



Sustainable Valorization of Plant-Derived Agri-Food Side-Streams Through Fungal Biorefinery: Supporting Bioeconomy Strategy

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Abstract

Purpose of Review The rapid expansion of agricultural and agri-food production has generated substantial volumes of byproducts and side-streams rich in organic matter. Despite their potential, these residues remain largely underutilized, contributing to environmental pressures and constraining the economic sustainability of food systems. Filamentous fungi, with a long history of assimilating agri-food side-streams (AFS), offer a promising solution by enabling the conversion of organic-rich side-streams into nutrient-dense fungal biomass suitable for novel food and feed applications. This review synthesizes recent advances in the use of filamentous fungi to valorize AFS into value-added, bio-based products and compounds relevant to food and feed sectors.

Recent Findings A comprehensive analysis of 268 peer-reviewed research articles was conducted to identify prevailing trends, technological developments, and key factors influencing the bioconversion of AFS. Emphasis is placed on bioprocessing strategies for producing commercially relevant fungal-derived ingredients, including proteins, enzymes, polysaccharides, lipids, and bioactive compounds. Innovative approaches aimed at improving production efficiency and addressing industrial-scale challenges, including fungal biomass recovery, downstream processing, and functional compound extraction, are also discussed.

Summary The review highlights significant opportunities for innovation in upcycling AFS through integrated fungal biorefinery platforms. Advancements in fungal bioprocessing support the development of sustainable, cost-effective, and environmentally friendly food and feed products within a circular bioeconomy framework, emphasizing both ecological and economic benefits.

Keywords Agri-food side-streams · Fungal biorefinery · Valorization · Food and feed applications · Bioeconomy strategy

Introduction

Across the world, the bioeconomy is gaining momentum [1], as global challenges related to food security, sustainable development, environmental protection, and climate change

mitigation have intensified in recent decades, demanding urgent and coordinated responses. Ensuring that agricultural and food systems can sustainably provide sufficient food, feed, and essential resources is critical. In response to these challenges, the United Nations General Assembly adopted the 2030 Agenda for Sustainable Development, which provides a global framework to promote long-term peace, prosperity, and environmental stewardship for humanity and the planet [2].

While modern agriculture and industrialized food production have significantly increased global food availability, they have also generated enormous amounts of agri-food waste and losses. These residues, estimated at approximately 150×10^6 Mt and projected to grow at an annual rate of 7.5% [3], impose severe environmental, economic, and social pressures. Globally, approximately one-third

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of all food produced is lost or wasted across the supply chain [4]. Food losses occur at multiple stages of the supply chain, with approximately 13% occurring before retail (harvesting, transport, storage, and processing) and 19% at the retail and consumption (grocery stores, households, and food service). From an environmental perspective, agri-food side-streams (AFS) and losses account for 8–10% of global greenhouse gas emissions, including methane (CH₄) and carbon dioxide (CO₂), thereby significantly contributing to climate change [5]. Moreover, AFS accelerate the depletion of natural resources, consuming approximately 23% of global fertilizer inputs and 25% of freshwater used in agriculture, as well as occupying extensive arable land [6]. These inefficiencies accelerate ecosystem degradation and biodiversity loss, illustrating the unsustainable nature of current food systems. In parallel, the economic and social costs of agri-food waste undermine food security and nutrition, particularly in vulnerable populations. Collectively, these interconnected impacts amount to approximately USD 2.6 trillion in losses [7] and underscore the urgent need for sustainable resource management and integrated valorization strategies that simultaneously advance food security, environmental protection, and socioeconomic development.

Recognizing the untapped potential of secondary biomass, including agricultural residues, byproducts, and organic waste streams, the European Commission has emphasized their valorization in the latest EU Bioeconomy Strategy [1]. This strategic focus supports the global transition toward clean industries and circular, decarbonized bioeconomies by promoting the sustainable supply and use of biomass, fostering innovation, improving resource efficiency, and reducing dependence on fossil-based and imported materials. In particular, biomass processing, biomanufacturing, and biotechnology can drive economic growth, generate environmental benefits, and produce high-value sustainable products, while creating synergies across agriculture, forestry, fisheries, and aquaculture. Europe's circularity rate currently stands at 12.2% [8], with the ambition of reaching 24% by 2030. This target is supported by complementary policy frameworks such as the Circular Economy Strategy, the Competitiveness Compass, and the Clean Industrial Deal, which collectively aim to strengthen industrial competitiveness and achieve climate neutrality. To advance these objectives, the European Investment Bank Group has identified critical investment needs across nine bioeconomy sectors, highlighting priority areas where targeted action is required to close financing gaps and enable a sustainable transition [9]. In parallel, the EU has conducted detailed assessments of agro-industrial residual biomass across Member States, demonstrating its significant potential as a sustainable feedstock for the emerging bioeconomy [10]. Looking ahead to 2040, the EU envisions

a bioeconomy that is circular, sustainable, and technologically advanced, fully integrated into global markets and supported by traceable, regionally anchored supply chains. This vision aims to deliver environmental, economic, and social benefits through the integration of regenerative land and water management, resilient biomass value chains, carbon and biodiversity markets, and knowledge-driven innovation [1].

Emerging technologies offer critical solutions to reduce food loss and waste across the supply chain. Precision farming, smart packaging, traceability, artificial intelligence, and consumer-focused digital tools can enhance efficiency, transparency, and sustainability, yet their adoption is hindered by high costs, limited infrastructure, and behavioral barriers [11]. Concurrently, side-streams bioconversion into value-added products biofuels, biochar, and biomaterials shows immense potential, although scalability remains a challenge [12]. However, conventional biological and thermochemical methods for food waste valorization are often limited by long operating times, low-value products, and the generation of unwanted byproducts [13]. Novel biotechnological valorization approaches of agri-food side streams, particularly via fungal biorefineries, provide a transformative route to recover valuable compounds, reduce environmental impact, and generate sustainable products for food, feed, and industry [14].

Agri-food side-streams, including grain straw and bran, oilseed cakes (OCs), soapstocks, and fruit and vegetable byproducts, and other agri-food processing side-streams are inherently rich in nutrients and bioactive compounds, yet they remain largely underutilized, often relegated to low-value applications such as composting, bioenergy, or animal feed [14–21]. Harnessing these residues through innovative biotechnological strategies aligns directly with the UN's Sustainable Development Goal Target 12.3 [2], and the new EU Bioeconomy Strategy [22], providing practical pathways to recover valuable resources, reduce environmental impacts, and generate high-value products for food and feed applications within a circular bioeconomy framework.

Bioprocessing, particularly via fungal biorefineries, offers a promising approach to upcycle low-cost AFS into nutrient-dense, functional products such as proteins, fibers, oils, bioethanol, organic acids, polysaccharides, and prebiotics. This strategy enhances sustainability by reducing reliance on food-grade sugars, increasing the value of agro-industrial byproducts, and expanding the portfolio of functional ingredients for human and animal consumption [16, 19]. In addition, fungal fermentation can yield a diverse portfolio of food and feed ingredients, such as protein-rich biomass (including single-cell proteins and mycoproteins) [19, 23–27], functional fermented foods and beverages [28], organic acids suitable for food applications, polysaccharides

and prebiotics [29], and nutritionally enriched animal feed products [30]. By converting agri-food side-streams into high-value products, microbial fermentation advances circular bioeconomy strategies, mitigates environmental impacts, and supports sustainable food systems, thereby addressing critical global challenges [31].

Most previous reviews on agri-food waste valorization have focused on individual strategies, such as composting, bioenergy, biodegradable materials, or phytochemical recovery. While informative, they offer limited insight into the potential of filamentous fungi fermentation to convert agro-industrial side-streams into high-value bio-based products. This review addresses these gaps by providing a comprehensive and up-to-date overview of the biovalorization of AFS through fungal biorefineries (FBRs). It integrates recent advances in fermentation technologies, process optimization, and valorization strategies, providing insights into the efficient conversion of low-value biomass into products with enhanced nutritional, functional, and economic value. Beyond technological developments, it addresses broader sustainability implications of fungal-based valorization, including improved resource efficiency, reduced food loss, and the promotion of a circular bioeconomy. Key challenges, opportunities, and future research directions are also discussed, positioning fungal biovalorization as a promising approach for sustainable food systems aligned with the UN SDGs including SDG 2 (Zero Hunger), SDG 9 (Industry, Innovation and Infrastructure), SDG 12 (Responsible Consumption and Production), and SDG 13 (Climate Action), and the EU Bioeconomy Strategy.

Materials and Methods

A search of published, peer-reviewed articles was conducted on the Web of Science Core Collection, ScienceDirect, and PubMed. The search targeted studies on the sustainable valorization of agri-food industry side-streams via fungal biorefinery approaches, with a particular focus on the production of food- and feed-relevant ingredients and compounds, including proteins, lipids, polysaccharides, enzymes, and bioactive molecules. Only English-language articles published between 2015 and 2025 were considered.

The search strategy combined the following keywords: (fungi OR filamentous) AND (waste OR side-streams OR residues OR byproducts OR biomass) AND (agricultural OR agrifood OR food) AND (fermentation OR bioprocess OR biorefinery) AND (valorization OR upcycling OR bioconversion OR circular) AND (protein OR feed OR food OR bioactive). The Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 framework guided the study selection process [32]. Of 438 articles

initially identified, 268 met the inclusion criteria and were included in this review. Figure 1 presents the PRISMA flow diagram illustrating the inclusion and exclusion process.

The included studies comprised original research articles, including Early Access and Open Access papers that met the inclusion criteria. Exclusions were applied to review articles summarizing existing literature without primary experimental data, invited reviews, associated datasets, and Enriched Cited References.

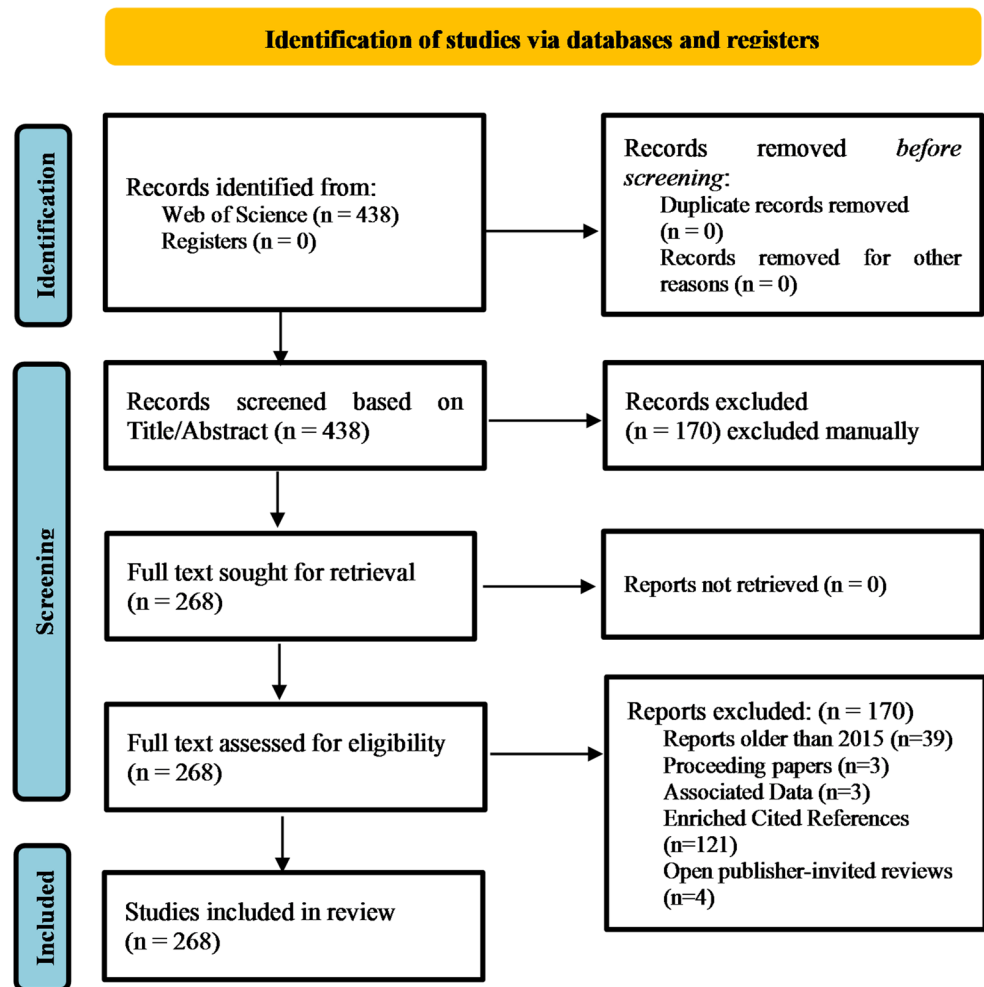
The final dataset was exported in plain text format and analyzed using VOSviewer software (version 1.6.18, Leiden University, The Netherlands) to identify major research clusters, co-occurrence patterns, and emerging trends in the valorization of AFS into value-added products via FBR approaches. A co-occurrence map based on titles and abstracts was generated using full counting, with a minimum occurrence threshold of 10. This initially yielded 7,583 terms, of which 222 met the threshold. Irrelevant terms were further refined using a thesaurus, removing 60% of the least relevant terms and resulting in six main thematic clusters comprising 133 items (Fig. 2c). In the visual representation, node size corresponded to keyword frequency, while link thickness indicated the strength of co-occurrence between terms.

Results and Discussion

Global Research Trends in Bio-Based Feedstocks Valorization

The geographic distribution of the 268 studies is illustrated in Fig. 2a, where the choropleth map highlights the concentration of research activity across countries, providing insight into global research trends in this field. The five leading countries in publications on the sustainable valorization of agri-food industry side-streams through fungal biorefineries are India (9%), China (8%), Spain (6%), Brazil (5%), and Sweden (5%). When geographic patterns are examined alongside thematic trends, regional differentiation becomes apparent. India and China are most frequently linked with topics related to agricultural residue valorization, lignocellulosic bioconversion, enzyme production, and bioenergy applications, consistent with the scale of crop-derived side-streams in these regions. Brazil focuses on enzymatic valorization of agro-industrial by-products, particularly those from sugarcane and fruit processing. European countries led by Spain and Sweden, show relatively stronger research emphasis on circular-economy frameworks, environmental assessment, waste-stream management, and integrated biorefinery design, alongside food and feed applications. This distribution likely reflects the high availability of bio-based

Fig. 1 PRISMA flow diagram illustrating the article selection and screening process used in this review



feedstocks, the growing emphasis on circular bioeconomy strategies that promote biomass valorization, the adoption of technological solutions, increased awareness, and an expanding research focus on innovative approaches for their sustainable utilization.

The cumulative number of publications reflects changes in research output over the past decade, showing a clear upward trend from 2015 to the present (Fig. 2b), with the peak was observed in 2024, with 44 publications. This rising volume of research underscores the growing scientific interest in the valorization of bio-based feedstocks through biorefinery approaches and highlights the increasing recognition of their potential for sustainable food, feed, and bio-based product and services development. Furthermore, the bibliometric co-occurrence analysis highlights key research trends and thematic structures in agri-food side-stream valorization via fungal biorefineries platforms. The network (Fig. 2c) reveals a tightly connected, interdisciplinary landscape, where fungal valorization strategies converge with applications in food and feed production. Central terms, agricultural and food side-streams,

enzymes, organic acids, pigments, proteins, fibers, lipids, and bioactive compounds, reflect the dual priorities of efficient alternative feedstock conversion and production of high-value bio-based products within a circular economy framework.

Furthermore, the identified thematic clusters underscore the strategic diversity and interconnectedness of research and innovation, emphasizing the expanding scientific emphasis on sustainable, value-oriented biorefinery solutions. The red cluster underscores the foundational role of microbial and fungal bioprocesses in transforming food waste and associated byproducts into bioeconomically relevant outputs. Strong associations with keywords such as nutritional value, minerals, vitamins, lipids, metabolites, antioxidant activity, single-cell protein, biorefinery, and bioeconomy reflect a shift in the literature from energy-centered applications toward nutrient recovery and functional product generation. This cluster underscores sustained interest in revalorizing fungal biomass for animal feed and, increasingly, human food applications, particularly in response to global demand for sustainable protein sources.

