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Fusarium-based mycoprotein: Advancements in the production of sustainable meat substitutes

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ABSTRACT

Background: Pursuing sustainable and nutritious food has positioned *Fusarium*-based mycoprotein as a promising solution to the environmental and health challenges posed by some traditional agricultural practices and types of food. As consumer awareness grows and the demand for alternative proteins increases, *Fusarium* species offer a scalable, environmentally friendly, and nutritious option to address these issues.

Scope and approach: This review delves into the unique characteristics of certain *Fusarium* species, which make them ideal candidates for mycoprotein production. It explores advancements in fermentation technologies, metabolic engineering, and process optimisation that have; enhanced production efficiency and product quality. The review also examines the technical, economic, and regulatory challenges hindering large-scale production and commercialisation, such as the high costs of fermentation, the need for robust; regulatory frameworks, and consumer acceptance. Furthermore, it highlights the significance of interdisciplinary collaboration and continuous innovation to overcome these challenges and unlock the full potential of *Fusarium*-based mycoprotein.

Key findings and conclusions: By synthesizing recent research and market trends, this review provides a comprehensive understanding of the potential of *Fusarium*-based mycoprotein to contribute to a sustainable and resilient food system. It emphasizes the need for targeted research, streamlined production processes, and strategic partnerships to advance its development and adoption, ultimately shaping the future of sustainable nutrition.

1. Introduction

1.1. Feeding the increasing global population sustainably

Meat is a critical component of daily diets, providing essential proteins, vitamins, and minerals for balanced nutrition (Majeed et al., 2024). However, excessive consumption of certain types of meat, especially processed and red meat, is likely associated with adverse health effects and contributes to climate change (Klurfeld, 2018). With the global population projected to reach 9 billion by 2050 (Chesnaye et al., 2024), the demand for meat, especially in rapidly developing economies, is expected to skyrocket. Given meat's critical role in human diets, reducing its demand is nearly impossible, necessitating the development of sustainable meat alternatives (Kumar et al., 2023).

Research has increasingly focused on alternatives such as cultured meat, plant-based substitutes, macroalgae, insects, and single-cell proteins (SCPs) based on microorganisms. These innovations address health and environmental challenges while meeting the rising global demand for meat products (Hadi & Brightwell, 2021). The high demand for microbial proteins, as evidenced by the proliferation of companies such as Quorn (Marlow Foods) (https://www.quorn.co.uk/), Nature's Fynd (https://www.naturesfynd.com/), Adamo Foods (https://www.adamofoods.com/), Better Meat Co. (https://www.bettermeat.co/), Enough (https://www.enough-food.com/), Mycotechnology (https://www.mycoiq.com/), Aqua Cultured Foods (https://www.aquaculturedfoods.com/), Mush Foods (https://mush-foods.com/), Mycorena (https://mycorena.com/), Mycovation (https://www.mycovation.asia/) and Infinite Roots (https://www.infiniteroots.com/process/),

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underscores the growing interest in this field (Table S1) (Banach et al., 2023).

SCPs are derived from microbial sources, either as biomass or extracted protein. Various microorganisms such as bacteria (e.g., *Rhodobacter capsulatus*), yeast (e.g., *Saccharomyces cerevisiae*), microalgae (e.g., *Chlorella*), and filamentous fungi (e.g., *Fusarium venenatum*) are utilised in SCP production. Filamentous fungi, in particular members of the genera *Fusarium*, *Aspergillus*, and *Rhizopus,* have received much attention for their environmentally friendly manufacturing processes and robust nutritional profiles, resulting in fungal biomass known as mycoproteins (Amara & El-Baky, 2023).

Mycoprotein derived from certain *Fusarium* species stands out for its high protein and fibre content, as well as its low levels of saturated fats, making it an efficient, relatively low-energy input food source with positive impacts on metabolic markers of health (Coelho et al., 2020). Unlike animal proteins, it contains negligible cholesterol while offering abundant dietary fibre, micronutrients, and biologically active compounds (Jakubczyk & Dussart, 2020).

The versatility of *Fusarium* species extends beyond food production. They produce a wide range of enzymes and secondary metabolites valuable to the food, cosmetics, cleaning, biofuel, and pharmaceutical industries (Pessôa et al., 2017). However, challenges such as low product yields, pathogenicity, and mycotoxin production persist. To address these challenges, optimisation of bioprocess and fermentation technologies, strain improvement, efficient downstream processing, synthetic biology, and stringent regulatory measures are essential. Integrating these approaches could significantly enhance mycoprotein yields, productivity, quality, and sustainability, further increasing its adoption worldwide as an alternative to traditional protein sources (Ibrahim et al., 2021).

This review examines the distinct properties and advantages of *Fusarium* species in mycoprotein production, emphasising their suitability for creating sustainable meat alternatives. It covers the various production methods, detailing their efficiency and the nutritional benefits of *Fusarium*-based mycoprotein. Importantly, the review also delves into the potential applications of metabolic engineering to enhance production and quality. Furthermore, it discusses the associated challenges, providing a holistic view of the obstacles and opportunities in this field. By integrating the latest research findings and industry trends, it aims to present a thorough analysis of the prospects for *Fusarium* species in the realm of sustainable food solutions.

1.2. *Fusarium* species: the history of sustainable protein sources

Fusarium species, such as *Fusarium graminearum*, *Fusarium oxysporum*, *Fusarium solani*, *Fusarium verticillioides*, and *Fusarium proliferatum*, are filamentous fungi within the *Ascomycota* division. They were first identified by Link in 1809 and can be distinguished by their unique canoe- or banana-shaped conidia (Leslie & Summerell, 2006). The genus comprises as many as 300 different species with varied morphological, physiological, and ecological features, making its taxonomy particularly complex (Munkvold, 2017). Commonly found as saprophytes in soil, many *Fusarium* species, such as *F. oxysporum, F. graminearum* and *F. solani,* are also notorious plant pathogens that can inflict substantial economic damage to cereal, fruit, legume and other arable crops (Munkvold, 2017). In addition, many species can cause toxicosis in humans and animals, and there are rare but increasingly reported cases of opportunistic human infections (Munkvold, 2017).

At the end of World War II, Europe faced significant challenges in restoring prewar food production and security levels. By the mid-1960s, Lord Rank of the Rank Hovis McDougall (RHM) group sought innovative solutions to address perceived future global protein shortages. The goal was to convert abundant starch, a by-product of cereal production, into protein, which was considered to become an ever more scarce resource. Initial attempts using environmental selection for fungi preferentially metabolising starch led to the isolation of a *Penicillium notatum* strain. However, it proved unsuitable for growth in continuous culture, which prompted a broader search (Whittaker et al., 2020).

Starch can be hydrolysed into fermentable sugars using enzymes from yeast and moulds. The Symba process in Sweden utilised starchy waste with a sequential mixed culture of *Endomycopsis fibuligira* (amylase producer) and *Candida utilis* (fast grower) (Amara & El-Baky, 2023). Liu et al. (2014) reported a two-step fermentation converting potato starch waste into single-cell protein for high-quality feed (Liu et al., 2014). A mutant strain of *Aspergillus niger H3* enhanced cellulose degradation by 80.5 %, achieving 38 % protein content. *Bacillus licheniformis* was used in a liquid fermentation step to further process the biomass (Amara & El-Baky, 2023).

In 1967, RHM embarked on an extensive screening of over 3000 fungi species worldwide, ultimately identifying *F. venenatum* A3/5 (initially classified as *F. graminearum* A3/5) (Fig. 1) from a compost heap from a garden in Marlow Bottom, Buckinghamshire, just 4 miles from the RHM research facility (Whittaker et al., 2020). This strain emerged as an ideal candidate for mycoprotein production due to its high protein content, desirable texture, lack of mycotoxin production and pathogenicity, and ease of cultivation on starch- or glucose-based media. Over the next 12 years, RHM invested in rigorous safety research to ensure that the organism and its biomass were safe for human consumption. This led to its approval by the UK Ministry of Agriculture, Fisheries, and Food in 1984 (Whittaker et al., 2020).

F. venenatum A3/5 biomass, marketed as Quorn, has since become a significant commercial protein source, offering a sustainable and nutritious alternative to meat in over 20 countries worldwide (Whittaker et al., 2020). Continuous monitoring and testing have ensured that the product remains free from mycotoxins, solidifying its position as a safe and reliable food source. This journey reflects the innovative and persistent efforts required to develop new food sources in response to global food security challenges (Wiebe, 2002). More recently, another *Fusarium* strain has been used by Nature's Fynd (USA) to produce a protein source called Fy protein, which is derived from processed fungal biomass, as seen in *F. venenatum.* The fungus was originally isolated from springs in Yellowstone Park in the USA and was named *F. flavolapis*, and is phylogenetically placed in the *F. fujikuroi* species complex conspecific with certain *F. proliferatum* strains (Furey et al., 2022).

1.3. *Fusarium as a fabricator of biomaterials*

The biotechnological potential of *Fusarium* species lies in their ability to produce a diverse array of enzymes and secondary metabolites, which are valuable across various industries such as the food, biofuel, medical, and pharmaceutical sectors (Bleackley et al., 2020) (Fig. 2). *Fusarium* species are known for producing cellulases, xylanases, and pectinases, which are crucial for degrading plant cell walls and converting lignocellulosic biomass into fermentable sugars. This makes them particularly useful in the biofuel industry for producing bioethanol from agricultural residues (Prasoulas et al., 2020). In the food industry, *Fusarium*-derived enzymes such as lipases and proteases are used to hydrolyse fats and proteins, thus enhancing the production of flavours, fragrances, and other food additives. Additionally, *Fusarium* species produce secondary metabolites such as fusaric acid and gibberellins, which have applications in agriculture as biopesticides and plant growth regulators (Iqbal et al., 2024).

