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Cultivated meat meets upcycling: Unlocking the potential of agricultural side-streams

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ABSTRACT

Background: Scaling-up cultivated meat production could enable sustainable production of a nutritious protein source, much needed for a growing population. However, to progress cultivated meat, low-cost, high-volume resources must be used as production inputs. Agricultural side-streams present an underutilised resource, rich in favourable components for cultivated meat inputs.

Scope and approach: The term “agricultural side-stream” encompasses all plant-based by-products and waste-streams generated from the harvest stage through to food product processing. This review explores the potential to valorise these agricultural materials to support the production of cultivated meat as both cell media supplements and scaffolding materials.

Key findings and conclusions: Production of cultivated meat could become more economically feasible through repurposing agricultural side-streams as production inputs. Through assisting cultivated meat scale up, this could lead to the production of a quality protein source, which reduces the environmental impact and animal welfare concerns of conventional meat production while potentially contributing to lowering global antibiotic resistance and zoonotic disease spread. Furthermore, upcycling agricultural side-streams could provide an additional income stream for agricultural producers while contributing to lowering global food loss. These added benefits could increase consumer acceptance for this novel technology. The utilisation of agricultural side-streams in cell media and cell scaffolding is a relatively new area of investigation requiring thorough research into identifying optimal side-streams, optimised processing techniques and side-stream variability.

1. Introduction

With an expected population of 9.7 billion people by 2050, the FAO has predicted a need to increase global food production by 70 % compared to 2009 levels (Alexandratos and Bruinsma, 2012). This demographic growth will demand increased food production while economic growth will support consumption of more animal derived products (Xu et al., 2021).

However, the production of animal products is inefficient. Meat and dairy account for 83 % of agricultural farmland while only contributing 18 % of the world’s calories and 37 % of the world’s protein (Poore and Nemecek, 2022). Livestock production accounts for 18 % of global greenhouse gas emissions while also contributing to deforestation, degradation of habitats and eutrophication of water ways (FAO 2006). High throughput herding and slaughtering involved in livestock production has raised concerns for animal welfare and public health (Post, 2012). Considering these issues, there is a need to innovate how animal products can be produced efficiently, with a reduced environmental and ethical cost.

One emerging technology challenging conventional animal farming is the production of cultivated meat (CM). Also known as ‘cultured meat,’ ‘cell-based meat,’ ‘clean meat’ or ‘*in-vitro* meat,’ this effort aims

Abbreviations: CM, cultivated meat; FBS, fetal bovine serum; BSCs, Bovine satellite cells; DMEM, Dulbecco’s Modified Eagle Medium; F12, Ham’s F-12 Nutrient Mixture; BSA, bovine serum albumin; ITS-X, insulin-transferrin-selenium-ethanolamine; hIL-6, human interleukin 6; FGF-2, fibroblast growth factor 2; VEGF, vascular endothelial growth factor; IGF1, insulin-like growth factor 1; HGF, hepatocyte growth factor; PDGF-BB, platelet-derived growth factor BB; HEPES, 4-(2-Hydroxyethyl)piperazine-1-ethane-sulfonic acid; TGF-β3, transforming growth factor–beta 3; NRG1, neuregulin 1; ITS, insulin-transferrin-selenium; MEM, minimum essential media; PSA, penicillin/streptomycin/amphotericin; 3D, three-dimensional; ACF, animal component free.

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to produce meat external to the animal through tissue culturing (Post et al., 2020). Lifecycle assessments indicate that CM could have a reduced environmental impact compared to traditional beef and pork production (Stephens et al., 2018; Sinke et al., 2023). This includes significant reductions in greenhouse gas emissions, water and land use as well as eutrophication potential (Stephens et al., 2018; Roy et al., 2021). Furthermore, due to the *in vitro* production method, there would be a considerable reduction in animal slaughter, which could cater to ethically minded omnivores and vegetarians (Hopkins and Dacey, 2008). However, for CM to demonstrate any of these benefits as a livestock replacement, it must be industrially scaled with widespread adoption.

A major challenge being faced to achieve this are the high production costs (Garrison et al., 2022). Unlike the pharmaceutical industry, food as a commodity is a high volume, low margin product, requiring mass output to be profitable. To become commercially viable, CM production must compete with the price of traditionally produced meat. Cell media, which supplies nutrients and bioactive compounds for the growth and functioning of cells, is high in cost. This presents a limitation prohibiting CM from competing with conventional meat products.

To advance CM, cell media costs must decrease to less than $1 USD per litre (Negulescu et al., 2023). If unable to achieve this, CM products risk entering a luxury, niche category. With CM purchased as a low volume premium food, the environmental, animal welfare and food security benefits, which are driving the development of this technology, will not be met.

Widespread adoption of CM also relies on the ability to mimic a range of meat products including both mince meats and highly structured products such as steaks. Often scaffolds are incorporated into CM to mimic the *in vivo* extracellular environment, guiding the adhesion, proliferation and differentiation of cells. An ideal scaffold should be low-cost, edible or biodegradable and able to provide biochemical, physical and mechanical cues to direct cell behaviour (Bomkamp et al., 2022).

Innovative approaches are needed to lower the cost of CM production while mimicking the textural experience of complex meat products. One approach to achieve this is through implementing the use of agricultural side-stream as CM inputs (Hubalek et al., 2022; Perreault et al., 2023; Flaibam et al., 2024; Xiang and Zhang, 2023). This review aims to provide insights into how agricultural side-streams could serve as low-cost inputs for cultivating meat (Fig. 1). The underlying hypothesis for this concept is that plant-based materials contain nutrients and bioactive compounds which can be used in cell media and physical matrices which can be used as cell scaffolds. This underutilised resource could provide efficient, sustainable and low-cost production inputs enabling the commercial realisation of CM.

2. Cultivated meat production

The production method for CM begins with a biopsy being taken from a live animal and the cells of interest being cultivated (Goswami et al., 2023). These cells are rapidly expanded in a suitable nutrient medium before differentiation is induced to produce the muscle fibres or adipose tissue of interest (Post, 2012; Goswami et al., 2023). At this stage, a scaffold can be incorporated to provide texture and three dimensionality to the product. The resulting meat analogue is then harvested, processed and packaged as needed. Agricultural side-stream products could feed into this process in two main areas: as bioactive compounds and nutrients for cell media or as scaffolding materials.

