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Review

The Role of Fungi in Food Production and Processing

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Abstract: Fungi play an important and multifaceted role in the production and processing of food, influencing various stages from cultivation to consumption. This paper explores the complex relationship between fungi and food systems, highlighting their diverse contributions. Firstly, fungi serve as essential agents in food cultivation, aiding in the breakdown of organic matter and the recycling of nutrients, and promoting plant growth through symbiotic relationships. Moreover, fungi such as yeasts and molds are integral to fermentation processes, yielding a wide array of fermented foods and beverages with unique flavors and textures. Additionally, fungi are indispensable in the creation of enzymes and bioactive compounds utilized in food processing, enhancing the nutritional value, shelf life, and safety. However, certain fungal species pose significant challenges as food spoilage agents and mycotoxin producers, necessitating stringent quality control measures. Understanding the intricate interplay between fungi and food systems is essential for optimizing food production, ensuring food security, and mitigating the risks associated with fungal contamination. This paper synthesizes current research to elucidate the important role that fungus play in shaping the modern food industry and underscores the importance of ongoing scientific inquiry in harnessing their potential for sustainable and safe food production.

Keywords: fermentation; food processing; food safety; fungi; mycotoxin contamination

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1. Introduction

1.1. Overview of the Significance of Fungi in the Context of Food Microbiology and Processing

The fungal kingdom represents an extraordinary diversity of organisms with profound impacts across animal and plant species and ecosystem health. The growth and metabolic activity of fungi can have different effects. On the one hand, fungi form beneficial symbioses with plants, leading to the production of valuable materials like food, and on the other hand, they are the main factors contributing to changes such as food spoilage, decay, and toxin formation. Despite these dual roles, humans have comprehended the utility of fungi in their everyday life and are utilizing them for various purposes. For many years, fungi and fungal by-products have been extensively used in the area of food science. They are either consumed directly or used as additives to facilitate further food-processing techniques for producing specific food products. Fungi are utilized in food biotechnology as mushrooms, fermentative yeasts, and filamentous fungi, and they are known for their rich nutritional profile, thus contributing to cost savings within the food industry. Manufacturing of food and large-scale production of higher-quality products with the use of fungi is cheaper and easier, resulting in an increase in cultivation just to meet the demands of consumers during recent years. Fungi not only serve as a source of food but also have various value-added applications [1]. The prevalent reasons for employing fungi as substitute proteins stem from their enhanced resource utilization efficiencies [2,3], full complement of amino acids and additional nutritional advantages [3–5]. Fungi may constitute a source of biomass and secondary metabolites, and they can be genetically manipulated in order to create products possessing specific properties with great impact in the food industry [6–9]. In addition to the previously listed applications of fungi, it is worth noting their capability to release valuable enzymes during their metabolic activities, which are of considerable value for the production of specific food items. These enzymes serve numerous functions in food production. Fungal lipases are employed to improve the taste of dairy products such as cheese and butter and to eliminate fat found in fish and meat [10]. Another enzyme used in the food industry is pectinase, which is derived from the fungi *Aspergillus niger*. The primary application of these enzymes lies in the extraction of fruit juices from the fruit pulp, followed by the subsequent clarification process [11]. Furthermore, proteases obtained from fungal sources have been recognized for their significant contribution to brewing and the preparation of baked food products [12]. Other fungal enzymes, which are employed in various food techniques, are lactases, hemicellulases, pullulanases, glucanases, α-amylases, and β-amylases [13]. Apart from the manufacture of the desired products, fungi also play a role in upholding the quality and safety of food products and contribute to environmental integrity. Strains of fungi are used to produce antibiotics that can be used to control bacterial growth in food products and participate in food preservation. Recent studies indicated that some strains of fungi are involved in the biodegradation of food waste, which is important for environmental sustainability. They also help in converting food by-products into usable forms, thereby reducing waste [14].

Mushrooms (macrofungi) are typically cultivated on a large scale in industrial settings. Numerous studies demonstrate that mushrooms have the potential to serve as an adjunct in the promotion of advantageous health effects. These fungi are renowned for their elevated protein content and abundance of antioxidants, vitamins, dietary fiber, carbohydrates, and minerals [15]. Additionally, it is noteworthy that mushrooms also contain lower cholesterol, fat, and caloric value. Considering the rich nutritional content of mushrooms, they can serve as a prebiotic source, promoting the development and balance of beneficial gut bacteria known as probiotics, leading to various health advantages [16,17]. Furthermore, Beelman et al.'s [18] research indicates that mushrooms serve as a repository of various bioactive compounds (terpenes, phenolic compounds, and polysaccharides), which aid in bolstering the immune system. Due to these components, mushrooms demonstrate antioxidant, anti-inflammatory, and antimicrobial properties. These advantages of mushrooms for health and their consumption can potentially lead to the creation of a diet that is well-balanced [7]. For thousands of years, filamentous fungi, a class of fungi, have been used for food production. These fungi are consumed by humans, often not in their raw state but as additives in various food items. Filamentous fungi are renowned for producing numerous secondary metabolites with potential health benefits [19] and are typically engaged in the creation of well-known culinary items such soy sauce, miso, and tempeh. Some filamentous fungi species have a higher protein content compared to most mushrooms, making them promising candidates for alternative protein sources. Recently, filamentous fungi have garnered significant attention in research circles for their potential innovative applications across a wide range of food products, including their established role as alternative proteins [20]. Another type of fungi commonly used in the food industry is yeast. Yeast cells and fungal mycelium are cultivated to produce protein-rich, nutritious food for both human and animal consumption. Yeasts are favored for their ability to carry out fermentation processes [21]. They contribute to the production of essential food items such as bread and cheese, which can enhance flavor and preserve the food. Fermentation is one of the oldest ways of food processing and is of great economic importance. However, only specific strains of yeast are chosen to conduct the fermentation process. The occurrence, production, characteristics, and utilization of fermented foods are extensively documented [22–24]. The selection of specific yeast strains depends on three primary factors: their ability to survive the processing conditions, their capacity to generate gas during fermentation, and their capability to contribute a desired flavor to the food product [7,25]. They also have a notable role in industrial fermentation for the production of various organic substances, such as amino acids [17]. Additionally, yeasts serve a significant function role in alcoholic and non-alcoholic beverages. The most commonly used strain for this purpose is *Saccharomycescerevisiae* [17]. Finally, yeasts are employed not only for fermentation processes but also to improve the flavor and texture or initiate maturation in various products [7,26].

Inevitably, naturally existing impurities in food may originate from either chemical or biological sources. Mycotoxins act as harmful secondary metabolites that are produced by fungi and are a major source of worry. Toxic fungi are abundant in nature and are regularly found in food sources worldwide, despite efforts to minimize fungal contamination. This is mostly because of mold growth on vulnerable agricultural goods, such as cereal grains, nuts, and fruits. Although a variety of mycotoxins are present in nature, only a notably small quantity can lead to food degradation. The three main genera of fungi associated with toxins in food are the *Aspergillus*, the *Fusarium* and the *Penicillium*. The mycotoxins produced by these fungi are highly diverse. In summary, fungi and their by-products have the potential to induce food spoilage; thus, comprehending their physiological characteristics and chemical composition is essential for enhancing food production quality [27].

Throughout the past few centuries, numerous scientists have contributed to a vast body of knowledge about fungi, underscoring the significance of comprehending their role in food production. This review provides insights from previous work to accelerate fungal research in food production and to highlight the research advances in the following six major topics: 1. Exploration of the diverse fungal species present in various food products; 2. Methodology for fungal identification and characterization in food samples; 3. Fungi as food spoilage agents; 4. Mycotoxins and food safety; 5. Fungal fermentation; and 6. Current trends and future directions.

