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Plant proteins for human consumption – from local to global opportunities and challenges in a full value chain context

Eva Johansson[a,*], Georg Carlsson[b], Åsa Grimberg[a], William R. Newson[a], Thomas Prade[b], Sara Spendrup[c], Sven-Erik Svensson[b]

[a] Department of Plant Breeding, The Swedish University of Agricultural Sciences, Box 190, SE-234 22, Lomma, Sweden
[b] Department of Biosystems and Technology, The Swedish University of Agricultural Sciences, Box 190, SE-234 22, Lomma, Sweden
[c] Department of People and Society, The Swedish University of Agricultural Sciences, Box 190, SE-234 22, Lomma, Sweden

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ABSTRACT

Environmental concerns together with a growing global population and health benefits call for an increased use of plant proteins in the human diet. This review paper summarizes opportunities and challenges of such an increased use and reveals the way forward for plant proteins for human consumption. The results clearly emphasize the increased consumer interest, especially in certain consumer segments, of the use of plant protein-based food alternatives, the positive environmental impact of the use of such alternatives and the wide array of crops available to be developed into novel protein-rich food choices. Major challenges identified are; i) how to combine different plant sources to receive highly nutritional and tasty food products, ii) how to produce crops with a high and easily extractable protein content, which simultaneously contain low amount of unwanted components such as antinutritional factors, iii) environmental effects of the production of the plant protein to be utilized for the protein-rich food items, and iv) economic feasibility of the plant protein food products. Opportunities exist to develop the processing methods for protein fractionation, although consumer preferences, environmental effects, economic feasibility and impact on protein functionality have to be taken into account in such developments. Plant breeding is summarized as a major way forward to target crops high in easily available protein and low in unwanted components, thereby fitting consumer desires simultaneously as contributing to economic feasibility and reduced environmental impact. Cultivation is the main source of the environmental impact in the plant protein value chain, while protein content, composition and extractability affect consumer preferences and both their economic and environmental impact.

1. Introduction

Protein is a key nutritional component within the human diet and is required for a range of body functions (WHO, 2007). Human daily requirement reference values for protein consumption are 60–80 g for an adult person (Trumbo et al., 2002; FNB, 2005), although, requirements differ based on age, weight, gender and physical activity. Therefore, it has been suggested (Richter et al., 2019) that the daily requirement should be based on age and body weight, resulting in that infants should have the highest daily requirements (1.4–2.5 g protein per kg body weight) while adults have the lowest (0.8 g protein per kg body weight). Currently, the global mean daily protein consumption is around 80 g per person (Henchion et al., 2017), indicating no absolute need to increase the total world protein consumption. However, opportunities for protein intake across the global population are not equal, i.e. mean daily protein consumption is 100 g per person in the developed countries, while it is 78 g per person in developing countries (Henchion et al., 2017). Also, in low income countries, the differences in protein intake among various sections of the population often differs more than in middle and high income countries. Thus, poor and vulnerable people often have a lower total intake of proteins, and often also from a single source (e.g. from maize) than those being wealthier (Smith et al., 2024). However, even in the high-income countries, certain segments, e.g. elderly, are known to often consume a too low amount of protein in relation to requirements (Lonnie et al., 2018).

Protein consumption has increased from a global daily mean of 60 g per person in the early 1960ies to around 80 g per person today, simultaneously as the world population has increased significantly,

* Corresponding author.
E-mail address: eva.johansson@slu.se (E. Johansson).

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resulting in a current demand of over 200 million tonnes of protein globally per year (Henchion et al., 2017). At the same time, a sharp reduction in greenhouse gas (GHG) emissions from human activities, including *e.g.* reduced use of fossil energy and nitrogen fertilizers in agriculture, reduced losses or even increases in soil carbon and reduced GHG emissions from livestock, is a necessity to limit the predicted climate change (Lamb et al., 2021). A range of studies have verified the particular higher climate cost of the production of animal-based proteins compared to protein-rich plant-based food sources (Cellura et al., 2022). These facts have also reached consumers, resulting in trends to partly replace animal-based food with plant-based alternatives for satisfying the human protein needs (Aschemann-Witzel and Peschel, 2019). Besides the consumers' will to contribute to a better climate, also the health effects, claimed by several studies, from replacing animal derived proteins in food with plant-based alternatives, has contributed to this trend (Lonnie and Johnstone, 2020).