2.1. Cell media for cultivating meat

Traditionally, basic cell medium is composed of glucose, amino acids, vitamins, inorganic salts, buffers and growth factors (Lee et al., 2024; O'Neill et al., 2021). However, additional supplementation is required to facilitate proliferation, differentiation and cell survival (Lee et al., 2024). This includes the use of the animal derived supplement, fetal bovine serum (FBS). FBS has been widely used in tissue engineering media due to its desirable composition of growth factors, hormones, amino acids, proteins, vitamins and inorganic salts (Gstraunthaler et al., 2013; Lee et al., 2022). It has also demonstrated effective results across most animal cell species, making it highly reliable (Gstraunthaler et al., 2013). However, FBS poses many concerns of use including risk of microbial contamination, variation between batches in quality and composition as well as rising ethical concerns due to its animal origin (Habowski and Sant'Ana, 2024; Batish et al., 2022). Furthermore, as the demand for FBS continues to rise, its price has surged to over USD 1000 per litre (Reiss et al., 2021). Since the use of FBS is antithetical to the aims of cultivating meat and price prohibitive, there is a need to develop serum-free media to allow the field to progress.

As shown in Table 1, developments have been made toward formulating chemically defined, serum-free media formulations for CM using insights from biomedical tissue engineering ([26–29].

Although the studies in Table 1 present the ability to develop effective chemically defined media (Kolkmann et al., 2022; Stout et al., 2022; Messmer et al., 2022; Skrivergaard et al., 2023), the cost of components used within these formulations limit their applicability for industrially

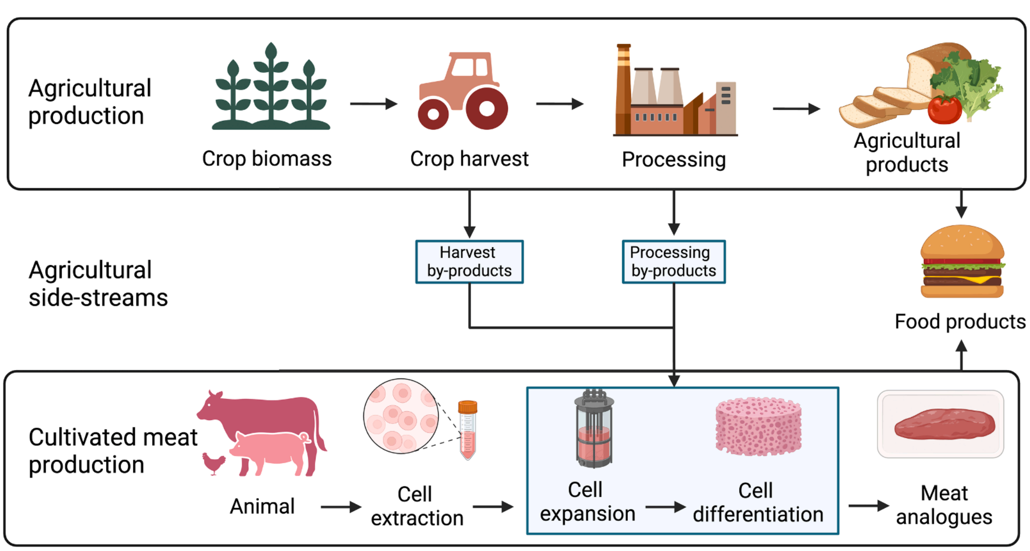

Fig. 1. The use of agricultural side-streams within cultivated meat production. Harvest and processing by-products can feed into the cell expansion and differentiation stages of cultivated meat production by providing cell media and cell scaffolding inputs.

Table 1
Chemically defined media formulations for the proliferation and differentiation of primary bovine satellite cells (BSCs).

Cell media purpose	Formulation	Reference
Cell proliferation	DMEM/F12, l-ascorbic acid 2-phosphate, fibronectin, hydrocortisone, GlutaMAX™, BSA, ITS-X, hIL-6, α-linolenic acid, FGF-2, VEGF, IGF-1, HGF, and PDGF-BB	(Kolkmann et al., 2022)
	Beefy-9: DMEM/F12, HEPES, insulin, l-ascorbic acid-2-phosphate, transferrin, sodium selenite, FGF-2, TGF-β3, NRG1 and human albumin	(Stout et al., 2022)
	Tri-basal 2.0+: DMEM/F-12, FGF2, fetuin, BSA and ITS	(Skrivergaard et al., 2023)
Cell differentiation	DMEM/F-12, EGF1, human serum albumin, l-ascorbic acid 2-phosphate, MEM Amino Acids Solution, NaHCO3, PSA, sodium selenite, Insulin, lysophosphatidic acid, transferrin and acetylcholine	(Messmer et al., 2022)

scaled production.

Hubalek et al. outlined components with the highest priority for replacement within cell media based on their cost and concentration required (Hubalek et al., 2022). They found that components with the highest priority for replacement in cell media are the proteins; albumin, transferrin and insulin which fall within the high cost and high concentration category. Following this are growth factors, a high cost, low concentration input. Hubalek et al. (2022) justify this as a second priority for replacement, as this expense can be reduced by utilizing fermentation systems in their manufacture, which are efficient and scalable (Hubalek et al., 2022).

By contrast, due to the high concentrations needed of albumin, transferrin and insulin, the sheer volume required will make them the primary cost drivers of media, even when a fermentation system is optimised to minimise costs (Hubalek et al., 2022). As cell media is expected to account for 40–60 % of CM production costs (Pasitka et al., 2024; Humbird, 2021), considering cheaper replacements to these proteins is important for competitive development of CM.

2.2. Scaffolding materials for cultivating meat

Another area where agricultural side-streams could be utilised is as scaffolding material in the CM process. Scaffolds are a necessary part of CM production as they replicate the *in vivo* extracellular matrix (ECM), providing a platform for cell adhesion, proliferation and differentiation (Nurul Alam et al., 2024). Scaffolds provide physical and biological support during tissue development via their mechanical integrity, flexibility and nutrition (Nurul Alam et al., 2024; Murugan et al., 2024; Yen et al., 2023). Furthermore, as is relevant for CM, a scaffold presents an opportunity to provide texture and three dimensionality to a final product, enhancing the meat-like sensory experience for consumers.