1.2. Historical Perspectives and Milestones in the Study of Fungi in Food

For millennia, humans have relied on fungi as a source of sustenance [28], even though only a small amount of fungi is edible and can be used in food processing. Since early agricultural practices, men have used the natural ability of fungi to ferment various grains and fruits in order to enhance the sensory and beneficial traits in the production of specific foods such as alcoholic beverages and bread [29]. Fungi are used in the production of beverages (like beer, cider, and wine) and fermented food items (like bread, cheese, and rice, including other foods) [30]. *Saccharomyces* yeasts are mostly utilized to maintain the safety and quality of foods and beverages because, in contrast to other microorganisms, they can withstand high amounts of ethanol. Initially, fungal species were accidentally used to ferment and produce alcohol, which ultimately resulted in the identification of efficient strains. Although *S. cerevisiae* is the primary species used in wine production, other species also play important roles. Numerous types of fungi can infect grapes before they are harvested, with the main culprits being species from the genera *Alternaria*, *Aspergillus*, *Botrytis*, *Plasmopara*, *Penicillium*, *Rhizopus*, *Oidium*, *Uncinula* and *Cladosporium* impacting the wine flavor and quality [31]. These species are considered domestic because they have adapted and possess improved traits in comparison to their wild ancestors [32]. Edible mushrooms are globally cultivated and considered a component of a healthy human diet [33].

Fungi, as mentioned above, are considered a source of nutrients since they produce important proteins and high-value biochemicals [7,34]. For a century, there has been intense interest in the production of proteins from fungi. Indeed, vigorous efforts are being made to replace animal-derived proteins with proteins produced by fungal cells [35]. In numerous instances, fungi are employed in food products due to their capability to decompose biomass and generate improved flavors and textures. It is noteworthy to mention some examples of the milestones achieved through the utilization of fungi and their enhanced biochemical products in food production and cultivation. *Aspergillus awamori*, which is one variant of *Aspergillus niger*, since 1919, has been commercially utilized for large-scale submerged culture fermentations to produce citric acid [36]. *Penicillin*, derived from *Penicillium* mold, revolutionized food safety, alongside the advancement of mycoprotein as a meat alternative due to its nutritional benefits [37]. Some phytopathogenic edible portions of fungi are also consumed, such as a delicacy comprised of *Ustilago maydis*. In Mexico, this fungus induces the formation of black tumors on maize, resulting in a delicacy known as huitlacoche [38].

One of the earliest documented instances of using fungi for human consumption was reported in China. Since then, its utilization has continued in various forms [39]. For over 3000 years, the fungus *Aspergillus sojae* has been utilized in the production of soy sauce because of its capacity to secrete enzymes, break down soybeans, and impart a distinctive flavor to the sauce [40]. *Aspergillus oryzae* has also been employed in the production of koji, using solid-state cultivation (koji is used as a starter for secondary fermentations). This technique is believed to have originated in China and has been utilized for centuries in Japanese fermentations. The commercialization of koji can be traced back to the Heian and Muromachi periods (13th to 15th century) [41]. This filamentous fungi is also utilized for the production of traditional alcoholic beverages, sauces, and condiments. In Japan, *A. awamori* has been extensively employed in the production of an alcoholic beverage called awamori, converting starch into glucose. Yeast-form fungi have been cultivated since 7500 BCE (e.g., *Saccharomyces cerevisiae* and *Saccharomyces pastorianus*) and are used for making bread, wine, and beer, while filamentous fungi are used for the maturation of cheeses [42] and for rice-alcohol production (yielding sake, also using *A. oryzae*), [43,44]. This rich history underscores the interconnected relationship between fungi and culinary practices throughout human civilization. Various cultures worldwide have a long and distinguished tradition of consuming wild edible fungi, exemplified by products like Roquefort and Camembert cheeses [45,46]. The earliest evidence of cheese making dates back to the 6th millennium BCE in Poland. Discoveries of milk fat in sieve vessels were initially documented [43] from the early Bronze Age (ca. 3800 years ago), while residues of old cheese were discovered in tombs [47]. Neolithic farmers also practiced the production of cheese, enabling the preservation of milk during transportation in a nonperishable form. Additionally, cheese became more digestible for adults due to its lower lactose content compared to fresh milk [48]. In ancient times, lactic acid bacteria (LAB) were incorporated into fresh milk for cheese production to prevent milk from curdling. Subsequently, various mechanical methods were developed to drain the curd, such as carving, brewing, pressing, and grinding, and to mature cheeses. These advancements, occurring later in history, led to the wide variety of cheeses known today, including soft cheeses, blue-veined cheeses, and hard cheeses, including other cheeses [29]. Furthermore, the earliest evidence of human wine production dates back to the Neolithic period, coinciding with the development of winemaking techniques. Tartaric acid and terebinth resin were identified in a pottery jar dating from 5400 to 5000 BCE in Hajji Firuz, Iran, marking a significant early milestone in the history of winemaking [49]. There is also evidence indicating that the yeast *S. cerevisiae* was responsible for wine fermentation in Egypt as early as 3150 BCE [50]. The techniques for wine fermentation originated in Mesopotamia and gradually expanded toward Europe, eventually spreading to the New World [51]. An example of fungi use in wine is the plant pathogenic fungus, *Botrytis cinerea*, “noble rot”, which is known for its ability to concentrate sugar in the berry of the grape, producing a sweet and expensive wine. Noble rot wine is mainly produced in the South of France [52]. *S. cerevisiae* can also be utilized for bread-making, hence its alternative name, baker’s yeast. Scenes depicting bread-making have been uncovered in tombs dating back to the Ancient Egyptian civilization. The remains of cereals and bread on pottery have deepened our understanding of the baking techniques [53]. However, the documentation regarding the origin and spread of leavened bread is incomplete, leaving uncertainty about whether yeasts originated from cereals or from the process of fermenting beer [54]. This uncertainty persisted until the late 19th century, when the exclusive production of baker's yeast for bread dough commenced. Initially, the production of distiller's yeast involved extracting it from mashed grains before transitioning to the more economical source of assimilable sugar, molasses [55]. Moreover, the variation in yeast's physiological traits, along with the quality of other ingredients and the mechanical processes employed, yield two primary types of beers: ale or lager-style beers. Ales have been brewed since ancient times, potentially as early as 6000 BCE [56]. Lager beer production, initially confined to cool seasons, underwent significant expansion following two key developments: the invention of the refrigerating machine by Linde in 1871 and the development of pure yeast cultures by E.C. Hansen in 1883. Regarding truffles, while they may have been initially gathered as a natural resource, direct reports confirming this are lacking. Truffles, including species such as truffles, morels, and boletus, are esteemed as culinary delicacies despite the challenges associated with their cultivation [57]. The inconspicuous nature of their vegetative stage likely hindered a comprehensive understanding of their exact ecology. Truffles were highly prized by the Romans, although the specific species collected two thousand years ago remain unidentified.

2. Understanding the Research Prospects

For this review article, a comprehensive literature search was conducted to gather relevant studies elucidating the role of fungi in food production and processing. The search strategy encompassed electronic databases, including Google Scholar, PubMed, Web of Science, and ResearchGate. Keywords such as "fungi", "food production", "food processing", "fermentation", "mycotoxins", and "food spoilage" were utilized in various combinations to identify peer-reviewed articles, reviews, and book chapters published between 2000 and 2024. The initial search yielded a broad selection of literature, which was subsequently refined based on the relevance to the scope of the review. Studies focusing on fungal ecology, physiology, enzymology, and their implications in food systems were prioritized. Additionally, articles detailing fungal interactions with food substrates, biotechnological applications, and food safety concerns were included. The selected literature was critically analyzed to extract the key findings, trends, and insights regarding the diverse roles of fungi in food production and processing. Special attention was paid to studies elucidating fungal-mediated processes such as fermentation, enzymatic activities, mycotoxin production, and spoilage mechanisms. Moreover, efforts were made to incorporate recent advancements in fungal biotechnology and their implications for enhancing food quality, safety, and sustainability. Overall, this literature review provides a comprehensive synthesis of existing knowledge on the multifaceted interactions between fungi and food systems, serving as a foundation for understanding their pivotal role in shaping the modern food industry.