The protein source plays an important role while discussing human daily protein requirement. Generally, the total amount of protein is not the limiting factor but instead some of the so called essential amino acids (Reeds, 2000). Protein with a high level of essential amino acids is found in most animal-based food products. The plant proteins consist of four different types of proteins; albumins, globulins, prolamins and glutelins (Rasheed et al., 2020), classified basically by their solubility in various solvents (Osborne, 1907). The two latter types are primarily present as storage proteins in the grains of cereals (Rasheed et al., 2020), while albumins and globulins are the major storage proteins in the grains of legumes (Singh, 2017). Prolamins and glutelins are known to be low in essential amino acids (especially lysine), while most of the albumins and globulins have a more sufficient essential amino acid composition (as concerns lysine, arginine, aspartic acid, threonine and tryptophan) for human consumption (Johansson et al., 2023a). Thus, legumes are known as good sources of proteins for human consumption (Siddiqi et al., 2020) although most show limiting amounts of the essential amino acids methionine, tryptophan and cysteine (Singh, 2017), while cereals are low in the essential amino acids lysine and threonine (Temba et al., 2016; Poutanen et al., 2022). Thus, intake of protein from different grain sources might contribute complementary amino acids for the benefit of human health (Han et al., 2021). A large part of the plant-based proteins consumed are present in the grains of the plants, which are often rather dense in protein content (approximately 10–40 %) as the proteins are a storage compound of nutrition for the germinating grain (Rasheed et al., 2020). Also, tubers of potatoes, seed-cakes of oil crops and green biomass (photosynthetic green parts of plants that can be harvested, *e.g.* ley or residual leaves from root and tuber crops) are good protein sources for human consumption, although with a high starch (tubers) and water content (tubers, green biomass), thereby reducing protein concentration on a wet-mass basis (Chandrasekara and Josheph Kumar 2016). Additionally, several of the mentioned crops are not edible on a direct basis as a protein source for human consumption, since the digestibility might be low and the majority of them contain antinutritional factors (ANFs) or anti-taste compounds, that tend to end up in the protein fraction at extraction (Sim et al., 2021).

The high number of different crops (legumes, cereals, pseudocereals, potatoes, oilcrops and green biomass from various crops) that can serve as plant-based sources of protein for human consumption, opens a wide range of opportunities to support the consumer trend towards a diet with a higher share of plant-based food. However, research is required to understand how cultivation, plant breeding and processing can provide sustainable, nutritious, tasty, secure and safe plant-based food alternatives to the current animal-based products. Consumer desires, acceptance and perception have to be taken into account with the change in the food system. What crops and varieties should be utilized, and how should they be used in the cropping system, what novel characteristics should be included in novel varieties to fit the new products requested and how should the protein be fractionated and processed for products to reach the market? Furthermore, economic feasibility and environmental effects have to be evaluated for cropping systems, crops, varieties and products created for the plant-based food society.

The state-of-the-art research on novel plant-based food and systems is currently moving forward quickly due to the high interest from both consumers, politicians and industry. However, large gaps in the knowledge is still present, in particularly as regards systems studies, involving the whole value chain from field production to consumer, in order for a change to take place towards a larger share of plant-based protein in the human food system.

The aim with this paper was to describe, review and compile information about opportunities and bottlenecks along the whole value chain, including field production, plant breeding, processing methods, economic feasibility, environmental effects and consumer analyses, impacting the use of plant proteins for human consumption. Furthermore, the aim was to use a systems perspective in searching to understand and synthesize the current state-of-the-art knowledge in order to facilitate the description of future directions to take. For a holistic understanding of their potential, this manuscript is compiling results in a multidisciplinary context on a broad array of plant protein sources. An additional aim was to compare the local (Swedish), regional (Europe) and global (the World) context in terms of plant-based protein consumption and production. Sweden was chosen as the local case study as it is known as an outstanding country in Europe and the World and is defined as having a high quality of life and strong commitments to social welfare including equality, environmental concerns and trust in institutions (Sanandaji et al., 2023).