Scaffolds used for CM have additional constraints placed on them as compared to those used in a biomedical tissue engineering context. This includes a need for a low-cost production process with high volumes of input materials available (Perreault et al., 2023). As discussed previously, cost and volume are major considerations for commercialising CM, with all stages of the production process needing to be scaled (Rybchyn et al., 2023). Additionally, attention must be paid to the impact a scaffold has on the nutrition, colour, flavour and cooking properties of the final meat product (Bomkamp et al., 2022; Rybchyn et al., 2021). To compete with conventionally produced meat, consumers must be offered a comparable and desirable food. Moreover, the design of the scaffold must either be entirely edible to meet food-safety requirements or it must somehow be removed from the final product (Bomkamp et al., 2022). With these challenges in mind, there have been multiple effective approaches to designing scaffolds for cultivating meat utilising protein and polysaccharide components (Murugan et al., 2024; Wollschlaeger et al., 2022; Ben-Arye et al., 2020; Gershlak et al., 2017; Jones et al., 2021; Cheng et al., 2020; Thyden et al., 2022; Song et al., 2022; Jeong et al., 2024). Many agricultural side-streams are rich in these components (Good Food Institute 2023), providing favourable, low-cost materials for progressing CM scaffolding.

3. Agricultural side-streams to support cultivating meat

Within the agricultural value chain, crop biomass is grown and harvested before being processed into food products. During the harvesting and processing stages, residue plant-based by-products and waste-streams are created (Good Food Institute 2023; Girón-Calle et al., 2008). Although biogas is gaining traction as a use for these secondary products (Alengebawy et al., 2024), they are often used as low-value animal feed, animal forage and fertilizer, or they are disposed of as landfill mass or incinerated (Good Food Institute 2023; Almaraz-Sánchez et al., 2022). With millions of tons of agricultural waste discarded and burned annually, these disposal methods are costly for producers and environmentally damaging (Riseh et al., 2024). Moreover, approximately one-third of food produced for human consumption is lost or wasted globally, totalling around 1.3 billion tons per year (FAO, 2011). This highlights the need to optimise food supply chains to reduce wastage.

By valorising side-streams for cultivating meat, a circular bioeconomy is enforced, which can assist in reducing food-losses. This would contribute to achieving the United Nations Sustainable Development Goal 12; ensuring sustainable production and consumption patterns by 2030 (United Nations (UN) 2015). Additionally, this valorisation presents agricultural producers with new economic opportunities, decreasing production costs of the initial high-value crop product (Salvatore et al., 2024). As consumers are increasing looking for more ethical and environmentally friendly foods, the utilisation of agricultural by-products could increase positive consumer perception of cultivating meat (Dutra da Silva and Conte-Junior, 2024).

Currently, pharmaceutical grade materials are used for cultivating meat, reflecting the technique's origins from biomedical tissue engineering. These inputs are of high-cost due to their high purity. As CM aims to produce a food product, only feed or food grade ratings are required for CM inputs (Hubalek et al., 2022). Therefore, harvest and food processing residues are advantageous for cultivating meat as they are naturally feed and food grade materials. These inputs would be significantly lower in cost than pharma grade supplements that are currently used. A report by the Good Food Institute (GFI) estimated that key side-streams of interest as cell media supplements, *i.e.* soy meal, canola meal, corn DDGS, barley brewer's spent grains and corn gluten meal had raw unit costs of $0.53, $0.49, $0.25, $0.49 and $0.60 USD per kilogram respectively (Good Food Institute 2023). By contrast, current cell media supplements; albumin, transferrin and insulin are estimated to cost; $45,000, $400,000 and $380,000 USD per kilogram respectively (Specht, 2020; Stout et al., 2023). If products of these agricultural side-streams could replace chemically defined supplements, extreme cost savings would occur for CM production.

Moreover, the high availability of input materials needed to support large-scale production of CM is of added importance. As global agriculture is increasing, millions of tons of by-products and waste are generated annually (Riseh et al., 2024). These high volumes indicate agricultural side-streams as potentially abundant resources, which could support CM scale-up. With this in mind, Table 2 displays cell media supplements and cell scaffolds developed from agricultural side-stream

Table 2
Agricultural side-streams used as inputs for cultivated meat production.

Agricultural side-stream	Processed form	Application	Reference
Rapeseed meal	Rapeseed protein isolate	Albumin replacement in serum-free cell media	(Stout et al., 2023)
Soybean meal	Protein hydrolysate (enzymatic hydrolysis)	FBS replacement for serum-free cell media	(B. Flaibam et al., 2024)
	Protein hydrolysate (microbial fermentation)	FBS replacement for serum-reduced cell media	(Kim et al., 2023)
Okara	Hydrolysed extract (microbial fermentation)	FBS replacement for serum-reduced cell media	(Teng et al., 2023)
Peanut meal	Protein hydrolysate (enzymatic hydrolysis)	FBS replacement for serum-free cell media	(B. Flaibam et al., 2024)
Textured soy protein flakes	Porous protein material	Cell scaffold	(Ben-Arye et al., 2020)
Peanut wire-drawing protein	Porous protein material	Cell scaffold	(Song et al., 2022)
Corn husks	Decellularised plant material	Cell scaffold	(Perreault et al., 2023)
Jackfruit rind	Decellularised plant material	Cell scaffold	(Perreault et al., 2023)
Cereal prolamins	3D printing bioink	Cell scaffold	(Su et al., 2023)
Zein	3D printing bioink	Cell scaffold	(Su et al., 2023)

materials for use in CM. To date, no techno-economic assessment has been conducted on the ability for agricultural side-streams to support large-scale CM production.

The following sections provide further detail into the use of plant-based materials in cell media and cell scaffolding to provide insight into how agricultural side-streams could support CM production.

4. Agricultural side-streams as inputs for cell media

4.1. Protein isolates

The key purpose for agricultural side-streams in the development of cell media is to source low-cost protein and amino acids to replace high-cost, pharma-grade protein media supplements (Specht et al., 2018). Stout et al. used this insight, forming protein isolates from the oilseed processing residues of Inca peanut, soybean, rapeseed and cottonseed (Stout et al., 2023). The study then compared the growth promotion of these oilseed protein isolates to recombinantly produced albumin within the serum-free medium, Beefy-9. The rapeseed protein isolate (RPI) medium demonstrated enhanced performance to the albumin medium with BSCs exhibiting 11.7 population doublings compared to 10.6 over 13 days of growth (Stout et al., 2023).