2.1. Fungal Diversity and Identification in Food

Exploration of the Diverse Fungal Species Present in Various Food Products

Among the most prevalent fungal inhabitants encountered in our exploration are the filamentous fungi of the genera *Aspergillus* and *Penicillium*. These molds, adept at colonizing a wide array of substrates, contribute to both the beneficial processes of fermentation and the detrimental phenomenon of spoilage. The enzymes produced by *Aspergillus oryzae* during fermentation contribute to the breakdown of proteins and carbohydrates, enhancing the flavor and nutritional value of these fermented products [58–60]. *Aspergillus* species, such as *Aspergillus flavus* and *Aspergillus niger*, are renowned producers of mycotoxins, secondary metabolites that pose significant health risks when present in contaminated food [61–63]. Similarly, *Penicillium* species, such as *Penicillium roqueforti* and *Penicillium camemberti*, play pivotal roles in the production of various fermented food, including blue cheese and Camembert, where they contribute to flavor development and texture modification through their enzymatic activities [64,65]. In addition to filamentous molds, yeasts constitute another prominent component of the fungal communities inhabiting food products. *Saccharomyces cerevisiae*, in particular, stands out as a key player in fermentation processes, contributing to the production of bread, beer, and wine [50,66]. This versatile yeast species ferments sugars to produce carbon dioxide and alcohol, imparting characteristic flavors and textures to these culinary delights [67]. *Debaryomyces hansenii*, a yeast species commonly found in dairy products, contributes to the ripening and flavor development of certain types of cheese [68]. Similarly, molds such as *Rhizopus oligosporus* and *Rhizopus oryzae* are used in the production of tempeh, a traditional Indonesian fermented food made from soybeans [69]. These molds produce enzymes that break down the proteins and carbohydrates in the soybeans, leading to the formation of a firm texture and a nutty flavor in the final product. However, not all fungal inhabitants within food products are as benign as *Saccharomyces cerevisiae*. Certain yeast species, such as *Candida albicans* and *Candida tropicalis*, may pose health risks when present in high numbers, particularly in immunocompromised individuals or those with underlying medical conditions. These opportunistic pathogens have the potential to cause invasive candidiasis, a serious bloodstream infection associated with high mortality rates if left untreated [70]. Furthermore, our study uncovers the presence of potentially pathogenic molds within food matrices, including species of *Fusarium*, *Alternaria*, and *Cladosporium*. *Fusarium* species, such as *F. graminearum* and *F. verticillioides*, are notorious producers of mycotoxins [71], including deoxynivalenol (DON) [72] and fumonisins [73], which contaminate cereal grains and pose risks to human and animal health. Similarly, *Alternaria* species, such as *A. alternata*, are known to produce allergenic compounds and mycotoxins, causing adverse reactions in sensitive individuals [74,75]. *Cladosporium* species, although frequently encountered in both indoor and outdoor settings, may also contaminate food products and trigger allergic reactions [76]. The diversity of fungal species encountered in our exploration varies across different food categories, reflecting the diverse ecological niches and environmental conditions present within food ecosystems. Grains and cereals, rich in carbohydrates and moisture, provide favorable conditions for fungal proliferation, resulting in a diverse array of fungal inhabitants, including both beneficial and detrimental species [77]. In contrast, fruits and vegetables, with their acidic pH and antimicrobial compounds, exhibit a more limited fungal diversity, although certain spoilage fungi may still colonize these substrates under favorable conditions [78].

In conclusion, the fungal diversity within food products unveils a dynamic and intricate microbial landscape, teeming with myriad interactions and metabolic activities. Understanding the ecological dynamics of these fungal communities is paramount for devising effective strategies to preserve food quality, ensure safety, and mitigate the risks posed by spoilage and contamination. By elucidating the roles and interactions of specific fungal taxa within food ecosystems, we can harness the potential of beneficial fungi while minimizing the risks associated with detrimental species, thereby safeguarding both human health and the integrity of our food supply.

2.2. Methods for Fungal Identification and Characterization in Food Samples

2.2.1. Microscopic Examination

Microscopic examination represents one of the earliest and simplest methods for fungal identification in food samples. Direct microscopic observation of fungal structures, such as hyphae, spores, and conidia, provides valuable morphological information that can aid in species identification. Staining techniques, such as lactophenol cotton blue or potassium hydroxide mounts, enhance the visualization of fungal structures under the microscope. While microscopy is rapid and cost-effective, it requires expertise to accurately differentiate fungal species based on morphological characteristics, and it may be limited by the lack of specificity in some cases [79].

2.2.2. Culture-Based Methods

Culture-based methods involve the isolation and cultivation of fungi from food samples on selective or non-selective agar media. Samples are plated onto suitable media, such as Sabouraud dextrose agar (SDA) or potato dextrose agar (PDA), and incubated under appropriate conditions to promote fungal growth. Colonies are then characterized based on their morphology, growth characteristics, and biochemical profiles. Additionally, selective media containing specific nutrients or inhibitors may be used to selectively isolate certain fungal species. While culture-based methods allow the isolation and identification of viable fungal species, they are time-consuming, labor-intensive, and may underestimate fungal diversity due to the inability to culture all the fungal species present in a sample.

2.2.3. Molecular Methods

Molecular methods have revolutionized fungal identification and characterization in food samples, offering unparalleled specificity, sensitivity, and accuracy [80]. Polymerase chain reaction (PCR) techniques target conserved regions of fungal DNA, such as the internal transcribed spacer (ITS) region, allowing the rapid amplification and detection of fungal DNA in food samples [81]. Sequencing of PCR products, followed by comparison with reference databases, enables precise species identification. Next-generation sequencing (NGS) technologies, such as amplicon sequencing and metagenomic sequencing, provide comprehensive insights into the fungal diversity [82] and community structure in complex food matrices. Additionally, quantitative PCR (qPCR) allows the quantification of fungal species in food samples, providing valuable information for risk assessment and monitoring purposes [83]. While molecular methods offer high specificity and sensitivity, they require specialized equipment, technical expertise, and may be cost-prohibitive for routine analysis in some settings.

2.2.4. Immunological Methods

Immunological methods, such as enzyme-linked immunosorbent assays (ELISAs) and lateral flow immunoassays, utilize specific antibodies to detect fungal antigens or toxins in food samples. These methods offer rapid and convenient detection of fungal contamination, particularly mycotoxins, with minimal sample preparation [84]. However, immunological methods may lack specificity and cross-reactivity with structurally similar compounds, leading to false-positive results.

2.3. Fungi as Food Spoilage Agents

2.3.1. In-Depth Analysis of Fungi Responsible for Food Spoilage

Fungal contamination continues to pose a significant challenge in the food industry, resulting in financial losses and potential health hazards for consumers [85]. This scientific investigation provides an in-depth analysis of the fungal species responsible for food spoilage, elucidating their ecological characteristics, metabolic activities, and mechanisms of action. Through a comprehensive literature review and critical analysis, this manuscript aims to enhance our understanding of fungal spoilage in food products and inform strategies for prevention and control. Fungi play a pivotal role in the spoilage of various food products, leading to changes in the taste, texture, odor, and nutritional quality. While some fungal species are benign, others possess enzymatic capabilities and metabolic activities that promote food degradation and deterioration. Understanding the diversity and behavior of spoilage fungi is crucial for implementing effective control measures and ensuring food safety and quality.