2. Consumer aspects on plant protein for human consumption

The consumption of meat has increased dramatically during the last 50 years and is currently above 300 000 tons per year globally, which according to IPCC (Intergovernmental Panel on Climate Change) is the direct reason for the need to shift consumption habits to mitigate climate change and reduce the ecological footprint (Pais et al., 2021). Therefore, an increased consumption of plant-based protein as an alternative to meat is being highlighted by international and national frameworks indirectly or directly encouraging such a development and adoption. Thus, the UN Sustainable Develoment Goals (UN, 2015) e.g. 2 – zero hunger, 12 – responsible consumption and production and 13 – climate action, contribute incentives for an increase in plant-based protein consumption. The push from FAO (the Food and Agriculture Organization of the United Nations) on pulses e.g. with the example of initiating the International year of pulses 2016 (FAO, 2016) is another such incentive. Additionally, the EU "Farm to Fork" strategy aiming at a more sustainable food system, including changes in food choices, profitability for companies and decreased climate impact, has identified a more plant-based diet as an important part of this transition (EC, 2020). The importance of protein crops has also been highlighted by the European Parliament by adopting a resolution on a European strategy for the promotion of protein crops (EP, 2023), although, there is at present a deficit of plant protein in the EU and it is not sustainable to rely on imports. Also, the tipping point, i.e. when a shift in consumption habit will contribute to a decrease in carbon footprint, is dependent on that a majority of the consumers actually eat plant-based instead of meat-based diets (Aschemann-Witzel et al., 2023).

A crucial step for the implementation of an increasingly sustainable (economic, environmental and social) food consumption (more plant-based and less meat protein) is an alteration of eating habits by consumers (Godfray et al., 2018; de Boer and Aiking, 2019, Graça et al., 2019; Willett et al., 2019). As illustrated in Fig. 1 (raw data given in Supplementary Table S1), the proportional intake of plant- and animal-based protein (incl. fish and egg) differs substantially between the global average consumption as compared to the consumption in Europe and Sweden. From a global perspective, as much as 60 % of the protein supply in 2019 was of plant origin, while in Europe and Sweden, the corresponding proportions were 43 and 35 %, respectively. Total

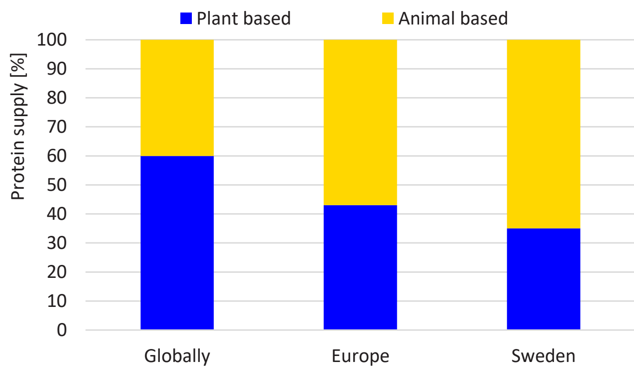

Fig. 1. Share of protein supply from plant and animal sources (FAO, 2022b).

protein consumption (g/capita/day) was also higher for Europe (104 g) and Sweden (108 g) as compared to the global amount (83 g; (FAO, 2022b)).

Thus, especially in high-income countries (which the majority of Europe represents), a transition towards higher proportions of plant-based protein in human diets is necessary to fulfil environmental goals related to *e.g.* resource use and climate impact (*e.g.* Willett et al. (2019). Despite a high environmental concern among Swedish consumers, this has not been transferred to a significant impact on the meat consumption, as shown in Fig. 1. For several years European and Swedish markets for both amount and product range of plant-based products have been steadily increasing, (Niva et al., 2017; Estell et al., 2021). However, during the last few years Swedish sales have decreased, a development mainly explained by inflation and price as well as arguments questioning the nutritional quality of plant-based products, compared to meat (AGFO, 2023). Similar findings are reported from the US retail which is also reporting declines in sales (GFI, 2024) for products rich in plant-based proteins.

Several studies state that drivers explaining why consumers buy plant-based protein are primarily linked to environmental and health arguments (Hartmann and Siegrist, 2017, He et al., 2020; Onwezen et al., 2021). However, some consumers do not change to a completely vegetarian diet, but instead the amount of vegetarian food in the diet increases gradually. An increase in this consumer segment has been identified in *e.g.* Sweden, where approximately 30 % of the population in 2021 had adopted a flexitarian (consumers who actively choose plant-based protein products, but also eat meat), food behaviour (Axfood, 2022). Changes in protein consumption by such a gradual increase in vegetarian food may be perceived less demanding as well as both reasonable and encouraging (Lacroix and Gifford, 2020; Dagevos, 2021).