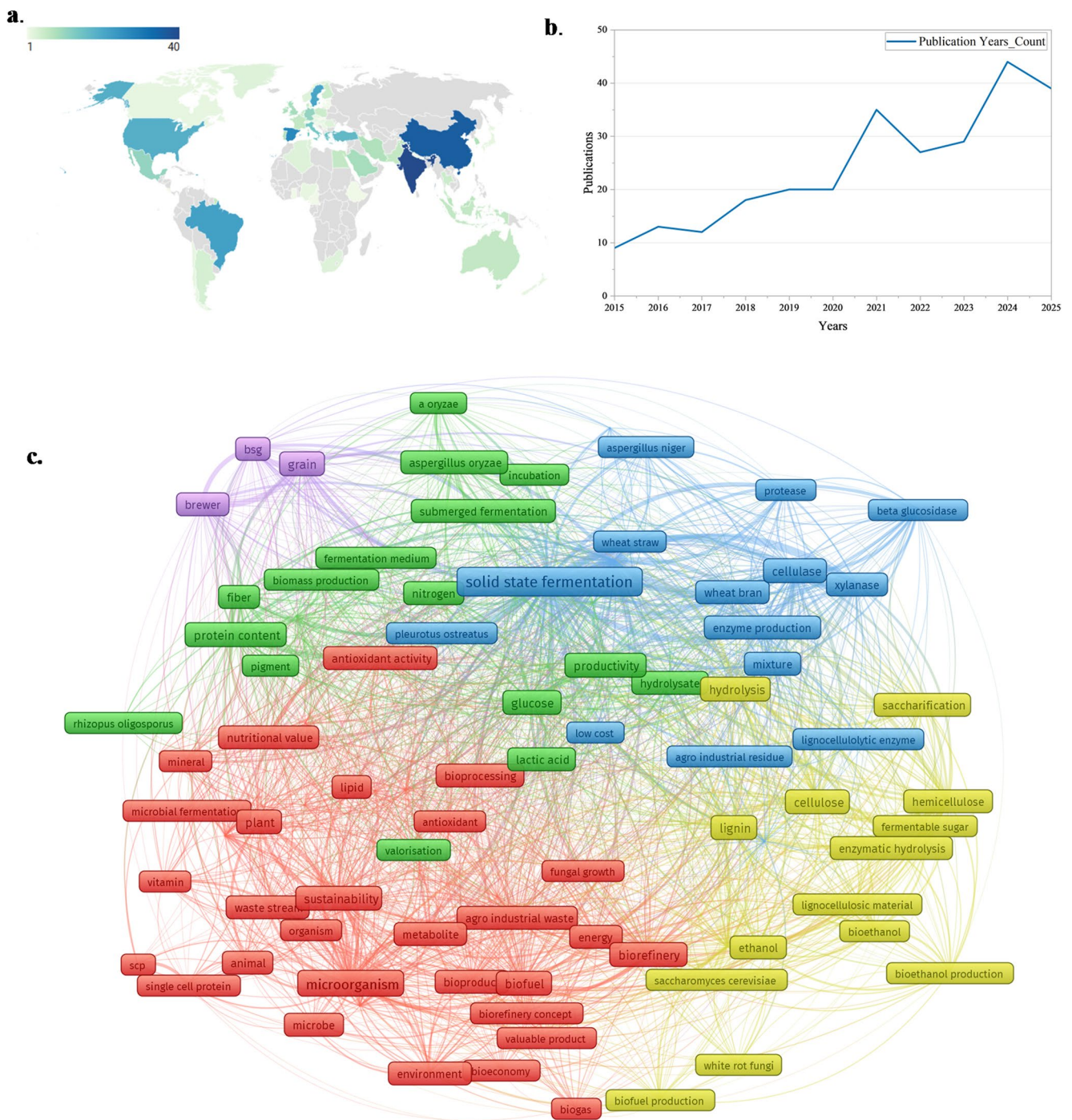


Fig. 2 (a) Choropleth map illustrating the geographic distribution and concentration of research activity across countries over the past decade. (b) Publication trends in the valorization of bio-based feedstocks using biorefinery-based approaches over 2015–2025. (c) Bib-

liometric network visualization of research trends on the sustainable valorization of AFS through FBR approaches (2015–2025). The network was constructed using VOSviewer and resolved into five main thematic clusters

The green cluster centers on fermentation media, biomass production, and compositional quality indicators such as protein content, fiber, glucose, and pigments. This cluster emphasizes optimization strategies in fungal cultivation, primarily through submerged fermentation,

aimed at enhancing nutritional profiles and producing functional food ingredients and biocolorants. The prominence of these terms highlights the growing convergence of fermentation technology and food-grade biomass development.

The blue cluster comprises enzyme-related terms (cellulase, xylanase, protease, β -glucosidase, lignocellulosic enzymes), low-cost substrates (agro-industrial residues, wheat straw, bran), and solid-state fermentation. This cluster represents methodological advances in fungal enzyme production and lignocellulosic biomass processing, which are critical for efficient substrate deconstruction and downstream biorefinery integration.

The yellow cluster reflects sustained interest in lignocellulosic biomass components such as cellulose and hemicellulose, linking enzymatic activities to fermentation outputs, including bioethanol and other biofuels. This cluster highlights hydrolysates as both technical and conceptual hubs, integrating pretreatment, enzymatic saccharification, and microbial fermentation into unified biorefinery pathways. The prominence of this theme aligns with recent experimental advances demonstrating improved saccharification yields through fungal enzyme cocktails and co-cultivation strategies.

The purple cluster emphasizes specific agri-industrial side-streams such as brewer's spent grain, bread waste, and other grains, underscoring their widespread adoption as low-cost, readily available substrates. Their strong association with edible filamentous fungi reflects increasing research on direct valorization routes aimed at producing consumable or feed-grade products. This cluster highlights practical pathways toward industrial scalability and alignment with circular bioeconomy principles.

In summary, the co-occurrence network provides a comprehensive overview of the evolution of research on the fungal valorization of agri-food waste. It demonstrates the transition from foundational fermentation studies to the development of integrated biorefineries and the production of high-value products. The prominence of enzymes, hydrolysates, and nutrient-rich biomass highlights the field's alignment with sustainable and circular bioeconomy objectives. Future research should prioritize bridging laboratory-scale advancements with industrial implementation, addressing challenges such as scalability, regulatory frameworks, and market acceptance.

Major Agri-Food Side-Streams of Plant Origin: Production and Characteristics

Plant-based agri-food side-streams (AFS) arise from agricultural production, harvest losses, and processing of crops, including cereals, sugar crops, fruits, vegetables, roots, tubers, oilseeds, pulses, and tree nuts. These residues, such as straw, husks, peels, pomace, and oil cakes, are generated in substantial quantities worldwide and represent a largely underutilized resource [33]. Depending on crop and

processing practices, these side-streams can account for 12–85% of production [3]. Traditionally, they have been used as animal feed or processed into humic compounds via composting for application as fertilizers in fields [34], whereas open-field burning or uncontrolled dumping of these wastes poses significant environmental and health risks [12]. Their pronounced compositional heterogeneity, influenced by feedstock, climate, and agricultural practices, complicates the development of standardized, scalable valorization strategies [35].

Figure 3 presents the global production of major crops (million tonnes, Mt), categorized as cereals and starchy crops, sugar crops, fruits and vegetables, roots and tubers, oilseeds, and pulses and tree nuts, illustrating their potential as sources of plant-derived agri-food side-streams.

Cereals and Starchy Crops

Corn, or maize (*Zea mays* L., Poaceae), is one of the world's most important crops, with global production projected to reach approximately 1,298 Mt in 2025–2026. Utilization is dominated by feed applications (about 762 Mt), followed by industrial uses (around 346 Mt), while direct human consumption remains comparatively limited (approximately 140 Mt) [37]. Corn residues include husks (8.4%), leaves (18.5%), stalks (57.8%) and cobs (12.2%) [38]. Corn cobs are an underutilized lignocellulosic biomass characterized by compact tissue, high cellulose content, and low ash and nitrogen levels. Recent studies highlight their strong potential for biotechnological valorization, including the production of bioenergies (e.g., bioethanol, biohydrogen, biodiesel, and biobutanol), industrial enzymes (cellulases, xylanases, amylases, glucosidases, and pectinases), and value-added bioproducts such as xylooligosaccharides, fermentable sugars, organic acids, and pigments [38]. Corn husks accounts for approximately 104 Mt of biomass and is characterized by high cellulose content and low moisture (5.6%). It contains moderate amounts of protein (4.3%) and ash (3.9%), low lipid content (1.8%), and is rich in carbohydrates (84.5%), including cellulose (49%) and hemicellulose (37%), with moderate lignin (12%) and a small fraction of total reducing sugars (0.24%). It has shown promise for sustainable applications, including the production of bio-textiles, reinforced composites, nanocomposites, bioplastics, pollutant adsorbents, and paper [39, 40]. Corn stover, another residue of this crop, consisting of cellulose (43.2%), structural carbohydrates (62.9%), acid-soluble lignin (2.4%), acid-insoluble lignin (21.3%), ash (11.8%) [41], and has demonstrated great potential to be used for biofuel production [42].

Wheat (*Triticum aestivum* L.) with global production projected to reach ~ 830 Mt for 2025–2026 dominated by food

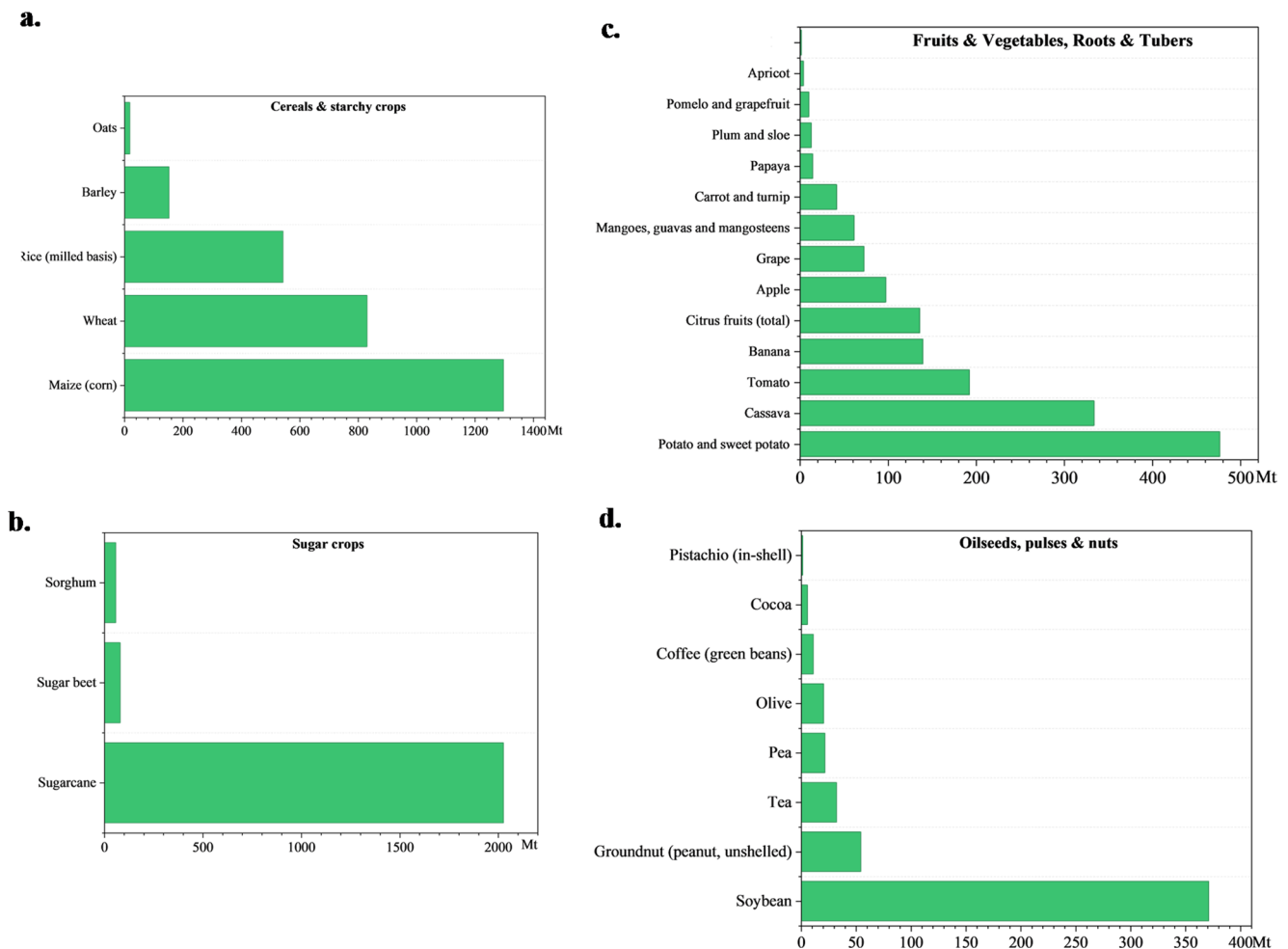


Fig. 3 Global production of major crops (million tonnes, Mt) as potential sources of bio-based feedstocks: **(a)** cereals and starchy crops; **(b)** sugar crops; **(c)** fruits and vegetables, roots and tubers; **(d)** oilseeds, pulses and tree nuts. (Source: FAOSTAT [36], and International Grains Council [37])

use (~ 571 Mt), followed by feed (~ 154 Mt) and industrial applications (~ 29 Mt) [37]. Wheat bran, a major by-product of wheat flour milling, has an annual global production of approximately 150 Mt and is primarily burned or used as an animal feed additive [43]. Wheat bran is a rich source of dietary fiber (35–60%), encompassing both soluble and insoluble fractions such as hemicellulose, cellulose, and starch, also contains 15.6% protein, 2.9% sugars, 3.3% fat, and 3.39% phosphate (P_2O_5). Despite its high carbohydrate content, wheat bran remains an underutilized resource with significant potential as a substrate for bioprocesses [43, 44]. Wheat straw, the dry stalk remaining after grain and chaff removal, is a recalcitrant agro-industrial by-product rich in lignocellulose (~ 27% cellulose, 21% hemicellulose, 23% lignin, plus minerals, proteins, silica, ash, and ADF) traditionally used in medicine, soil amendment, biochar, basketry, pulp, and bioremediation [45].

Rice (*Oryza sativa*) is the world's third most-produced cereal crop, following corn and wheat, with global production ~ 548 Mt (on a milled basis) projected in 2025–2026 [37]. Paddy

straw (PS), a lignocellulosic biomass, is estimated at around 731 Mt and represents a versatile agro-residue with multifaceted benefits for agriculture, environment, and bioenergy. PS is primarily composed of carbohydrates, including cellulose (28–45%) and hemicellulose (12–34%), lignin (5–24%), and silica (5–24%) [46]. Its incorporation into soils enhances nutrient cycling, organic matter content, soil structure, moisture retention, and microbial activity, while contributing to erosion control and carbon sequestration. On a proximate basis, it contains 10–20% moisture, 82% organic matter, 4% crude protein, 37% crude fiber, 43% non-fatty ester, and 18–22% ash, with NDF and ADF ranging 54–75%, phosphorus (0.05%) and calcium (0.14%). Beyond traditional agronomic uses, PS is a promising feedstock for energy, chemical, food, medical, and industrial sectors into biofuels, biogas, biohydrogen, alcohols, organic acids, enzymes, biopolymers, biochar, and fertilizers using diverse microbial and thermal processes [47]. A total of 72.6 Mt of rice bran, the brown outer layer of the rice kernel was generated in 2022 [48]. Although nutrient-rich, containing ~ 50% carbohydrates (mainly cellulose, hemicellulose, xylan,

and starch), 20% fat, 15% protein, 15% dietary fiber, and substantial amounts of vitamins and minerals, rice bran remains underutilized, or often used as animal feed or discarded as waste [49]. Rice husk is a lignocellulosic agro-industrial residue characterized by low protein content (1.9% DM) and a high ash fraction (16.2%), reflecting its elevated silica content. Its structural carbohydrate fraction is dominated by cellulose (37.4%) and hemicellulose (11.2%), while lignin accounts for a substantial proportion (25.5%) [50].

Barley (*Hordeum vulgare* L.) is an ancient and important functional crop global barley total production is projected to reach ~ 152 Mt in 2025–2026 [37]. Almost 80–90% of barley is used in animal feed (~ 101 Mt), and for malt preparation (~ 27 Mt), while only a small part is used directly for human consumption (~ 7 Mt). Barley straw contains soluble and insoluble dietary fibers, fermentable sugars, amino acids, and vitamins; however, its high cellulose content and unique protein composition can limit palatability [51, 52].

Brewers' spent grain (BSG), the insoluble solid residue of malted barley, is the most abundant byproduct of the brewing process, representing 85% of the total brewing waste material produced, ~ 36 Mt of BSG is generated globally per annum. BSG has a short shelf life, and traditionally is utilized as animal feed or in landfill, if dried, it can be incorporated as a food ingredient in products such as bread, pasta, muffins, sponge cakes, pizza crust, biscuits, crackers, yogurt and beverages, due to its dietary fiber (40–50%, with main fiber constituent hemicellulose, 20–40% of the total) and protein content (30%); however, the inclusion of BSG in food systems can negatively affect the techno-functional and sensorial properties of the products [53].