2.3.2. Fungal Species Responsible for Food Spoilage

Numerous fungal species have been implicated in the spoilage of different food products, each exhibiting specific preferences for substrates and environmental conditions. Common spoilage fungi include species of *Aspergillus*, *Penicillium*, *Fusarium*, *Alternaria*, and *Mucor* [86,87]. These fungi thrive in various food matrices, including grains, fruits, vegetables, dairy products, and processed foods, where they utilize the available nutrients and water to proliferate and produce metabolites that degrade the food quality.

2.3.3. Ecological Characteristics and Metabolic Activities

Spoilage fungi possess diverse ecological adaptations that enable them to colonize and degrade different food substrates. Filamentous fungi, such as *Aspergillus* and *Penicillium* species, produce hyphae and mycelium that penetrate and colonize food matrices, leading to visible signs of spoilage, such as mold growth and discoloration. These fungi secrete a plethora of extracellular enzymes, including proteases [88], lipases [89], and amylases [90], which break down the proteins, lipids, and carbohydrates in food, resulting in changes in the texture, flavor, and aroma.

2.3.4. Mechanisms of Food Spoilage

The mechanisms underlying fungal-mediated food spoilage are multifaceted and involve enzymatic degradation, metabolic activity, and the production of secondary metabolites. Proteolytic enzymes produced by spoilage fungi hydrolyze the proteins in food, leading to the production of peptides and amino acids that contribute to off-flavors and odors. Lipolytic enzymes degrade lipids, causing rancidity and off-flavors in fatty foods. Moreover, the formulation of organic acids and volatile compounds by spoilage fungi contributes to the souring and fermentation of food products. Additionally, some fungal species produce mycotoxins. These are secondary metabolites with toxic effects on humans and animals [91].

2.3.5. Strategies for Prevention and Control

Preventing fungal-mediated food spoilage requires a multifaceted approach encompassing good agricultural practices, proper hygiene, temperature control, and adequate food preservation techniques. Implementing stringent quality control measures throughout the food supply chain, including monitoring and testing for fungal contamination, can help identify and mitigate potential sources of spoilage. Furthermore, utilizing natural preservatives, such as antimicrobial compounds derived from plants or microorganisms, can inhibit fungal growth and extend the shelf life of food products [92].

2.4. Factors Influencing Fungal Growth and Spoilage in Different Food Matrices

2.4.1. Intrinsic Factors

Intrinsic factors refer to the inherent properties of the food matrix that influence fungal growth and spoilage. The composition and availability of nutrients play a crucial role in supporting fungal proliferation, with high-carbohydrate and high-moisture foods serving as ideal substrates for fungal growth. Additionally, the pH levels can impact fungal growth, with acidic environments inhibiting the growth of some fungal species while promoting the growth of acid-tolerant fungi [93]. Food’s water content is another critical intrinsic factor, as fungi require water for metabolic activities and enzymatic reactions. Foods with a high moisture content, such as fruits, vegetables, and dairy products, are particularly susceptible to fungal spoilage due to their favorable water activity levels.

2.4.2. Extrinsic Factors

Extrinsic factors encompass environmental conditions and external influences that affect fungal growth and spoilage in food products. Temperature is one of the most significant extrinsic factors, as fungi exhibit specific temperature requirements for growth and proliferation. Mesophilic fungi, such as *Aspergillus* and *Penicillium* species, thrive in moderate temperatures (20–30 °C) [94], while psychrophilic fungi, such as molds of the genus *Cladosporium*, can grow at lower temperatures (0–10 °C) [95]. Thermophilic fungi can grow at temperatures above 45 °C and have a minimum temperature for growth of or above 20 °C [94]. Oxygen availability also plays a crucial role in fungal growth, with aerobic fungi requiring oxygen for respiration and anaerobic fungi thriving in oxygen-deprived environments [96]. Furthermore, the storage conditions, such as the humidity levels, packaging materials, and exposure to light, can influence fungal growth and spoilage in food products.

2.4.3. Interactions with Microorganisms

Fungal spoilage of food products often occurs in conjunction with the activities of other microorganisms, including bacteria, yeasts, and molds. Interactions between fungi and bacteria can result in synergistic or antagonistic effects on food spoilage, with certain bacterial species producing metabolites that inhibit fungal growth or vice versa [97]. Understanding these complex interactions is essential for predicting and controlling fungal spoilage in food products.

2.5. Mycotoxins and Food Safety

2.5.1. Examination of Mycotoxins Produced by Fungi and Their Implications for Food Safety

Representative genera of mycotoxigenic fungus are *Aspergillus*, *Penicillium*, and *Fusarium*; significant food contaminants or plant pathogens have been identified to include *Trichoderma*, *Trichothecium*, and *Alternaria* [98,99]. Certain environmental conditions drive the formation of mycotoxins; however, the degree of contamination varies depending on the location, agricultural practices, and the vulnerability of commodities to fungal penetration throughout the storage and processing periods. As a result, depending on their ecological growth needs, fungi that produce food toxins are divided into two categories: fungi of the fields and storage fungi [100]. Industrialized countries have lower risks of mycotoxin exposure due to agricultural practices, efficient quality control, and storage systems, although a recent survey [101] revealed that a large number of developing regions are at high risk due to the severe to extreme prevalence of mycotoxins. For example, mycotoxins are especially common throughout South Asia and throughout North and Central America. In other regions, there is a moderate to strong presence, including Europe, Oceania, and Southeast Asia. Remarkably, by-products from both housed and free-range animals have been shown to contain mycotoxins, in addition to grains, concentrates, and silage. The AFM1 toxin (aflatoxin M1) has been found in free-range cow milk even above European borders. The T-2 (trichothecene 2) and HT-2 (hydroxy trichothecene 2) toxins are members of the TH (trichothecenes) and ZEA (zearalenone) families. These mycotoxins have been discovered in pasture grasses. In other words, mycotoxins have been found in animals regardless of whether they are reared with an intermediate, extensive or intensive method of production. As a result, nomadic and mixed crop–livestock systems based on fodder, crops and animal waste have a risk of mycotoxin contamination (Table 1). Aflatoxin (AF), ochratoxins (OTA), fumonisins, trichothecenes (TH), patulin (PAT), citrinin (CIT) and zearalenone (ZEA) are commercially important mycotoxins that have been detected in the research. Mycotoxins have an equivalent impact on growers and consumers in terms of health and profitability. Wheat, millet, corn, sorghum, soybeans, peanuts and their products, as well as by-products created from contaminated staples, are the most sensitive crops to mycotoxins. Food scraps, moldy bread, cottonseed, spices and other foods, as well as cereals, pulses, oilseeds and industrial by-products diverted into animal diets, can all contain mycotoxins [102]. The most common contaminants that damage crops during the preand post-harvest periods are fungi (*Aspergillus*, *Fusarium*, *Penicillium Alternaria and Claviceps*) and saprophytic fungi.

Table 1. Some important mycotoxins and their effects on humans and animals [101].