Compared to traditional chemical methods, using *Fusarium* in biotechnological processes offers several advantages, including milder reaction conditions, lower operating temperatures, reduced toxic waste, and fewer emissions and by-products. Their proficiency in extracellular protein production is particularly notable, with applications in producing industrial enzymes and biopharmaceuticals (Ibrahim et al., 2021). Moreover, *Fusarium* species exhibit efficient nutrient absorption and metabolism of various carbon sources, underscoring their versatility and efficiency in fermentation processes. This adaptability allows for optimising fermentation conditions to enhance yield and productivity,

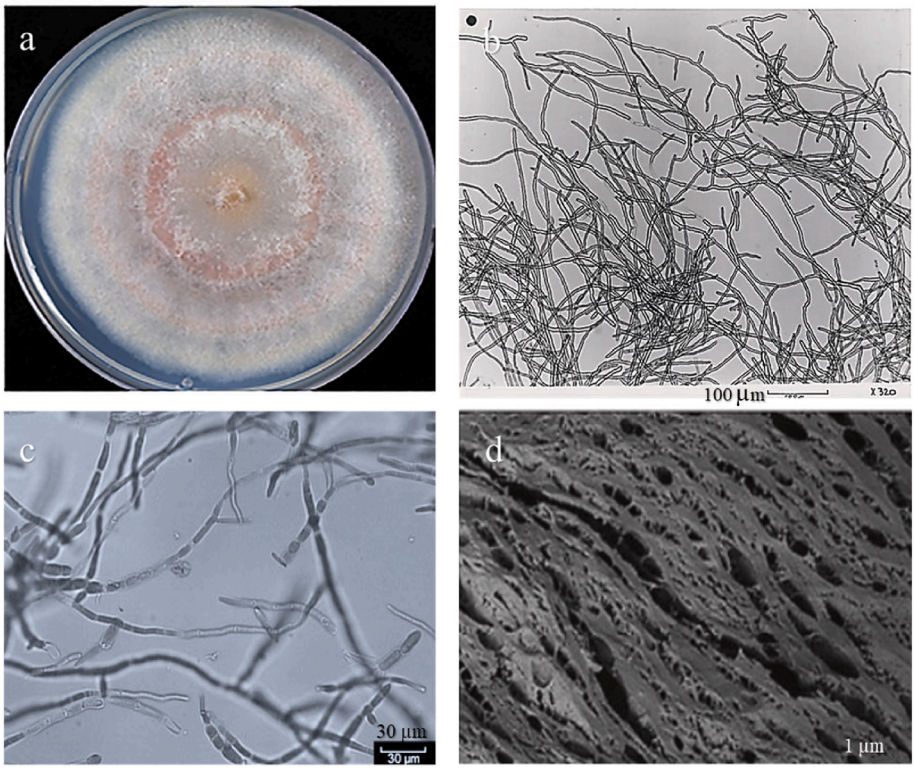

Fig. 1. *Fusarium* culture morphology. a) Macroscopic observation of colony culture *Fusarium* (Cutuli et al., 2015), b) the appearance of *Fusarium venenatum* A3/5 as collected from the outlet of the Quorn fermenter (Ugalde & Castrillo, 2002), c) The filamentous nature of mycoprotein and d) Ice crystal growth on freezing forms highly packed hyphal domains and gives rise to fibrous structure (Ahmad et al., 2022; Finnigan, 2011; Finnigan, Mach, & Edlin, 2024).

making *Fusarium* a promising candidate for large-scale industrial applications (Bleackley et al., 2020).

The diverse enzymatic capabilities and secondary metabolite production of *Fusarium* species, combined with their efficiency and adaptability in various biotechnological processes, make them invaluable across multiple industries. They offer sustainable and eco-friendly alternatives to traditional chemical methods.

2. Fermentation strategies to produce *fusarium*-based mycoprotein

Over the years, submerged fermentation (SmF), surface culture methods (SCM), and solid-state fermentation (SSF) techniques have been utilised for mycoprotein production (Ahmad et al., 2022). SmF involves the growth of microorganisms in a liquid medium rich in carbohydrates under aerobic conditions, allowing precise control of growth conditions. The SCM involves the growth of microorganisms on a solid or semi-solid surface (Gong et al., 2023). SSF involves the growth of microorganisms on solid materials without free-flowing water (Ahmad et al., 2022). The most widely used techniques for mycoprotein production are the SmF and SCM methods (Landeta-Salgado et al., 2021). SmF is the dominant method in commercial production, exemplified by Quorn, which employs airlift bioreactors to optimise oxygen transfer and minimise shear stress, ensuring long hyphal growth for a fibrous, meat-like texture. SmF allows precise control over pH, oxygen levels, and nutrients, leading to high biomass yield and consistent quality. Additionally, its closed-system design reduces contamination risks, making it preferable for large-scale food-grade applications. On the other hand, SCM is a viable alternative, where fungi are cultivated on solid substrates under controlled conditions. Although it enables structured biomass formation with good textural properties, SCM is less economically feasible at an industrial scale compared to SmF, primarily due to higher operational costs and challenges in scalability.

Quorn mycoprotein is produced using continuous SmF processes, offering significant advantages over batch systems by enabling continuous biomass production over extended periods, thereby enhancing efficiency. Initially, the production relied on a 40 m^3 pilot-scale fermenter, yielding 1000 tons annually. The development of 155 m^3 airlift fermentation technology through a joint venture between Imperial Chemical Industries (ICI) and RHM significantly increased the production to 10,000–14,000 tons per year; annual sales reached £74 million by 1997 (Sadh et al., 2018) (Fig. 3).

These Quorn submerged fermenters are among the largest continuous flow culture systems in biotechnology and can be distinguished from conventional stirred-tank bioreactors, which allow mycoprotein to be harvested continuously for more than 30 days (Finnigan, Mach, & Edlin, 2024). The low-shear design in airlift fermenters fosters the development of long hyphal lengths essential for replicating meat-like textures and reduces energy consumption for mixing. Sterile air bubbles achieve oxygen saturation and facilitate mixing; most oxygen transfer occurs at the base of the riser, leveraging hydrostatic pressure and air turbulence. This continuous circulation ensures optimal oxygen levels, promoting rapid fungal growth and making SmF a highly efficient method for mycoprotein production. It has been calculated that *F. venenatum* mycelium circulates around the fermenters at an approximate speed of 4 m/s^{-1} (Whittaker et al., 2020).

Several studies have investigated mycoprotein production by *Fusarium* using submerged fermentation (Table 1). Wiebe (2002) used *F. venenatum* A3/5 to produce mycoprotein in 150,000-L pressure reactors in a continuous flow process utilising glucose and ammonium as carbon and nitrogen sources. Similarly, Ahangi et al. (2008) produced mycoprotein using *F. oxysporum* PTCC 5115 by optimising the fermentation conditions to achieve a high biomass concentration of 8.2 g/L and with a protein yield of 42 % w/w (% dry biomass weight). Prakash et al. (2014) employed statistical designs to optimise medium components to improve the biomass yield of *F. venenatum*. Key factors included

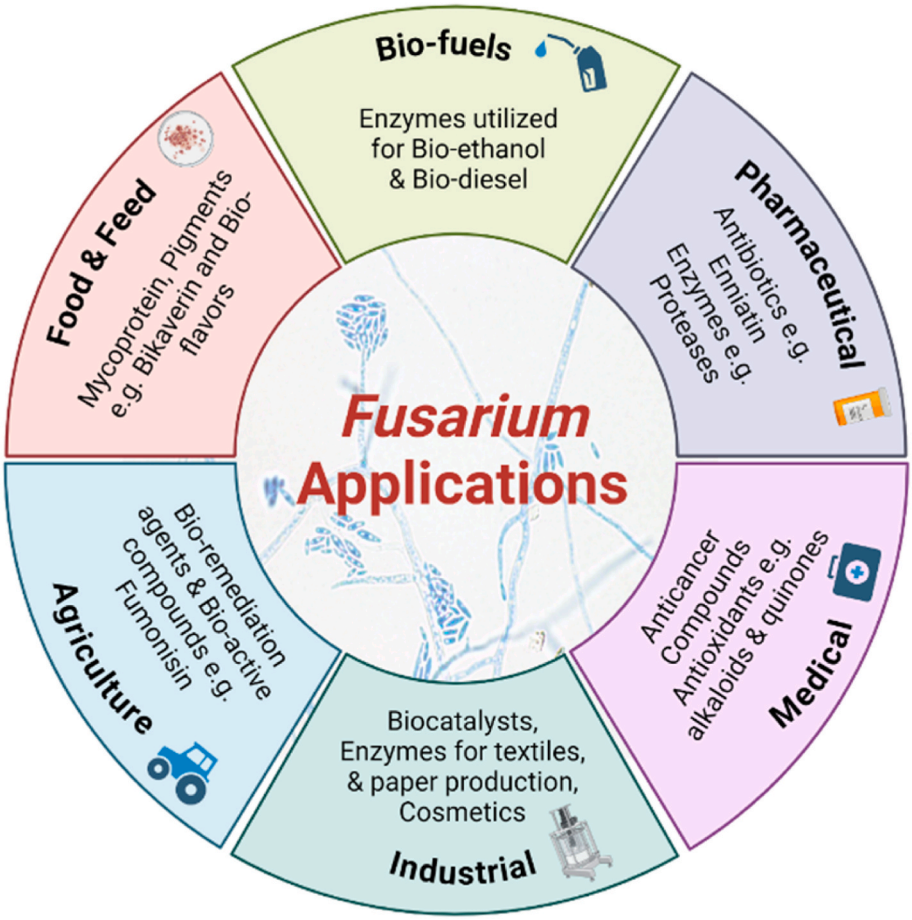

Fig. 2. Diverse applications of *Fusarium* species in biotechnology.

liquefied jaggery, date extract, KH_2PO_4, and K_2HPO_4, achieving a maximum biomass yield of 5.7 g/L and a protein content of 33 % w/w. Souza Filho et al. (2018) investigated the potential of a pea-processing by-product (PpB) as a substrate for producing mycoprotein using various edible filamentous fungi in a bench-scale airlift bioreactor, including *F. venenatum*. The optimised conditions achieved a protein content ranging between 55.3 and 59.8 % w/w. Additionally, Reihani and Khosravi-Darani (2018) utilised *F. venenatum* IR372C to produce mycoprotein from date sugar, achieving an average biomass of 7.2 g/L and 65–76 % w/w protein in a bioreactor.

Few studies have reported the cultivation of *Fusarium* using SCM (Table 1). Hosseini et al. (2009) investigated mycoprotein production using *F. venenatum* grown on a modified Vogel medium with date sugar as the carbon source. They evaluated the effect of various parameters, including medium components, temperature, incubation time, and inoculum conditions, on mycoprotein production. Under these optimal conditions, they achieved a crude protein content of 47.3 % w/w. Hosseini et al. (2010) further studied the effect of process variables on the yield of mycoprotein production by *F. venenatum* ATCC 20334 in surface culture. They aimed to determine the maximum protein production using suitable concentrations of date juice, nitrogen concentration, and seed size. The optimal conditions for mycoprotein production yielded 46.5 % w/w of mycoprotein. Meanwhile, a form of surface fermentation is used in the production of Fy protein by *F. flavolapis*, in which semi-solid fungal biomass is harvested after batch fermentation and then mechanically pressed to remove water, although precise details are lacking (Furey et al., 2022). This leads to a final product with 12 % w/w protein wet weight but between 40 and 50 % amino acid dry weight (Table 1).