Consumers who choose plant-based products, such as flexitarians, consist to a greater extent of women, and also the level of education tends to be higher as compared to those staying with a meat-based diet (Wozniak et al., 2020; Eckl et al., 2021; Deliens et al., 2022). Findings also show that the adoption of a more plant-based diet is more common among younger than older consumers (Stoll-Kleemann and Schmidt, 2017; Bryant and Sanctorum, 2021) and that female consumers are more inclined than male consumers to reduce their meat intake due to environmental concerns (Sanchez-Sabate and Sabaté, 2019).

Despite identified positive signs of change, there are also consumers who do not want to change their food choices, *e.g.* increase the proportion of plant-based protein. Drivers and barriers identified for these consumers have *e.g.* been linked to a bond with meat, and a perceived social limitation in eating plant based meat alternatives (Eckl et al., 2021). Additional explanatory factors are linked to unfamiliarity and lower sensory attractiveness of substitutes compared with meat (Hartmann and Siegrist, 2017; Stoll-Kleemann and Schmidt, 2017, Collier et al., 2021). Findings by Cliceri et al. (2018) highlight the importance of developing plant-based food that is perceived as positively hedonic as meat-based food. Looking at socio-demographic variables, several studies identify a gender gap, with men dominating the consumer group that prefers meat (Keller and Siegrist, 2015; Love and Sulikowski, 2018; Lemken et al., 2019; Rosenfeld and Tomiyama, 2021), as do also persons with a lower level of education (van Bussel et al., 2020).

Today's range of plant-based protein rich food can broadly be divided into two categories, plant-based meat alternatives (Estell et al., 2021) and less processed products, such as different types of pulses (edible seeds of grain legumes). More processed products are presently gaining momentum through *e.g.* media attention and interest from entrepreneurs and actors with financial power and investment initiatives (Blease, 2015; Smith, 2017, van der Weele et al., 2019). Also, a consumer resistance has been identified, towards replacing meat with the less processed plant-based, protein-rich products such as beans and peas (Lemken et al., 2019; Melendrez-Ruiz et al., 2019). Suggested explanatory factors for this consumer resistance are a long-term decline and neglect of use (within the western cuisine), and as a consequence the product category is now associated to poverty and being out of date (van der Weele et al., 2019). However, there is also a skepticism from consumers regarding taste, familiarity and attractiveness of plant-based meat alternatives (Röös et al., 2022). Plant-based protein products resembling processed meat have been shown to have the best chance to replace meat (Michel et al., 2021).

A substantial proportion of the plant-based meat alternatives consumed in Sweden (and Europe) today are produced using imported soy beans (*Glycine max* (L.) Merr.), even though it is possible to grow protein-rich crops such as faba beans (*Vicia faba* L.) and peas (*Pisum sativum* L.) domestically in *e.g.* Sweden (Niva et al., 2017). However, recent findings suggest an increased consumer interest in labelling linked to origin and plant-based products produced from Swedish raw materials (Axfood, 2022; Spendrup and Hovmalm, 2022). All in all, there is both knowledge of how to grow and a consumer interest in buying plant-based products where the raw materials have been grown domestically (in *e.g.* Sweden). Finally, it should be noted that beside plant-based protein sold as meat alternatives, plant-based protein is also available in other types of products, not always perceived as sources of protein, *e.g.* cereals, potatoes, fruit and vegetables (Fig. 2). This means that consumers in general eat plant-based protein, without reflecting or noticing this, for example when eating a sandwich or a fruit. Thus, it is a complex issue for the consumer to understand the origin of the daily consumption of protein, as protein is present in a large amount of the foods we eat, although in varying amounts and compositions.

3. Cultivation to produce plant protein for human consumption

A range of crops are available that are currently used or have the potential to be used to produce plant protein for human consumption, as summarized in Table 1. Each of these crops contributes opportunities and challenges as related to their cultivation.