Mycotoxins	Genus/Species	Major Food	Toxic Effects and Diseases
Aflatoxin	*A. flavus* *A. parasiticus* *A. nomius* *Penicillium sp.*	Cereals, feeds, oilseeds and pulp, coconut	Hepatotoxicity, teratogenicity, immunological system suppression, altered DNA structure, hepatitis, bleeding, and kidney lesions are among the factors that can cause cancer
Ochratoxin OTA	*Aspergillus* *A. ochraceus* *Penicillium* *P. nordicum* *P. verrucosum*	Herbs, cereals, oilseeds, figs, beef jerky, fruits, and wine	Damage to the kidneys and liver, appetite loss, nausea, and vomiting, weakened immune system, and carcinogenic
Fumonisin	*Fusarium* *F. verticillioides* *F. Culmorum*	Corn, cereals	Esophageal cancer, heart failure, liver damage, neurotoxicity, carcinogenicity, human encephalomalacia, and pulmonary edema
Patulin	*A. terreus* *A. clavatus* *Penicillium* *Penicillium carneum* *P. clavigerum* *P. griseofulvum*	Silage, wheat, feeds, apples, pears, grapes, peaches, apricots, olives, cereals	Hemorrhage of brain, neurological conditions, skin cancer, skin lesions, lung, mutagenicity, and antimicrobial effect
Zearalenone	*Fusarium* *F. graminearum* *F. culmorum*	Cereals, corn, fodder, silage, timothy grass,	Carcinogenic, estrogenic effect from imbalance of hormones, reproductive issues, and teratogenic

2.5.2. Aflatoxin

Aflatoxin derivatives are difuranocoumarins. They are constructed of a pentanone ring, or in some other cases, of a lactone ring (for AFBs: aflatoxin B). It is also possible to be constructed of a lactone ring attached to the coumarin core (for AFGs: atoxin G). Between the 20 known aflatoxins, aflatoxin B1 (AFB1), aflatoxin B2 (AFB2), aflatoxin G1 (AFG1), and aflatoxin G2 (AFG2) are the four most important. AFB1's and AFB2's hydroxylated metabolites are aflatoxin M1 (AFM1) and M2 (AFM2). *A. flavus* creates B types, while *A. parasiticus* creates G sorts [103]. AFs can be found in many different types of foods and feeds. Peanuts, nuts, figs, corn, rice, spices and dried fruits are among the most affected foods and feeds [104]. Contamination of crops from aflatoxin commonly occurs in the field before the harvest and is usually due to unfavorable conditions of storage. These conditions can be low substrate moisture content and relative humidity, as well as growing dryness. Increased farm animal mortality has been associated with aflatoxin contamination, and the indirect form of aflatoxin present in milk and dairy products (aflatoxin B1 is biotransformed to aflatoxin M1, a hydroxylated form) is caused by consuming polluted feed [105]. Aflatoxin has been linked to toxicity and carcinogenesis in humans and also in animals. Aflatoxin-related disorders are referred to as aflatoxicosis. Aflatoxin ingestion is thought to be a significant reason for the onset of primary hepatocellular carcinoma, especially in people with a history of hepatitis B. Complicating epidemiological studies is the existence of hepatitis B virus infection, a significant factor in liver cancer [106].

Aflatoxins biosynthesis occurs through a polyketide pathway initially proposed by Birch in 1967. Presently, research indicates that the biosynthetic pathway of aflatoxins involves 27 enzymatic reactions. Among the natural secondary metabolites, aflatoxin biosynthesis stands out as one of the most extensive and intricate processes, largely due to the multitude of oxidative rearrangements it encompasses. In 1988, Dutton identified three pivotal oxygen elements crucial to this pathway:

(i) Monooxygenases: These enzymes are responsible for integrating a single oxygen atom into another molecule while reducing it, with nicotinamide adenine dinucleotide phosphate (NADPH) serving as a co-factor.
(ii) Dioxygenases: Involved in ring-cleavage reactions, dioxygenases play a crucial role in the rearrangement of molecular structures.
(iii) Baeyer–Villiger reactions: These reactions facilitate the insertion of oxygen atoms between two carbon atoms, leading to structural modifications.

Aflatoxin production is also significantly influenced by cytochromes P-450. These enzymes play a significant role in the biosynthesis process by attaching functional groups like methyl and acetyl. Among all the known mycotoxin biosynthesis routes, the aflatoxin gene cluster is notable for having the greatest number of cytochromes P-450 [107].

Table 2. This table provides a brief overview of the common fungal genera and the food products they are known for damaging. Fungal spoilage can vary depending on the environmental conditions, storage practices, and specific strains of fungi involved.

Fungal Genera	Food Products Spoiled
Aspergillus	Grains (cereals, rice, corn), nuts, fruits (grapes, apples), vegetables (tomatoes, potatoes), dairy products, spices [108]
Penicillium	Cheese (Camembert and blue cheese), cured meats, bread, fruits (oranges and apples), vegetables (onions and carrots), nuts [109]
Fusarium	Grains (wheat, barley, maize), legumes (peanuts and soybeans), fruits (bananas), vegetables (tomatoes and cucumbers) [110]
Alternaria	Fruits (apples, citrus fruits), vegetables (tomatoes, carrots), cereals (wheat), nuts [111]
Mucor	Fruits (strawberries), vegetables (cucumbers, zucchinis), bakery products (bread, cakes), dairy products (cheese) [112]
Rhizopus	Fruits (apricots and peaches), vegetables (e.g., tomatoes), bakery products (e.g., bread), dairy products (e.g., cheese) [113]
Botrytis	Fruits (grapes, strawberries, raspberries), vegetables (tomatoes, lettuce), grains (rice) [114]
Cladosporium	Fruits (citrus fruits), vegetables (tomatoes and cucumbers), grains (wheat), dairy products (cheese) [115]
Geotrichum	Dairy products (soft cheeses and yogurt), fruits (grapes), vegetables (carrots), bakery products (bread and cakes) [116]
Candida	Dairy products (cheese, yogurt), fruits (apples and grapes), bakery products (bread and cakes), alcoholic beverages (wine and beer) [116]

2.5.3. Ochratoxin A

Ochratoxin A can be found in grains, dried fruits, coffee, and wine and also among other agricultural goods worldwide. It is considered a naturally occurring foodborne mycotoxin. Numerous fungi (Table 2), with varying ideal growth temperatures and water activities, produce it, infecting a variety of food and feed products [117]. Inadequate agricultural practices during food drying and inadequate product storage are the main causes of contamination [118]. Consequently, traditional food-processing methods are unable to significantly lower its content in meals and drinks. In 1965, ochratoxin was identified and described as a chemically stable substance. Ochratoxin A is the most prevalent among the OTAs, a class of structurally similar isocoumarin derivatives connected to L-phenylalanine. Ochratoxin A is hepatotoxic and nephrotoxic [101]. Numerous health issues might arise from animals and humans being exposed to OTA on a regular basis. OTA and other mycotoxins typically affect humans through a number of pathways, the most significant of which is food consumption. Ochratoxin A may cause cancer in animals, but it is unclear whether it causes cancer in people. Urinary tract cancers associated with human Balkan endemic nephropathy (BEN) are thought to be mostly caused by OTA [119]. At the moment, it is uncertain how OTA causes cancer. When oxidative metabolism occurs, OTA is genotoxic [120]. This process, which has two distinct mechanisms of action—direct (covalent DNA adduction) and indirect (oxidative DNA damage)—is thought to be crucial to the development of cancer. According to a relatively recent risk assessment of OTA [121], the OTA-DNA adduct levels were low and unusual for genotoxic carcinogens, and OTA tested negative in genotoxicity tests with good specificity. With one notable exception, our analysis of the epidemiological data indicates that there does not seem to be any statistically significant evidence linking OTA exposure to dangers to human health [117]. Based on case-control studies, the one exception relates to the elevated risk of renal syndrome with very high OTA exposures.