Oats (*Avena sativa*) are among the most prominent cereal crops globally, ranking seventh in cereal production, with a global production of approximately 18 Mt in 2023, of which Europe contributed ~ 11 Mt [36]. Oat processing generates oat hulls, representing ~ 25% of the total grain mass. These hulls are rich in lignocellulosic materials, comprising up to 84% of their dry weight, with approximately 23% cellulose, 35% hemicellulose, 25% lignin, and 3% starch, though exact composition varies with growth conditions [54]. As a lignocellulosic feedstock, oat hulls have been primarily used for ethanol production [55]. Oat bran is a rich source of β -glucan, a soluble dietary fiber consisting of cellotriase, cellotetraose, and longer cellooligosaccharide units linked by (1→3)- β -D-glycosidic bonds [56].

Sugar Crops

Sugar beet (*Beta vulgaris* var. *Saccharifera*) has an annual global production of ~ 80 Mt, with the EU contributing ~ 46% of this output. Processing one tonne of sugar beet

yields ~ 500 kg of wet sugar beet pulp (SBP), a byproduct rich in polymeric carbohydrates (75–85% DW), including cellulose (20–25%), hemicelluloses (25–36%), and pectin (20–25%), with low lignin (1–3%) and ~ 8% protein. Its heterogeneous composition makes SBP a promising substrate for biobased products, although its nutritional and industrial potential remains underexplored. Traditionally used as animal feed or for biogas production, SBP applications now include bioplastics, biofuels, organic acids, microbial enzymes, feed proteins, and pectic oligosaccharides [57].

Sugarcane (*Saccharum officinarum*) is one of the most widely produced crops, with an annual production of 2,026 Mt, representing 21% of global crop output. Its primary residue, sugarcane bagasse (SCB), is produced at ~ 700 Mt annually. SCB is a lignocellulosic biomass with potential as sustainable ruminant feed, however, its low crude protein content (~ 10%) and high lignin–(hemi)cellulose fraction (> 85%) limit its digestibility. While chemical, physical, and physicochemical treatments can break down lignin–polysaccharide complexes, these methods are costly, energy-intensive, require specialized equipment, and may generate toxic waste.

Sorghum (*Sorghum bicolor* L. Moench) is a globally important cereal, with an estimated production of approximately 57 Mt in 2023, of which Europe contributed ~ 1 Mt [36]. It is the fifth most important cereal worldwide and is valued for its nutritional content, being the second most used grain for cattle feed [58, 59]. The sorghum bagasse (SSB), a lignocellulosic by-product from food processing and agriculture, is an attractive feedstock for biofuels, enzymes, and value-added bioproducts [60]. On a dry matter basis (DM), sorghum contains high carbohydrates (71.3–71.5%), moderate protein (6.8–10.9%) and lipids (4.0–13.8%), low crude fiber (1.9–2.0%), ash (1.3–2.01%), and structural polysaccharides including neutral detergent fiber (NDF: 69.6%), ADF (20.1%), acid detergent lignin (ADL: 3.0%), hemicellulose (49.5%), and cellulose (17.1%). Essential minerals include potassium (11.2–12.3 mg/g), phosphorus (1.99–2.29 mg/g), and calcium (1.95–2.19 mg/g), supporting its applications in food, feed, and bioprocessing [58, 59]. Despite its nutritional value, sorghum utilization is constrained by condensed tannins, which reduce protein and carbohydrate digestibility.

Fruits and Vegetables, Roots and Tubers

In the EU, approximately 96 Mt (8.5%) of global fruit and vegetable production is generated annually, yet nearly 30% of this is lost as byproducts (peels, pulp, seeds, kernels, pomace, cores, stems, and leaves) or remains uneaten. Fruits, vegetables, roots, and tubers account for 40–50% of all agri-food industry byproducts [61]. Fruit byproducts account for

over one-third of the fruit mass and, after consumption or industrial processing, are largely underutilized, often being used as animal feed, incinerated, or sent to landfills. They are rich in carbohydrates, dietary fiber, lipids, and essential minerals such as calcium and potassium, but contain low protein, representing a largely untapped resource [62]. Most plant-derived phenolic antioxidants occur in conjugated forms with sugar residues, which reduce their bioavailability [63].

Apples (*Malus domestica*) are among the most widely cultivated fruits globally, with a 2023 production of approximately 97 Mt, of which Europe contributed about 18% [36]. Industrial processing generates substantial solid byproducts, which constitute about 25–35% of the fresh fruit. Of the pomace produced, approximately 3% consists of seeds, ~ 95% skin and ~ 1% stems. These byproducts are primarily generated during apple juice and sauce production [63], with 89.1% resulting from slicing and 10.9% comprising seed and pulp [64]. Apple pomace is rich in carbohydrates (34–45%), phenolic antioxidants (1–289 mg gallic acid equivalent (GAE)/100 g), and minerals (1.5–3%), with smaller amounts of proteins, lipids, and carotenoids. Apple byproducts serve as a valuable substrate to produce a variety of high-value compounds, including enzymes, proteins, organic acids, ethanol, carotenoids, aroma compounds, natural antioxidants, and pectin [63, 65, 66].

Grape (*Vitis* spp.) is among the most widely cultivated fruits worldwide, with global production reaching ~ 73 Mt in 2023, over 34% of which originated in Europe [36]. Grape pomace, a major byproduct of winemaking and juice production, represent approximately 30% of processed grapes [14] and contains 55–75% water and varying amounts of protein (6–15%), lipids, carbohydrates, minerals, and antioxidants. The pomace is primarily composed of fruit skins and stems (77%), with seeds accounting for 8–23%. Grape seeds yield oil rich in unsaturated fatty acids, mainly linoleic and oleic acids (> 68%) [67].

Plum (*Prunus* spp.) and sloes had a global production of approximately 13 Mt in 2023, with Europe contributing around 3 Mt [36]. Industrial processing generates significant byproducts, including pomaces, kernels, and brandy distillery wastes. Plum kernels contain over 45 g/100 g oil, rich in oleic acid, moderate in linoleic acid, low in saturated fatty acids, and also provides beneficial phytosterols and tocopherols [68].

Fig fruit (*Ficus carica* L.) had an estimated global production of 1.30 Mt in 2023, with Europe contributing 0.10 Mt [36]. Figs are typically consumed fresh or dried, and are also used in wine, liquor, juice, jelly, and jam production. Byproducts from fig processing include leftover fruits and fig skins, which consist of moisture (11.9%), protein (8.7%), fat (2.6%), fiber (8.8%), and ash (4.5%), with carbohydrates

predominating (75.4%). These byproducts also provide a rich source of phenolic compounds, including phenolic acids, flavanols, flavones, and proanthocyanidins [69].

Citrus production including oranges, tangerines/mandarins/clementines, and other citrus fruits totaling consist 69.8 Mt, 52.6 Mt, and 13.4 Mt, respectively, of which Europe contributed 5.73 Mt, 3.03 Mt, and 0.043 Mt [36]. Citrus processing generates approximately 0.025 Mt of waste per year, posing significant management challenges [70]. Mandarins yield roughly 16% peel and 84% usable products [64]. Orange peels, a major byproduct, are rich in carbohydrates (41.25%) and protein (3.5%) but low in lignin, with a carbon content of 22.56%, low nitrogen (0.735%), and a C/N ratio of 30:1 [71].

Pomelos and grapefruits had a global production of 9.93 Mt in 2023, with Europe contributing 0.10 Mt [36]. Grapefruit byproducts are rich in carbohydrates (~ 76.2%) and crude fiber (~ 10.6%), contain moderate crude protein (~ 5.8%) and low lipids (~ 0.7%), and also include moisture (~ 3.7%) and ash (~ 3.1%) [72].

Carrot (*Daucus carota* L.) roots and turnips global production reached 41.4 Mt in 2023, with the Europe contributing ~ 19% [36]. Carrot processing can generate up to 30% waste [64], but only 10–15% of carrot pomace is currently used as animal feed or fertilizer, with the remainder discarded [73]. Carrot byproducts are rich in carbon (> 40%) and protein (14%), and cellulose (10–28%), hemicellulose (5–20%), lignin (2.5–8%), pectin (2–8%), and free sugars, including sucrose (14.3–47.2%), glucose (7.9–30.4%), and fructose (5.4–14.2%), and beneficial minerals (notably Ca and Zn, with low Cu). Carrot peels contain 1.5% carbohydrates and 0.5% proteins [40] and are a source of α - and β -carotene, which can be processed into antioxidant-rich dietary fiber powder [74].

Papaya (*Carica papaya* L.) production was ~ 14.2 Mt [36], byproducts consist of ~ 8.5% peel, 6.5% seeds, 32% pulp, and 53% as the final product [64]. Papaya contains ~ 69–91% moisture, 7–8% carbohydrates (mainly fiber), 1–11% protein, 0.3–1.9% fat, and 1–7% ash. Sugars are dominated by sucrose (~ 2.66 g/100 g fresh weight, FW), with glucose and fructose around 1.1 g/100 g FW each. Organic acids total ~ 334 mg/100 g FW (mainly malic acid), and major minerals include K (~ 320 mg/100 g FW), Na (~ 69 mg/100 g FW), P (~ 35 mg/100 g FW), and Ca (~ 33 mg/100 g FW). Papaya peels are rich in carbohydrates (61.8%) but low in protein (4.1%) [75].

Bananas (*Musa* spp.) are among the most widely produced fruits, with a global production of 139.3 Mt in 2023, including 0.71 Mt from Europe [36]. Bananas are consumed fresh or processed into products such as ketchup, sauces, and chips. Processing generates substantial peel waste, accounting for approximately 30–40% of the fruit's mass,

which is often discarded or used as animal feed [64, 76]. Banana peels are rich in carbohydrates, including cellulose, hemicellulose, starch, and pectin, and can serve as a renewable feedstock.

Mango (*Mangifera* spp.) ranks as the second most traded tropical fruit worldwide and fifth in total production. Together with guavas, and mangosteens, global production reached approximately 61 Mt in 2023 [36]. Although traditionally consumed fresh, the fruit can be processed into a wide range of food products; however, over 35% of mangoes are discarded during processing, comprising roughly 13.5% seeds, 18% unusable pulp, and 11% peels [64]. Mango byproducts, including the seed kernel and seed shell/epicarp, contain 4.0–7.3% protein, 0.8–5.4% lipids, and 1.7–5.7% ash, with carbohydrates predominating (81.9–93.6% dry weight). Hemicellulose accounts for 9.6–14.1%, reducing sugars range from 14.8 to 15.2 mg glucose/g, and antioxidant activity is high (59.2–93.1% DPPH scavenging) [77]. Pineapple (*Ananas comosus* L.) generates about 15% of pulp, 15% of the top 14% of peels, 9% of the core, and 48% as the final product [64]. Pitahaya (*Hylocereus undatus*) peel accounts for approximately 33% of the fruit's weight, and its disposal poses significant challenges for the pitahaya juice processing industry. Processing of pineapple, grape, apple, pitahaya, and mango processing generate substantial byproducts that are rich in bioactive compounds including phenolics, flavonoids, and carbohydrates and lipids [63, 78].

Apricot (*Prunus armeniaca* L.) had a global production of ~ 4 Mt in 2023, with Europe contributing 0.78 Mt [36]. Apricot fruits are rich in nutrients and phenolic compounds, including neochlorogenic and chlorogenic acids, proanthocyanidin dimers and trimers, quercetin and kaempferol glycosides, and cyanidin-3-glucoside, the main pigment. Composition varies by cultivar and fruit part (skin or flesh) [79]. These characteristics highlight the potential of apricot byproducts (peels and stones) as valuable sources of natural antioxidants and bioactive compounds.

Chokeberry (*Aronia melanocarpa*) has attracted global interest due to its high polyphenolic content and strong antioxidant activity and is increasingly cultivated in Eastern Europe. Over 90% of the fruits are processed into juice, generating byproducts rich in dietary fiber (63–78% DM), flavanols and highly polymerized proanthocyanidins (88–90.5% of total polyphenolics), and anthocyanins (7.7–9.3%). Chokeberry pomaces, particularly seed-rich fractions, also contain saccharides (2.7–3.5% DM), proteins (18–24% DM), and lipids (9.8–13.9% DM), with a high proportion of unsaturated fatty acids [80].

Tomato (*Lycopersicon solanum*) is a major commercial and nutritional crop, with global production of ~ 192.3 Mt in 2023, including ~ 21.5 Mt from Europe [36]. While commonly consumed fresh, over 80% of tomatoes are

processed into products such as juice, paste, puree, ketchup, and sauces, generating up to 0.05 Mt of byproducts annually. During processing, 3–7% of the raw material is lost as waste, of which approximately 10% consists of seeds [64]. Tomato pomace, composed of peels and seeds, contains approximately 60% fiber, 25% total sugars, 20% proteins, 8% pectin, 6% total fat, and 4% minerals. Tomato seed meal provide high-quality protein, which might find application in food formulations [74]. Moreover, these residues are rich in bioactive compounds, including carotenoids (lycopene, 60–64% of total), phenolics, and vitamins [81].

Potato (*Solanum tuberosum*) and sweet potato (*Ipomoea batatas*) are major global crops, with total production reaching 476.6 Mt in 2023, of which Europe contributed approximately 100 Mt [36]. Farming and food processing generate substantial potato byproducts, including pulp and peel from alcohol, chips, and starch production, potato distillery wastewater [82], and potato cell fluid from starch processing [83]. Potato peels account for 8–40% of the initial tuber mass generated during industrial, household, and restaurant peeling operations [64, 84]. These byproducts are nutrient-rich, containing 79.4–90% moisture and 2.43% protein, with high carbohydrate content, primarily starch (66.8%) and dietary fibers including cellulose, hemicellulose, lignin (14.7%), and pectin (3.4%) [85, 86], as well as bioactive compounds [84]. Potato cell fluid is also nutrient-rich, containing 94.5 g/L sugars (glucose 32.2, fructose 27.4, galactose 20.9, mannose 1.9, sucrose 30.6 g/L), 5.4 g/L organic acids (mainly lactic 3.8 and acetic 1.7 g/L), 10 g/L glycerol, and 16.9 g/L nitrogen. It has a pH of 5.5, 12.2% ash, 34.7% dry matter, 2.76% insoluble solids, and a density of 1.22 kg/L [83]. The composition of potato byproducts make them promising feedstocks for microbial valorization into biohydrogen, biogas, biobutanol, bioethanol, lactic acid, enzymes, carotenoids, lipids, nutraceuticals, and fertilizers [84, 85, 87]. They are also explored for agricultural applications as biofertilizers and soil amendments, contributing to nutrient recycling [84].

Cassava (*Manihot esculenta* Crantz) is a major tuber crop, with global production reaching approximately 334 Mt in 2023 [36]. Cassava peels, consisting of the thin pericarp and thicker inner ring, contain 81.9–93.9% organic matter, 47.2% starch, 34.4% hemicellulose and cellulose, 8.4% lignin, 6.3% ash, 4.1–6.5% crude protein, and 0.93% cyanide [88].

Oilseeds, Pulses and Tree Nuts

Olive (*Olea europaea* L.) production in 2023 is ~ 20 Mt, with Europe contributing around 12 Mt [36]. Olive oil production (> 3.2 Mt) generates substantial byproducts,

including semisolid mill waste, pomace, and wastewater, which are challenging to dispose of due to high organic load, acidity, and complex phenolics. Olive pomace is rich in carbohydrates, polyphenols, minerals, and residual lipids, while stones are mainly used for energy. Valorization efforts focus on recovering bioactive compounds such as polyphenols, carotenoids, phytosterols, squalene, and dietary fiber for sustainable applications in food, nutraceutical, and cosmetic industries [74].

In 2023, global soybean and sunflower production reached ~ 371 Mt and ~ 59 Mt, respectively, with Europe contributing ~ 15 Mt and ~ 42 Mt, respectively [36]. Soybean (*Glycine max*), rapeseed (*Brassica napus*), and sunflower (*Helianthus annuus*) are the main oilseed crops, with industrial processing dominating their use. About 380 Mt of soybeans are processed into oil and meal, while food and feed uses remain limited (~ 25 Mt and ~ 14 Mt, respectively) [37]. Oil extraction generates oilseed cakes (OCs), which are rich in protein (300–500 g kg⁻¹), carbohydrates, and minerals, making them suitable for animal feed or soil amendment. However, high fiber and lignin contents may reduce digestibility. Given their large volumes and nutrient richness, OCs, including sunflower, rapeseed, and soybean cakes, represent promising substrates for sustainable valorization and biotechnological processing [89].

Soapstock is an alkaline, lipid-rich byproduct produced during the refining of various vegetable oils, including grape seed, soybean, olive, canola, corn, sunflower, cotton seed, and palm oils, typically accounting for 5–10% of the crude oil mass. Its composition varies with oil type and refining conditions, generally containing 29.7–52.6% water, 31.8–47.5% fatty fraction, 17–25.1% neutral oil, 3.6–7.2% ash, and pH 8.22–8.80. Soapstock is nutrient-dense, containing free fatty acids, triacylglycerols, phospholipids, pigments, and other minor nonpolar compounds. Although storage, handling, and disposal present challenges soapstock holds significant potential as a feedstock for fungal conversion into value-added bioproducts [90].