In a later study by the same group, protein isolates from low-cost sources were tested as albumin replacements for growing Atlantic Mackerel cells of the MACK1 cell line (Lim et al., 2024). This included protein isolates from lupin, pea, rapeseed cake, chlorella, red algae, spirulina and yeast flakes. In serum-free conditions, no change or decreased growth was observed. However, when 2.5 % FBS was added, rapeseed protein isolate demonstrated significantly improved growth promotion ($p < 0.001$) (Lim et al., 2024). The findings from both studies (Stout et al., 2023; Lim et al., 2024) highlight the applicability for rapeseed protein isolate to act as a potential albumin replacement within cell media across CM relevant cell types. However, a low protein extraction yield was observed by both studies (Stout et al., 2023; Lim et al., 2024). Additionally, Lim et al. speculate that the alkaline protein precipitation method used, may change the molecular weight profile of the protein isolate, impacting cell growth promotion (Lim et al., 2024). Research into improving protein extraction methods and the yield obtained is needed to progress using protein isolates from agricultural processing residues in cell media.

In general, processing residues in their raw form contain potentially undesirable components for cell media such as fibre, polyphenols or phytic acids. These compounds may interfere with the growth promoting ability of the proteins present (Chabanon et al., 2007). To remove these antinutritive compounds, forming a higher purity protein fraction is desirable such as a protein concentrate or protein isolate (Good Food Institute 2023; Stout et al., 2023; Chabanon et al., 2008). This may improve the availability of these side-stream sourced proteins to contribute bioactive and nutritional value to cell media.

4.2. Protein hydrolysates

An additional processing step, which can make proteins from agricultural processing residues more favourable for cell growth is hydrolysis (Flaibam et al., 2024; Kim et al., 2023; Teng et al., 2023; Obaidi et al., 2021; Charlesworth et al., 2024). By hydrolysing proteins, smaller peptides and amino acids are produced which demonstrate increased functionality (Girón-Calle et al., 2008). Furthermore, peptides in cell media have previously demonstrated an ability to exhibit bioactive properties such as antiapoptotic, antioxidant and immunomodulatory effects as well as antibacterial properties (Ho et al., 2021; Amirvaresi and Ovissipour, 2024).

Commonly, enzyme hydrolysis is used as this enables specificity in which peptide bonds are broken (Flaibam et al., 2024; Lobo-Alfonso et al., 2010). Nevertheless, in a study by Kim et al., soybean meal protein was hydrolysed using Alcalase (Kim et al., 2023). The resulting hydrolysate was able to replace up to 50 % of FBS in cell media while maintaining the proliferative and differentiative capacity of pig muscle stem cells.

The degree of hydrolysis and the peptide fractions achieved are variable depending on the protein substrate, enzyme, and reaction conditions applied (temperature, pH, enzyme/substrate ratio and protein concentration) (Chabanon et al., 2007; Flaibam and Goldbeck, 2024). As demonstrated by Flaibam et al., soybean meal and peanut meal exhibited different degrees of hydrolysis even when the same reaction conditions and enzyme were applied (Flaibam and Goldbeck, 2024). Moreover, Alcalase 2.4 L® enabled a maximum degree of hydrolysis for both substrates with 22.44 % for soybean meal protein and 16.44 % for the peanut meal protein. However, a study conducted by Chabanon et al., the degree of hydrolysis for a rapeseed meal protein isolate was greatest using Pronase (19.2 %), while Alcalase 2.4 L ® only achieved 13.3 %. This can be attributed to different reaction temperatures, pH values, protein substrates used, and concentrations differing between the two studies (Chabanon et al., 2008; Flaibam and Goldbeck, 2024). Therefore, to compare the degree of hydrolysis achieved across processing residues, identical hydrolysis conditions must be achieved to account for variability.

In a separate study by Flaibam et al. (2024) the Alcalase 2.4 L® hydrolysed soybean meal and peanut meal proteins developed previously (Flaibam and Goldbeck, 2024) were added to a basal medium for growing L929 murine fibroblast cells. Both hydrolysates were able to significantly increase cell growth compared to the negative control. However, this growth did not match the positive control containing 10 % FBS (Flaibam et al., 2024). Remarkably, when the hydrolysates were added to media containing 2.5 % FBS, superior growth was observed compared to the 10 % FBS containing control.

Furthermore, the rapeseed hydrolysate developed by Chabanon et al. (Chabanon et al., 2008), demonstrated an ability to replace transferrin, insulin and albumin (TIA) supplementation within a serum-free medium for growing CHO cells, compared to the medium depleted of TIA. However, the cell growth exhibited was not to the same extent as the medium containing TIA (Chabanon et al., 2008). Nonetheless, these studies (Chabanon et al., 2008; Flaibam et al., 2024) showcase the potential for protein hydrolysates from agricultural processing residues to replace expensive media supplements.

Commonly, enzymatic hydrolysis is considered less harsh than acid hydrolysis, which can destroy vitamins and sensitive animo acids due to the combination of strong acid and high temperature (Lobo-Alfonso et al., 2010). However, acid hydrolysed plant materials have demonstrated an ability to enhance cell growth in serum free conditions (Charlesworth et al., 2024). As acid hydrolysis presents a lower cost technique, further exploration is warranted on the production of other hydrolysates through this method.

In addition, combining hydrolysates from different raw material in cell media, has also demonstrated an ability to impact animal cell growth (Flaibam et al., 2024). Although little exploration has been undertaken, using multiple hydrolysates from different agricultural side-streams may prove beneficial as this variation may result in a range of peptide products and amino acids within the cell media.

4.3. Fractionation of protein hydrolysates

Fractioning protein hydrolysates based on molecular weight (MW) into size grouped peptides and amino acids enables a more controlled peptide supplement to be achieved (Teng et al., 2023; Farges-Haddani et al., 2006). This enables increased nitrogen matter within the media supplement, decreasing the presence of potentially antinutritive components while also decreasing the heterogeneity of the initial hydrolysate composition (Farges-Haddani et al., 2006).