3.1. Grain legumes

In this review, we use the term grain legumes, as also information on *e.g.* soybeans and peanuts is presented, which are crops that are not included in pulses, a partly synonymous term (FAO, 2022b). Grain legumes are large-seeded, often annual, crops belonging to the *Fabaceae* family, where the harvested dry grains (as enough dry when harvested or dried after harvest) are used mainly to produce food or feed (Röös et al., 2018). The main grain legume cultivated globally is soybean, grown on 58 % (ca 133 million ha) of the total acreage used for legume production, resulting in 87 % (ca 387 million tons) of the total amount of grain legumes produced (Table 1). Soybean grown in Europe is only ca 4 % of the global production both in terms of acreage and total amount produced, but despite that, soybean is the major grain legume (although several other beans and peas are more high yielding; FAO, 2022a),

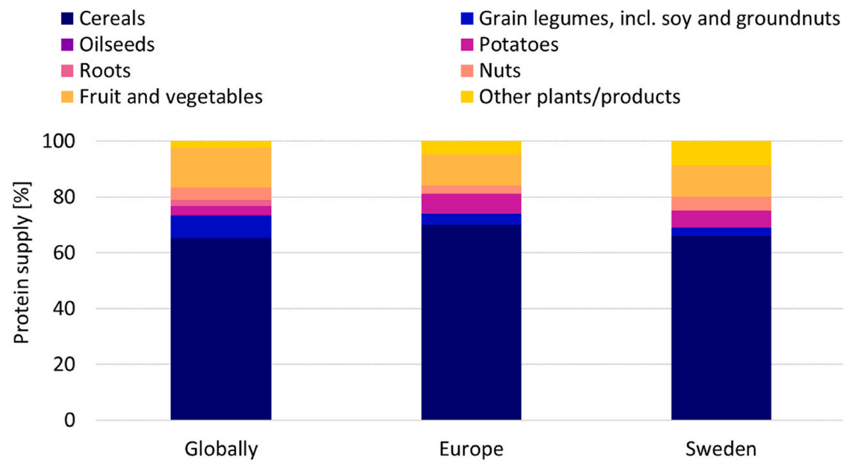

Fig. 2. Relative plant-based protein supply based on data from FAO (FAO, 2022b). Note that oilseeds represent only approx. 0.1 g/capita/day and are therefore not visible in the figure.

Table 1
Amount of crops in terms of cultivation (ha) and production (ton) that constitute the raw material for plant protein, and predicted possible protein harvest (ton; given within brackets). Data are for the year 2022, collected from FAOSTAT (www.fao.org/faostat) except for the category Green biomass, for which data are collected from Eurostat (https://ec.europa.eu/eurostat/data/database). NA: data not available.

Crop group	Sweden, thousand ha	Sweden, thousand ton[a]	Europe, thousand ha	Europe, thousand ton[a]	World, thousand ha	World, thousand ton[a]
Grain legumes	46	164 (38)	11 485	23 771 (5519)	229 750	444 846 (103 293)
Soybeans as % of all grain legumes	*0*	*0*	*54*	*52*	*58*	*87*
Cereals[b]	953	5823 (550)	115 498	521 842 (49 366)	729 124	3 057 246 (289 215)
Pseudocereals[c]	0	0	1238	1388 (155)	2430	2394 (268)
Oil crops[d]	132	436 (83)	33 289	70 796 (13 529)	155 317	283 531 (53 800)
Potato	23	852 (17)	4063	89 113 (1987)	17 788	374 778 (7589)
Green biomass[e]	1120	5001 (650)	19 349	NA	NA	NA

[a] For grain legumes, cereals, pseudocereals and oil crops, production data concern the dry grains (14 % water content except for oil crops, which are at 9 % water content). Data for potato are fresh matter yields (75–80 % water content). For green biomass, production is reported as dry matter (0 % water content). Predicted possible amounts of protein (given within brackets) are calculated based on the following assumed average protein concentrations (percent of dry matter): 27 % in grain legumes, 11 % in cereals, 13 % in pseudocereals, 21 % in oil crops, 9 % in potato and 13 % in green biomass).
[b] Including maize and rice.
[c] Buckwheat and quinoa, of which buckwheat is 100 % in Europe and 92 % (area) or 93 % (production) in the world.
[d] In Sweden, this group includes linseed and rapeseed (of which rapeseed is 96 % of area and 98 % of production). In Europe, additional crops are *e.g.* mustard seed, safflower, seed cotton and sunflower seed. On the world level, this group also includes *e.g.* peanuts (actually a legume, but here included in the oil crop category), melon seed and sesame seed. Soybeans are included in grain legumes, and therefore not counted again here. Coconuts, oil palm fruits, olives and other fruits and nuts from trees/shrubs are not included.
[e] Mainly temporary grass, grass-legume mixtures, silage maize and other forage crops from arable land.