These findings highlight that choosing the most appropriate fermentation method, strain selection, and culture conditions is crucial for maximising mycoprotein production. They offer various avenues for optimising and scaling up production processes. The design of new bioreactors is particularly pivotal, as innovative designs can enhance aeration, mixing, and nutrient distribution, ensuring optimal growth conditions for *Fusarium* strains. Consequently, understanding and appropriately manipulating these factors can provide multiple strategies to enhance mycoprotein production, making it possible to scale up the process efficiently for commercial purposes. However, it is important to note that many of the previously mentioned studies did not evaluate potential impacts on mycotoxin production or changes in the amino acid composition of the Fusarium biomass. Nonetheless, certain regulatory frameworks - such as Nature's Fynd's GRAS application - do allow for low levels of mycotoxins in food products, provided those levels remain significantly below the thresholds established for other foods, like cereals (Canton, 2021). It is known that *Fusarium* species can show significantly increased tricothecene production on different carbon sources (e.g. Jiao et al., 2008) and also that amino acid composition can vary according to growth substrate (Szepe et al., 2021). Therefore, there are safety and nutritional concerns to consider when implementing new fermentation, strain and culture conditions (Whittaker et al., 2020). In addition, many *Fusarium* species may be considered inherently unsuitable for mycoprotein production, given the known production of mycotoxins and their roles as animal and plant pathogens (Munkvold, 2017).

2.1. Nutritional properties of fusarium biomass

The nutritional properties of *Fusarium* biomass have been most extensively studied in *F. venenatum* used for the production of Quorn

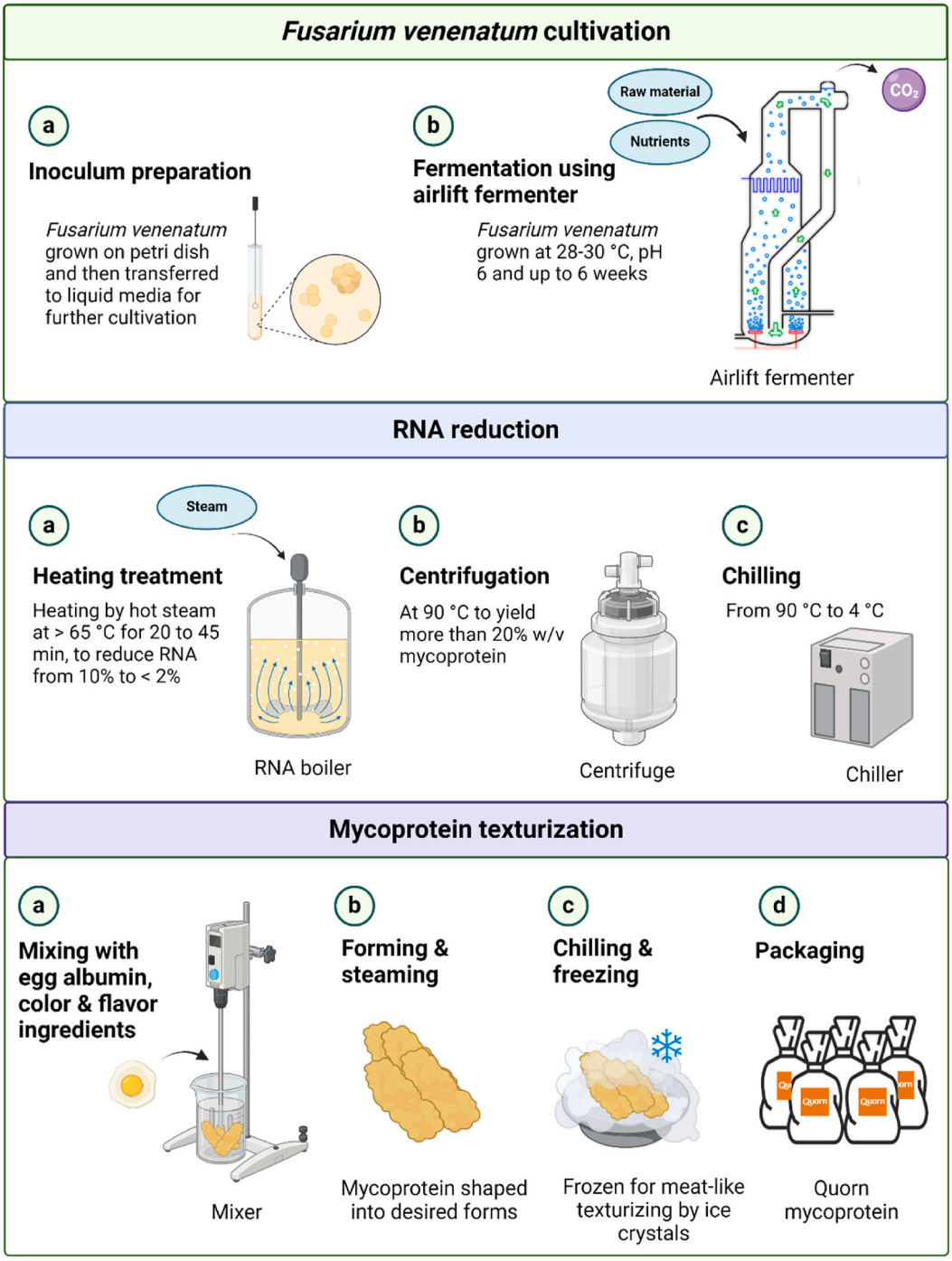

Fig. 3. Schematic representation of the process for Quorn mycoprotein production.

mycoprotein, but also with some comparative studies for *F. oxysporum* and *F. flavolapis*. In the case of *F. venenatum*, the fungal biomass is beneficial for a healthy diet due to its high protein content, elevated fibre levels, and low saturated fat (Fig. 4). Studies have shown that it offers several nutritional advantages, such as enhancing satiety as well as regulating blood sugar and cholesterol levels (Majumder et al., 2024). Prior to processing, the wet weight of *F. venetaum* biomass consists of 11.3 % protein, 6 % fibre, 2.9 % fat, and 3 % carbohydrates, with an energy content of 85 kcal (data from Marlow Foods; Derbyshire & Delange, 2021). It offers a balanced nutritional profile, being lower in calories and fat than beef and chicken while providing more fibre than these traditional protein sources (Fig. 4).

The nutritional profile of *Fusarium* biomass is significantly influenced by the species and strain utilised for its production, which impacts the composition of the amino acids, fatty acids, polysaccharides, minerals and vitamins present in the biomass (Ahmad et al., 2022). Several studies have indicated that *Fusarium* biomass is rich in both essential and non-essential amino acids that are comparable in profile to that of animal protein (Szepe et al., 2021) (Table 2). Notably, *F. venenatum* PTA-2684 (a patent deposit of the original A3/5 strain) exhibits high levels of essential amino acids such as lysine (8.3 % w/w), leucine (8.6 % w/w), and arginine (7.3 % w/w), which are crucial for human nutrition. Lysine supports protein synthesis and tissue repair, leucine aids in muscle growth and blood sugar regulation, and arginine promotes

Table 1
Summary of species, substrates, fermentation conditions, and mycoprotein yields of *Fusarium* strains.

Species	Substrate	Culture type	Cultivation condition	Biomass yield (g/L)	Mycoprotein content (% w/w)	Reference
Fusarium venenatum	Pea-processing by-product (PpB)	Submerged culture	250 mL Erlenmeyer flasks kept in a water bath shaker at 35 °C and 150 rpm for 36h, with and without amylase. The produced fungal mycelium was collected using a sieve, washed with ultra-pure water, and dried at 70 °C.	–	55.3–59.8	Souza Filho et al. (2018)
Fusarium venenatum (ATCC 20334)	Date juice	Surface-culture	Inoculum preparation on Vogel slants with date juice for 30 °C for 3 days. Filtration: after rinsing and oven-drying at 50 °C.	–	46.5	Hosseini & Khosravi-Darani 2010
Fusarium venenatum (IR372C)	Date sugar	Submerged culture	Inoculum preparation on Vogel slants. In the first phase of the study, submerged fermentation was conducted in 500 ml flasks, and a 3l stirred-tank bioreactor was used to perform the submerged fermentation in the second phase. Substrate: date waste. Incubation: at 26 °C with an agitation of 200 rpm for 3 days. Filtration: after rinsing and oven drying at 60 °C.	7.2	65–76	Reihani & Khosravi-Darani (2018)
Fusarium venenatum (ATCC 20334)	Date sugar	Surface culture	Inoculum preparation on Vogel slants. Fermentation was conducted in 500 mL flasks containing 100 mL of production medium. Incubation: 25 °C for 3 days.	–	47.3	Hosseini et al. (2009)
Fusarium venenatum	Date extract	Submerged culture	The fungus was cultivated in 100 ml of Vogel's minerals medium.	5.0	33.0	Prakash et al. (2014)
Fusarium venenatum	Jaggery water, date extract	Submerged culture	Jaggery and dates were dissolved separately in 1000 mL of filtered distilled water, and the collected filtrate was mixed with trial sources of K_2HPO_4, KH_2PO_4, and $MgSO_4$, sterilised by cold sterilisation. After sterilisation, 5 % of inoculum was added and incubated for 72 h under shaking conditions.	5.7	0.6	Prakash et al. (2014)
Fusarium venenatum A3/5	Glucose	Large-scale pressure-cycle reactors in a continuous flow process	Glucose is provided as the carbon source. Ammonium is provided as the nitrogen source. Incubation temperature (28–30 °C) and pH (6.0) are controlled.	2.0–2.3	–	Wiebe (2002)
Fusarium oxysporum PTCC 5115	Glucose	Submerged culture	Inoculum preparation on Vogel medium with 5 % fungal suspension, Glucose 5 g/L, 3.4 g/L $NH_4H_2PO_4$. Incubation: at 25 °C with an agitation of 200 rpm.	8.0	42.0	Ahangi et al. (2008)
Fusarium venenatum CGMCC NO. 20740	Glucose	1 L shake flask and 5 L stirred-tank bioreactor	Fermentation was performed at 29 °C with ventilation at 1 vvm and rotation at 100 rpm for 0−12 h, 200 rpm for 12−24 h, and 300 rpm for 24−72h, respectively. The pH was adjusted to 6.0 by adding a 6 M ammoniacal solution during the experimental period.	10.2	61.9 %	Tong et al. (2023)
F. strain flavolapis	–	Semi-solid fermentation	The medium is prepared using sources of carbon, nitrogen, phosphate, sulfate, chloride, yeast extract, water, and trace metals. Growth is initiated by inoculating the sterilised media with a frozen pure culture isolate. As the medium is consumed during the growth, the semi-solid fungal biomass is formed and physically harvested from the cultivation chamber at the end of fermentation.	–	50.0	Furrey et al., 2022

immune function and wound healing. Additionally, non-essential amino acids such as aspartic acid and glutamic acid are found in significant quantities, with *F. venenatum* PTA-2684 containing 10.3 % w/w of aspartic acid and 12.5 % w/w of glutamic acid (Finnigan, Mach, & Edlin, 2024). These amino acids play vital roles in metabolic processes and neurotransmission. Similarly, *F. oxysporum* has a notable concentration of glutamic acid (17.4 %) and aspartic acid (9.8 %), which further enhances its nutritional profile. Additionally, lysine (6.6 %) and leucine (6.2 %) are present in significant amounts, thus enhancing the protein's nutritional quality (Ahangi et al., 2008). These amino acids are crucial for various metabolic processes and contribute to the overall nutritional quality of mycoprotein. Comparatively, the lysine content of *F. venenatum* (8.3 % w/w) is similar to that found in lean beef (8.1 g/100 g protein) and chicken breast (8.5 g/100 g protein), while its leucine concentration (8.6 % w/w) aligns closely with beef (8.6 g/100 g protein) but is slightly lower than in chicken (9.2 g/100 g protein) (Dohlman et al., 2022). The high glutamic acid content (12.5 % w/w) in *F. venenatum* is also comparable to that found in beef and pork (13–14 % w/w), contributing to the umami taste and nutritional value. Meanwhile, for *F. flavolapis*, glutamic acid (1.4 %) is the most abundant, contributing to flavour and metabolism. Aspartic acid (1.2 %) and valine (1.3 %) are also present at higher levels compared to other amino acids in this strain. In contrast, certain amino acids such as tryptophan (0.2 %), cysteine (0.1 %) and methionine (0.2 %) are found in minimal amounts (Furrey et al., 2022). This limited amino acid profile suggests that *F. flavolapis* may require supplementation or blending with other protein sources to meet specific nutritional requirements.