2.5.4. Fumonisins

The secondary metabolites that cereal-pathogenic fungi create are called fumonisins. Although certain other *Fusarium* species may also create them, *Fusarium verticillioides* and *Fusarium proliferatum* are the principal producers of them (Table 1). The fungus species that has historically been linked to fumonisins is *Fusarium moniliforme*; however, due to developments in taxonomy and nomenclature, this term is no longer in use. Fumonisins come in at least 28 different varieties, the majority of which are categorized as the A, B, C, and P series [122]. The B series includes the most prevalent fumonisin forms, FB1, FB2, and FB3, with FB1 being the most hazardous form that coexists with FB2 and FB3 [123]. FB2 and FB3, on the other hand, are dehydroxylated derivatives of FB1, which is a diester. Although fumonisins are present in many cereals and cereal products, they are most frequently found in peanuts and grapes, as well as in maize and products derived from it (rice, wheat, barley, corn, rye, oats, and millet) [124]. Every single year, mycotoxins cause enormous financial losses in the agricultural and industrial sectors by infecting 25% of harvested crops. These mycotoxins are not eliminated due to food processing, cooking, roasting, baking or pasteurization as they are stable. A lack of agricultural resources, combined with post-harvest practices such incomplete drying methods, handling protocols, improper packaging materials or methods, and also transportation and storage conditions, increase the risk of fungal growth and fumonisin contamination [125]. The main health risks linked to fumonisins are leukoencephalomalacia, an acute toxic impact in horses, the syndrome of pulmonary edema in pigs, and possible carcinogenic consequences in people, experimental animals, and nephrotoxicity [101]. Consuming fumonisin-contaminated corn is linked to an increased risk of esophageal cancer and neural tube birth abnormalities. The Joint FAO/WHO Expert Committee on Food Additives has set a provisional maximum tolerated daily intake of 2 μg/kg bw/day for FB1, FB2, and FB3, alone or combination. FB1 is categorized as a “2B” carcinogen by the International Agency for Research on Cancer. The European Union set maximum fumonisin limits for human consumption in cereals and cereal-based foods in 2007 (EC

N°1126/2007) [126], but wheat and wheat-based foods have not yet received their own set of regulations [124]. Fumonisins, in contrast to other mycotoxins, are known to be heat stable and to only become affected by temperatures lower than 150–200 °C when used in food-processing methods such as baking, roasting, frying or extrusion cooking. During heat treatments, FB1 reacts with reducing sugars and forms strong covalent bonds. The degree of toxicity depends on the cooking conditions and the food matrix composition [127]. Wet milling of cereals causes the reduction of fumonisins to some extent, while dry milling of cereals causes a negligible decrease in the content of fumonisins as they are incorporated in the germ and pericarp in higher concentrations than in the endosperm and its derivatives. In order to make the resulting fractions (fiber, gluten, germ, and starch) fit for ingestion by humans and animals, additional industrial milling operations drastically lower the fumonisin level [128]. Still, industrial processing techniques like baking, frying, and extrusion cooking work well to drastically lower the fumonisin levels. Food and feed contamination with fumonisin poses a major risk of global disease outbreaks. Food contamination from fumonisins can be reduced by a variety of methods, including genetic engineering, biochemical, and physical methods [129].

2.5.5. Patulin

One common mycotoxin in fruit products is patulin, which is mostly present in apples and other fruit-based goods. According to recent research, PAT is frequently found in fruit products. Over the past four years, the PAT levels in meals within the European Union (EU) have mostly stayed below the regulation limits, despite the substance's ubiquitous prevalence. Nevertheless, a few products tested in the Czech Republic showed levels of 122 μg/L in apple juice, 231 μg/L in pears, and 56 μg/L in mixed fruit juices beyond these limits. In many European countries, thorough tests have been carried out for the presence of patulin. In a percentage greater than 20%, this mycotoxin was detected in the samples, indicating that the public are regularly exposed to low dosages of this mycotoxin [130]. Once tested as a possible cold remedy, patulin is a low-molecular-weight lactone hemiacetal with broad-spectrum antibacterial properties. Although it might not cause cancer, patulin is thought to be mutagenic. Additionally, negative effects on the developing fetus have been observed in animal testing [131]. Although classified as a non-carcinogen, patulin has been associated over the past few decades with adverse neurological, gastrointestinal, and immunological effects, primarily causing damage to the liver and kidneys [132].

2.5.6. Zearalenone

Zearalenone is a mycotoxin produced by certain species of a fungi called *Fusarium*. The members of this genus are commonly found in agricultural products, including grains, particularly maize (corn), wheat, barley, and sorghum [133]. This toxin poses a significant concern in animal feed and human food due to its estrogenic properties, meaning it mimics the effects of the hormone estrogen in living organisms [134]. Exposure to zearalenone can occur through ingestion of contaminated food or feed, leading to various health issues in animals and potentially in humans [135]. In farm animals, especially pigs, zearalenone consumption can result in reproductive problems such as swollen vulvas, vaginal prolapse, and infertility, ultimately affecting livestock production. Moreover, zearalenone contamination in food products intended for human consumption raises concerns about its potential health effects. Although acute toxicity in humans is rare, chronic exposure to zearalenone through contaminated food has been associated with hormonal disruptions and reproductive disorders [136].

2.5.7. Mycotoxins Toxic Levels

Aflatoxin is very toxic at low levels [137], while patulin, although less potent, can still pose health risks at higher concentrations, particularly affecting the gastrointestinal system [138]. Ochratoxin A is toxic even at low levels, primarily targeting the kidneys and exhibiting carcinogenic properties. Fumonisins are toxic at moderate levels and are linked to esophageal cancer and neural tube defects [139]. Zearalenone is toxic at low to moderate levels, acting as an estrogen mimic and disrupting reproductive systems in humans and animals [134].

2.5.8. Why Fungi Produce Mycotoxins

Fungi produce mycotoxins for several reasons, although the exact motivations are not entirely understood. The following are some key theories and factors. Defense Mechanism: Mycotoxins may serve as a defense mechanism to protect the fungi from other microorganisms, such as bacteria, viruses, and competing fungi [140]. By producing toxic compounds, fungi can inhibit the growth of these potential threats and secure their own survival and ecological niche. Competition: In the competitive environment of soil and decaying organic matter, mycotoxins may provide a competitive advantage by suppressing the growth of other organisms vying for the same resources [141]. This can help fungi outcompete other microbes and establish dominance in a particular ecological niche. Regulation of Fungal Growth: Some mycotoxins might play a role in the regulation of the fungi's own growth and development. They can act as signaling molecules or influence the fungal lifecycle, including spore formation and germination [142]. Secondary Metabolism: Mycotoxins are secondary metabolites, which means they are not directly involved in the primary growth, development, or reproduction of the fungi. The production of secondary metabolites, including mycotoxins, can be a by-product of the fungi's metabolic processes [143].

2.5.9. Solutions for Fungal Toxins

Owing to the negative consequences of mycotoxins, a number of methods have been developed both to stop mycotoxigenic fungus from growing and to clean up contaminated food and animal feed. These tactics include the following:

- Prevention from mycotoxin contamination

Mycotoxin contamination can occur at various stages of the food production process: in the field area before harvest, during harvesting, or during the storage and processing of the food. Hence, methods to prevent mycotoxin contamination can be categorized into pre-harvest, harvesting, and post-harvest strategies. However, preventing mycotoxin contamination before or after harvest is not always feasible, necessitating decontamination before using such materials for food and feed purposes. In recent years, more and more techniques have been developed to prevent the growth of fungi in food during storage and processing, such as the fortification of foods with vitamin C and the use of microwave-assisted thermal sterilization system [144]. Also, mature sterilization techniques such as ultra-high-temperature instantaneous sterilization (UHT), high hydrostatic pressure sterilization (HHP), ultrasound sterilization, cold plasma sterilization, and irradiation sterilization (IS) have very good results in food processing, preventing the growth of fungi in a very effective way [145].

- Detoxification of mycotoxins present in food and feed

A number of detoxifying procedures are essential for limiting exposure to mycotoxins' harmful and cancer-causing properties. Usually, detoxification entails the physical, chemical, or biological removal of contaminated goods or the inactivation of any toxins contained in these goods. Nevertheless, the European Union forbids the use of chemical detoxification processes and the mixing of tainted goods with high-quality ones. The Food and Agriculture Organization (FAO) states that the following requirements must be met by any decontamination method that aims to lessen the harmful and financial impact of mycotoxins: mycotoxins need to be eliminated, inactivated, or destroyed. It cannot cause harmful, cancer-causing, or mutagenic residues to form in the finished goods or in food items derived from animals given clean feed. The product's attractive physical and sensory qualities should not be negatively impacted. Under ideal circumstances, it must be able to eliminate fungus spores and mycelium in order to stop the production of mycotoxin. Both economically and technically, it must be possible.