Okara, a fibrous by-product of soymilk and tofu (~ 4 Mt annually), retains 15–33% protein, 8–11% fat, minerals, and bioactive isoflavones. Its high insoluble fiber (40–51%), low digestibility, and a grassy off-odor limits its utilization [91]. Similarly, soybean hulls (SBH), which constitute 8–10% of the soybean weight, are rich in cellulose (28.6–52.3%), hemicellulose (12–33.8%), and pectin (6–15%), with lignin levels of 1–13.1%, constraining direct valorization [92, 93]. These nutrient-rich byproducts present promising substrates for sustainable upcycling.

Pea (*Pisum sativum* L.) is the second most widely cultivated leguminous crop globally, with an annual production exceeding 21.5 Mt, of which the EU contributes 1.13 Mt [36]. Peas are among the most popular seasonal legumes

globally, being commercially available in fresh, frozen, or shelled forms. Industrial processing of peas generates a substantial amount of byproducts, with pea pod waste accounting for approximately 30–40% of the total biomass [94]. Rich in proteins, carbohydrates, dietary fiber, vitamins, and minerals, the peas are used to produce food ingredients such as proteins, starches, flours, and fibers [95]. Despite their nutritional value, peas contain naturally occurring antinutritional factors, including phytic acid, tannins, and raffinose that may limit nutrient absorption and digestive efficiency [94].

The pistachio (*Pistacia vera* L.) is a major dried fruit, with global in-shell production reaching 1.30 Mt in 2023 [36]. Pistachio dehulling residues (leaves, clusters, and green hulls) are nutrient-rich lignocellulosic wastes (~ 600,000 t/year) containing phenolics, carbohydrates, and minerals. While previous studies focused on composting or animal feed, PBM shows significant potential for sustainable, high-value valorization via fungal fermentation [96]. Pistachio kernels contain 18–23% proteins, 18% carbohydrates, and lower amounts of fiber, minerals, and bioactive compounds such as total phenolics. The non-edible green hull, comprising 45–60% of the fruit, is a rich source of phenolic compounds, but remains largely underutilized [97].

Groundnut (*Arachis hypogaea* L.) or peanut global production (excluding shelled) reached approximately 54.27 Mt in 2023 [36]. It is a nutritious leguminous crop, grown mainly for seed and oil worldwide. Groundnut shells are abundant residues after the removal of seed 20% of the dried peanut pod by weight, which has a very slow degradation rate under natural conditions, while commercially, it is used as a feedstock, food, filler in fertilizer and even in bio-filter carriers, while deserted groundnut shells are burnt or buried. Groundnut shells contain various bioactive and functional components, and are composed of cellulose, hemicellulose and lignin, it can be utilized in multiple ways. Efficient management can be converted in various bio-products such as biodiesel, bio-ethanol, nano-sheet and also has applications in enzyme and hydrogen production, dye and heavy metal degradation [98].

The coffee sector ranks among the largest globally, with green coffee (*Coffea* spp.) production estimated at approximately 11 Mt in 2023 [36]. Processing generates roughly 0.65 t of byproducts per tonne of green coffee (~ 7 Mt globally), including husk, mucilage, and parchment removed during green bean extraction. Additionally, soluble coffee production produces about 2 kg of spent coffee grounds per kg of product [99]. Coffee residues are rich in antioxidants and contain bioactive compounds such as caffeine, chlorogenic acid, caffeic acid, and tannins, along with 24% protein, 39.7% carbohydrates, 16.9% lipids, 16.6% fiber, 2.7% ash, 10.9% cellulose, 27.1% hemicellulose, and 14.9% lignin [100].

Cocoa (*Theobroma cacao* L.) is a key global commodity, with production reaching 5.60 Mt in 2023 [36]. Cocoa beans, primarily used in chocolate production, represent only ~ 10% of the fruit's dry weight (DW), while ligno-cellulosic residues such as cocoa pod husk and bean shells are generated at a ~ 10:1 ratio [101]. This generates an estimated ~ 5 Mt of biomass annually worldwide. Cocoa meal residue, composed mainly of the bean peel (mesocarp equivalent), is often used as animal feed despite containing anti-nutritional compounds like theobromine [102]. These abundant byproducts, including cocoa shells and pod husks, present significant opportunities for sustainable valorization through biotechnological processes to recover valuable bioactive compounds [101, 102].

In recent years, the rapid development of the instant tea industry has resulted in significant economic benefits, with global production of tea (*Camellia sinensis* L.) reaching 32.2 Mt in 2023 [36], and a substantial increase in the generation of tea residue. Tea residue is commonly disposed of through incineration, composting, and used as animal feed. Also, they containing various nutrients, such as proteins and polysaccharides, with a complex network structure composed of cellulose, hemicellulose, and lignin [103]. Tea residues have acidic pH, contain 20–30% polyphenols, 4–5% caffeine, and 2–4% sugars and around 6.4% tannic acid [104, 105].

Table 1 shows the main composition of agri-food side-streams (AFS), which strongly influences fungal selection, fermentation strategy, and product yield. Beyond bulk proximate composition, the bioavailable fractions in AFS determine what fungi can assimilate, including soluble sugars and starch, structural polysaccharides (cellulose, hemicellulose, pectin, β -glucans, inulin); proteins; and lipids [12, 112, 113].

Filamentous fungi access these resources primarily through secretion of extracellular hydrolytic and oxidative enzymes, converting polymers to transportable monomers/oligomers (e.g., glucose, xylose, arabinose; amino acids/peptides; fatty acids/glycerol) that are then assimilated into central metabolism for biomass formation and metabolite synthesis. For example, co-cultures of *A. niger* and *T. reesei* on wheat bran generate enzyme consortia (xylanases, amylases, cellulases) that depolymerize lignocellulosic biomass into sugar monomers (D-glucose, D-xylose, L-arabinose). Similarly, several filamentous fungi grown on wheat straw produce cellulases, laccases, α -amylases, xylanases, and β -xylosidases. In starchy residues, fungi such as *Rhizopus* deploy amylases and related carbohydrate-digesting enzymes (alongside cellulases/hemicellulases), enabling efficient hydrolysis and conversion without extensive chemical pretreatment [43, 114–116].

For phenolic-rich matrices, enzymatic action can also release bound antioxidants (e.g., via carbohydrase-assisted

cell-wall deconstruction and related activities), improving phenolics and flavonoids recovery and antioxidant functionality. Specific bioactives can be directly transformed by specialized enzymes; for instance, tannase-producing fungi hydrolyze tannins, and tannase can convert tannic acid to gallic acid. Consequently, carbohydrate- and starch-rich residues (cereal stovers, potato, carrot) support cellulolytic and amylolytic fungi (*Trichoderma*, *Aspergillus*, *Penicillium*, *Neurospora*) for enzymes, fermentable sugars, and protein-enriched biomass, while fiber- and lignin-rich substrates (wheat bran, rice husk, sugar beet pulp) favor white-rot and hydrolytic fungi (*Pleurotus*, *Trametes*, *Ganoderma*, *Aspergillus*) that restructure lignocellulose (including lignin modification) and enhance downstream sugars and antioxidants recovery [117–119].

It implies that the substrate composition determines the accessible nutrient pool, which in turn dictates fungal enzyme portfolios, process design, and the resulting bio-product classes (protein-rich biomass, enzymes, organic acids, pigments, and released bioactives).

Filamentous Fungi Biorefinery for the Biovalorization of Plant-Derived Agri-Food Side-Streams

Microbial fermentation has long been utilized to extend the shelf life of foods such as bread, cheese, beer, and wine, while simultaneously enhancing their nutritional content, texture, and sensory characteristics. Advances in fermentation technology over the years have been driven by the changing needs of food, nutraceutical, and industrial sectors [120]. Table 2 summarizes the major plant-derived (cereals, starchy crops, sugar crops, fruits, vegetables, roots, tubers, oilseeds, pulses, and nuts) AFS and the FBR strategies applied. In particular, the use of filamentous fungi in solid-state and submerged fermentation (SSF and SmF), or in combination, has proven to be an efficient approach for converting agri-food processing residues into value-added functional ingredients. From this analysis, the main fungal genera and species were successfully applied, including *Aspergillus* spp. (*A. niger*, *A. oryzae*, *A. awamori*, *A. brasiliensis*), which were primarily applied for enzyme production (cellulases, xylanases, amylases, proteases), phenolic and flavonoid release, and enhancement of antioxidant activity.

Rhizopus spp. (*R. oligosporus*, *R. oryzae*, *R. delemar*, *Rhizomucor miehei*) contributed to polyunsaturated fatty acids (γ -linolenic acid), enzymes, and carbohydrate/lignocellulose bioconversion. White-rot fungi (WRF), including *Pleurotus* spp. (*P. ostreatus*, *P. djamor*, *P. pulmonarius*) and *Trametes* spp. (*T. versicolor*, *T. villosa*), were used for lignin degradation, protein enrichment, and bioethanol production.

Table 1 Main composition of plant agri-food side streams

Crop/Side-streams	Moisture (%)	Protein (%)	Fat (%)	Carbohydrates (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	Reducing Sugars (%)	Ash (%)	Total Solids (%)	Key characteristics	References
Corn (<i>Zea mays</i> L.)/Husk, Cobs, Stover, Stalks	5.6–6.4	4.3	1.8	43.2–84.5	49–62.9	6.9–37	12	10.8–11.8	3.9	97.7	High cellulose, low ash and nitrogen, total reducing sugars 10.8–11.8%	[3, 38–42]
Wheat (<i>Triticum aestivum</i> L.)/Bran, Straw	7–20	4–15.6	3.3	27–33	21–24	8.9–23	–	3.39–6.7	–	96	Dietary fiber, minerals, starch	[3, 43–45]
Rice (<i>Oryza sativa</i>)/Paddy straw, Bran, Husk, Straw	6.58–20	1.9–15	20	37.4–50	11.2–45	25.5–36.1	5–24	12.4–18–22	–	98.62	Nutrient-rich, lignocellulosic residue, high silica P:0.05; K:0.14%	[3, 46–50]
Barley (<i>Hordeum vulgare</i> L.)/Straw, Brewers' spent grain	–	30	20–40	33.8	21.9	13.8	–	–	–	–	Lignocellulosic residue, high hemicellulose and protein, starch 11%	[3, 51–53]
Oats (<i>Avena sativa</i>)/Hulls, Bran, Straw	–	–	–	23–39.4	27.1–35	17.5–25	–	8	–	–	Rich in β-glucan, fiber, lignocellulosic feedstock	[3, 54–56]
Sugar beet (<i>Beta vulgaris</i>)/Pulp	12.4–75	8	–	26.3–85	18.5–25	2.5–36	1–3	4.8	–	87.5	Rich in polymeric carbohydrates, low lignin, pectin 20–25%	[3, 57]
Sugarcane (<i>Saccharum officinarum</i>)/Bagasse	4.8–55	10	0.5–1	85–90	30.2–50	35–56.7	20	1–3	–	91.6	Rich in cellulose and hemicellulose, low protein P:0.5; K:0.1%; C: 42–44%; N: 1.5–2, C/N: 22–29	[3]
Sorghum (<i>Sorghum bicolor</i> L.)/Bagasse	10–12	6.8–10.9	4–13.8	71.3–71.5	17.1	49.5	3	1.3–2	1.3–2	88–90	Residual stalks, lignocellulosic by-product, contains P:1.99–2.29; K:1.95–2.19%	[58–60]
Apple (<i>Malus domestica</i>)/Peel, seeds, core	25–35	1–3	0.5–1	34–45	–	–	–	1.5–3	–	–	Rich in carbohydrates, phenolics, minerals	[63, 65, 66]
Grape (<i>Vitis</i> spp.)/Pomace (skins, seeds, stems)	55–75	6–15	6–15	–	–	–	–	–	–	–	Rich in antioxidants, unsaturated fatty acids	[14, 67]
Plum (<i>Prunus</i> spp.)/Pomace, Kernels, Seed cake	5.96–7.66	36.9–61.9	–	–	–	–	–	–	–	–	High oleic acid, phytosterols, > 45 (kernel oil), 6.36–9.85% crude fiber	[68, 106]
Fig (<i>Ficus carica</i> L.)/Skin, Over-ripe figs	11.9	8.7	2.6	75.4	8.8	–	–	4.5	–	–	Rich in carbohydrates, fiber, phenolics	[69]
Carrot (<i>Daucus carota</i>)/Pomace	69–91	1–14	0.3–1.9	7–8	10–28	5–20	2.5–8	14.3–47.2	1–7	–	Rich in carbon, protein, fiber, carotenoids; pectin 2–8%	[40, 74]
Orange (<i>Citrus sinensis</i>)/Peel	11.86	3.5	–	41.25	9.21	10.5	0.84	–	3.5	–	Rich in carbohydrates; C: 22.56%, 0.735%, C/N: 30	[3, 71]
Papaya (<i>Carica papaya</i>)/Peel	–	4.1	–	61.8	–	–	–	–	–	–	Rich in carbohydrates	[75]
Banana (<i>Musa</i> spp.)/Peel	7.36	16.4	10.4	23.1	–	–	–	–	12.1	–	High cellulose, hemicellulose, starch, pectin, 30.5% crude fiber	[64, 76, 107]
Mango (<i>Mangifera indica</i> L.)/Seed kernel, Shell/epicarp	–	4–7.3	0.8–5.4	81.9–93.6	–	9.6–14.1	–	1.48–1.52	–	–	High carbohydrate, antioxidants	[77]
Pineapple (<i>Ananas comosus</i>)/Peel (dried)	3.94	4.20	2.53	73.3	18.11	–	1.37	–	3.98	–	Lignocellulosic residue, 12% crude fiber, TPC 729.93 mg GAE/100 g	[3, 108]
Tomato (<i>Solanum lycopersicum</i>)/Pomace (peel, seeds)	–	20	6	25	60	–	–	–	4	–	High-quality protein, carotenoids, phenolics, vitamins, pectin 8%	[74, 81]
Potato (<i>Solanum tuberosum</i>)/Peel	9.89–90	2.43	–	–	2.2–14.7	–	–	–	7.7	–	High starch, pectin 3.4%	[3, 84, 85]
Cassava (<i>Manihot esculenta</i>)/Peel	10.3	4.1–6.5	–	–	34.4	34.4	8.4	–	6.3	–	Rich in starch and fiber, contains cyanide 0.93%; starch 47.2%	[88]

Table 1 (continued)

Crop/Side-streams	Mois- ture (%)	Pro- tein (%)	Fat (%)	Car- bohy- drates (%)	Cel- lulose (%)	Hemi- cel- lulose (%)	Lig- nin (%)	Reduc- ing Sugars (%)	Ash (%)	Total Solids (%)	Key characteristics	Refer- ences
Olive (<i>Olea europaea</i> L.)/Pomace	48	5.47– 7.53	17.21– 19.4	–	45.8– 53.3	–	–	0.08– 0.09	–	–	Rich in carbohydrates, polyphenols, minerals, tocopherols 31.94–47.63 mg/kg; TPC 46.87–65.87 mg/g GAE	[74, 109]
Soybean (<i>Glycine max</i>)/Okara, Hulls, Stalk	7.7–85	9.84– 33	0.82–11	–	28.6– 52.3	12– 33.8	1– 13.1	–	3.9– 10.39,9,39	0.235	High protein, insoluble dietary fiber, isoflavones, pectin 6–15%, TPC 1.2 mg GAE/g DM, phytic acid 0.051%	[3, 91–93]
Sunflower (<i>Helianthus annuus</i>)/ Seed hulls	12	3.6	1.98	–	42.1	29.7	5–13.4	–	2.7	97.3	High protein and carbon, indigestible fiber, C: 44–50%, NDF 65.7%, ADF 30.4%	[3, 89, 110]
Rapeseed (<i>Brassica napus</i> L.)/Pod hulls	7.7	9.57	3.22	–	–	–	–	–	–	83.4	NDF 48.2%, ADF 26.3%	[110]
Pea (<i>Pisum sativum</i>)/Pod	–	16.7	–	55.0	–	–	–	–	–	–	Proteins, starches, flours, 13.1 dietary fiber, TPC 463 mg GAE/100 g	[94, 95]
Pistachio (<i>Pistacia vera</i> L.)/Dehull- ing residues	–	18–23	–	18	–	–	–	–	–	–	Lignocellulosic waste; green hulls rich in phenolics	[96, 97]
Groundnut (<i>Arachis hypogaea</i> L.)/ Shells	6	5.08	0.90	–	–	–	–	–	4.22	95.8	Bioactive components; cellulose, hemicellulose, lignin, NDF 73.3%, 59.3% ADF	[98, 110]
Cocoa (<i>Theobroma cacao</i> L.)/Pod husk & shells	87.1	0.31	0.12	11.03	–	–	–	–	1.48	–	Lignocellulosic residues; theobromine	[101, 102, 111]
Coffee (<i>Coffea</i> spp.)/Spent grounds	–	24	16.9	39.7	10.9	27.1	14.9	–	2.7	–	Caffeine, chlorogenic acid, tannins; antioxidant-rich	[99, 100]
Tea (<i>Camellia sinensis</i> L.)/Tea residue	–	4–5	–	2–4	–	–	–	–	–	–	Polyphenols 20–30%, caffeine 4–5%, tannic acid 6.4%	[103–105]