Comparatively, the nutritional profile of *Aspergillus* and *Rhizopus* species exhibits high protein content but differs in amino acid composition. *Aspergillus oryzae* biomass contains approximately 45–55 % protein, with high levels of glutamic acid, alanine, and proline, making it a flavorful and nutritious source for fermented foods (Hong et al., 2004). However, it has lower lysine and methionine content than *F. venenatum*, which may require supplementation for a complete amino acid profile. *Rhizopus oryzae*, commonly used in tempeh production, has a protein content of around 40 %, with a well-balanced amino acid profile but slightly lower leucine and isoleucine levels compared to *F. venenatum* (Nout & Kiers, 2005). The amino acid composition of *Rhizopus* biomass makes it a viable protein source, particularly in combination with legumes, to ensure sufficient lysine intake.

The fatty acid composition further enhances the nutritional value of mycoprotein. A diverse saturated and unsaturated fatty acid profile exists across different *Fusarium* species and strains (Table 3). For instance, *F. venenatum* PTA-2684 has a low saturated-to-unsaturated fatty acid ratio of 0.10, suggesting a higher proportion of health-beneficial unsaturated fatty acids (Finnigan, Mach, & Edlin, 2024).

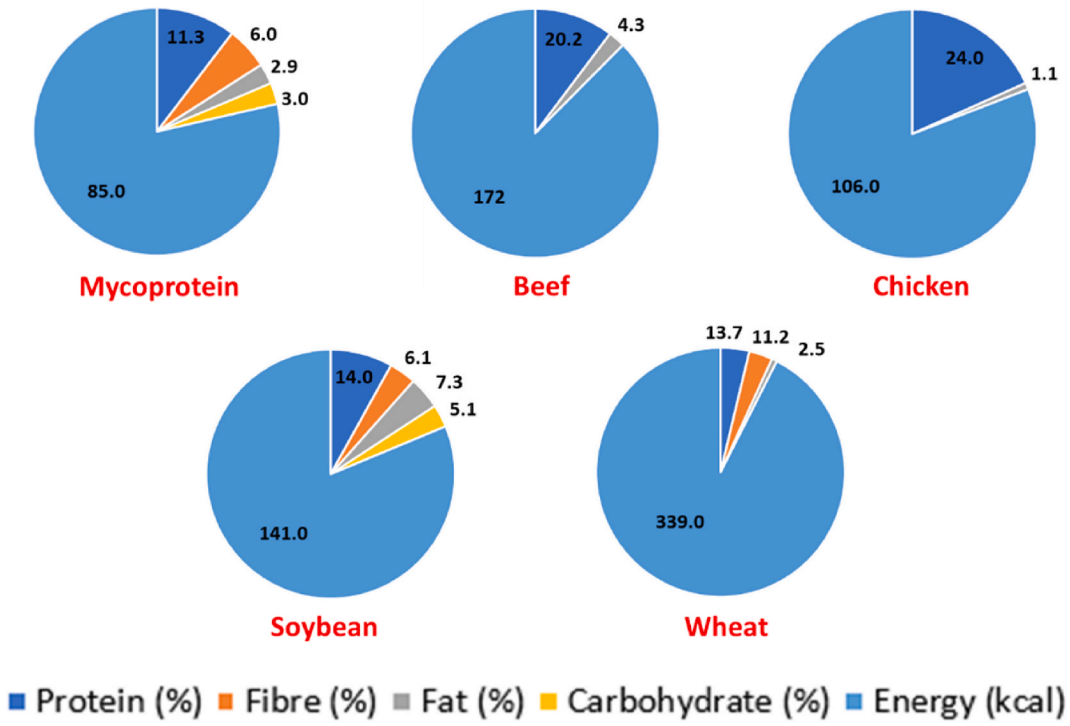

Fig. 4. Nutritional composition of fungal mycoprotein (wet weight) compared to animal meat and plant-based alternatives (Derbyshire & Delange, 2021; Khan et al., 2024). The numbers on the pie charts represent the protein (%, blue), fibre (%, grey), fat (%, orange), carbohydrate (%, yellow) and energy content (kcal, light blue) of each protein source. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

This ratio is similar to that of oily fish such as salmon (0.12) and mackerel (0.15), both of which are known for their high omega-3 content and cardiovascular benefits. Conversely, *F. venenatum* IR372C exhibits a higher ratio of 1.33, indicating a higher presence of saturated fatty acids, although a different growth substrate was used, which might have impacted the fat content and quality (Reihani et al., 2018). This saturated-to-unsaturated fatty acid ratio is more comparable to red meats such as beef (1.2–1.5) rather than fish. Meanwhile, for *F. oxysporum*, the fatty acid profile reveals a balanced composition with a saturated-to-unsaturated fatty acid ratio of approximately 0.35, indicating a predominance of unsaturated fatty acids that contribute to its nutritional benefits (Ahangi et al., 2008). This ratio is close to that of lean fish such as tilapia (0.40) and cod (0.38), suggesting that *F. oxysporum* could be a viable alternative protein source similar to certain fish species. Overall, the data suggests that certain *Fusarium* strains with a lower saturated-to-unsaturated fatty acid ratio could offer enhanced cardiovascular benefits, making them preferable for producing health-optimised mycoprotein.

Analysis of polysaccharide composition has highlighted notable amounts of N-acetyl glucosamine (9.7 % w/w) and glucose (8.8 % w/w) in *F. venenatum* PTA-2684, considered essential for cellular functions and energy supply (Table 4) (Finnigan, Mach, & Edlin, 2024). Analysis of mineral content has revealed a diverse range of essential minerals, including calcium (0.2 % w/w, 0.1 % w/w and 0.3 % w/w) and potassium (0.4 % w/w, 0.1 % w/w and 0.12 % w/w) in *F. venenatum* PTA-2684, *F. venenatum* ATCC 2684 (another derivative of the original A3/5 strain) and *F. flavolapis*, respectively, crucial for bone health, muscle function, and electrolyte balance (Table 5) (Finnigan, Mach, & Edlin, 2024; Saeed et al., 2023). The vitamin profile shows significant levels of riboflavin (9 mg/kg), niacin (14 mg/kg), and pyridoxine (5 mg/kg) in *F. venenatum* PTA-2684, important for energy metabolism, skin health, and cognitive function (Table 6) (Finnigan, Mach, & Edlin, 2024; Saeed et al., 2023). Meanwhile, *F. flavolapis* contains only thiamin (1 mg/kg) and pyridoxine (0.25 mg/kg). Further studies are required to detail its full vitamin spectrum in *F. flavolapis*. These findings highlight the potential of *Fusarium* species as a sustainable and nutrient-rich source for mycoprotein production, offering essential nutrients necessary for a balanced diet.

Comparing the amino acid and fatty acid profiles across different *Fusarium* strains and species overall (Tables 2–6), it is evident that each strain and species can contribute uniquely to the nutritional composition of mycoprotein. The variations in the amino acid and fatty acid, minerals and vitamins compositions of the different strains imply that factors such as fermentation conditions, carbon sources, and downstream processing are crucial in shaping the metabolic pathways of the fungi, thereby affecting amino acid, fatty acid, minerals and vitamins synthesis. Additionally, the nutrient composition of the growth medium, particularly nitrogen and phosphorus availability, can also modulate amino acid production (Whittaker et al., 2020). Moreover, evidence suggests that different sugar sources can alter the amino acid content in *Fusarium* species. Anderson and Solomons (1984, pp. 231–250) compared the total amino acid content in *F. venenatum* when grown on glucose and ribose. They found that cultures fed with ribose showed a reduction in total amino acid content compared with those grown on glucose (394 mg/g and 494 mg/g, respectively) (Whittaker et al., 2020). The observed variation in the amino acid content of *F. venenatum* when grown on different carbon sources, such as glucose and ribose, can be attributed to the organism's metabolic pathways and their efficiency in processing these sugars. Glucose is metabolised through glycolysis and the tricarboxylic acid (TCA) cycle, leading to efficient energy production and the generation of key intermediates necessary for amino acid biosynthesis. In contrast, ribose enters metabolism via the pentose phosphate pathway, which may not supply the same level of energy or precursors required for amino acid synthesis, resulting in a reduced total amino acid content (McGeorge, 2019)."

Beyond its high protein and amino acid content, one of the most significant nutritional advantages of *Fusarium* biomass is its high fibre content, primarily composed of chitin and β-glucans, which are structurally distinct from plant-based fibres (Finnigan, Mach, & Edlin, 2024). Unlike traditional dietary fibres, chitinous fibre has been shown to

Table 2
Overview of the amino acid profiles in mycoprotein from various *Fusarium* species (g per 100 g protein).

Species/Amino Acids	Alanine	Arginine	Aspartic	Cysteine	Glutamic	Glycine	Histidine	Isoleucine	Leucine	Lysine	Methionine	Phenylalanine	Proline	Serine	Threonine	Tryptophan	Tyrosine	Valine	Reference
Fusarium oxysporum	5.7	6.4	9.8	–	17.4	7.1	2.4	4.6	6.2	6.6	1.4	4.2	6.8	4.3	9.2	–	1.3	6.0	Ahangi et al. (2008)
Fusarium venenatum	6.3	7.3	10.3	0.8	12.5	4.3	3.5	5.2	8.6	8.3	2.1	4.9	4.5	5.1	5.5	1.6	4.0	6.2	Ahangi et al. (2008)
Fusarium venenatum IR372C	5.9	6.9	4.2	1.2	12.9	4.1	3.2	4.8	6.7	7.5	2.9	–	–	5.3	4.7	–	4.3	5.0	Hashempour-Baltork et al. (2020)
Fusarium venenatum IR372C	0.2	0.7	–	0.2	2.2	0.4	0.7	0.2	0.2	0.3	0.4	0.3		15.5	0.3	–	0.3	0.3	Reihani et al., 2018
Fusarium venenatum, PTA-2684	6.0	7.3	10.3	0.8	12.5	4.5	3.5	5.2	8.6	8.3	2.1	4.9	4.5	5.1	5.5	1.6	4.0	6.2	Finnigan, Mach, and Edlin (2024)
Fusarium venenatum ATCC 20334	5.2	6.1	5.7	3.2	13.1	4.7	3.0	4.2	2.7	7.2	3.0	4.5	2.2	5.7	3.5	–	4.5	5.0	Hosseini and K. Khosravi-Darani, 2010
Fusarium strain flavolapis	0.7	0.7	1.2	0.1	1.4	0.6	0.3	0.6	1.0	1.0	0.2	0.5	0.6	0.6	0.6	0.2	0.4	1.3	Furrey et al., 2022

Table 3
Overview of the fatty acids profiles in mycoprotein from various *Fusarium* species (g per 100 g lipid).