grown on 54 % of the total acreage used for grain legume production, thereby producing 52 % of the total amount of grain legumes in Europe (Table 1). Other main grain legumes cultivated globally are beans (*Phaseolus vulgaris* L.), peas, faba beans, chickpeas (*Cicer arietinum* L.), peanuts (*Arachis hypogaea* L.), lentils (*Vicia lens* (L.) Coss & Germ.), lupins (*Lupinus* spp.), and several species in the *Vigna* genus (*e.g.* cowpea (*Vigna unguiculata* (L.) Walp.); FAO (2022b)). Based on the size of the mature grains of the grain legumes and their relatively high protein concentration (20–30 % in most species, and from 35 to above 40 % in soybeans and lupins), they show a high potential as a protein source for human consumption. Also, the content of the essential amino acid lysine is normally relatively high in the grain legumes, although the content of the sulphur-containing amino acids are lower (Allen, 2013).

Cultivation of grain legumes is positive for the environment, as it provides several services to the cropping system, such as i) adding biologically fixed nitrogen (through symbioses with nitrogen-fixing bacteria), leaving N-rich residues in the field that contribute to the N acquisition of other crops, and ii) acting as break crops (reducing the pressure of diseases and pests) in cereal-dominated crop rotations (e.g. Voisin et al. (2014), Preissel et al. (2015); Stagnari et al. (2017)). Grain legumes are also considered as the most promising plant-based protein alternative for human consumption (Magrini et al., 2016; Zander et al., 2016; Watson et al., 2017).Despite this, the cultivation of legumes (except for soybean) is generally low (Table 1), and only around 2 % of the arable land is used for grain legume cultivation in Europe (Watson et al., 2017). The main challenges that hinder increased cultivation of grain legumes are i) low profitability for farmers (compared to *e.g.* cereals and oil crops), ii) low yield stability and iii) under-developed value chains for human consumption (*e.g.* logistics in post-harvest handling, processing facilities such as dehulling, milling or cooking and packaging, but also for extraction/isolation of proteins for the production of meat substitutes) (Zander et al., 2016; Röös et al., 2018; Tidåker et al., 2021). An increase in legume production might take place to replace animal-based food and thereby reduce the land needed to produce feed crops (*e.g.* Röös et al. (2018)). Yield may be increased by measures in plant breeding (see 4.1) and cultivation practices, e.g. control of weeds, diseases and pests, ensuring adequate availability of water and nutrients (except nitrogen) and intercropping (growing a mixture of two or more species). The latter has been shown to increase yield stability and improve the overall efficiency in the use of land and nitrogen (Jensen et al., 2020; Weih et al., 2021).

3.2. Cereals, pseudocereals, oil crops and potatoes

Cereals is the crop group with globally by far the largest production amount and cultivation area (wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.) and maize (*Zea mays* L.) are ranked as the three largest crops), and wheat is the most traded crop. Among the annual crops, cereals are also the largest group of crops in Sweden and in Europe (Table 1). Thereby, cereals contribute a significant amount of protein (25–35 %; Poutanen et al. (2022)) to the human diet, although the grain protein concentration in cereals is lower (8–13 %) than in grain legumes (Table 1). Cereal proteins are readily available from industrial fractionation of starch or ethanol production, where the protein (gluten) is a co-stream with good functional properties, contributing strength and structure to end-use products, as preferred by consumers (Godschalk-Broers et al., 2022). However, the protein in cereals contains low proportions of some essential amino acids such as lysine, methionine and tryptofan (Klose and Arendt, 2012; Koehler and Wieser, 2013). Combining protein from different plant sources, *e.g.* cereals and grain legumes has the potential to generate food products that meet both structural and nutritional requirements for human consumption (Han et al., 2021).

Cultivation of cereals as sources of plant protein for human consumption has many benefits, *e.g.* the value chains are well developed, there is abundant knowledge about varieties/genotypes, cultivation, post-harvest handling and processing (Pingali, 2012, Magrini et al., 2019). Cultivation practices, notably nitrogen fertilization, can be used to govern the total grain protein concentration, while the cereal amino acid composition is limitedly affected by cultivation practices. However, the cereal proteins are important not only as contributors of amino acids to the human diet, but they also contribute largely to functional properties of their products, and these characters are significantly impacted by environmental conditions, including cultivation (Johansson et al., 2013; Johansson et al., 2020).