Table 2 Valorization of plant-derived agri-food side streams (AFS) through fungal biorefinery (FBR) using solid-state (SSF) or submerged fermentation (SmF)

Plant derived AFS	Filamentous fungus	Fermentation strategy	FBR and main outcome	Target application	Reference
Corn cob	<i>Pleurotus ostreatus</i> , <i>Ganoderma annularis</i>	SSF, 28–30 °C, 7–10 days	Enhanced protein, soluble fiber, β -glucan; reduced sugars and phenolics	Functional foods, bioactive ingredients	[38]
Corn stover	<i>Phanerochaete chrysosporium</i> , <i>Trametes versicolor</i>	SSF, 30 °C, 10–15 days	Improved lignin degradation, sugar release, ethanol yield, enzyme production	Bioethanol, enzyme production	[121]
Corn stover	<i>Phanerochaete chrysosporium</i>	SSF, 28–32 °C, 7–12 days	Production of cellulase, hemicellulase, ligninase, amylase, manganese peroxidase	High-value enzymes production	[41]
Corn husks	<i>Cladosporium</i> sp.	SSF, 28–30 °C, 5–8 days	Cellulase production	Enzyme production	[40]
Corn byproducts	<i>Aspergillus niger</i>	SSF, 30 °C, 5–7 days	Bioactive extracts enriched in phenolics (caffeic, ferulic, quinic acids) and organic acids (oxalic, citric)	Nutraceuticals, functional ingredients	[39]
Wheat bran	<i>Aspergillus niger</i>	SSF, 28–32 °C, 5–7 days	Release of bound phenolic acids; increased antioxidant and anti-inflammatory activity	Functional foods, nutraceuticals	[122]
Wheat bran	<i>Fomitopsis pinicola</i>	SSF, 25–30 °C, 7–10 days	Increased total phenols and alkylresorcinols	Nutritionally enriched bread	[123]
Wheat bran	<i>Isaria cicadae</i> , <i>Cordyceps militaris</i> , <i>Inonotus obliquus</i>	SSF, 28–30 °C, 6–10 days	Enhanced soluble dietary fiber, total flavonoids/phenolics, swelling capacity, oil absorption, antioxidant activity	Functional foods	[44]
Wheat bran	<i>Aspergillus niger</i> , <i>Trichoderma reesei</i> (co-culture)	SSF, 28–32 °C, 6–8 days	Enzyme consortia (xylanases, amylases, cellulases); depolymerization of lignocellulose into sugar monomers (D-glucose, D-xylose, L-arabinose)	Bioethanol	[43]
Wheat straw	<i>Penicillium janthinellum</i> , <i>Trichoderma harzianum</i> , <i>Penicillium chrysogenum</i> , <i>Paecilomyces thermophila</i> , <i>Aspergillus ochraceus</i> , <i>A. niger</i>	SSF, 28–32 °C, 7–12 days	Production of industrial enzymes (cellulases, lactases, α -amylases, xylanases, β -xylosidases)	Paper-pulp, feed, biofuels	[45, 124, 125]
Paddy straw	<i>Trichoderma</i> spp. (consortia)	SSF, 28–30 °C, 6–8 days; supplemented with deoiled neem cake	Cellulase-free xylanase production; β -xylanase and α -L-arabinofuranosidase; enhanced enzyme yield	Enzyme production	[46]
Rice bran	<i>Aspergillus niger</i> var. phoenicis, <i>A. terreus</i> , <i>Penicillium</i> spp.	SSF, 28–32 °C, 5–7 days	Lignocellulolytic enzymes, bioactive peptides, proteases, antifungal proteins	Nutraceuticals, enzyme production	[48]
Rice husk	<i>Aspergillus brasiliensis</i> BLf1	SSF/SmF, 28–30 °C, 6–10 days	Lignocellulolytic enzymes (xylanase, β -xylosidase, β -glucosidase, cellulase); xylooligosaccharides	Functional ingredients	[50]
Rice straw	<i>Phanerochaete chrysosporium</i> , <i>Aspergillus niger</i>	SSF, 28–30 °C, 15 days; 2.5 g/L N, 40 g/L material-liquid ratio, 3% inoculum, pH 9	42% degradation lignocellulosic biomass; increased humic acid-like substances; reduced protein-like compounds	Enzymes, organic acids production	[126]
Hulled barley	<i>Aspergillus oryzae</i>	SSF, 30 °C, 5 days	High enzyme levels (amylase 31,310 U/g; protease 2,615 U/g); β -glucan 14.6%	Enzyme production, functional ingredients	[52]
Barley straw	<i>Trametes villosa</i>	SSF, 28–30 °C, 6–10 days	Enzymatic cocktails for biofuel hydrolysis	Bioethanol	[51]
Brewer's spent grain	<i>Trametes versicolor</i> , <i>Pleurotus ostreatus</i> , <i>Rhizopus</i> spp.	SSF, 28–32 °C, 5–10 days	Increased protein (11–50%), enhanced functional properties; enzymes, organic acids, xylitol, volatile fatty acids	Functional foods, feed	[53, 127, 128]
Brewer's spent grain	<i>Aspergillus ibericus</i> , <i>A. niger</i> CECT2088	SSF, 28–30 °C, 5–7 days	Xylanase (300–313 U/g), cellulase (51–62 U/g), β -glucosidase (94 \pm 4 U/g)	Enzyme production	[129]
Oat hulls	<i>Neurospora intermedia</i> , <i>Rhizopus oryzae</i>	SSF, 28–32 °C, 6–8 days	Nutritionally enriched ingredient; synergistic metabolic interactions	Sustainable protein	[54]
Oat bran	<i>Aspergillus niger</i> , <i>Rhizopus oryzae</i>	SmF, 28–30 °C, 5–7 days	Enhanced β -glucan extractability; improved solution viscosity	Functional foods, nutraceuticals	[56]

Table 2 (continued)

Plant derived AFS	Filamentous fungus	Fermentation strategy	FBR and main outcome	Target application	Reference
Oat bran	<i>Aspergillus niger</i> (acid pretreatment)	SSF, 30 °C, 6 days	TPC: 58.11 mg GAE/g; vanillic acid: 77.42 µg/g; lipid: 4.66–7.33%; antioxidant activity (DPPH) 83.33%)	Functional ingredients, nutraceuticals	[130]
Sugar beet pulp	<i>Aspergillus niger</i> , <i>A. nidulans</i> , <i>Botrytis cinerea</i> , <i>Rhizopus arrhizus</i> , <i>Fusarium solani</i> , <i>Penicillium oxalicum</i>	SSF, 28–32 °C, 5–10 days	Protein-rich biomass (protein 52.7–68.3%); enhanced polyunsaturated fatty acids, especially α-linolenic acid; lignocellulose depolymerization; production of cellulolytic enzymes and fermentable reducing sugars	Animal feed, integrated, enzyme production	[57, 131]
Sugarcane bagasse	<i>Agaricus bisporus</i> , <i>Pleurotus djamor</i> , <i>Calocybe indica</i> , <i>Pleurotus ostreatus</i>	SSF, 28–30 °C, 7–12 days	Increased crude protein (from 1.98–2.08% to 3.98–5.02%); reduced NDF, lignin, hemicellulose; decreased in vitro methane production, improved digestibility	Animal feed, functional ingredients	[132]
Sweet sorghum (juice or stalks)	<i>Aspergillus oryzae</i> , <i>A. niger</i>	SSF, 28–32 °C, 5–7 days	Release of phenolic compounds with antioxidant potential	Functional foods, nutraceuticals	[58]
Sweet sorghum stalks	<i>Pleurotus ostreatus</i> , <i>P. djamor</i> , <i>Trametes versicolor</i>	SSF, 28–32 °C, 7–10 days	Mycelial biomass; increased crude protein, ash, improved NDF (81.5%) and ADF (56.2%) degradability; enhanced volatile fatty acid and propionate production	Animal feed, functional ingredients	[59]
Sorghum, wheat bran	<i>Aspergillus niger</i> , <i>A. fumigatus</i>	SSF, 28–32 °C, 6–8 days	Optimized cellulase and hemicellulase production	Enzyme production	[133]
Sorghum bagasse	<i>Coriolus versicolor</i> , <i>Ganoderma lucidum</i> , <i>Pleurotus</i> spp.	SSF, 28–32 °C, 7–10 days, supplemented CuSO ₄ , gallic acid, syringic acid	Enhanced lignin degradation (1.56-fold), selectivity (3.58-fold); up to 2.2-fold increase in fermentable sugars	Bioethanol, fermentable sugar	[60, 134]
Apple pomace	<i>Phanerochaete chrysosporium</i>	SSF, 28–30 °C, 6–10 days	Increased polyphenols, antioxidant activity	Functional foods, nutraceuticals	[78]
Apple pomace	<i>Actinomucor elegans</i> , <i>Umbelopsis isabellina</i>	SSF, 28–32 °C, 6–12 days	γ-linolenic acid (~ 3.85 g/kg), carotenoids (β-carotene, lutein, zeaxanthin), enhanced polyphenols and antioxidant activity	Functional foods, nutraceuticals	[65]
Apple pomace	<i>Rhizopus delemar</i> F2	SSF, 28–30 °C, 6–10 days	Thermostable carbohydrases: cellulase, xylanase, pectinase, amylase	Bioethanol, textiles, food	[135]
Apple peel	<i>Aspergillus</i> spp.	SSF, 28–32 °C, 5–7 days	TPC up to 1440 mg GAE/100 g; flavonoids up to 495 mg CE/100 g; antioxidant activity ↑3–5×	Functional ingredient	[66]
Apple peel	<i>Rhizomucor miehei</i>	SSF, 28–32 °C, 5–7 days	Increased phenolic content and antioxidant capacity	Functional ingredient	[78]
Grape pomace	<i>Actinomucor elegans</i> , <i>Umbelopsis isabellina</i>	SSF, 28–32 °C, 7–10 days	γ-linolenic acid (up to 378.85 mg/100 g), carotenoids (β-carotene > 50 mg/100 g), polyunsaturated fatty acids, moderate antioxidant activity	Food, feed, functional ingredients	[67]
Black grape, apple, pitahaya residues	<i>Rhizomucor miehei</i> , <i>A. niger</i> (enzyme treatment)	SSF, 28–30 °C, 5–7 days	Enhanced release of free phenolics: (+)-catechin, (–)-epicatechin, gallic and vanillic acids	Natural antioxidants, functional foods	[63]
Citrus reticulata peel	<i>Aspergillus niger</i>	SSF, 28–32 °C, 5–7 days	TPC ↑70%, flavonoids ↑26.8%, enriched hesperidin, tangeretin; ↑71.6% radical scavenging activity	Functional foods, nutraceuticals, medicine	[70]
Orange peel	<i>Aspergillus awamori</i>	SSF, 28–30 °C, 5 days	Xylanase (40.6 IU/g) and exo-polygalacturonase (16.3 IU/g); reducing sugars 24.4 g/L for lactic acid fermentation	Functional ingredients, organic acid production	[71]
Fig fruit byproducts	<i>Aspergillus niger</i> HT4	SSF, 40 °C, 36 h, 60% moisture, pH 5.0, mineral supplementation	TPC 10.19 mg GAE/g; ↑5.48–98.5% antioxidant activity	Functional foods, nutraceuticals	[69]
Apricot press residues	<i>Aspergillus niger</i> , <i>Rhizopus oligosporus</i>	SSF, 28–32 °C, 5–7 days	TPC ↑30–70%, flavonoids ↑12–38%; chlorogenic acid, rutin, quercetin 3-acetyl-glucoside; improved lipid recovery	Functional ingredients, antioxidant-rich oils	[79]

Table 2 (continued)

Plant derived AFS	Filamentous fungus	Fermentation strategy	FBR and main outcome	Target application	Reference
Grapefruit byproducts	<i>Aspergillus niger</i> GH1	SSF, 70% moisture, 28–30 °C, 5–7 days	Increased antioxidant compound recovery; solids reduced ~ 50%	Natural antioxidants, functional products	[72]
Saba banana peel	<i>Monascus purpureus</i>	SSF, 28–32 °C, 6–10 days	Pigments: red, orange, yellow; Enzymes xylanase and cellulase	Natural colorants, enzyme production	[76]
Orange and banana peels	<i>Aspergillus ibericus</i> , <i>Rhizopus oryzae</i>	SSF, 28–32 °C, 5–7 days	Increased protein, antioxidant activity, fiber, minerals, lipids	Functional food ingredients	[62]
Pineapple residues	<i>Kluyveromyces marxianus</i>	SSF, 28–32 °C, 5–7 days	Enhanced phenolic content, antioxidant activity, anticancer potential	Functional foods, nutraceuticals	[61]
Mango seed	<i>Aspergillus niger</i>	SSF, 28–32 °C, 5–7 days	Increase TPC; enhanced radical scavenging activity	Natural antioxidants, functional ingredients	[77]
Chokeberry pomace	<i>Aspergillus niger</i> , <i>Rhizopus oligosporus</i>	SSF, 28–32 °C, 5–7 days	Extractable phenolics ↑1.7×; total flavonoids ↑; enriched linoleic acid (57–61% FA); enhanced antioxidant and nutritional quality	Functional foods, nutraceuticals	[80]
Orange, carrot, papaya peels	<i>Blakeslea trispora</i>	SSF, 28–32 °C, 5–7 days	Carotenoid yield β-carotene (0.127 mg/mL); antioxidant activity; high purity (> 76%)	Food, feed, nutraceutical, cosmetic, pharmaceutical	[75]
Carrot pomace	<i>Penicillium oxalicum</i> BGPUP-4	SSF, 90% moisture, pH 7, 28–30 °C, 4 days	Inulinase (322 IU/g); high inulinase/invertase ratio (3.38)	Enzyme production, functional ingredients	[136]
Carrot pomace	<i>Aspergillus niger</i> <i>Trichoderma viride</i>	SSF, 28–32 °C, 5–7 days	Release of polyphenols (80.88 mg GAE/10 g); 17 polyphenolic compounds; enhanced α-amylase inhibition and antioxidant activity	Functional foods, nutraceuticals	[137]
Carrot peel, corn husk	<i>Cladosporium</i> sp. V3	SSF, 28–32 °C, 5–7 days	Cellulase production; endoglucanase	Enzyme production	[40]
Tomato byproducts	<i>Fusarium solani</i>	SSF, 28–32 °C, 5–7 days	Lycopene extraction; enhanced antioxidant activity	Functional ingredients, natural antioxidants	[81]
Potato waste	<i>Aspergillus ficuum</i>	SSF, 28–32 °C, 5–7 days	High-value phytase production; enzyme activity ↑2.5× with N supplementation	Enzyme production	[86]
Potato peel and other agri-waste	<i>Rhizopus oryzae</i>	SSF/SmF, 28–32 °C, 5–7 days	Ethanol (16.8–29.2 g/L), lactic acid (3.1–50.5 g/L); carbohydrate-digesting enzymes (amylases, cellulases, hemicellulases, isoamylase, glucoamylase)	Biofuels, lactic acid	[85]
Potato peel, wheat straw, spent coffee grounds	<i>Pleurotus ostreatus</i>	SSF, 28–32 °C, 6–10 days	Enhanced mushroom powder quality; improved water- and oil-holding capacity, emulsifying ability, bioactive compounds, antioxidant activity	Functional foods, bioactive ingredients	[87]
Potato residues	<i>Rhizopus oligosporus</i> , <i>Paecilomyces variotii</i> , <i>Trichoderma reesei</i> , <i>Penicillium oxalicum</i>	SSF/SmF, 28–32 °C, 5–10 days	Lactic acid, gluconic acid, poly-β-hydroxybutyrate, starch films, enzymes, enhanced protein	Functional ingredients, biofuels, chemicals platform, biopolymers, single-cell protein	[84]
Potato cell fluid	<i>P. variotii</i> , <i>R. oligosporus</i> , <i>T. reesei</i>	SSF/SmF, 28–32 °C, 5–7 days	Biomass with 17–27% amino acids, 23–30% dietary fiber	Functional ingredients	[83]
Potato proteins	<i>F. venenatum</i>	SSF, 28–32 °C, 5–7 days	Structured, fibrous hybrid gels with tunable hardness	Textiles, functional food gels	[138]
Cassava peels	<i>Trichoderma pseudokoningii</i>	SSF, 24 °C, 60–70% moisture, pH 5.0, with urea/ammonium sulfate	Protein enrichment (~ 48.1%)	Protein-rich feed, functional ingredients	[88]
Exhausted/ crude olive pomace	<i>Rhizopus oryzae</i>	SSF, 28–32 °C, 5–10 days	Enhanced phenolics recovery; 12.9-fold increase in antioxidant activity	Bioactive compounds, functional ingredients	[129]