Farges-Haddani et al. found that the level of processing applied to rapeseed hydrolysate significantly varied CHO cell growth when added as a supplement to cell media (Farges-Haddani et al., 2006). The acid-precipitated hydrolysate without fractioning displayed an inhibitory effect on cell growth. This was speculated to be due to the sample's lower purity, with antinutritive compounds potentially present within the solution (Farges-Haddani et al., 2006). In contrast, one of the nano- and ultra- filtrated samples displayed an enhanced final cell density (6×10^5 cells/ml) compared to that of the reference media (4.2×10^5 cells/ml) (Farges-Haddani et al., 2006). It was hypothesised that this growth-promotion was due to the fraction's composition of small peptides (<500 Da) and large peptides (500–5000 Da) with the smaller peptides acting as nutrients and the larger peptides behaving as growth factors with bioactive properties (Farges-Haddani et al., 2006). The impact of fractioning fermented okara extract (a soy by-product) has also been explored (Teng et al., 2023). Similar results were observed, where fractioning the okara hydrolysate led to increased cell viability in C2C12 cells (Teng et al., 2023). However, in both studies (Teng et al., 2023; Farges-Haddani et al., 2006), the proteome profiles of the fractions were not analysed. Identifying and characterising these peptones and peptides is an important future step in progressing the use of fractioned hydrolysates.

4.4. Processing of agricultural by-products for use in cell media

To improve the make-up of agricultural processing residues for use as cell media supplements, three distinct steps have been identified; increasing protein purity, undergoing hydrolysis and fractioning of the resulting hydrolysate (Fig. 2).

As discussed throughout this section, cell growth has been observed using agricultural residues without employing all three steps. Protein isolates demonstrated cell growth without needing hydrolysis or ultrafiltration (Stout et al., 2023; Lim et al., 2024). Simultaneously, non-purified hydrolysates with and without ultrafiltration promoted cell growth (Chabanon et al., 2008; Flaibam et al., 2024; Teng et al., 2023; Farges-Haddani et al., 2006). However, each step adds additional costs and complexity to the cell media production process. As commercialising CM requires low costs and crude processing, all added complexity to the process must be evaluated to ensure its necessity. It is important that future research evaluates and identifies the most appropriate processing of agricultural side-streams for cell media use to maximise cell growth promotion while minimising complexity and costs.

It has also been observed that hydrolysates from agricultural processing residues promote cell growth in low concentrations but exhibit cytotoxicity at increased levels (Stout et al., 2023; Teng et al., 2023; Andreassen et al., 2020). This may be due to beneficial compounds becoming cytotoxic at high concentrations (Teng et al., 2023). Similar findings have been observed when incorporating hydrolysates of non-agricultural origin including insects and cyanobacteria (Batish et al., 2022; Ghosh et al., 2023). This highlights the need to test a range of concentrations when assessing the potential of a protein hydrolysate for use in cell media to ensure maximal potential cell growth is achieved.

In addition, little exploration has occurred in using side-stream materials as cell media inputs beyond the use of proteins and amino acids. As cell media also provides energy and additional nutrients, this could involve the incorporation of side-streams for glucose, vitamins and minerals. However as lowering the cost of cell media is the main priority for scaling up CM production, the replacement of the most expensive cell media components (proteins and growth factors) is of the highest priority. This favours the use of side-stream proteins as replacement sources of FBS nutrients and bioactive compounds (Hubalek et al., 2022).

5. Agricultural side-streams as scaffolding materials

Within agricultural food production, both the protein and the polysaccharides from product processing and from harvest stage can be used to form CM scaffolds (Fig. 3). The cell wall of higher order plants is comprised of polysaccharides including cellulose, hemicellulose and lignin (Brethauer et al., 2020). Harvest waste is rich in these biopolymers and with approximately 3.8 billion metric tons of agricultural harvest waste produced annually, there is an abundant global source (Perreault et al., 2023). Fresh fruit and vegetable produce, which is declared unsellable due to damage or unappealing aesthetic features, could also be used as source of polysaccharides for scaffolding.

5.1. Polysaccharide-based decellularised scaffolds

One method of scaffolding utilises polysaccharides from agricultural side-streams through a process of decellularisation. This technique removes the cellular contents and DNA from the plant material, leaving

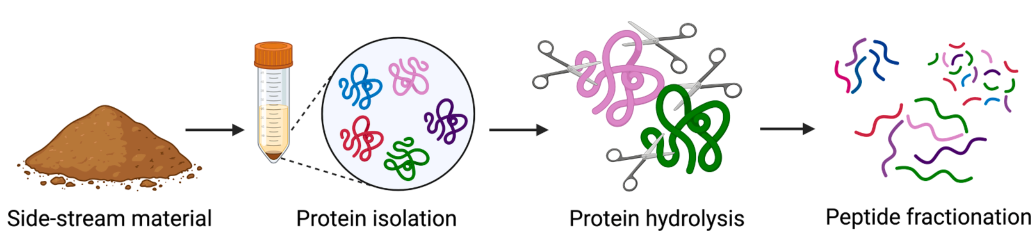

Fig. 2. Processing techniques applied to agricultural side-stream materials for use as protein and growth factor replacements within cultivated meat cell media. This includes producing a protein isolate, undertaking protein hydrolysis and separating peptide fractions.

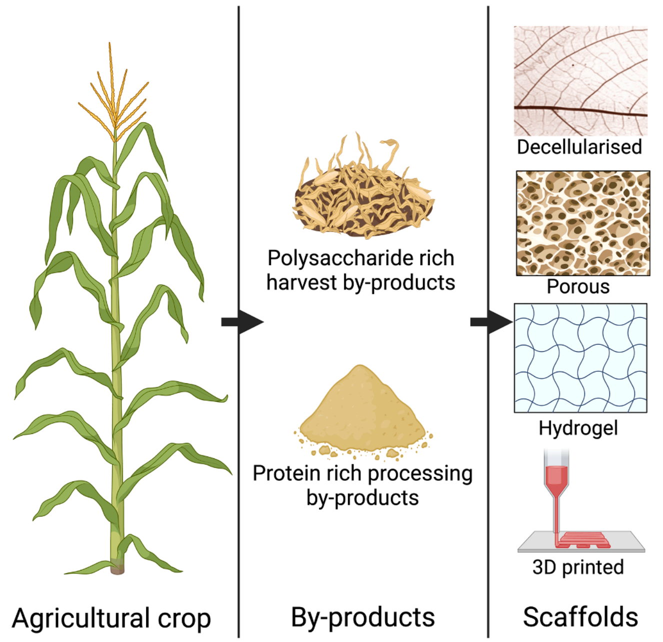

Fig. 3. Protein and polysaccharide components from harvest and processing by-products as cell scaffold materials. These components can be used to develop various scaffold structures for cultivated meat including decellularised scaffolds, porous scaffolds, hydrogel scaffolds and three-dimensional (3D) printed scaffolds.

the lignocellulose structure (Murugan et al., 2024; Rybchyn et al., 2023; Gershlak et al., 2017; Jones et al., 2021; Cheng et al., 2020; Thyden et al., 2022).