Pseudocereals, *e.g.* buckwheat (*Fagopyrum esculentum* Moench), quinoa (*Chenopodium quinoa* Willd.), amaranth (*Anaranthus* spp.; of which the first two are most common; Table 1) are crops that are not cereals, since they do not belong to the grass family, although, the pseudocereals have similar uses as the harvested mature grains of cereals (Johansson et al., 2023a). Pseudocereals typically have higher grain protein concentration than cereals, and as their storage proteins consists of albumins and globulins instead of prolamins and glutelins (the two latter are mainly found in cereals), they also have higher proportions of essential amino acids for human consumption (Janssen et al., 2017; Johansson et al., 2023a), which make them increasingly popular by consumers (Mir et al., 2018). The fact that pseudocereals belong to different plant families than cereals is an advantage in cropping systems, since they can act as break crops that do not host the same crop diseases or pests as cereals (Cheng, 2018). Pseudocereals are still considered niche crops in most contexts, and as such, they have the potential to provide high profitability for farmers who successfully grow and sell them. However, for niche crops, bottlenecks normally exist for upscaling of the production, notably related to the low yield of the pseudocereals and the need for specialized equipment for harvest (as the pseudocereals often have an indetermined growth with unequal maturation of grains) and post-harvest handling (normally small grains that need to be dehulled). Cultivation practices are unlikely to contribute enough changes to these traits to make the pseudocereals a major alternative vegetable protein source for human consumption, although the pseudocereals might contribute positively in crop rotations and make a valuable – albeit minor – contribution to the total mix of plant proteins in human diets.

Oil crops, notably oilseed rape (*Brassica napus* L.) but also *e.g.* sunflower (*Helianthus annuus* L.), linseed (*Linum usitatissimum* L.), groundnuts (*Arachis hypogaea* L.) etc. are also sources of protein. For example, oilseed rape (the most common oil crop in Europe) contains around 20 % protein in the mature grains. Furthermore, the press cake after oil extraction has a protein content of up to 40 % and the amino acid composition is excellent for human consumption (Wanasundara et al., 2017). Currently, oilseed press-cakes are mainly used to feed animals. The major drawback in using them for human consumption products is their high level of ANFs (Nour-Eldin et al., 2017; So and Duncan, 2021), which are difficult to get rid of by cultivation measures, but might be handled through breeding or processing.

Potato (*Solanum tuberosum* L.) tubers contain considerably less human-edible protein than grain legumes, cereals and oil crops, but more than pseudocereals (Table 1). Similar to oil crops, the protein-rich residues after starch extraction from potatoes contain protein with excellent amino acid composition for human consumption (Hussain et al., 2021). The major challenges, which currently limit their applications, are the denaturation of the proteins during precipitation from the potato fruit juice, and the presence of ANFs (Waglay and Karboune, 2016). Again, these ANFs are difficult to influence by cultivation practices.

3.3. Green biomass including e.g. cover crops and ley

Green biomass includes a heterogeneous group of biomass sources, and the quantification of several of them is difficult. Numbers on the quantity of ley and green forage crops are available for Sweden, but data are lacking or inconsistent for Europe and the world both in FAOSTAT and Eurostat (Table 1). Also, the amount and quality (dry matter and protein content, hygienic quality) of green biomass vary widely and depend on the source (crop, harvest time, location).

Ley and other green forage biomass do contain large amounts of protein (Table 1), but the protein in unprocessed green biomass is not available for uptake in the human digestive system. Thus, in order to play a role in human nutrition, green biomass needs to be processed to extract and purify the protein (see section 5).

In Sweden, ley is the dominating crop within the green biomass category (SBA, 2021). Ley has important values and benefits in the cropping systems and as a feed to ruminant animals. In cropping systems, leys, which are typically perennial crops, are kept two to three years in the field before changing to another crop in a crop rotation, increase soil carbon content (or at least reduces the losses of soil carbon) and reduce the risks of nutrient losses and soil erosion (Persson et al., 2008; Glover et al., 2010). Ley also acts as a break crop with a high pre-crop value in cereal-dominated crop rotations, and it reduces the need for use of fertilizers and pesticides (Martin et al., 2020). Currently, the vast majority of ley and forage biomass produced is used as animal feed. The production of leys has the potential to be intensified (Prade et al., 2017a), while, for use in human consumption, investment is required in processing facilities that can extract and purify protein from green biomass with sufficient energy- (including transportation of biomass) and cost-efficiency.