Table 2 (continued)

Plant derived AFS	Filamentous fungus	Fermentation strategy	FBR and main outcome	Target application	Reference
Vine trimming shoots, exhausted grape marc, grape stalks	<i>Rhizopus oryzae</i>	SSF, 28–32 °C, 5–10 days	Increased phenolic release, antioxidant capacity	Bioactive compounds, functional ingredients	[129]
Sunflower, rapeseed, soybean cakes	<i>Aspergillus niger</i> , <i>Aspergillus ibericus</i> , <i>Rhizopus oryzae</i> , <i>Trichoderma</i> spp.	SSF, 28–32 °C, 5–10 days	Reduced NDF and ADF; extracellular enzyme production (cellulase 109 U/g, xylanase 692 U/g, protease 157 U/g, β -glucosidase 503 U/g); increase TPC and antioxidant activity	Nutritional/functional feed	[89, 139]
Okara	<i>Rhizopus oligosporus</i> , <i>Yarrowia lipolytica</i>	SSF, 28–32 °C, 5–7 days	Increase soluble fiber, free amino acids, isoflavone aglycones, free phenolic acids, flavor improvement	Functional foods, protein enrichment, nutraceuticals	[91]
Soybean hulls	<i>Aspergillus niger</i> NRRL3	SSF, 28–32 °C, 5–7 days	High cellulase (endoglucanase 5914 U/L, exoglucanase 4551 U/L, β -glucosidase 984 U/L); robust colonization; high volumetric productivity	Enzyme production, biofuels, pulp/paper, detergents, textiles	[140]
Soybean hulls	<i>Trichoderma reesei</i> (Rut C30), <i>Aspergillus</i> spp. (<i>A. niger</i> , <i>A. aculeatus</i> , <i>A. cinnamomeus</i> , <i>A. foetidus</i> , <i>A. phoenicis</i>)	SSF/SmF, 28–32 °C, 5–10 days	Carbohydrases (cellulase, xylanase, pectinase, polygalacturonase, β -galactosidase, sucrase) and proteases production	Enzyme production	[92]
Pea-processing byproducts	<i>Aspergillus oryzae</i> , <i>Fusarium venenatum</i> , <i>Monascus purpureus</i> , <i>Neurospora intermedia</i> , <i>Rhizopus oryzae</i>	SmF, 28–32 °C, 5–7 days	Protein-rich fungal biomass (~ 680 kg protein/tonne)	Vegan protein, sustainable food ingredients	[95]
Pistachio green hulls	<i>Aspergillus niger</i> GH1	SSF, 28–32 °C, 5–7 days	Phenolics recovery (23.83 mg/g); bioactive compounds (gallic acid 4-O-glucoside, geranine); enhanced antioxidant activity	Functional ingredients, nutraceuticals	[97]
Pistachio dehulling	<i>Neurospora intermedia</i>	SSF, 30 °C, 72 h, pH 5.5	Fungal biomass with protein 20.4–27.1%	Protein-rich ingredients	[96]
Groundnut shells	<i>Aspergillus niger</i>	SSF, 28–32 °C, 5–7 days	Converted to eco-friendly adsorbents; improved Pb(II) removal	Bioremediation (Pb(II) removal from waste water)	[141]
Peanut meal, coconut residue, soybean meal	<i>Monascus purpureus</i>	SSF, 28–32 °C, 5–7 days	Red pigment production; enhanced antioxidant activity	Natural colorants, functional ingredients	[61]
Cocoa pod husk	<i>Rhizopus stolonifer</i>	SSF, 28–32 °C, 5–7 days	Increased protein; antioxidant activity; bioactive metabolites (methyl 3-hydroxybutyrate, 10,12-tricosadiynoic acid, palmitic acid)	Functional foods, nutraceuticals	[101]
Cocoa shells	<i>Penicillium roqueforti</i>	SSF, 28–32 °C, 5–7 days	Increased TPC and carotenoid content; improved fatty acid composition (oleic, linoleic, γ -linolenic acids)	Functional foods, nutraceuticals	[102]
Tea residues	<i>Lentinus edodes</i> , <i>Lentinus sajor-caju</i> , <i>Flammulina filiformis</i> , <i>Hericium erinaceus</i> , <i>Pleurotus pulmonarius</i> , <i>Monascus kaoliang</i> B6	SSF, 28–32 °C, 5–10 days	Degradation of cellulose, hemicellulose, lignin; enhanced nutrient release and production mycelial biomass	Functional foods, Protein rich biomass	[103]
Green and black tea residues	<i>Aspergillus niger</i> TBG 28 A, <i>Aspergillus glaucus</i> NRC8	SSF, 28–32 °C, 5–7 days	High tannase (tannin acyl hydrolase) production; tannin hydrolysis; conversion of tannic acid to gallic acid	Enzyme production, application in animal feed, grape wine, Production gallic acid	[104, 105]

Penicillium spp. (*P. chrysogenum*, *P. roqueforti*, *P. oxalicum*) and *Ganoderma* spp. (*G. lucidum*, *G. annularis*) supported enzyme production, lignocellulose depolymerization, and enrichment of bioactive compound. *Monascus* spp. (*M. purpureus*, *M. kaoliang*) were employed for pigment and enzyme production. *Trichoderma* spp. (*T. reesei*, *T. harzianum*, *T. viride*, *T. pseudokoningii*) and *Neurospora intermedia* mainly produced cellulolytic and hemicellulolytic enzymes and protein-rich biomass.

Fusarium spp. (*F. solani*, *F. venenatum*) contributed enzymes, antioxidants, and protein enrichment, while *Lentinula/Lentinus* spp. (*L. edodes*, *L. sajor-caju*) and other basidiomycetes (*Cladosporium* sp., *Cordyceps militaris*, *Isaria cicadae*, *Actinomucor elegans*, *Umbelopsis isabellina*, *Hericium erinaceus*, *Flammulina filiformis*, *Calocybe indica*, *Agaricus bisporus*, *Paecilomyces variotii*, *Blakeslea trispora*) were applied for bioactive metabolites, pigments, antioxidants, enzymes, and protein production.

Valorization of Cereals and Starchy Crops Side-streams

Valorization of corn byproducts via filamentous fungal fermentation demonstrates significant biotechnological potential. Solid-state fermentation of corncob with *Pleurotus ostreatus* and *Ganoderma annularis* enhances protein, soluble fiber, and β -glucan content while reducing sugars and phenolics [38]. Corn stover treatments with fungi such as *Phanerochaete chrysosporium* and *Trametes versicolor* improve lignin degradation, sugar release, ethanol yield, and enzyme production, supporting integrated biorefinery applications [121]. Both untreated and alkali-pretreated corn stover were employed for enzyme production including cellulase, hemicellulase, ligninase, amylase and manganese peroxidase, via solid-state fermentation using *Phanerochaete chrysosporium*, highlighting corn stover's potential as a renewable substrate for high-value enzyme production in biorefinery applications [41]. Corn husks fermented by solid-state fermentation with *Cladosporium* sp. provide a sustainable route for producing value-added bioproducts, including industrially relevant enzymes such as cellulases [40]. Whereas, fermentation with *Aspergillus niger* generates bioactive extracts enriched in phenolics, including caffeic, ferulic, and quinic acid esters, highlighting their nutraceutical potential, as well as organic acids (oxalic and citric) [39].

Wheat bran valorization via SSF with filamentous fungi enhances both nutritional and functional properties. *Aspergillus niger* releases bound phenolic acids, increasing antioxidant and anti-inflammatory activity beyond standard ferulic acid [122], while fermentation with *Fomitopsis*

pinicola elevates total phenols and alkylresorcinols, supporting the development of nutritionally enriched whole-grain bread [123]. Medicinal fungi such as *Isaria cicadae*, *Cordyceps militaris*, and *Inonotus obliquus* further improve soluble dietary fiber, total flavonoid and phenolic content, swelling capacity, oil absorption, and antioxidant activity, promoting functional food applications [44]. Co-cultures of *A. niger* and *Trichoderma reesei* on wheat bran generate enzyme consortia, including xylanases, amylases, and cellulases, capable of depolymerizing lignocellulosic biomass into sugar monomers (D-glucose, D-xylose, L-arabinose) [43]. Similarly, wheat straw can be efficiently valorized through fungal fermentation. Filamentous fungi such as *Penicillium janthinellum*, *Trichoderma harzianum*, *Penicillium chrysogenum*, *Paecilomyces thermophila*, *Aspergillus ochraceus*, and *A. niger* convert wheat straw into industrially relevant enzymes, including cellulases, laccases, α -amylases, xylanases, and β -xylosidases, applicable in paper-pulp processing, animal feed, food, and biofuel production from cellulosic biomass [45, 124, 125].

The valorization of paddy straw (PS) using *Trichoderma* spp. consortia under SSF demonstrates a sustainable approach for producing cellulase-free xylanase while contributing to zero-waste management. Incorporation of nitrogen-rich de-oiled neem cake effectively enhanced enzyme production, with the partially purified enzyme comprising β -xylanase and α -L-arabinofuranosidase [46]. Filamentous fungi, particularly species of *Aspergillus* and *Penicillium*, efficiently valorize rice bran through the production of lignocellulolytic enzymes and bioactive peptides. *Aspergillus niger* var. *phoenicis* and *A. terreus* exhibit high cellulase and xylanase activities, while *Penicillium* species contribute proteases and antifungal proteins, supporting rice bran valorization [48]. Furthermore, under SSF and SmF, rice husk fermented with *Aspergillus brasiliensis* BLf1 enabled the production of lignocellulolytic enzymes (xylanase, β -xylosidase, β -glucosidase, and cellulase) and value-added xylooligosaccharides [50]. A filamentous fungal consortium of *Phanerochaete chrysosporium* and *Aspergillus niger* was developed for rice straw degradation; under optimized conditions (2.5 g/L nitrogen, 40 g/L material-liquid ratio, 3% inoculum, pH 9), the consortium achieved 42% lignocellulosic degradation in 15 days, effectively breaking down lignocellulosic components, increasing humic acid-like substances, and reducing protein-like compounds [126].

Hulled barley can be valorized via solid-state fermentation (SSF) with *Aspergillus oryzae*, yielding high enzyme levels (amylase 31,310 U/g; protease 2,615 U/g) and β -glucan (~14.6% of fermented biomass) [52]. Barley straw fermented with *Trametes villosa* enables cost-effective production of enzymatic cocktails suitable for biofuel hydrolysis [51].

Fermentation transforms BSG into a substrate with enhanced nutritional, functional, and prebiotic properties, enabling the production of high-value compounds such as enzymes, organic acids, xylitol, volatile fatty acids [53], protein-rich biomass [142] and improving feed digestibility in European seabass [128]. SSF with fungi such as *Trametes versicolor*, *Pleurotus ostreatus*, and *Rhizopus* spp. increases protein content by 11–50%. Functional properties of BSG are further improved: *Rhizopus oligosporus* fermentation enhances emulsifying, foaming, and water/oil-binding capacities [127], while *Aspergillus awamori* increases ferulic acid content in bread, albeit with potential textural impacts [143]. Combined fermentation with *Rhizopus oryzae* and protein extraction further optimizes protein functionality [144]. Additionally, *Aspergillus ibericus* produces xylanase (300–313 U/g) and cellulase (51–62 U/g) from BSG, whereas *A. niger* CECT2088 efficiently generates β -glucosidase (94 U/g) [129].

Co-cultivation of the edible filamentous fungi *Neurospora intermedia* and *Rhizopus oryzae* under SSF effectively transformed oat hulls into a nutritionally enriched ingredient, demonstrating synergistic metabolic interactions that support sustainable protein production and FBR applications [54]. SmF of oat bran with *Aspergillus niger* and *R. oryzae* significantly enhanced β -glucan extractability and improved solution viscosity [56]. Furthermore, SSF of oat bran with *A. niger*, particularly after acid pretreatment, increased total phenolic content (TPC) to 58.11 mg GAE/g DW, vanillic acid to 77.42 μ g/g DW, and lipid content from 4.66% to 7.33% by day six. Antioxidant activity, measured via DPPH assay, peaked at 83.33% on day four, highlighting the potential of this approach for generating functional ingredients with enhanced nutraceutical value [130].

Valorization of Sugar Crops Side-streams

Sugar beet pulp (SBP) serves as an effective substrate for filamentous fungi in solid-state fermentation (SSF), producing protein-rich biomass with a total protein content of 52.7–68.3% using species such as *Aspergillus niger*, *A. nidulans*, *Botrytis cinerea*, *Rhizopus arrhizus*, *Fusarium solani*, and *Penicillium oxalicum*. Fungal fermentation also enhances polyunsaturated fatty acids, particularly α -linolenic acid, increasing SBP's value as a sustainable feedstock for integrated biorefineries [131]. Concurrently, the lignocellulosic matrix is depolymerized, generating cellulolytic enzymes and fermentable reducing sugars, which are key intermediates for biorefinery processes [57].

SSF of sugarcane bagasse (SCB) with WRF such as *Agaricus bisporus*, *Pleurotus djamor*, *Calocybe indica*, and *P. ostreatus* enhances nutritional value and digestibility, increasing crude protein from 1.98 to 2.08% DM to

3.98–5.02% DM, while reducing NDF, lignin, hemicellulose, and in vitro methane production [132].

Sweet sorghum can be valorized via its sugar-rich juice through submerged fermentation or directly from stalks via SSF. SSF with *Aspergillus oryzae* and *A. niger* releases phenolic compounds with antioxidant potential [58]. WRF, including *Pleurotus ostreatus*, *P. djamor*, and *Trametes versicolor*, convert sorghum into myceliated biomass, increasing crude protein (68–330%) and ash (40–190%), improving NDF and ADF degradability (81.5% and 56.2%), and enhancing volatile fatty acid and propionate production [59]. SSF of genetically enhanced sorghum with *A. niger* and *A. fumigatus*, combined with wheat bran, optimizes cellulase and hemicellulase production for lignocellulosic waste valorization [133]. Similarly, SSB, supplemented with CuSO_4 , gallic acid, and syringic acid, and fermented with fungi such as *Coriolus versicolor*, *Ganoderma lucidum*, and *Pleurotus* spp. improved lignin degradation (1.56-fold) and selectivity (3.58-fold), yielding up to 2.2-fold more fermentable sugars [60, 134]. Collectively, these studies highlight SSF with filamentous fungi as an effective biorefinery strategy to enhance sorghum nutrient bioavailability while enabling the co-production of feed, enzymes, antioxidants, and fermentable sugars.

Valorization of Fruits, Vegetables, Root and Tubers Side-streams

Solid-state fermentation (SSF) effectively enhances the nutritional and functional properties of fruit and vegetable residues. Apple pomace fermented with *Phanerochaete chrysosporium* showed increased polyphenols and antioxidant activity. Similarly, fermentation of grape, pomegranate, chokeberry, and mango residues using *Aspergillus* spp., *Rhizopus* spp., and *Lentinula* spp. enriched phenolics, flavonoids, ellagic acid, and β -carotene. Fruit peels from fig, grapefruit, plum, apricot, pineapple, orange, and mixed fruits fermented with *Aspergillus niger*, *Rhizopus oligosporus*, and *R. miehei* displayed enhanced antioxidant capacity along with elevated tannase, phytase, and β -glucosidase activities. *Kluyveromyces marxianus* NRRL Y-8281 increased phenolic content and anticancer potential in pineapple byproducts, while *Paecilomyces variotii* and *Blakeslea trispora* boosted antioxidant levels and β -carotene in orange, carrot, and papaya peels [61]. Mixed fruit and vegetable residues, including apple, pomegranate, black carrot, and red beet pulps, were successfully converted into fungal pigments by *Aspergillus carbonarius* under optimized SSF conditions (pH 6.5, particle size < 1.4 mm, 15 days), with melanin identified as a major compound [145].

Apple pomace fermented with Zygomycetes fungi, such as *Actinomucor elegans* and *Umbelopsis isabellina*,

produced high-value compounds, including γ -linolenic acid (up to 3.85 g/kg DW), carotenoids (β -carotene, lutein, zeaxanthin), and other polyunsaturated fatty acids, along with enhanced polyphenol content and antioxidant activity, enabling its use in functional foods and nutraceuticals [65]. The fungus *Rhizopus delemar* F2 efficiently utilized apple pomace to produce thermostable carbohydrases, such as cellulase, xylanase, pectinase, and amylase, highlighting applications in bioethanol, textiles, and food industries [135]. SSF of apple peel with *Aspergillus* spp. significantly increased TPC (up to 1440 mg GAE/100 g DM), flavonoids (up to 495 mg CE/100 g DM), and antioxidant activity by 3–5 times, converting the peel into a functional ingredient [66]. Fermentation with *Rhizomucor miehei* similarly enhanced phenolic content and antioxidant capacity [78].