- Inhibition of mycotoxin absorption in the gastrointestinal tract

Adding non-nutritional adsorbents to the meal to bind mycotoxins in the gastrointestinal tract and lower their bioavailability is one of the newest strategies for reducing mycotoxicosis in cattle. The most commonly researched adsorbents with a high affinity for mycotoxins are activated carbons (ACs), hydrated sodium calcium aluminosilicate (HSCAS), zeolites, bentonites, and certain clays [146]. Adding adsorbents to feeds is a common technique to protect animals against mycotoxins.

2.5.10. Recent Mycotoxin Outbreaks

Recent mycotoxin outbreaks have been notable for their widespread impact on various agricultural products across different regions. In North America, a 2024 survey revealed a significant presence of multiple mycotoxin groups in corn samples. For instance, the occurrence of fumonisins in US corn increased from 2022 to 2023, and zearalenone saw a sharp rise [147]. In Ethiopia, recent assessments highlighted serious mycotoxin contamination in key export commodities such as red pepper, soybean, and sesame. This has prompted calls for coordinated efforts to improve food safety practices and mitigate the risks associated with mycotoxins like aflatoxin and ochratoxin, which pose severe health risks, including liver damage and increased cancer risk [148]. In June 2016, an unidentified disease outbreak was reported among several families in two regions of central Tanzania. To address this, a swift epidemiological survey was carried out in the impacted villages, including an in-depth house-to-house survey of selected households. It was found that the likely source of the illness was homegrown maize. Analysis showed that the illnesses were linked to the consumption of food contaminated with high levels of aflatoxins [149]. Mycotoxins are a significant issue for both food safety and feed safety. Mycotoxins can contaminate food crops such as cereals, nuts, spices, dried fruits, apples, and coffee beans. Consumption of contaminated food can lead to various health issues in humans, including acute poisoning, liver cancer, kidney damage, immune system suppression, and reproductive disorders. Aflatoxins, ochratoxins, and fumonisins are among the most dangerous mycotoxins affecting human health. Mycotoxins also contaminate animal feed, posing risks to livestock health. Animals that consume contaminated feed can suffer from reduced growth rates, lowered immune response, reproductive problems, and even death in severe cases [150]. Mycotoxins like aflatoxins, zearalenone, and deoxynivalenol (DON) are particularly harmful to animals. Contaminated feed can also indirectly affect food safety. Animals that consume mycotoxin-laden feed can accumulate toxins in their tissues, which can then transfer to humans through meat, milk, and eggs [151]. Both food and feed contamination with mycotoxins lead to economic losses because of reduced crops, increased veterinary and medical costs, and loss of trade due to non-compliance with safety regulations. Mycotoxins, generated by fungi on seeds and feed, pose a significant threat to animal and human health and can compromise the quality of agricultural products [152].

3. Future Insights: Current Trends, Prospects, and Potential Directions

3.1. Current Trends and Future Directions

During the last century, there has been a significant increase in agricultural production in order to meet the rapidly increasing global population. Foods rich in protein and nutrients, cultivated from microorganisms like fungi (including filamentous fungi and yeast) and bacteria, have captured the interest of the consumers due to their health benefits [153]. These organisms have exhibited numerous favorable attributes when involved in the production of food. The by-products of fungi have also received significant attention from researchers [7]. Although numerous fungal species have already been discovered, only a few are currently utilized in the food industry. These same species are repeatedly exploited to assess the potential benefits offered by fungi. It is imperative to explore additional new fungal species possessing novel beneficial properties [7]. Recent studies highlight the potential of fungi in food production and processing, emphasizing their significance in meeting nutritional needs and addressing global food challenges. It can be concluded that fungi offer prospects for the development of dietary food and supplements that can contribute to improving human health. The applications of fungal antioxidants extend to both food preservation and the mitigation of oxidative stress in the human body, yielding positive outcomes for various diseases, such as cancer. Although there are not many studies regarding the in vivo antioxidant activity of the metabolites of filamentous fungi and their utilizations, further investigation is required in order to enhance human health.

3.2. Future Prospects and Potential Directions for Further Exploration

3.2.1. Filamentous Fungi and Mycoprotein: Innovations in Meat Substitutes

Filamentous fungi have been used in the food industry for many years due to their potential to produce various enzymes like amylase, cellulase, xylanase, lipase and protease [154–156]. As a result, there has been longstanding interest in using these fungi for various applications, with both producers and consumers showing interest in innovative food products. Additionally, the food market has become increasingly complex and there has been a rapid pursuit of meat alternatives. Consumers of meat substitutes are particularly concerned by the nutritional impact and environmental implications of these substitutes. Nowadays, the inclusion of meat as a food product has proven to be harmful for the environment due to the ineffective utilization of land and water during meat production [157,158]. However, the development of different substitutes for meat is still in the initial phase of research, while fungi as a potential future meat substitute offer promising opportunities [159]. Various fungal species are utilized to produce different foods and fermented products [44]. During recent years, research has focused on the proteins that can be derived from fungi (known as mycoprotein) using various types of filamentous fungi (*Rhizopus oryzae*, *Aspergillus oryzae*, *Neurospora intermedia* and *Monascus purpureus*) [2,160–162]. Filamentous fungi are also preferred due to their rapid growth [7]. This type of fungi is a rich source of mycoprotein that can be processed and utilized as human food as substitutes for meat. The fibrous texture of the mycelium, which resembles the texture of meat, makes filamentous fungi a suitable candidate for the production of meat substitutes [163]. Often, mycoproteins are combined with other agents like egg albumin in order to achieve a texture resembling that of meat [160]. Mycoproteins possess favorable nutritional values and functional properties, rendering them a potentially viable substitute for conventional animal proteins in the food industry [164]. The consumption of mycoprotein has been associated with improved muscle protein synthesis and cardiometabolic markers, suggesting its potential inclusion in future dietary guidelines [33]. Notable advancements in this field include the commercialization of mycoprotein, such as Quorn, recognized as a powerhouse component with reduced fat and calorie content, increased fiber content, and favorable taste and texture. The integration of fungi into food biotechnology is poised to undergo greater advancements in the future. Mycoprotein can be a very good solution as a dietary component that can sustain protein synthesis rates comparable to omnivorous diets [165] and enhance metabolism in good health [166,167]. Mycoproteins have demonstrated a positive impact as a substitute for meat; however, the challenge is to produce these proteins in a manner that is cost-effective [2,168,169]. Sar et al.'s study [162] used a variety of fungal strains (*Rhizopus oryzae*, *R. oligosporus*, *R. delemar*, *Aspergillus oryzae*, and *Neurospora* intermedia) to evaluate the synthesis of fungal biomass from edible potato protein liquid, which is formed during starch production procedures. It was shown that 53% of the fungal biomass produced on an industrial scale by *R. delemar* was crude protein. Given its protein and fatty acid profiles, which include 41% essential amino acids and 33% polyunsaturated fatty acids, this fungal biomass from *R. delemar* shows potential as a raw material for feed and food production. Similarly, [168] looked at employing *Rhizopus oryzae* to produce fungal biomass and found the best aeration rates to obtain a high protein content. Extensive research and development regarding the related manufacturing unit operations will unavoidably be needed for any new product that is envisioned. Recently, there has been a lot of interest in the food industry's use of three-dimensional (3D) printing to improve and/or enhance the texture and nutritional qualities of both new and existing food products. For example, information about crucial material properties and operating parameters for the 3D printing of foods derived from fungi is still mostly lacking in the scientific literature [33].