Species/Fattyacid	DecaneC10 : 0, undecane(C11 : 0)dodecane(C12 : 0),	Myristicacid(C14 : 0)	Pentadecanoic(C15 : 0)	Palmiticacid(C16 : 0)	Palmitoleicacid(C16 : 1)	Margaricacid(C17 : 0)	Heptadec – 9 – enoic(C17 : 1)	Stearicacid(C18 : 0)	Isostearic(C18 : 0)	OleicAcid(C18 : 1)	Linoleicacid(C18 : 2)	Alpha – Linolenicacid(C18 : 3)	Gamma – Linoleicacid(C18 : 3)	Nonadecanoic(C19 : 0)	Arachidicacid(C20 : 0)	Gadoleicacid(C20 : 0)	Behenicacid(C22 : 0)	Erucicacid(C22 : 1)	Linocericacid(C24 : 0)	References
Fusarium oxysporum		0.2		13.2	0.9			9.0		37.9	31.6	4.5	0.1		0.9		0.5			Ahangi et al. (2008)
Fusarium venenatum IR372C		0.5		21.2	–	0.5	0.2	0.0		18.2	29.4	18.1	0.3		0.5	0.2	0.4	0.1	0.7	Hashempour-Baltork et al. (2020)
Fusarium venenatum IR372C	2.0	0.5	0.1	23.2	2.2	2.1		5.7	0.7	18.0	39.4			2.6	1.4					Reihani et al., 2018
Fusarium venenatum, PTA-2684				1.3				0.2		1.4	4.3	0.9								Finnigan, Mach, and Edlin (2024)
Fusarium venenatum ATCC 20334		0.3	0.1	14.2	0.5	0.2	0.1	6.9		18.4	0.1	25.1	0.3		0.5	0.2	0.4	0.1	0.7	Hosseini1 and K. Khosravi-Darani 2010

Table 4
Overview of the polysaccharides of mycoprotein from various *Fusarium* species (g/100 g).

Species/Amino Acids	N-acetyl galactosamine	N-acetyl glucosamine	Arabinose	Mannose	Galactose	Glucose	Uronic acid	Reference
Fusarium venenatum, PTA-2684	0.3	9.7	0.2	3.3	1.1	8.8	2.4	Finnigan, Mach, and Edlin (2024)

Table 5
Overview of the mineral profiles in mycoprotein from various *Fusarium* species (g/100 g).

Species/Amino Acids	Calcium	Phosphorus	Potassium	Sodium	Magnesium	Iron	Zinc	Copper	Manganese	Reference
Fusarium venenatum ATCC 2684	0.05	0.29	0.07	0.01	0.05	0.00	0.01	–	–	Saeed et al. (2023)
Fusarium venenatum, PTA-2684	0.17	0.10	0.40	0.02	0.19	0.00	0.04	0.00	0.03	Finnigan, Mach, and Edlin (2024)
Fusarium flavolapis	0.025–0.05	0.175–0.225	0.125–0.162	0.002	0.007–0.011	0.007	0.002	–	–	Furrey et al., 2022

Table 6
Overview of the vitamin profiles in mycoprotein from various *Fusarium* species (mg/kg).

Species/Amino Acids	Thiamin	Riboflavin	Niacin	Pyridoxine	Pantothenic acid	Folic acid	Biotin	Folate	Cobalamin	Reference
Fusarium venenatum, PTA-2684	0.4	9	14	5	10	0.4	0.6	–	–	Finnigan, Mach, and Edlin (2024)
Fusarium venenatum ATCC 2684	–	–	–	1	–	–	–	0.11	0.01	Saeed et al. (2023)
Fusarium flavolapis	1	–	–	0.25	–	–	–	–	–	Furrey et al., 2022

enhance satiety, regulate lipid metabolism, and support gut microbiota diversity, contributing to overall digestive health (Finnigan, Mach, & Edlin, 2024; Saeed et al., 2023). Given that Western diets are often fiber-deficient, the inclusion of mycoprotein-rich foods could serve as an important dietary intervention to address this gap (Cherta-Murillo & Frost, 2022). Recent studies have highlighted the positive metabolic effects of diets rich in mycoprotein, particularly in the context of obesity, cardiovascular health, and glycemic control. A large-scale population study analysed by Cherta-Murillo and Frost (2022) found that mycoprotein consumers had a significantly higher fibre intake (+22 %) and better diet quality scores compared to non-consumers. Additionally, mycoprotein consumption was associated with lower BMI (−4.77 %), reduced fasting blood glucose (−0.31 mmol/L), and lower glycated haemoglobin (HbA1c) (−0.15 %), suggesting a role in blood sugar regulation and diabetes prevention (Cherta-Murillo & Frost, 2022). These findings align with clinical trials demonstrating that mycoprotein intake leads to lower postprandial glucose and insulin responses, which are crucial factors in metabolic disease management (Finnigan, Mach, & Edlin, 2024). Moreover, dietary modelling studies have attempted to quantify the population-level health benefits of shifting toward mycoprotein-based diets, predicting significant reductions in obesity, type 2 diabetes, and cardiovascular disease prevalence with increased dietary adoption. Given these emerging insights, mycoprotein-rich foods not only offer a sustainable and nutritionally complete protein source but also hold significant potential as functional foods for metabolic health improvement."

In summary, the relatively high protein content and also quality based on the presence of essential amino acids, together with the fatty acid, mineral and vitamin profiles of the studied *Fusarium* species, highlight the potential of these fungi in producing nutritionally rich biomass as an excellent alternative to conventional protein sources, particularly for vegetarian and vegan diets. The differences in composition not only reflect the metabolic diversity of *Fusarium* strains and species - they also provide valuable insights for selecting optimal strains, cultivation conditions, and downstream processing for mycoprotein production. In particular, *F. venenatum* stands out for its balanced amino acid profile and substantial amounts of health-promoting unsaturated fatty acids. This makes it a promising candidate for developing nutritionally enhanced food products.

2.2. Nucleic acid removal and sensory quality

In 1985, the sale of Quorn mycoprotein was approved by the Ministry of Agriculture, Fisheries and Food (MAFF) on the condition that its nucleic acid content be reduced to meet World Health Organization (WHO) recommendations (Khan et al., 2024). These guidelines state that for human consumption of fungal biomass, RNA intake should not exceed 2 g per day for adults. This restriction was imposed due to concerns that high dietary RNA could be metabolised into purines, subsequently increasing uric acid levels in the body (Coelho et al., 2022). Elevated uric acid is associated with the development of gout, a form of inflammatory arthritis characterised by severe pain and swelling in the joints (Majumder et al., 2024). Recent research by Coelho et al. (2022) investigated the impact of consuming mycoprotein with high nucleotide content on serum uric acid levels. The study found that twice-daily consumption of such mycoprotein for one week led to increased serum uric acid concentrations above baseline levels (Coelho et al., 2022). Under modern fermentation conditions, F. venenatum biomass contains 8–9 % RNA by dry weight, which would limit its daily consumption to around 20 g of dry mycoprotein. However, in its wet form, the RNA content is significantly lower (approximately 2 %), meaning that about 100 g of non-RNA-depleted mycoprotein would reach the daily recommended RNA threshold. Since the mycoprotein content of finished Quorn products varies (e.g., around 90 % in pieces versus lower percentages in processed forms like sausages), reducing RNA levels in the fungal biomass was essential to ensure broader commercial viability and dietary flexibility (Khan et al., 2024).

A heat treatment method was developed for *F. venenatum* in which the harvested fungal biomass is exposed to 60–70 °C for 15–30 min. This process activates endogenous RNases, which degrade cellular RNA into nucleotides that diffuse out of the cell wall into the culture broth. As a result, the RNA content is significantly reduced, reaching approximately 0.5 % on a wet weight basis. This depletion allows for the consumption of approximately 400 g of finished mycoprotein products, such as Quorn

pieces, without exceeding the WHO-recommended daily RNA intake limit.

The increased temperature also inactivates proteases, minimising protein loss and ensuring the non-viability of the source organism, *F. venenatum*. However, this process also causes the cell membranes to become leaky, resulting in a significant loss of dry biomass, approximately 33 %, during subsequent centrifugation, reducing the amount of mycoprotein available for commercial sale (Finnigan, Mach, & Edlin, 2024; Whittaker et al., 2020). Heat treatment has also been used to reduce RNA content in biomass of *F. oxysporum*, with reduction of RNA to less than 1 % achieved either by exposure at 65 °C for 15 min or 72 °C for 10 min. Significantly, the weight loss of biomass was lower in the 65 °C treatment (18.6 %) than in the 72 °C treatment (36.7 %) (Ahangi et al., 2008). Post-heat treatment, the biomass is centrifuged to yield a pulp with ca. 20 % dry matter. The final mycoprotein product undergoes steaming, cooling, and freezing, which develops a meat-like texture suitable for human consumption (Fig. 3) (Majumder et al., 2024).

The texture is a critical component in evaluating the mouthfeel, softness, and chewiness of food products (Fu et al., 2022). To meet consumer expectations, meat substitutes must exhibit sensory qualities such as texture, bite resistance, and flavour that closely resemble those of meat. Quorn products, including Quorn mince and pieces, achieve this by integrating mycoprotein with gelling agents such as agar, alginate, and egg albumin (Finnigan et al., 2019, 2024). This mixture is heated to 80–85 °C, then cooled and frozen at −10 °C, resulting in a gel composite with a fibrous texture like chicken, as well as desirable softness and chewiness. Elzerman et al. (2011) conducted a sensory evaluation of Quorn products that were compared to other meat substitutes, such as Tivall stir-fry pieces, tofu strips, and Goodbite chicken style. The study involved 93 participants in a central location test evaluating meals with meat substitutes. The participants were meat-eaters recruited in Wageningen, Netherlands, with the majority (77 %) being women and an average age of 35 years. Most participants (97 %) had Dutch nationality, and 54 % had a university degree. Interestingly, their findings indicated that Quorn was preferred for its texture, taste, aroma, colour, and appearance. Finnigan et al. (2019) also reported that Quorn mycoprotein foods have a texture similar to meat products due to their comparable breakdown in the oral cavity. Moreover, Quorn items were noted for their superior fibrous texture and less rubbery consistency, compared with chicken and soybean products, attributable to their densely packed laminations.