De-stoned plum residues and brandy distillery byproducts, including spent pulp and peels, can be enriched in phenolic antioxidants by over 30% through solid-state fermentation (SSF) with *Rhizopus oligosporus* and *Aspergillus niger*. Additionally, these fungi improve plum kernel oil recovery by 21.9%, yielding lipids of superior quality characterized by high sterol ester content and phospholipids rich in n-3 polyunsaturated fatty acids, highlighting their potential for commercial applications [68].

Grape pomace from winemaking can be enriched with functional biomolecules through SSF using oleaginous Zygomycetes fungi, such as *Actinomucor elegans* and *Umbelopsis isabellina*. Fermentation increases γ -linolenic acid (up to 378.85 mg/100 g DW), carotenoids (β -carotene > 50 mg/100 g DW, lutein), and lipids with over 94% nutritionally valuable polyunsaturated fatty acids at the sn-2 position, alongside phenolic extracts exhibiting moderate antioxidant activity, highlighting its potential for food and feed applications [67]. Increases in TPC and flavonoids are primarily attributed to enzymatic hydrolysis during fermentation; however, certain fungal strains may degrade phenolics over extended periods. Among wine industry residues, grape marc, stalks, and vine shoots display variable phenolic content depending on prior processing, with grape stalks generally retaining the highest levels [78].

SSF with *Rhizomucor miehei*, combined with enzymatic treatments using *R. miehei* cellulase and *Aspergillus niger* pectinase cocktails, effectively increased the release of free phenolics from black grape, apple, and pitahaya residues, offering a promising source of natural antioxidants. The composition of individual phenolics was substrate-dependent: (+)-catechin and (–)-epicatechin were predominant in black grape and apple residues, whereas gallic and vanillic acids were more abundant in pitahaya [63].

Fermentation of *Citrus reticulata* peel with *Aspergillus niger* significantly increased TPC by 70% and total flavonoids by 26.8%, with marked enrichment of hesperidin,

nobiletin, and tangeretin. Radical scavenging activity improved by up to 71.6%, highlighting the potential of citrus peel as a source of bioactive compounds for food, nutraceutical, and medicinal applications [70]. Orange peels can also serve as a substrate for enzyme-free lactic acid production using *Aspergillus awamori*, which produces xylanase (40.6 IU/g) and exo-polygalacturonase (16.3 IU/g) to hydrolyze peels into 24.4 g/L reducing sugars suitable for fermentation by lactic acid bacteria [71]. Optimization of *Aspergillus niger* HT4 fermentation on fig byproducts (36 h, 40 °C, 60% moisture, pH 5.0, with mineral supplementation) increased TPC to 10.19 \pm 0.04 mg GAE/g DM and enhanced antioxidant activity by 5.48- to 98.5-fold [69].

Apricot press residues fermented with *Aspergillus niger* and *Rhizopus oligosporus* exhibited 30–70% increases in TPC and 12–38% increases in flavonoids, while antioxidant activity also improved. HPLC–MS analysis identified chlorogenic acid, neochlorogenic acid, rutin, and quercetin 3-acetyl-glucoside as the dominant phenolics. Lipid recovery from apricot kernels was enhanced, yielding oils rich in linoleic acid, demonstrating the potential of these byproducts as bioactive- and antioxidant-rich ingredients [79].

Grapefruit byproducts, rich in carbohydrates and fiber, were used as a solid support and carbon source in SSF with *Aspergillus niger* GH1. Fermentation at 70% moisture promoted fungal growth, increased recovery of antioxidant compounds, and reduced solids by approximately 50%, highlighting their value for producing natural antioxidant-rich products [72].

Monascus species are well known for synthesizing valuable pigments, including red (monascorubramine, rubropunctamine), orange (monascorubin, rubropunctatin), and yellow (ankaflavin, monascin), which are widely applied in food products such as koji and Anka. Agro-industrial residues like Saba banana peel can support the simultaneous production of these pigments and enzymes (xylanase, cellulase) by *Monascus purpureus*, offering a cost-effective strategy for natural colorant and enzyme production [76].

Growth of *Aspergillus ibericus* and *Rhizopus oryzae* on untreated orange and banana peels significantly increased protein content, antioxidant activity, fiber, mineral, and lipid contents, supporting their use in the development of functional food ingredients [62].

Pineapple residues, including pulp, peels, skin, core, and crown, subjected to SSF with *Kluyveromyces marxianus*, show enhanced phenolic content, antioxidant activity, and anticancer potential. Similarly, mango seed waste fermented with *Aspergillus niger* exhibits increased TPC and radical scavenging activity. Pitahaya residues undergoing SSF with *Rhizomucor miehei* demonstrate higher phenolic content and antioxidant activity, particularly in freeze-dried samples [78]. In particular, mango seed fermented with *Aspergillus*

niger GH1 via SSF significantly increases polyphenolic content from 984 to 3288 mg GAE/100 g, primarily by converting bound phenols such as gallotannins into the free fraction, thereby enhancing antioxidant activity and highlighting its potential as a natural antioxidant source [77].

Extractable phenolics increased by over 1.7-fold, enhancing free radical scavenging activity, when chokeberry pomace was valorized via SSF with *Aspergillus niger* and *Rhizopus oligosporus*. Total flavonoids showed a similar increase, while prolonged fermentation caused substantial anthocyanin loss. SSF also enriched pomace lipids, particularly linoleic acid (57–61% of total fatty acids), demonstrating that fermentation improved both the antioxidant and nutritional quality of chokeberry byproducts [80].

Fermentation of orange, carrot, and papaya peels with *Blakeslea trispora* increased carotenoid yield (β -carotene 0.127 mg/mL), comparable to synthetic media and other agro-industrial residues such as cabbage, watermelon husk, and peach peels. The extracted carotenoids, confirmed by LC-MS, FTIR, and HPLC, were highly pure (> 76%) and exhibited strong antioxidant activity, demonstrating their potential for large-scale applications in food, feed, nutraceutical, cosmetic, and pharmaceutical industries [75].

Carrot pomace has been successfully valorized through fungal bioprocessing. *Penicillium oxalicum* BGPUP-4 produced inulinase under solid-state fermentation, achieving 322 IU/g at 90% moisture, pH 7, and 4 days, with a high inulinase/invertase ratio (3.38), indicating strong inulin specificity and suitability of carrot pomace as a substrate [136]. Mixed fermentation with *Trichoderma viride* and *Aspergillus niger* enhanced the release of bound polyphenols (80.88 mg GAE/10 g DW), identifying seventeen polyphenolic compounds and elevated levels of p-coumaric and other organic acids. These changes improved α -amylase inhibition and antioxidant activity in *Caenorhabditis elegans*, driven by hemicellulose degradation, lignin modification, and xylanase activity [137]. Enzymatic pretreatment followed by submerged fermentation with *Rhizopus delemar* released soluble sugars and produced fungal biomass enriched in protein, fiber, chitin, and chitosan, while retaining 28–33% glucan in the insoluble cellulose fraction for potential applications in biobased textiles, membranes, and other cellulose-derived materials. Hemicellulose, pectin, and sucrose provided essential nutrients that supported efficient fungal growth and biomass accumulation [73]. Similarly, co-fermentation of carrot peel and corn husk with *Cladosporium* sp. V3 effectively produced cellulases, with endoglucanase identified as the predominant active enzyme, demonstrating the substrate's suitability for enzyme production [40].

Crude enzymes produced by *Fusarium solani* through solid-state fermentation efficiently extracted lycopene from tomato byproducts, achieving higher recovery and enhanced

antioxidant activity compared with conventional methods, highlighting a sustainable strategy for food waste valorization [81].

Potato waste has been effectively valorized through fungal fermentation and bioprocessing. *Aspergillus ficuum* produced high-value phytase via solid-state fermentation, with enzyme activity enhanced up to 2.5-fold through optimized incubation and nitrogen supplementation [86]. *Rhizopus oryzae* converts potato peel and other agro-industrial residues, including cassava pulp, yam peel, pineapple residues, wheat wastewater, and mixed agri-food wastes, into ethanol (16.8–29.2 g/L) and lactic acid (3.1–50.5 g/L), with yields influenced by substrate, particle size, loading rate, and pretreatment. Its carbohydrate-digesting enzymes, including amylases, cellulases, hemicellulases, isoamylase, and glucoamylase, enable efficient hydrolysis without chemical pretreatment [85]. Incorporation of 10–20% potato peel into wheat straw and spent coffee grounds improved *Pleurotus ostreatus* mushroom powders, enhancing water- and oil-holding capacities, emulsifying ability, bioactive compounds, protocatechuic acid, tannins, and antioxidant activity [87]. Filamentous fungi, such as *Rhizopus oligosporus*, *Paecilomyces variotii*, *Trichoderma reesei*, and *Penicillium oxalicum*, applied via submerged or solid-state fermentation, can transform potato residues into biofuels, platform chemicals, lactic acid, gluconic acid, biopolymers, poly- β -hydroxybutyrate, starch films, enzymes, single-cell protein, and functional ingredients, exploiting their enzymatic capacity to hydrolyze starch and polysaccharides without extensive chemical pretreatment [84].

Potato cell fluid also supports fungal growth (*P. variotii*, *R. oligosporus*, *T. reesei*), producing biomass containing 17–27% amino acids and 23–30% dietary fiber, suitable as a functional ingredient [83]. Hybrid gels combining *Fusarium venenatum* mycoproteins with potato proteins form structured, fibrous gels with tunable hardness, in which mycelial hyphae provide the fibrous network and potato proteins enable firm, heat-set gel formation [138].

Cassava peels fermented with *Trichoderma pseudokoningii* under SSF, in optimized conditions (pH 5.0, 24 °C, 60–70% moisture, with urea or ammonium sulfate supplementation) achieved up to 48.1% protein enrichment, emphasizing the importance of fungal strain selection and nutrient strategy for maximizing protein yield during lignocellulosic residue valorization [88].

Valorization of Oilseeds, Pulses and Nuts Side-streams

Exhausted olive pomace, crude olive pomace, and crude organic olive pomace fermented by *Rhizopus oryzae* under SSF exhibited enhanced phenolic compound extraction

and a 12.9-fold increase in antioxidant activity. Multivariate analysis revealed strong correlations between enzyme production, phenolic release which are often bound within the lignocellulosic plant cell wall matrix, and antioxidant capacity, underscoring SSF as a promising biotechnological strategy for recovering bioactive compounds. Comparable trends were observed in vine trimming shoots, exhausted grape marc, and grape stalks [129]. In particular, fungal enzymes such as laccases and other lignolytic enzymes, which catalyze oxidative reactions that break down lignin structures; hydrolytic enzymes such as β -glucosidases, xylanases, and cellulases, which cleave glycosidic bonds in complex carbohydrates [146]; and esterases, which break ester-linked phenolics from structural polymers [147], collectively promote the release of bound phenolic compounds from the cell wall matrix.

Fermentation of sunflower, rapeseed, and soybean cakes with *Aspergillus niger*, *Aspergillus ibericus*, *Rhizopus oryzae*, and *Trichoderma* species via SSF effectively upgraded their nutritional and functional properties. The process reduced NDF and ADF and enhanced extracellular enzyme production, including cellulase (109 U g^{-1}), xylanase (692 U g^{-1}), protease (157 U g^{-1}), and β -glucosidase (503 U g^{-1}), facilitating the release of total phenolic compounds and improving antioxidant activity [89]. Fermented aqueous extracts also exhibited lower minimum inhibitory concentrations against *Listeria monocytogenes* and phytopathogenic fungi, and some extracts provided protection against genotoxic agents such as camptothecin and bisphenol A [139]. Under SmF using *Aureobasidium pullulans*, *Aspergillus oryzae*, *Trichoderma reesei*, and *Aspergillus niger*, substrates were effectively upcycled into protein-rich, bioactive biomass with enhanced total phenolic content and antioxidant activity, while reducing phytic acid and residual sugars. Furthermore, co-product valorization proved to be an effective strategy, as fermentation of thin stillage supplemented with SBH markedly enhanced nutrient and total solids recovery (up to 71%), improved clarification and oil recovery, and supported robust fungal growth [93].

Soapstock serves as a natural carbon source for lipase production by *Aspergillus*, *Penicillium*, *Trichoderma*, *Mucor*, and *Fusarium solani* 7F under SSF or SmF, with enzyme activity reaching 5.95 U/mL/min [90].

Fermentation of okara with *Rhizopus oligosporus* and a coculture with *Yarrowia lipolytica* via SSF significantly improved its nutritional and functional properties. The coculture synergistically reduced insoluble dietary fiber by 33% and phytic acid by 16%, while increasing soluble fiber by 176%, free amino acids by 254%, isoflavone aglycones by 179%, and free phenolic acids by 197% compared with unfermented okara. Flavor was also enhanced through the production of alcohols, esters, acids, and volatile

phenols [91]. Soybean hulls fermented with *Aspergillus niger* NRRL3 yielded high activities of endoglucanase (5914 U L^{-1}), exoglucanase (4551 U L^{-1}), and β -glucosidase (984 U L^{-1}), with robust fungal colonization and high volumetric productivity at shorter fermentation times, suggesting cost-effective scale-up potential. These cellulases have broad industrial applications, including biofuels, pulp and paper, detergents, and textiles [140]. Furthermore, soybean hulls are utilized as feedstock for enzyme production, where SSF or SmF with fungi such as *Trichoderma reesei* (Rut C30) and various *Aspergillus* species (*A. niger*, *A. aculeatus*, *A. cinnamomeus*, *A. foetidus*, *A. phoenicis*) produced a wide spectrum of carbohydrases, including cellulase, xylanase, pectinase, polygalacturonase, β -galactosidase, and sucrase, along with proteases [92].

Pea-processing byproducts under SmF using *Aspergillus oryzae*, *Fusarium venenatum*, *Monascus purpureus*, *Neurospora intermedia*, and *Rhizopus oryzae* yielded protein-rich fungal biomass ($\sim 680 \text{ kg protein/tonne}$), providing a sustainable vegan protein source while reducing the environmental impact of animal protein production [95].

Aspergillus niger GH1 applied to pistachio green hulls via solid-state fermentation enhanced phenolic recovery ($23.83 \text{ mg/g dry mass}$) through enzymatic cell wall degradation, increasing bioactive compounds such as gallic acid 4-O-glucoside and geranine, and improving antioxidant capacity [97]. Pistachio dehulling residues processed with *Neurospora intermedia* under optimized conditions (72 h, pH 5.5, 30°C) produced fungal biomass containing 20.4–27.1% protein, highlighting their potential as protein-rich ingredients for food, feed, and biorefinery applications [96]. Groundnut shells fermented with *Aspergillus niger* were converted into eco-friendly, high-performance adsorbents with improved Pb(II) removal, avoiding the use of toxic chemicals [141]. Fungal bioprocessing also enhanced pigments and antioxidant activity: *Monascus purpureus* generated red pigments from peanut meal, coconut residue, and soybean meal; *Rhizopus stolonifer* increased DPPH scavenging and ORAC values in cocoa pod husk and shells; and *A. niger* GH1 improved ABTS, DPPH, and FRAP activity in pistachio green hulls [61].

Spent coffee grounds processed with *Rhizopus oryzae* and *Trichoderma harzianum* (via SSF and SmF) showed increased protein ($\sim 26\%$) and lipid ($\sim 25\%$) content, while fiber, ash, cellulose, and hemicellulose decreased, reflecting microbial degradation and enzymatic conversion of carbon into protein-rich biomass and bioactive metabolites [100]. Additionally, SSF with *Lentinus crinitus* UCP 1206 and *Trametes* sp. UCP 1244 produced laccase (14.62 U/g), and the fermented biomass combined with chemically activated SCG served as effective biosorbents for Remazol dyes, comparable to commercial activated carbon, illustrating

integrated FBR applications for enzyme production and wastewater remediation [99].

Cocoa and nut byproducts have also been valorized through fungal fermentation. Fermentation of cocoa pod husk with *Rhizopus stolonifer* increased protein content ($11.33 \pm 0.86 \text{ mg g}^{-1}$), enhanced antioxidant activity, and promoted bioactive metabolites, including methyl 3-hydroxybutyrate, 10,12-tricosadiynoic acid, and palmitic acid, while improving phenolic bioavailability [101]. Similarly, cocoa shells fermented with *Penicillium roqueforti* exhibited higher phenolic and carotenoid content and favorable modifications in fatty acid composition (oleic, linoleic, and γ -linolenic acids) without significantly affecting anthocyanins or flavonols [102]. Fungi such as *Aspergillus*, *Trichoderma*, and *Penicillium* efficiently transform cocoa byproducts into antioxidant, anti-inflammatory, and antitumor bioactive metabolites, highlighting their potential for functional foods, nutraceuticals, and pharmaceutical applications [101, 102].

