer and more nutritious for livestock feed. Similarly, apple pomace fermented with *A. niger* yielded high titers of polygalacturonase, highlighting SSF's role in enzyme production for industrial applications. SSF also improves the nutritional profile of byproducts by increasing bioavailability of nutrients and degrading anti-nutritional factors such as phytic acid and tannins. Microorganisms—particularly filamentous fungi like *Aspergillus* and *Trichoderma* spp., and bacteria like *Bacillus* spp.—play critical roles in substrate degradation, enzyme secretion, and nutrient conversion. Aligning with circular economy principles, SSF reduces agricultural waste, limits environmental pollution, and conserves natural resources. While scale-up challenges persist due to heat accumulation, moisture heterogeneity, and process variability, emerging innovations such as genetically engineered strains and smart bioreactor systems are providing viable solutions. Importantly, SSF contributes to sustainable agriculture by repurposing residues, improving soil health through composted post-fermentation biomass, and supporting local economies via decentralized production models. It also offers a waste management solution by diverting biomass from landfills, thereby mitigating methane emissions and environmental degradation. As demonstrated in this review, SSF is not merely a tool for waste reduction, but a transformative approach that supports climate-smart agriculture, food security, and bioeconomic development. Its continued evolution—through microbial engineering, process optimization, and technological integration—will enhance its scalability and environmental impact, positioning SSF as a cornerstone of the future bio-circular economy.

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