Decellularised plant scaffolds can also be used to support cell differentiation and the formation of the final CM product. This has been demonstrated using scaffolds formed from spinach, green onion, and apple (Jones et al., 2021; Cheng et al., 2020; Hickey et al., 2018). Furthermore, porcine adipose-derived mesenchymal stem cell muscle and fat were successfully co-cultured on a decellularised asparagus scaffold (Murugan et al., 2024). The uncooked CM displayed a similar texture to the raw pork loin control. However once pan fried, the CM displayed decreased hardness and chewiness (Murugan et al., 2024). Although textural improvements can be made, the production of a co-cultured CM product using a decellularised plant scaffold is a significant milestone demonstrating the applicability of this technology for commercialising CM.

Agricultural harvest residues and inedible food waste have also been explored as decellularised scaffolds (Perreault et al., 2023). Perreault et al. investigated the use of corn husks and jackfruit rinds as scaffold materials in a simulated bioreactor environment (Perreault et al., 2023). Both scaffolds were successfully able to attach BSCs and quail myoblast cells (QM7) (Perreault et al., 2023). Furthermore, bead-to-bead transfer was successfully enabled, where cells migrate from populated scaffolds to unpopulated scaffolds (Perreault et al., 2023). Due to the jackfruit rind's loose fibrous structure it was deemed the more favourable scaffolding material as it exhibited a greater similarity in stiffness to native bovine tissue (Perreault et al., 2023). However, the study hypothesised that the scaffold mechanics observed would likely be altered by the additional co-culturing of adipose and connective tissues with the BSCs, which would occur in a more complex CM product (Perreault et al., 2023).

A potential advantage of decellularising agricultural side-streams is the use of simplistic and low-cost processing techniques. Decellularisation can be achieved using common food industry detergents and the process could be locally implemented on farms, streamlining scaffold production while minimising unnecessary resource and labour use (Thyden et al., 2022). An additional benefit is the presence of cellulose, an insoluble fiber within the final product (Thyden et al., 2022). As conventional meat has no fiber content, this would enhance the fiber content for CM products compared to what is currently provided, presenting a potential nutritional benefit.

Although the decellularised plant scaffolds discussed exhibited strong cell attachment to the scaffolds (Perreault et al., 2023; Murugan et al., 2024; Thyden et al., 2022), this may be due to the presence of ECM proteins within the serum fraction of the growth media. As ideal cell media should contain no animal derived components, it would be beneficial to test these scaffold materials within serum-free media to determine if the polysaccharide structures can support cell attachment without the addition of animal derived adhesive proteins.

5.2. *Porous scaffolds*

Proteins from agricultural processing residues can be used as porous scaffolds for growing CM relevant cell types (Ben-Arye et al., 2020; Song et al., 2022; Xiang et al., 2022; Wei et al., 2023). In the native muscular environment, a honeycomb-like structure called the *perimysium* provides mechanical support to the muscle tissue (Ben-Arye et al., 2020). Creating an edible porous scaffold from protein, mimics this cellular environment for cells to grow on. Additionally, a soft gel, the *endomysium* fills the *perimysium*. The *endomysium* in contrast, can be mimicked *in vitro* by the deposition of ECM by cells (Ben-Arye et al., 2020). Ben-Arye et al. used textured soy protein to mimic this *perimysium* structure for cultivating meat (Ben-Arye et al., 2020). The study demonstrated the ability for BSCs, bovine smooth muscle cells and bovine endothelial cells to be co-cultivated within the scaffold. This tri-culture system supported myogenic differentiation and the formation of a complex ECM matrix, which mimicked the *in vivo endomysium*. As textured soy protein is naturally porous, it does not require further modification, minimising processing costs and increasing its applicability for scaled up production (Ben-Arye et al., 2020).

Similarly, peanut wire-drawing protein, a by-product of peanut oil production has been used to construct a porous scaffold for cultivating fat from porcine adipose-derived mesenchymal stem cells (Song et al., 2022). The cultivated fat displayed similarities to raw porcine subcutaneous adipose tissue in both texture and volatiles present (Song et al., 2022). These sensory properties were not tested after cooking the cultivated fat which may alter the results observed.

5.3. *Bioinks for 3D printed scaffolds*

3D printed scaffolds could make use of protein sourced from agricultural processing residues to form functional bioinks. 3D printing is an additive manufacturing process with potential for use in complex CM formation, although limited by scale-up. This production method enables the formation of scaffolds with specific and controlled layered structures (Gurel et al., 2024). The technology could assist in producing desirable thick pieces of muscle as opposed to the current thin monolayer structures achieved (Ianovici et al., 2022). As cells are encapsulated within the 3D print bioink, an even cell distribution is achieved throughout the produced scaffold, a challenge currently facing other types of scaffold use (Ianovici et al., 2022).

Traditionally, a protein-polysaccharide bioink has been employed with agricultural processing residues explored as sources of protein within these hydrogel structures (Wollschlaeger et al., 2022; Su et al., 2023). Su et al. utilised prolamin proteins from cereals and zein, a protein by-product of corn processing, to produce a bioink for 3D printing (Su et al., 2023). The formed hydrogel demonstrated an ability to support porcine skeletal muscle satellite cells to proliferate and differentiate (Su et al., 2023). However, the seeding of cells was performed post-printing, with no investigation into cellular printing. Such post-printing cell addition is unfavourable as it restricts the product thickness and evenness of the cell distribution achieved (Ianovici et al., 2024).

By contrast, Ianovici et al. successfully employed cellular 3D printing to produce cell inlayed scaffolds from pea protein isolate and modified alginate. This bioink enabled the formation of well-defined geometries and the printing of both BSCs and bovine mesenchymal stem cells with subsequent cell proliferation and differentiation observed (Ianovici et al., 2022). Culturing of these two cell types together on the same scaffold was not attempted.

Building on this, in a separate paper, Ianovici et al. then improved the 3D printing method with a focus on forming multicellular, thick and fibrous structures which resemble a scaled-down rib-eye structure (Ianovici et al., 2024). BSC and BMSC were successfully incorporated into the previously formed pea protein isolate and alginate bioink. The separate bioinks were then printed into different areas of the structure forming distinct marbled muscle and fat sections (Ianovici et al., 2024). Investigating the formation of thicker multicellular constructs, the cell viability and cellular activity significantly decreased when attempting to cultivate cells in a 1 cm thick structure compared to a 0.5 cm thick structure (Ianovici et al., 2024). This was expected due to the suggested inadequate transfer of nutrients, waste and gas in the thicker structure.