Xiao et al. (2016) similarly developed a chickpea-based bread incorporating 20 % mycoprotein and found that the final product had a colour comparable to the control group and a softer texture than wheat bread. Likewise, Finnigan et al. (2019) reported that Quorn food products displayed a more fibrous texture and a reduced rubbery consistency compared to chicken and soybean-based products, attributed to their highly compacted laminations. Additionally, Finnigan et al. (2017) highlighted the necessity of functional synergy between Quorn products and egg whites to achieve a meat-like texture.

Furthermore, Lonchamp, Akintoye, Clegg, and Euston (2020) investigated the interaction between mycoprotein retentate mixture and egg white, revealing that gels produced with 25/75 and 50/50 ratios of retentate mixture to egg white exhibited foaming properties comparable to 10 % egg white and superior to those containing 5 % or 7.5 % egg white. Their study also demonstrated that gels formed from a 75/25 egg white-retentate mixture developed a dense hyphal structure, encapsulating filaments and other particles around air bubbles. This interaction enhanced the foaming ability of egg white protein, leading to increased air bubble formation and a texture resembling meat. The findings confirmed a functional relationship between egg white protein and the retentate mixture in texture development. Finnigan, Mach, and Edlin (2024) emphasised that traditional Quorn products require functional synergy with egg white to achieve a meat-like texture, although vegan derivates have been developed in recent years using alternative plant-based binding agents.

Among all the unit processes involved in Quorn production, freezing and frozen storage have the most significant impact (Evans, 1996). Freezing transforms the rubbery mass produced after steaming into a fibrous, meat-like texture. Approximately 50 % of the texture develops during freezing, with further refinement occurring over approximately three weeks of frozen storage. For optimal texture, relatively slow freezing-slower than conventional food freezing processes, is required. Ice crystal formation compresses mycoprotein fibres into bundles, enhancing the meat-like mouthfeel (Rodger & Angold, 1991). Additionally, "Ostwald ripening" of ice crystals during storage appears to improve the perception of "meatiness" further. However, prolonged storage can lead to defects, often altering the distribution of expressible water. This can initially increase juiciness but may later result in a dry, woody texture.

The quality and quantity of mycoprotein-based products are influenced by various process variables (Fig. 5). Besides the strain type and fermentation conditions that are fundamental to the successful production of fungal biomass, downstream processing plays a crucial role in developing meat-like textures. Mixing is a significant challenge due to the viscoelastic nature of mycoprotein and the need to disperse powdered ingredients effectively at large scales. Rheological properties are closely linked to the RNA reduction process and the solids level in the biomass. Fibre alignment occurs during extensional flow and must be optimised during its formation to achieve the desired texture. Thermal gel creation is critical since heat setting "fixes" mixing effects and fibre alignments, transforming the texture to resemble meat. Different heating methods, such as steaming and microwaving, affect hyphae differently, impacting protein dispersion and gel formation. Air inclusion can create softer texture areas, mainly if CO_2 used for cooling is not adequately removed. Freezing and frozen storage are the most impactful processes; slow freezing compressing mycoprotein fibres into bundles can enhance a meat-like texture. However, prolonged storage can lead to defects, altering the water distribution and affecting the texture (Finnigan, Mach, & Edlin, 2024).

Therefore, advanced production technologies that enhance these qualities in meat analogues through innovative cultivation, purification and processing methods are vital for fungal biomass to succeed as a meat substitute. This underscores the importance of optimising mycoprotein production to offer consumers high-quality meat alternatives.

3. Molecular tools in *Fusarium* species

Recent advancements in the metabolic and genetic engineering of *Fusarium* species, particularly *F. fujikuroi*, have significantly enhanced the production of valuable secondary metabolites such as gibberellic acid (GA3). While metabolic engineering efforts have largely focused on optimising nitrogen metabolite repression (Zhang et al., 2020), other factors such as carbon source utilisation and oxidative stress responses remain underexplored, highlighting the need for a more comprehensive metabolic control strategy (Ge et al., 2024). Genetic engineering has benefited from the development of strong constitutive promoters (e.g., gpdA), efficient terminators (e.g., trpC), and selectable markers (e.g., hph, NPTII), yet comparative analyses on their efficiency across different *Fusarium* species are lacking (Hwang & Ahn, 2016; Brown et al., 2011; Darino et al., 2024). In the case of *F. venenatum,* such genetic engineering approaches have been greatly assisted by the release of publicly available whole genome sequence data in recent years (King et al., 2018).

The introduction of CRISPR/Cas9 has enabled precise genome editing, but challenges such as inconsistent transformation efficiencies, unintended mutations, and limited repair template integration remain significant hurdles (Tong et al., 2022). Additionally, homologous recombination strategies, particularly the use of long homologous arms and selectable markers, have improved gene disruption efficiency in *F. fujikuroi*, yet their reliability across other *Fusarium* species remains unclear (Hwang & Ahn, 2016). Electroporation has facilitated DNA

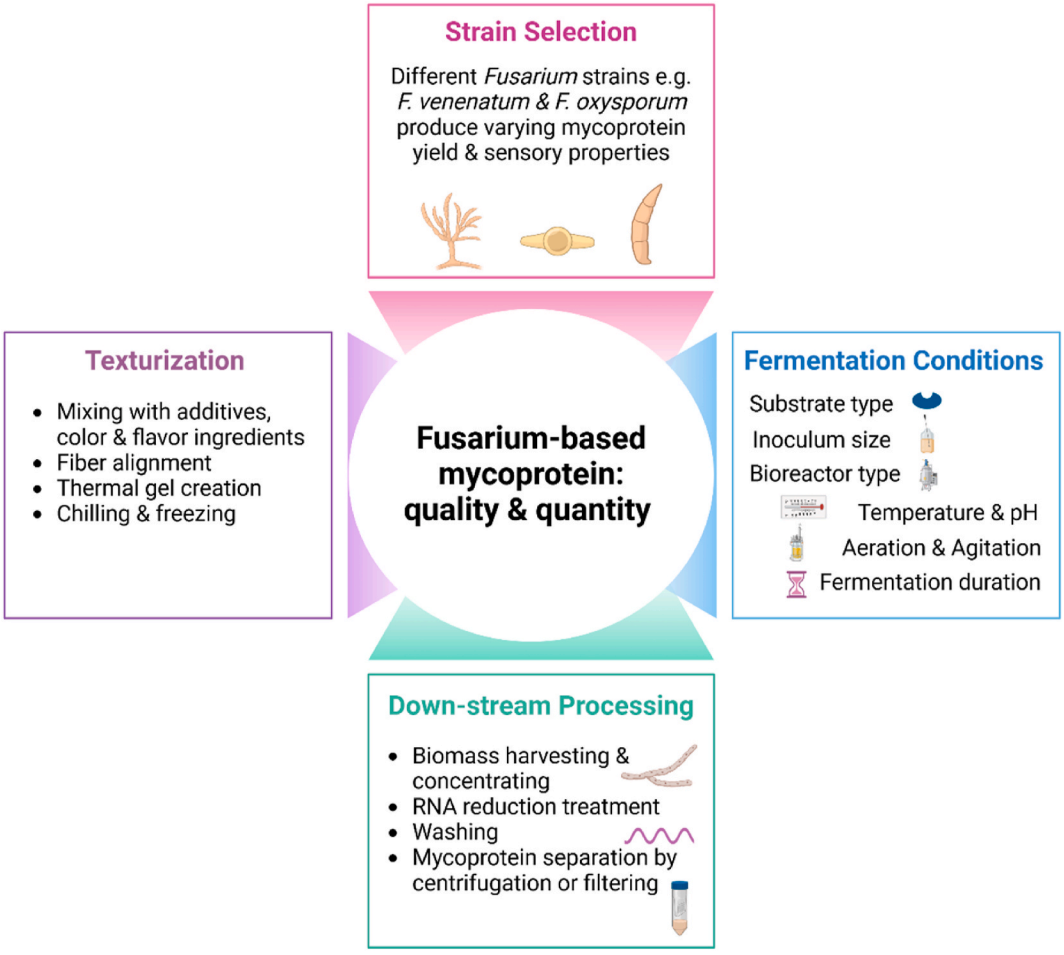

Fig. 5. Factors affecting the quality and quantity of *Fusarium* biomass.

transformation in *F. graminearum* and *F. culmorum* (Yörük & Albayrak, 2015), but its efficiency compared to traditional protoplast-mediated transformation requires further investigation, especially in industrial applications where scalability is critical. Traditional mutagenesis methods, such as chemical, physical, insertional and random mutagenesis, have also been employed to generate mutant strains, contributing to knowledge about the genetics of processes such as pathogenicity despite their lower precision compared with modern genetic tools (Chen et al., 2009; Heuts et al., 2007; Michielse et al., 2009; Sanchez et al., 1975; Seong et al., 2009; Zhang et al., 2020).

Despite these advancements, the metabolic engineering of *Fusarium* for mycoprotein production is still in its infancy, with a study reporting a CRISPR/Cas9-driven strategy to enhance protein yield and carbon conversion efficiency in *F. venenatum* (Tong et al., 2023). While this study demonstrated a 39 % reduction in CO_2 emissions, further research is needed to compare its environmental impact to conventional protein sources and to optimise fermentation conditions for industrial scalability. Moreover, regulatory challenges surrounding the commercialisation of genetically modified *Fusarium* strains, particularly for food production, pose significant barriers to market adoption. The European Union enforces strict GMO regulations, whereas the United States follows a more flexible GRAS framework, but consumer acceptance remains uncertain. Labelling strategies, such as branding genetically modified mycoprotein as "precision-fermented" or "precision breeding", may help mitigate public concerns and facilitate broader acceptance. Moving forward, research should expand beyond incremental genetic modifications to explore adaptive laboratory evolution, synthetic biology circuits, and consortia-based approaches that could further enhance metabolic efficiency. Furthermore, bioprocess optimisation, including bioreactor design and media formulation, should complement genetic engineering efforts to ensure commercial viability. While significant progress has been made in developing molecular tools for *Fusarium* species, a more integrative approach that combines metabolic and genetic engineering, process optimisation, and regulatory considerations is essential for advancing both fundamental research and biotechnological applications.

4. Technical challenges

Fusarium-based mycoprotein production faces several technical challenges, particularly in managing the emergence of morphological mutants that can negatively impact product quality. A continuous flow process, as used in Quorn production, reduces the time needed for decontamination, sterilisation, and batch growth. However, cultivation beyond 200 generations (>800 h) of *F. venenatum* may result in the appearance of highly branched colonial mutants, which can alter the texture of the final product in an undesirable fashion (Ugalde & Castrillo, 2002). Solomons (1987) observed that after 1000 to 1200 h of cultivation (250–340 generations), morphological changes, such as a decrease in hyphal length per tip, occurred, which negatively impacted the final product. Wiebe et al. (1992, 1994, 1995) found that in glucose-limited chemostat cultures of *F. venenatum* A3/5 at high dilution rates and pH 5.8, highly branched morphological mutants consistently appeared and quickly displaced the parent strain. These mutants exhibited a growth rate advantage under glucose-limited conditions but not when glucose was abundant (Wiebe et al., 1992). Conversely, highly

branched mutants isolated from a mycoprotein production plant showed a growth rate advantage under nutrient-rich conditions compared with the parent strain. Some of these mutants also demonstrated superior growth rates under nutrient-limited conditions (glucose-, ammonium-, sulfate-, and/or magnesium-limitation) (Wiebe et al., 2002).