Fungal growth on tea residues, including *Lentinus edodes*, *Lentinus sajor-caju*, *Flammulina filiformis*, *Hericiium erinaceus*, *Pleurotus pulmonarius*, and *Monascus kaoliang* B6, promotes degradation of cellulose, hemicellulose, and lignin, enhancing nutrient release and mycelial biomass production [103]. Tea-processing wastes can also be valorized using tannase-producing fungi such as *Aspergillus niger* TBG 28 A and *Aspergillus glaucus* NRC8, which exhibit strong tannin hydrolysis and high tannase yields on green and black tea residues, respectively [104, 105]. Other tannase-producing fungi include *Aspergillus*, *Penicillium*, *Fusarium*, and *Trichoderma* species. The high-value tannase (Tannin acyl hydrolase; E.C.3.1.1.20), is applicable in animal feed and grape wine production [104]. Moreover, tannase can efficiently convert tannic acid to gallic acid, demonstrating the strong potential of *A. glaucus* for black tea waste valorization and industrial tannase and gallic acid production [105].

Fungal Biorefinery: Opportunities, Challenges and Future Perspectives

Fungal biorefineries provide a sustainable framework for converting agri-food side-streams (AFS) into high-value products while simultaneously reducing environmental burdens. Effective biorefinery design requires an in-depth understanding of feedstock composition, the interactions among its constituents, and the intended end products [12, 112, 113, 148]. Biorefinery strategies are generally grouped into three categories: (i) biological approaches that utilize microorganisms or enzymatic processes to transform food waste; (ii) thermochemical approaches,

including pyrolysis, gasification, and liquefaction; and (iii) chemical methods, which rely on catalysts or solvents to convert the feedstock [82]. Increasingly, combining these strategies in an integrated manner is explored to enhance conversion efficiency, improve product yields, and reduce production costs [149].

Among these, biological valorization using filamentous fungi offers particularly significant opportunities. Key biotechnological approaches employed for fungal valorization include solid-state fermentation (SSF), submerged fermentation (SmF), and co-culture or mixed-substrate strategies. SSF is advantageous for lignocellulosic residues due to low water requirements and enhanced enzyme yields, whereas SmF allows easier process control and biomass recovery. Co-culture and mixed-substrate methods enable synergistic interactions between microorganisms or feedstocks, further improving the efficiency and diversity of bioproducts. Fermentation processes and microbial technologies have been employed for the cost-effective, large-scale production of single or cocktail of enzymes not only for use in the animal feed industry but also in the food and beverage, biofuel, cosmetic, detergent, textile, and pharmaceutical industries [59]. Combining fungal hydrolysis with physical or chemical pretreatments can shorten conversion times and lower processing costs [57]. Important factors to consider in fermentation processes include the correct selection of the substrate, moisture, and microorganisms [58].

Fungi can efficiently transform diverse AFS into a variety of bioactive compounds, industrially relevant enzymes (e.g., cellulases, β -glucosidase, xylanase), organic acids, pigments, mycoprotein, protein-rich fungal biomass, polysaccharides, also bioplastics such as polyhydroxyalkanoates (PHAs), and biofuels including ethanol and hydrogen, supporting circular bioeconomy initiatives [82]. Notably, species such as *Aspergillus*, *Trichoderma*, *Rhizopus*, *Penicillium*, *Fusarium*, and *Cladosporium*, and *Neurospora* demonstrate the capacity to convert lignocellulosic residues, including pistachio hulls, potato byproducts, and apple pomace, many into protein-enriched biomass, pigments, and organic acids and other valuable metabolites [57].

Lignocellulosic residues such as rice and wheat bran, coffee byproducts, mango peels, coconut husks, corn cobs, and grape skins, are particularly suitable substrates due to their high carbohydrate content, porosity, and water-holding capacity. These characteristics promote fungal colonization, enhance enzyme secretion, and provide low-cost carbon sources for the production of industrially relevant compounds, including pigments, cellulases, organic acids, and antimicrobial metabolites [140].

To further improve the efficiency of these processes, microbial engineering tools play a pivotal role in enhancing fungal biomass yields, improving substrate utilization,

increasing tolerance to environmental stresses, and maximizing the production of target compounds. Recent advances in metabolic and protein engineering of filamentous fungi, including CRISPR-Cas9-mediated strain optimization, have significantly expanded the potential of fungal cell factories for the sustainable production of biochemicals and high-value bio-based products [18, 150].

Despite these promising prospects, fungal biorefineries face several technical and economic/logistical challenges that constrain the industrial adoption of fungal biorefineries. Technical challenges primarily relate to the biological and process aspects of fungal valorization. These include feedstock heterogeneity, which can affect conversion efficiency; limited mechanistic understanding of enzyme-microbe interactions, relatively low conversion efficiencies in some processes, and difficulties in maintaining optimal conditions for fungal growth and metabolite production at industrial scale. Process design must also account for factors such as substrate selection, moisture content, and strain-specific requirements, all of which influence yields and reproducibility [151]. In contrast, economic and logistical barriers stem from market and operational realities, especially for large-scale implementation. Bio-based products often face economic competitiveness relative to fossil-based alternatives, which remain a critical barrier. Even high-value compounds, such as lycopene and β -carotene, are sensitive to fluctuations in raw material costs and market demand, impacting commercial feasibility [82]. Efficient collection, transport, and storage of feedstock present additional challenges, as do scaling up processes through automation and integration with existing industrial systems. These factors collectively affect the commercial viability, widespread adoption of fungal biorefineries, and integration with existing markets [152].

Looking forward, advancing fungal biorefineries will require improvements in biological conversion platforms and the development of hybrid process models. Expanding mechanistic knowledge, generating comprehensive experimental datasets, and integrating multi-stage kinetic and mathematical models can enhance process predictability and operational efficiency [153]. In parallel, policy support, including carbon taxation and incentives for bio-based products, can bolster economic competitiveness and encourage market uptake [149]. Effective waste sorting, minimizing source waste, and optimizing process design are also crucial for maximizing biomass utilization and ensuring that the resulting products meet market requirements sustainably [82].

Fungal biorefineries hold promise for the sustainable valorization of AFS, enabling the production of a diverse array of products for food, feed, and industrial purposes. Fully realizing this potential will require addressing

technical, economic, and regulatory constraints, while advancing integrated biorefinery modeling, process optimization, and the strategic development of market-oriented bioproducts. By carefully aligning feedstock characteristics, fungal metabolic potential, and product demand, these systems can significantly contribute to a sustainable circular bioeconomy.

In view of these perspectives, an integrated fungal biorefinery platform has been designed (Fig. 4) to enable the conversion of diverse agri-food side-streams into multifunctional, high-value bio-based products and ingredients. This platform supports their integration across food, feed, nutraceutical, and other industrial value chains, thereby fostering research and innovation while advancing circular bioeconomy strategies.

Policy Relevance and Bioeconomy Strategy Alignment

Recognizing the untapped potential of secondary biomass and organic residues, the European Commission has emphasized residue valorization in the EU Bioeconomy Strategy [1], explicitly linking biomass utilization, innovation, and resource efficiency to the circular bioeconomy agenda, while noting Europe's low circularity rate and the ambition to increase it by 2030.

The integration of biomass valorization and circular bio-based production into public policy has accelerated at both the European Union and international levels, driven by growing recognition that circular bioeconomy solutions are essential for achieving sustainability, climate, and economic goals. Recent EU policy developments not only articulate strategic priorities but also embed monitoring and measurement frameworks to track progress and inform policy implementation. Analyses of OECD member states and G20 national strategies reveal that many jurisdictions increasingly incorporate monitoring systems and governance tools that track bioeconomy outcomes [154]. There is also an ongoing challenge in integrating economic, environmental, and social dimensions into comprehensive indicator sets that fully capture circularity and sustainability outcomes [155].

Moreover, United Nations high-level agendas, notably the 2030 Agenda for Sustainable Development, provide overarching targets that intersect with bioeconomy policy objectives (e.g., SDG 12 on sustainable consumption and production, SDG 13 on climate action). These frameworks encourage the development of multidimensional indicator systems to monitor the contribution of bioeconomy pathways toward sustainable and circular development [156]. In this context, fungal biorefineries

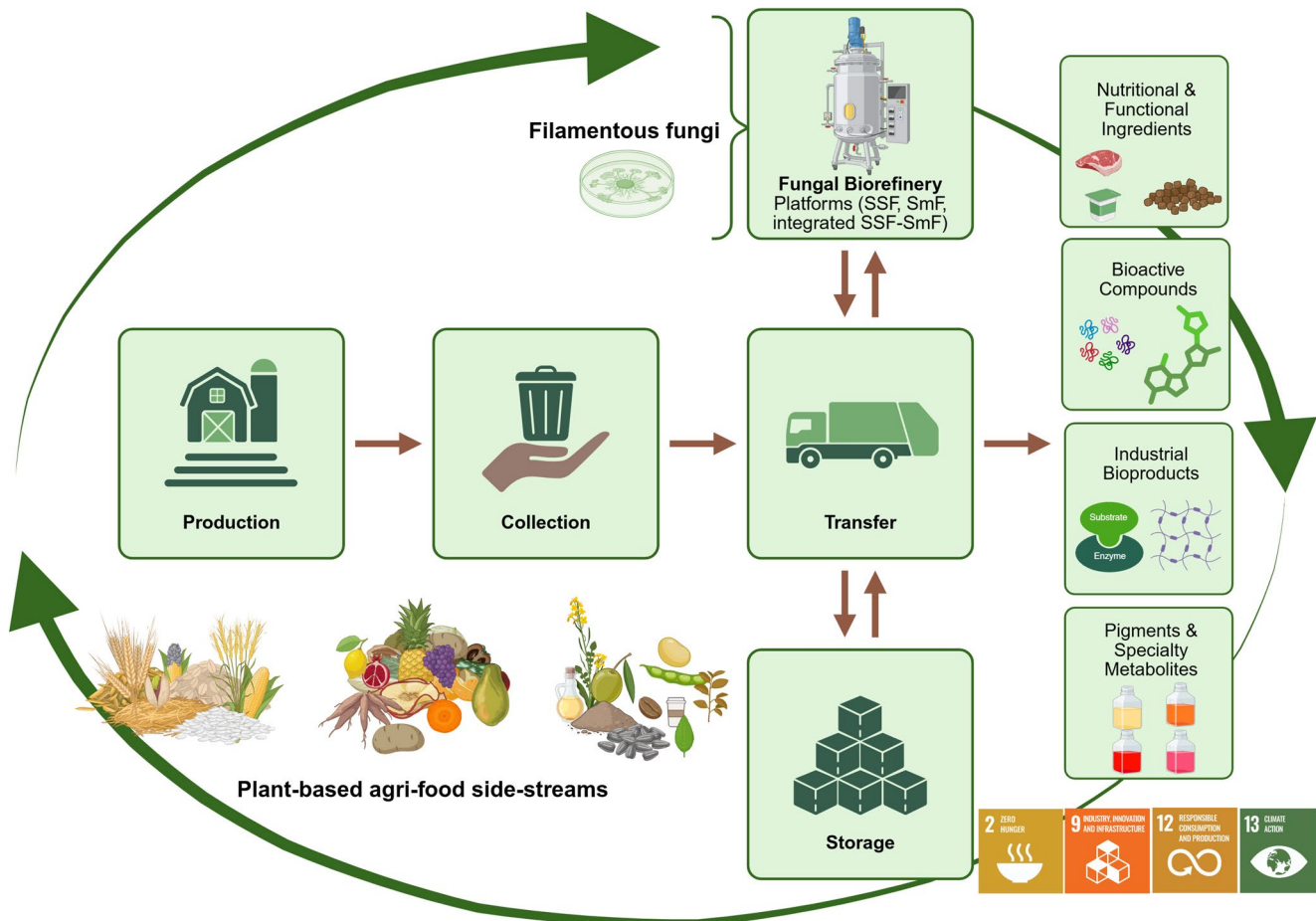


Fig. 4 Conceptual design of an integrated fungal biorefinery platform for the valorization of plant-derived agri-food side-streams into multifunctional, high-value bio-based products and ingredients, enabling

integration across different value chains and supporting circular bioeconomy models

represent a particularly actionable bioeconomy pathway because they directly convert regionally available agri-food side-streams into food-, feed-, and industry-relevant products, thereby shifting residues away from low-value outlets and toward higher-value circular use. This paper already frames fungal biorefineries as a transformative route to recover valuable compounds, reduce environmental impacts, and generate sustainable products within a circular bioeconomy framework aligned with the EU Bioeconomy Strategy and SDG Target 12.3 [157]. Alignments with SDG Target 12.3 (halving per-capita global food waste at the retail and consumer level and reducing food losses along production and supply chains) further strengthen policy relevance [1].

A distinctive advantage of fungal platforms is their capacity to produce a diversified portfolio of higher-value outputs, including mycoprotein and protein-rich fungal biomass, industrial enzymes, organic acids, pigments, polysaccharides, and other bio-based intermediates via SSF and SmF routes that can be adapted to heterogeneous plant-derived

residues. This diversity is strategically relevant for bioeconomy deployment because higher-value product slates can justify smaller, modular plant capacities and co-location with agri-food processors, which reduces transport and storage burdens for bulky side-streams and supports distributed, rural and regional bioeconomy development. At the same time, we should note that even high-value fungal products can remain sensitive to raw material cost variability and market demand, underscoring the importance of market-oriented product selection and integrated process design to ensure commercial robustness.

To translate this strategic alignment into implementation, the identified constraints, such as feedstock heterogeneity, logistics, and integration challenges, and economic competitiveness relative to fossil-based alternatives should be treated as policy-relevant deployment conditions rather than purely technical issues. In addition, policy support, including carbon taxation and incentives for bio-based products, together with improved waste sorting and source minimization, can strengthen competitiveness

and accelerate market uptake of fungal-derived ingredients and intermediates.

Accordingly, positioning fungal biorefineries as a bioeconomy instrument is strongest when the narrative links (i) locally available side-stream supply, (ii) fungal conversion routes and product portfolios, and (iii) the enabling conditions for scale (feedstock quality management, integrated downstream processing, and demand-side/policy measures) into a coherent deployment logic that supports circular bioeconomy objectives.

Conclusions

This study confirms that fungal biorefinery platforms constitute an efficient and flexible approach for converting plant-derived agri-food side-streams into value-added bioproducts. Diverse filamentous fungi have been successfully cultivated on both primary agricultural residues and secondary processing byproducts originating from cereals, sugar crops, oilseeds, legumes, nuts, and diverse fruit and vegetable side-streams. The use of solid-state and submerged fermentation systems enables the effective transformation of chemically complex and heterogeneous substrates into functional ingredients enriched in protein, bioactive compounds, and unsaturated fatty acids, as well as are produced high-value industrial enzymes, organic acids, biocolorants, and renewable bioproduct intermediates.

Different fungal taxa showed clear functional specialization. *Aspergillus* spp., *Trichoderma* spp., and *Penicillium* spp. were primarily associated with the production of carbohydrate-active enzymes and the release of bound phenolic compounds, whereas *Rhizopus* spp. and *Neurospora* spp. efficiently supported protein enrichment, organic acid formation, and lipid bioconversion. White-rot fungi, including *Pleurotus* spp., *Trametes* spp., and *Ganoderma* spp., proved particularly effective in lignin modification and biomass restructuring, thereby improving substrate digestibility and downstream sugar recovery. In parallel, pigment- and metabolite-producing fungi such as *Monascus* spp. and *Blakeslea* spp. expanded the portfolio of bioactive compounds obtainable from agri-food side-streams.

Collectively, these findings confirm that fungal biorefineries hold strong potential to enhance the nutritional, functional, and commercial value of agri-food side-streams, facilitating their integration into food, feed, nutraceuticals, and many bio-based products, services, and materials value chains. To translate these advances into industrial practice, future research should prioritize process standardization, scalability, and integrated biorefinery design in support of the bioeconomy strategy.

Abbreviations

ABTS	2,2'-Azino-bis(3-ethylbenzothiazoline-6-sulfonic acid)
ADF	Acid Detergent Fiber
ADL	Acid Detergent Lignin
AFS	Agri-Food Side-Streams
BRF	Fungal Biorefinery
BSG	Brewers' Spent Grain
DM	Dry Matter
DPPH	2,2-diphenyl-1-picrylhydrazyl
DW	Dry Weight
EU	European Union
FAOSTAT	Food and Agriculture Organization Corporate Statistical Database
FTIR	Fourier-Transform Infrared Spectroscopy
FRAP	Ferric Reducing Antioxidant Power
FW	Fresh Weight
GAE	Gallic Acid Equivalent
HPLC-MS	High-Performance Liquid Chromatography-Mass Spectrometry
IDF	Insoluble Dietary Fiber
LC-MS	Liquid Chromatography-Mass Spectrometry
Mt	Million Tonnes
NDF	Neutral Detergent Fiber
OCs	Oilseed Cakes
ORAC	Oxygen Radical Absorbance Capacity
PS	Paddy Straw
SBH	Soybean Hulls
SBP	Sugar Beet Pulp
SCB	Sugarcane Bagasse
SmF	Submerged Fermentation
SSB	Sorghum Bagasse
SSF	Solid-State Fermentation
TPC	Total Phenolic Content
WRF	White-Rot Fungi

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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