Although pea protein itself is not from an agricultural side-stream, these studies demonstrate the applicability of plant-based proteins as inputs for 3D printing bioinks for CM scaffold design (Ianovici et al., 2022; Ianovici et al., 2024). The use of zein and cereal prolamins, which are agricultural processing residues (Su et al., 2023), demonstrates that proteins can be used from abundant and low-cost agricultural side-streams, while providing functionality.

5.4. Protein-based fiber scaffolds

Zein has also been used to provide cytocompatibility to an alginate-based hydrogel fiber scaffold (Jeong et al., 2024). As anchorage-dependent cells lack the receptors to recognise alginate, alginate alone cannot support their proliferation and differentiation. By coating the alginate hydrogel fibers with the hydrophobic zein, high cell adhesion, proliferation and differentiation of C2C12 cells was observed (Jeong et al., 2024). The zein-alginate fibers were able to be bundled and stretched, with cells demonstrating tightly packed, unidirectional muscular alignment, resembling *in vivo* muscle formation (Jeong et al., 2024). Using this scaffold, Jeong et al. separately cultivated bovine muscle, fat and vessel cells and then assembled the cells into one product (Jeong et al., 2024). After pan-frying, the multi-cellular structure remained intact, providing a desirable fibrous texture (Jeong et al., 2024). This study demonstrates success in leveraging the functionality of an agricultural processing residue protein to form an impressive, multicellular CM product. This is a significant achievement which could serve as a model for implementing other processing by-product proteins to progress CM scaffold design.

Through incorporating low-cost proteins into porous, 3D printed and hydrogel fibrous scaffolds, there is the potential for added protein content within the final food product which would assist in increasing the protein content of CM products (Ianovici et al., 2022). This is a high priority for ensuring the success of CM, as *in vitro* developed products will have to present comparable nutritional contents to that of traditional meat.

5.5. Edible film scaffolds

The advantage of a film scaffold structure is the ability to overcome oxygen and nutrient diffusion limitations associated with constructing thicker scaffolds while utilising a patterned surface topography to encourage cellular interactions (Xiang et al., 2022). Furthermore, individual film scaffolds can be layered together to construct larger meat analogue structures (Shahin-Shamsabadi and Selvaganapathy, 2022). Mariano et al. formed a novel edible film scaffold utilising the self-assembly properties of soy extract, with no added chemical crosslinking agents (Mariano et al., 2024). The scaffold production process used minimal inputs and simple, inexpensive techniques, increasing the usability of the scaffold within hypothetical mass production. Multiple hypotheses have been posed to explain soy's ability to form gel films including protein denaturation, endothermic polymerisation and lipid-protein interactions (Mariano et al., 2024; Zhang et al., 2018; Wu and Bates, 1972). C2C12 cell attachment to the scaffold and myotube formation were demonstrated. However, the scaffold was unable to withstand the contractile forces generated by the myotubes. This led to scaffold degradation and the inability to facilitate further contractions as part of the formation of muscle (Mariano et al., 2024). Improving the mechanical stability presents a key area for improving the scaffold's usability.

Edible films constructed from wheat glutenin protein also displayed degradation during cell differentiation (Yao et al., 2024). During this time ECM proteins such as collagen were generated by the cells contributing to the final product elasticity and strength. Achieving sufficient mechanical properties in the final product involves an interplay of scaffold-cell interaction and the synthesis of contributing proteins.

Although both film scaffolds demonstrate the biocompatibility of soy and wheat derivatives (Mariano et al., 2024; Yao et al., 2024), the testing of these scaffolds in serum growth media may mask the source of cell adhesion. It is unclear whether the scaffold itself assists cell adhesion or if the adhesive proteins in serum are adsorbing to the scaffold surface. In this case, the use of the scaffold may be dependent on the presence of cell adhesive factors within the growth medium. Further research is necessary to clarify the source of cell adhesion within plant-based scaffolds.

6. Challenges of using agricultural side-streams

Agricultural side-streams present a promising resource for progressing CM, but many challenges still need to be resolved. The following section details these challenges and potential solutions.

6.1. Variation in side-stream composition

A major concern for using agricultural side-streams is their chemically undefined composition and the resulting variability. Batch-to-batch variability of side-streams may occur due to seasonal, regional or processing differences which then could alter performance in both cell media and scaffolding. In one study, Stout et al. produced two protein isolates from separate batches of rapeseed for use within serum-free media. (Stout et al., 2023). The results demonstrated a difference in cell growth between the two nutrient media used due to the variability between the batches of rapeseed (Stout et al., 2023).

Unfortunately, this reality could limit the reproducibility and repeatability of producing CM using agricultural side-streams (Flaibam et al., 2024). Currently, there is little research available into minimising batch-to-batch variability of agricultural side-streams for use within CM production. However, fractioning side-streams based on molecular weight may aid refinement of side-streams while reducing variation (Teng et al., 2023).

Based upon the prevalent use of FBS, the issue of batch-to-batch variability is not unfamiliar for the biomedical field (Gstraunthaler et al., 2013). Shifting away from undefined components in cell media is ideal, however, using undefined agricultural side-stream components may be manageable considering the current system is reliant on undefined components. Nonetheless, further research is necessary to limit variation between batches of agriculturally derived components to increasingly provide reliable inputs for cultivating meat.

6.2. Supply chain complexity

The availability of agricultural side-streams can vary between seasons, geographic locations or due to climate change (Salvatore et al., 2024; Giulia et al., 2020). This can create fluctuations in supply which may prove challenging for scaling up production of CM. Additionally, some side-streams may need to be collected within a specific time-frame of use or maintain adequate storage conditions to avoid microbial growth and spoilage occurring. This could increase the logistical complexity of CM production.

6.3. Contamination

Agricultural side-streams could provide an entry point for contamination within CM production. Microbial contamination is a major risk for cell culturing but not a new challenge for tissue engineering. Studies having demonstrated the applicability of plant-based materials in CM while mitigating microbial contamination through applying disinfecting and sterilising techniques such as soaking in ethanol, autoclaving or filtering (Ben-Arye et al., 2020; Stout et al., 2023; Yao et al., 2024; Liu et al., 2025). However, agricultural side-streams present additional contaminants such as pesticides and heavy metals. Proper testing, processing and treatment of side-streams have to be applied to ensure food-safety standards and regulations are met in the final product (Salvatore et al., 2024).