A critical infrastructure challenge in Quorn's continuous fermentation process is the need for frequent cleaning and sterilisation of the airlift fermenter to prevent the accumulation of morphological mutants. *F. venenatum* is cultivated in a glucose-limited airlift bioreactor under continuous flow conditions, allowing for high biomass productivity. However, as fermentation progresses, highly branched colonial mutants can emerge, outcompeting the parental strain and negatively impacting product texture (Wiebe, 2002). To mitigate this, rigorous cleaning and sterilisation protocols are required to remove residual mutant biomass and maintain strain stability. Despite implementing strategies such as pH adjustments, dilution rate modifications, and nitrogen source alterations, periodic fermenter cleaning remains essential to maintaining consistent product quality and preventing unwanted strain selection (Wiebe, 2002).

Several strategies have been proposed to prevent or delay the emergence of highly branched mutants by altering the selection procedures. For instance, at low dilution rates ($D \leq 0.10\ h^{-1}$), the appearance of these mutants is significantly delayed (Trinci, 1994; Wiebe et al., 1994). However, such slow dilution rates are unsuitable for producing growth rate-dependent products like biomass. Additionally, lowering the pH from 5.8 to 4.5 effectively delayed the appearance of morphological mutants; however, some highly branched mutants did appear but did not outcompete the parental strain (Wiebe et al., 1996). Modifying the nitrogen source also influences the displacement of the parental strain by morphological mutants. When nitrate replaced ammonium as the nitrogen source (Wiebe et al., 2001) or when ammonium cultures were supplemented with mycological peptone, highly branched mutants appeared but did not increase in the population (Wiebe et al., 2001). In parallel, it has been proposed that diploid strains may effectively buffer recessive mutations (such as those linked to c-variants) and allow fermentations to continue for a longer period, with some evidence for this in laboratory-scale trials (Wiebe, 2002). However, there may be unwanted side effects, and the long-term stability of diploid strains is unknown (Whittaker et al., 2020).

To address the challenges posed by morphological mutants in *Fusarium* biomass production, recent advances in omics technologies have provided deeper insights into the genetic basis of these mutations. Next-generation sequencing (NGS) has been utilised in many different research areas, including the identification of driver mutations of individual single-nucleotide polymorphisms (SNPs), copy number variations, insertions and deletions that are possibly linked to specific diseases and has been instrumental in identifying specific genes and regulatory pathways associated with these morphological changes (Kim et al., 2017). This understanding allows for targeted genetic engineering, mutagenesis, or adaptive laboratory evolution to develop strains resistant to undesirable changes (Connell et al., 2024). By manipulating key genes or pathways, it may be possible to enhance the stability of the parental strain and prevent the outgrowth of highly branched mutants, thus maintaining consistent product quality in large-scale production processes.

5. Safety of mycoprotein

The safety of mycoprotein, like any food or feed product, is paramount, necessitating stringent regulations to ensure its safe production and use (Pouris et al., 2024). Key concerns include RNA content, microbial toxins either from the host or contaminants, potential allergic reactions, and harmful substances from the feedstock, such as heavy metals (Saeed et al., 2023). Industrial methods have been developed to reduce RNA content to acceptable levels. RNA purines can be metabolised into serum uric acid (SUA), which may contribute to gout and other metabolic issues in some individuals (Lockyer & Stanner, 2016). However, the link between SUA and gout is complex (Duskin-Bitan et al., 2014). Current dietary guidelines align with general healthy eating recommendations, with some adjustments for specific foods and nutrients. More randomised controlled trials are needed to clarify dietary impacts on gout risk and improve prevention strategies.

The challenge of toxins is mitigated by carefully selecting production organisms, optimising process conditions, and formulating the product appropriately. Some fungi produce mycotoxins, making them undesirable sources of SCP (Salazar-López et al., 2022). *Fusarium* species produce toxic metabolites, e.g., zearalenone, fumonisins, trichothecene, and deoxynivalenol, which contribute to plant diseases and mycotoxicosis in humans (Noorabadi et al., 2021). Mycotoxins can cause allergic reactions, carcinogenesis, and even death, posing risks to both humans and animals. While regulatory agencies permit low levels of mycotoxins in certain foods, such as cereals, mycoprotein production requires particularly stringent control to ensure safety for human and animal consumption.

Quorn mycoprotein, produced from *F. venenatum*, underwent extensive testing to ensure the absence of mycotoxins or other toxic compounds before being approved for human consumption (Wiebe, 2004). The specific strain of *F. venenatum* used does not produce mycotoxins under production conditions and is classified as a biosafety level 1 microorganism. This process is continually monitored to ensure safety. The initial safety testing for Quorn mycoprotein spanned 16 years, with additional years required for approval outside the UK (Ritala et al., 2017). Similarly, Fy protein from *F. flavolapis* was subjected to testing for animal toxicity, mutagenic/genotoxic potential and mycotoxin production, with no safety issues raised (Furey et al., 2022).

Using various waste materials for mycoprotein production is attractive for cost and sustainability reasons but poses safety challenges, necessitating careful consideration of the feedstock's origin. For instance, Quorn is produced in a chemically defined medium from glucose (hydrolysed starch) in a process that meets Good Laboratory Practice (GLP) standards (Wiebe, 2004). Any product for human consumption derived from biomass hydrolysates or waste streams would need to demonstrate an equivalent safety record before gaining approval in Europe or North America, particularly given the risk of increased mycotoxin production on alternative feedstocks (Whittaker et al., 2020). Additionally, public perception and acceptance of waste-derived foods are critical factors when introducing fungal biomass into human diets.

Although mycoproteins undergo rigorous food safety testing for mycotoxins and mutagenic properties, some individuals may still develop sensitisation and, in rare cases, a specific allergy. However, a systematic review of the evidence indicates that the occurrence of allergic reactions remains exceptionally low (Finnigan et al., 2019). Consequently, careful monitoring of factors such as mycotoxin levels, microbial contamination, and allergenic compounds of all commercial mycoprotein batches is necessary to ensure product safety (Ritala et al., 2017).

6. Economics and market trends

Mycoproteins have been a part of the UK market since 1985 (Ahmad et al., 2022). In 2002, the FDA granted mycoprotein GRAS status, paving the way for the introduction of seven Quorn products in the USA, such as steaks, sausages, mince, chicken, nuggets, strips, and fishless fingers. Currently, mycoprotein is sold in several regions, including Europe (UK, Norway, Denmark, France, Germany, and Switzerland), Asia (Hong Kong, Singapore, and Thailand), and North America (USA and Canada). These proteins have been consumed in nearly 5 billion meals worldwide since their launch (Finnigan, Mach, & Edlin, 2024). The global mycoprotein market, valued at US$642 million in 2022, is expected to expand to US$1.1 billion by 2030, with a compound annual growth rate (CAGR) of 6.4 % from 2022 to 2030. In the United States, the mycoprotein market was estimated at US$175 million in 2022. China, the world's

second-largest economy, is anticipated to achieve a market size of US $239 million by 2030, reflecting a CAGR of 10.4 % over the same period. Other significant markets, including Japan and Canada, are projected to grow at CAGRs of 2.8 % and 5.5 %, respectively, from 2022 to 2030 (Derbyshire & Delange, 2021).

Quorn, a leading brand in the meat alternative industry, has experienced notable fluctuations in its market performance in recent years. In 2023, Marlow Foods, Quorn's parent company, reported a pre-tax loss of £63.4 million, a significant increase from the £15.4 million loss in 2022. This downturn was primarily attributed to inflationary pressures and decreased demand in key markets such as the UK and the US. Despite these challenges, Quorn maintained a strong presence in the UK, holding a 32 % market share in the meat substitute sector as of 2023. Brand awareness remained high, with 85 % of UK meat substitute users recognizing the Quorn brand and 55 % using its products in the past year.

Despite the health advantages of mycoprotein, it is vital to ensure its production and expansion are managed sustainably to prevent new environmental issues.

7. Environmental and sustainability of mycoprotein

It is acknowledged that large-scale animal husbandry has detrimental environmental impacts both in terms of emissions and land degradation, which might be partly mitigated by the use of plant and fungal-derived proteins (Rubio et al., 2020). Indeed, there is evidence of the environmental and sustainability benefits of mycoprotein compared to meat production. A number of 'cradle to processing' studies by the Carbon Trust comparing like-for-like Quorn products to beef, pork and chicken production established that Quorn had lower water usage (3.5-2.0x lower) and land usage (at least 2-6x lower) and a considerably lower carbon footprint (between 17.5-1.5x lower) (Finnigan, Mach, & Edlin, 2024). A separate modelling study comparing microbial protein to ruminant-meat-based protein also revealed considerable environmental benefits for mycoprotein production in terms of cutting deforestation and pasture use, as well as lowered CO_2 and methane gas emissions. This analysis took into account the need for sugars for microbial growth and land use effects (Humpenöder et al., 2020).

Life cycle assessments (LCA) of mycoprotein production are relatively limited, but existing studies consistently highlight its lower environmental footprint compared to conventional meat, particularly beef. For instance, Finnigan et al. (2010) found that Quorn mince has only 48 % of the global warming potential (GWP) of beef mince per unit weight. However, the inclusion of glucose and egg albumen in Quorn production could increase this to 60 % (Souza Filho et al., 2018). Similarly, Shahid et al. (2024) reported lower greenhouse gas emissions (GHGe) for mycoprotein-based products (0.73 kgCO_2eq/kg) compared to soy protein (1.21 kg CO_2 eq/kg) and pea protein concentrate (1.91 kg CO_2 eq/kg).

By contrast, some studies suggest that mycoprotein offers only marginal benefits compared to certain types of meat. Smetana et al. (2015) assessed mycoprotein made from sugar beet molasses and found that its environmental impact was comparable to chicken meat, with both being lower than cultured meat. Key contributors to mycoprotein's impact included processing (45 %), consumer frying (25 %), and ingredient sourcing (21 %; 10 % from egg white and 11 % from nitrogen fertiliser used for fungal substrates). The global warming potential for mycoprotein ranged from 5.55 to 6.15 kg CO_2 eq per kg, similar to chicken (2–4 kg CO_2 eq) and pork (4–6 kg CO_2 eq). However, mycoprotein was less favourable when evaluated on calorific energy and digestible protein content, with only cultured meat having a higher impact.