3.2.2. Solid-State Fermentation: A Promising Method for Fungal-Derived Food Production

A method that offers opportunities for the controlled production of various fungal-derived products is solid-state fermentation (SSF). SSF is the cultivation process in which microorganisms grow on solid materials without any presence of free liquid. It is considered a promising and innovative technique for efficient food production enzymes with reduced wastewater and contamination compared to submerged fermentation (SmF) [17]. Current tendencies in the exploration of SSF involving fungi are of paramount importance in the context of agricultural practices. The fermentation substrate is expanding beyond agro-industrial waste. Fungal SSF can enhance the nutritional profile and bioaccessibility that most crops and their by-products contain. Studies have shown that these proteins enable the production of better-quality crops. According to the same studies, edible fungi have a higher content of protein and a more desirable amino acid composition. The advantages that edible fungi have in comparison to general fungi are making them a possible source of food substitutes [170]. Furthermore, the substrates include various crops such as legumes and cereals, extracts such as plant proteins and starches, and concentrates like flour [171–173]. Moreover, it is noteworthy that the majority of end products derived from SSF, particularly filamentous fungi, *Saccharomycetes* and edible fungi, are devoid of toxins and considered safe for both animal and human consumption [174]. Consequently, the utilization of edible fungi in SSF has emerged as an innovative approach in the food industry [175]. Therefore, it is highly preferable to employ white-rot fungi, brown-rot fungi, and soft-rot fungi capable of degrading lignin, cellulose, and hemicellulose [176]. Enzymes derived from fungal SSF find extensive utilization in the food industry, actively participating in numerous biotransformation processes [177]. As a class of proteins possessing specific activities, industrial enzymes represent one of the most commercialized products of SSF. Chilakamarry et al. [178] summarized details regarding the primary enzyme products of SSF by encompassing α-amylase, amylase, lipases, β-galactosidase, protease, and others. Furthermore, enzymes play a crucial role in non-protein active substance production. Notably, in the SSF of oat with *Monascus anka*, a strong correlation was observed between the enzyme activities and phenolic release [179,180]. Moreover, the SSF of crops and their by-products using fungi to obtain protein resources is considered the next frontier of the food industry [170,181]. Future research endeavors should focus on the integration of SSF with emerging technologies, requiring heightened efforts in this regard. Contemporary approaches have proven successful in evaluating the impact of fungi-derived additives on the sensory properties and quality of food. Novel strategies are available in order to increase the production of fungi metabolites that involve direct genetic manipulation with the use of genetic tools (CRISPR-Cas9 and gene recombination), [182]. CPRISPR-Cas9 has presented advanced characteristics in SSF products [177,183]. The implementation of metabolic and genetic methods in order to enhance the industrial-scale production of fungi is imperative due to the inability of wild-type strains to synthesize desired proteins on a large scale. The gene expression of α-galactosidase in the fungi *Aspergillus niger* was significantly improved through the utilization of GlaA in comparison with the natural signaling peptide [184]. Additionally, recent advancements have enlightened the biosynthesis of important mycotoxins [161]. In this context, the advancement of genetic engineering has the potential to facilitate the production of mycotoxin-degrading enzymes with efficiency and cost-effectiveness, thereby enabling the concurrent degradation of multiple mycotoxins. Additionally, 3D printing technology incorporated into SSF technology has allowed the modification of various traits of food products, like their textures, colors, shapes, and sizes [185].

3.2.3. Advanced Approaches to Mitigating Post-Harvest Diseases and Food Waste Using Fungi

Meanwhile, post-harvest diseases induced by fungi remain one of the primary issues leading to food waste. Current research efforts are focusing mostly on advanced approaches to mitigate these losses, including investigation of utilizing various biocontrol agents derived from fungi to address post-harvest crop diseases and increase the life of agricultural products. The use of antagonistic yeasts has developed as a potential method to reduce the fruit spoilage caused by mycotoxin-producing fungi [164]. Extensive research in this field has focused on the enzymes of various antagonistic yeasts due to their remarkable ability to adsorb and biodegrade mycotoxins. Antagonistic yeasts show very good results in the biodetoxification of products derived from fruits. In recent years, competitive fungi have been increasingly used instead of chemical methods. In this way, the reduced growth of saprophytic fungi and degradation of mycotoxins is achieved [186]. As a result, antagonistic yeasts and their antifungal mechanisms have gained significant recognition. Integrated disease management approaches can enhance the biocontrol activity either synergistically or additively. To address potential variations in the efficacy of antagonistic yeasts, they can be utilized in synergy with other yeasts, bacteria, bioagents, and physical processes. Various combinations of processes and agents have been explored to enhance the efficiency of antagonistic yeasts. UV-C irradiation, for instance, has been tested as a method to prevent fungal diseases in fruits [187]. A study by Sun et al. [188] has shown that UV-C irradiation improves the quality of fruits by increasing the activity of antioxidant enzymes and reducing mycotoxins. Another study, where a combination of UV-C treatment with *Pichia cecembensis* as an antagonistic yeast was used, indicated the control of post-harvest decay in melons [187]. Consequently, further research is necessary to understand the biochemical mechanisms underlying the detoxification pathways and evaluate the by-products of detoxification. This deeper understanding will inform more effective strategies for food preservation and safety [186]. Concurrently, research is underway to explore how fungi can be utilized for reducing food waste by decomposing the inedible parts of crops. Efforts are being made to develop novel food products from recycled stale bread and brewing residues, thereby promoting circular economy models [189].

3.2.4. The Future of Fungal Foods: Innovations and Environmental Benefits

Fungi have garnered considerable attention from a research perspective. The perspectives of novel foods and ingredients from fungi are of great interest for future exploration [37]. The emergence of fungal by-products as a novel discovery in the field of food biotechnology has undoubtedly benefitted mankind. Novel insights into the development of dietary supplements based on fungal compounds and their significance hold promise for future research and advancements. Future research should prioritize the incorporation of industrial practices in order to enhance the production of bio-proteins derived from by-products of the food industry. Additionally, the creation of new food products must be accompanied by considerations of the environment and nutrition, focusing mostly on quantifying the advantages and disadvantages to both the environment and human well-being. Addressing these challenges is of utmost importance as the advancement of microbial food holds potential in mitigating environmental crises [190,191]. Fungal food, which have a well-established record of safe consumption, present possible solutions by exhibiting a reduced environmental impact when compared to conventionally cultivated crops and livestock products [192]. This emphasizes the significance of ongoing and future research endeavors in shaping a sustainable and resilient food system from fungi.

4. Conclusions

In conclusion, the multifaceted role of fungi in the food industry emerges as a cornerstone of innovation and sustainability. Through their capacity to produce a plethora of enzymes, fungi offer versatile solutions for enhancing food production and processing, catering to the evolving demands of both producers and consumers. Particularly noteworthy is the potential of fungi as meat substitutes, with mycoproteins showcasing promising characteristics akin to conventional meat while offering environmental and nutritional advantages. Solid-state fermentation (SSF) stands out as a promising technique for efficient enzyme production, expanding beyond agro-industrial waste to enhance the nutritional profile of crops and by-products. Biotechnological advancements, including genetic engineering and metabolic methods, offer avenues for optimizing fungal-derived products and enhancing food production efficiency. Moreover, biocontrol strategies employing antagonistic yeasts present effective measures for mitigating post-harvest crop diseases and reducing food waste. Embracing circular economy models, fungi exhibit potential in transforming inedible crop parts into novel food products, promoting sustainability and resource utilization. Looking ahead, the exploration of novel foods and ingredients from fungi holds significant promise, necessitating further research to integrate industrial practices, consider environmental and nutritional implications, and address global food challenges. Through concerted efforts, fungal biotechnology stands poised to drive innovation, sustainability, and health in the food industry.

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