6.4. Food allergens

The use of side-stream materials to produce CM could introduce a source of allergens into a mainstream product which is not inherently allergenic. As the presence of food allergies globally is increasing, novel food sources should assist in mitigating this risk (Wong, 2024). Soy and peanuts are considered two of the most common food allergens globally (Wong, 2024). Some consumers may also be allergic to the prolamin proteins found within cereals (Su et al., 2023). Using these side-streams as inputs for CM may limit the accessibility of the final product for global consumption. This is an important factor to consider when investigating the potential of side-streams as CM inputs. Additionally, before commercially producing CM, the allergenicity must be verified to ensure correct allergen labelling is provided, as per country specific guidelines (Flaibam et al., 2024).

6.5. Animal component free side-streams

Agricultural side-streams used in CM must be animal component free (ACF) to realise the full range of proposed benefits from this technology. Previously, Andreassen et al. utilised low-cost, food industry by-products within cell media for growing bovine skeletal muscle cells (Andreassen et al., 2020). This included using hydrolysates of chicken carcass, cod backbone, eggshell membrane, egg white powder and pork plasma (Andreassen et al., 2020). The results of the study revealed that serum-free media containing basal media (DMEM) with pork plasma hydrolysate were able to enhance cell proliferation by 48 % compared to cells grown in the control serum medium (Andreassen et al., 2020). The simplicity of this formulation and the high cell growth achieved by this short-term growth study is particularly promising. Animal derived by-products have also been explored for the development of micro-carriers (Andreassen et al., 2022). Andreassen et al. demonstrated the use of eggshell membrane and turkey collagen to successfully enable the attachment and proliferation of bovine skeletal muscle stem cells.

Although these studies support the valorising of food processing waste (Andreassen et al., 2020; Andreassen et al., 2022; Lee et al., 2024), by using animal derived components, many animal welfare and environmental issues associated with using FBS remain (Flaibam et al., 2024). If animal-products are used for the production of CM, this new industry would rely on the conventional livestock industry, making any progress of transitioning to CM questionable (Letti et al., 2021). However, as the shift away from relying on conventional agriculture will be over many decades, there may be a justification for using food-safe animal components within CM production in the interim to assist advancing CM technology. This being said, meaningfully progressing the CM sector toward achieving its animal welfare and sustainability goals will rely on all inputs being ACF.

7. Future prospects

To advance the development of cost-effective CM production, further research is required on the potential use of agricultural side-streams. With a variety of agricultural side-streams to investigate, high throughput testing should be optimised to minimise time and labour costs. Computational methods such as convolutional neural networks, multi-information Bayesian models and response surface methodologies have previously been used for optimising CM cell media and functional proteins (Skrivergaard et al., 2023; Cosenza et al., 2022; Gligorijević et al., 2021). In addition, it is important to not only consider the effectiveness of a side-stream for its intended purpose but also other external factors such as volume, environmental impact and cost (Good Food Institute 2023). Nikkhah et al. achieved this using a multi-objective artificial intelligence framework to optimise a reduced-serum media formulation considering; GWP, cost and cell-growth rate (Nikkhah et al., 2023). Therefore, utilising these technologies may enable a greater streamlined workflow for determining the most advantageous side-stream for use while considering multiple variables.

Some side-streams may provide multiple inputs for both cell media and scaffolding within the CM process. For instance, the formation of protein isolates from processing by-products for cell media leaves behind insoluble protein fractions, which could be useful within protein-based scaffolds (Stout et al., 2023). Corn husks have also been used as a form of decellularised scaffold while zein, a key corn protein has been used in hydrogel-based scaffolds (Perreault et al., 2023; Jeong et al., 2024; Su et al., 2023). Therefore, the applicability for agricultural side-streams to be used within cultivating meat is multifaceted. By employing different components of a side-stream as inputs, further economic value can be derived from specific side-streams.

To validate the potential economic benefits of using agricultural side-streams as inputs for CM, a techno-economic analysis (TEA) should be conducted. Although TEAs have been conducted for CM production previously (Negulescu et al., 2023; Pasitka et al., 2024; Humbird, 2021; Risner et al., 2021), a focus on agricultural side-stream inputs would enable a clear understanding of the impact utilising this resource could have.

Moreover, although not a focus of this review article, agricultural side-streams could also be used as potential smart packaging materials for the finished CM product (Adi et al., 2024). Processing residues including peels, pomace and seeds could be repurposed into bioplastics and biofilms, replacing plastic usage (Adi et al., 2024). This demonstrates an additional use case for agricultural side-streams to support the sustainable production of CM.

8. Conclusion

In conclusion, up-cycling agricultural side-streams could assist the scaling up of CM, aiding existing agricultural producers while decreasing global food losses. Using agricultural side-streams presents solutions to some of CMs most pressing challenges including sourcing low-cost, high-volume CM production inputs while minimising environmental impact. Agricultural side-streams could contribute to CM as sources of bioactive compounds and nutrients for cell media or as structural materials for cell scaffolds. Plant-based proteins and peptides have gained increased attention for their ability to support cell growth and reduce antioxidative stress (Stout et al., 2023; Kim et al., 2023; Teng et al., 2023; Charlesworth et al., 2024; Ho et al., 2021; Farges-Haddani et al., 2006; Mi et al., 2025). In addition, plant-based protein and polysaccharide structures can provide matrices for guiding cell growth on three dimensional structures (Perreault et al., 2023; Wollschlaeger et al., 2022; Ben-Arye et al., 2020; Gershlak et al., 2017; Jones et al., 2021; Cheng et al., 2020; Song et al., 2022; Xiang et al., 2022; Wei et al., 2023; Ianovici et al., 2022; Su et al., 2023; Kim et al., 2024; Kim et al., 2024; David et al., 2024). By using agricultural side-streams as inputs for CM, an opportunity presents itself to transform the global food system. A circular bioeconomy would be in reach, which could decrease the environmental impact of both crop and meat production, reduce global food loss and introduce new economic opportunities for agricultural producers.

Ethical statement

This is a review article, no studies in humans and animals have been conducted for this work.

CRediT authorship contribution statement

Charlotte Charteris: Writing – review & editing, Writing – original draft, Conceptualization. **Johannes le Coutre:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Johannes le Coutre reports a relationship with University of New South Wales that includes: employment.

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Data availability

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

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