Recent studies have refined these estimates. Finnigan et al. (2019) noted that mycoprotein production releases approximately 6.8 tons of CO_2, with eggs and glucose as primary contributors to GHGe. Meanwhile, Van Peteghem et al. (2022) reported lower emissions at around 2.7 tons of CO_2. Both studies emphasised that significant emissions occur during the conversion of mycoprotein to Quorn. Despite these variations, mycoprotein production consistently emits fewer greenhouse gases than animal-based proteins, with beef emitting 14.3 tons of CO_2 per ton (Finnigan et al., 2017; Smetana et al., 2023).

Mycoprotein production has significantly less land-use demand compared to traditional livestock farming. The cultivation of *F. venenatum*, the primary fungal species used for mycoprotein production, occurs in controlled fermentation systems, eliminating the need for vast agricultural lands. Energy, land, and water usage analyses further illustrate mycoprotein's environmental efficiency. According to Smetana (2015), the land use for producing mycoprotein is 10 times less than that required for beef production. In a follow-up study, Smetana et al. (2018) highlighted its low land use (<2 m^2a/kg compared to 5–7 m^2a/kg for chicken and 7–8 m^2a/kg for pork) and water use (~500 L/kg). However, energy consumption (15–20 kWh/kg) was higher than that of vegetables and insects but comparable to dairy alternatives. Furthermore, Van Peteghem et al. (2022) highlighted that mycoprotein production only occupies 0.13 m^2 of land per kilogram, whereas beef requires approximately 7.1 m^2 of land per kilogram.

This lower land footprint not only helps preserve natural ecosystems but also supports biodiversity by reducing deforestation and habitat destruction associated with livestock farming. The ability to produce mycoprotein using agricultural by-products as feedstock further minimises the need for croplands, making it a sustainable alternative in a growing global population context.

8. Consumer acceptance and regulation

Consumer acceptance of mycoprotein remains a critical issue that needs thorough investigation. While taste and texture are primary concerns, consumer perception of food safety can also influence acceptance. Specifically, concerns, whether scientifically justified or not, about microbial toxin production and potential allergic reactions may shape public perception and demand for mycoprotein products (Khosravi-Darani et al., 2020). In addition, the acceptance of GMOs in fungal biomass production varies globally; Europe shows resistance, whereas other regions are more receptive. As more data on GMO consumption becomes available and protein sources dwindle, public acceptance may increase, particularly for health-focused and personalised nutrition applications. Genetic engineering presents numerous benefits for mycoprotein production, such as the synthesis of essential nutrients, the elimination of toxin-producing genes to enhance safety, and the optimisation of carbon source metabolism to reduce costs. Advanced technologies like CRISPR allow for precise genome editing without introducing foreign DNA, potentially circumventing GMO classifications and mitigating the risk of spreading antibiotic resistance genes. Furthermore, genetic modifications can significantly be used to tune the composition of the biomass, thereby supporting the development of personalised nutrition solutions (Ritala et al., 2017). Thus, these advancements have the potential to significantly improve consumer trust and acceptance of mycoprotein as a sustainable and nutritious food source.

Recent studies have examined how the framing of mycoproteins as either "alternatives" or "replacements" affects consumer perception and acceptance. A study by Godley (2024) highlights that Quorn's early branding as a "meat replacement" faced resistance from traditional meat consumers, whereas positioning it as a complementary protein source improved acceptance. Similarly, De Cianni et al. (2024) found that health-conscious consumers were more receptive to mycoproteins when framed as an "alternative protein" rather than a direct "replacement" for meat, whereas environmentally motivated consumers responded more positively to the "replacement" narrative. D'Almeida and de Albuquerque (2025) further supported this finding, showing that framing mycoprotein as a "low-carbon protein alternative" reduced scepticism, particularly among those unfamiliar with fungal-based proteins. In a

study by Chezan et al. (2022), labelling mycoprotein as an "alternative protein" made it more appealing to general consumers, as the term "replacement" was associated with dietary sacrifice and a loss of familiar flavours or textures. Similarly, Chriki et al. (2024) found that regional and cultural preferences influenced framing effectiveness, with Spanish consumers responding well to the term "innovative food alternative", while French and German consumers were less accepting of the term "meat substitute", which they associated with artificiality. Furthermore, Fischer and Hilboesen (2025) demonstrated that neutral descriptors such as "fungal protein" increased consumer willingness to try mycoproteins compared to more direct terms like "meat replacement." These findings indicate that framing plays a crucial role in shaping consumer attitudes, with "alternative" positioning generally leading to higher acceptance, while "replacement" framing can trigger resistance, especially among traditional meat eaters. The success of mycoproteins in the market may, therefore, depend on targeted messaging strategies that align with consumer motivations, whether they are health-driven, environmentally conscious, or simply seeking variety in their diet.

Mycoprotein-based products like Quorn are marketed as meat alternatives but often come at a higher price than conventional meat (Apostolidis & McLeay, 2016; Moore & Chiu, 2001). These products appeal primarily to consumers who identify as vegetarian, flexitarian, vegan, or generally health-conscious groups that tend to be more willing and financially capable of paying a premium for alternative protein sources (Dufossé et al., 2014). While some studies suggest that consumers are indeed prepared to pay more for mycoproteins (Dufossé et al., 2014), others highlight the role of price sensitivity and demand elasticity in purchasing decisions (Ritchie et al., 2018). Additionally, mycoproteins are gaining popularity among consumers who prioritise sustainability (Apostolidis & McLeay, 2019). Compared to conventional meat, mycoprotein production is considered more environmentally sustainable due to the significant externalities associated with meat production, including ethical concerns over animal husbandry, inefficient resource utilisation, and high carbon and water footprints (Finnigan et al., 2017). In this regard, sustainability-focused consumers are likely to value Quorn's commitment to environmental responsibility, as evidenced by its third-party certifications, such as the Carbon Trust footprint label (Dean et al., 2022).

Recent studies have explored whether the increasing availability of alternative proteins has led to a measurable decline in traditional meat consumption, with findings indicating that while alternative protein consumption is rising, it has not yet significantly reduced overall meat intake. Jang et al. (2025) found that although younger and environmentally conscious consumers are reducing red meat consumption, the shift is gradual rather than immediate, suggesting that alternative proteins are supplementing rather than replacing traditional meat. Similarly, Samad et al. (2025) analysed purchasing data and found that consumers who try alternative proteins still consume meat, albeit with a slight reduction, particularly in processed meats. Drewnowski (2024) highlighted that cultural and economic factors continue to sustain meat demand, and significant reductions are more likely in regions with active policy support for plant-based diets. However, Costa et al. (2024) suggested that framing alternative proteins as "sustainable dietary transitions" rather than strict "meat replacements" could have a more effective long-term impact, as consumers are more open to integrating these products into their diets. Meanwhile, Khanashyam et al. (2025) emphasised that price competitiveness and taste parity remain critical in determining whether alternative proteins will significantly shift meat consumption patterns. While these findings indicate that alternative proteins are gaining market share, a substantial decline in traditional meat consumption will likely require a combination of economic incentives, sensory improvements, and policy-driven initiatives. The framing of alternative proteins as complements rather than replacements may also help broaden consumer acceptance, potentially leading to a more gradual transition away from meat over time.

9. Concluding remarks

Fusarium-based mycoprotein represents a promising, sustainable alternative to conventional meat, offering a high-quality protein source with a favourable nutritional profile, including essential amino acids, fibre, and low saturated fat content. Advances in fermentation technology, particularly submerged and airlift bioreactors, have optimised large-scale production while emerging genetic and metabolic engineering tools offer new opportunities for *fusarium* strain improvement. Despite the potential of *Fusarium*-based mycoprotein, key challenges remain, including optimising growth conditions, ensuring safety through effective mycotoxin control, and improving sensory properties for consumer acceptance. Addressing these issues through bioprocess optimisation, novel strain engineering, and sustainable feedstock utilisation will be essential for enhancing production efficiency and scalability. Looking ahead, integrating *Fusarium*-based mycoprotein production with circular bioeconomy approaches, such as valorising agricultural by-products, could further improve environmental sustainability. Additionally, expanding regulatory approvals and increasing public awareness will be critical in driving market adoption. With continued advancements in biotechnology and fermentation science, *Fusarium*-based mycoprotein can play a pivotal role in meeting global protein demands while reducing the environmental impact of food production.

9.1. Outstanding questions

- What genetic and physiological traits of *Fusarium* species most influence fungal biomass yield and efficiency?
- How can *Fusarium*-based mycoprotein production integrate with other biotechnologies for a circular, sustainable industrial ecosystem?
- What role does interdisciplinary collaboration play in overcoming technical and economic barriers to large-scale *Fusarium*-based mycoprotein production?
- What are the socio-economic impacts of adopting *Fusarium* biomass as a meat substitute on food security and agricultural employment?
- What are the ecological impacts of large-scale *Fusarium* production, and how can they be monitored and mitigated?
- How can academic advances in *Fusarium* cell factory development enable rapid industrial scaling?
- How can synthetic and engineering biology improve the quality, acceptance, and commercialisation of *Fusarium*-based mycoprotein?
- What factors shape consumer perception and acceptance of *Fusarium*-based mycoprotein, and how can sensory, nutritional, and branding strategies influence its market success?

CRediT authorship contribution statement

Rima Gnaim: Conceptualization, Project administration, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Paul S. Dyer:** Investigation, Visualization, Writing – review & editing. **Rodrigo Ledesma-Amaro:** Conceptualization, Investigation, Visualization, Writing – original draft, Writing – review & editing.

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Declaration of competing interest

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

Glossary

Mycoprotein Protein derived from fungi, specifically *Fusarium*, used as a meat substitute due to its high nutritional value and sustainability

Single Cell Proteins (SCP) Proteins produced from microbial sources, such as bacteria, yeast, algae, and fungi

Filamentous Fungi A type of fungi characterised by long, thread-like structures called hyphae; it includes genera such as *Fusarium*, *Aspergillus*, and *Rhizopus*

Fermentation A metabolic process whereby microorganisms convert carbohydrates to other products, often used for producing mycoprotein

Submerged Fermentation (SmF) A fermentation technique whereby microorganisms grow in a liquid medium, allowing precise control of the growth conditions

Surface Culture Method (SCM) A fermentation technique whereby microorganisms grow on a solid or semi-solid surface

Bioreactor A vessel used to grow microorganisms under controlled conditions to produce various bioproducts

Synthetic Biology An interdisciplinary field combining biology and engineering to design and construct new biological parts and systems

Metabolic Engineering The practice of optimising cellular processes to increase the production of desired compounds

Airlift Fermenter A bioreactor that uses air bubbles to mix the culture medium, promoting growth and reducing energy consumption

Nutritional Profile A food product's composition of nutrients, such as amino and fatty acids

Secondary Metabolites Compounds produced by microorganisms that are not essential for their growth but can have various applications, such as antibiotics and pigments

Pathogenicity The ability of an organism to cause disease

Mycotoxins Toxic compounds produced by certain fungi, which can contaminate food and pose health risks

Downstream Processing Steps involved in purifying and refining bioproducts after fermentation

CRISPR/Cas9 A genetic engineering tool used for precise editing of DNA sequences

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.tifs.2025.104981.

Data availability

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

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