Cover crops have similar benefits as ley, although their impact on soil carbon is often less pronounced since cover crops typically stay in the field for a much shorter period than ley: a few months or up to half a year. On the other hand, cover crops have the benefit of low or no risk for indirect land-use change (ILUC), *i.e.* cover crops do not compete in land use with food or feed crops (Prade et al., 2017b; Nilsson et al., 2024).

3.4. Contribution of cultivation to tailor plant proteins for the consumer

The major opportunities to tailor plant proteins to suit the consumer through cultivation is by i) the type of protein produced through the choice of the crop, and ii) the amount of protein produced which is determined by the crop, the genotype, the environment and input choices. However, the consumer might also be interested in environmental effects of the plant protein production, where a diversified crop production system, with suitable crop rotation and low chemical inputs are important measures.

4. Plant breeding for production of protein for human consumption

Consumers are generally slightly positive to traditional plant breeding, while more negative to the use of modern methods such as genetic modifications (GMO; Spendrup et al. (2021)). However, plant breeding has contributed significantly to the large increases in yield obtained during the last century and thereby to food security for consumers. A total of 74 % of the yield increase from 2000 to 2015 has been attributed to plant breeding (Noleppa and Cartsburg, 2021), although input of plant breeding has varied as regards to crops and traits. Thus, plant breeding is a strong tool, that has the potential to contribute to food security both in terms of quantity and quality of food crops for consumers at the local and global level.

4.1. Grain legumes

Soybean is globally the most economically important grain legume crop (see Table 1), and it is a dual-purpose crop, with a grain weight content of 40 % protein and 20 % oil (Kezeya Sepngang et al., 2020; FAO, 2022a). Breeding efforts on soybean have been substantial, as can be judged from the number or varieties registered (Fig. 3), which are classified into commodity- (used for edible or industrial oil and animal feed) or food-type. The major producing countries of soybean are Brazil, Argentina and USA (FAO, 2022a), and in those countries, the cultivation is dominated by GMO varieties, which use for human consumption worries consumers in Europe (Rotundo et al., 2024). The primary breeding targets for GMO soybean have been herbicide tolerance and insect resistance aiming at increased yield, but also oil quality (www.isaaa.org). For all grain legumes, increased yield has been a common breeding target (Abraham et al., 2019; Assefa et al., 2019, Desmae et al., 2019; Maalouf et al., 2019; Kumar et al., 2021, Parihar et al., 2022). Breeding for increased yield usually addresses tolerance and resistance to abiotic and biotic (fungal pathogens and insects) stresses. Additionally, breeding for a determinate plant architecture is important for most grain legumes, resulting in improvements in harvest index, and in a more consistent flowering and maturation time, although seed yield might be influenced (Benlloch et al., 2015; Lopez et al., 2021, Kim et al., 2022). Furthermore, winter hardiness is a cultivation trait of importance for varieties of *e.g.* faba bean and pea used as autumn-sown crops (Link et al., 2010).

If grain legumes should be used increasingly as a protein-rich resource replacing meat, grain protein content and composition will become important breeding goals, not least if they are to be used in novel food applications based on protein isolates or concentrates (Nadeeshani et al., 2022). A high grain protein content in soybean is already an important breeding target, as a majority of the economic returns in soybean comes from the protein-rich meal which is mainly used for feed (Jegadeesan and Yu, 2020). Among the minor grain legumes, lupin is one of few examples with a protein content comparable to soybean. In Asia, where the traditional use of soybean has been in diverse types of food products, research and breeding have targeted several grain quality parameters, of which high protein and sucrose content are the major ones. However, depending on the food product concerned, seed size and the levels of oil, carbohydrate, and oligosaccharides have also been of interest (Jegadeesan and Yu, 2020). Additionally, early flowering and maturation have been breeding goals in several legumes including faba bean with the purpose to expand the cultivation areas compared to those they were originally adapted for (Stoddard and Hämäläinen, 2011, Desmae et al., 2019). Furthermore, seed size, shape, colour, nutrient composition, cookability, texture and taste attributes are important quality traits of grain legumes for use in food (Santos et al., 2019; Bassett et al., 2021; Gupta et al., 2021), although the latter of these traits have not yet received much attention in breeding.

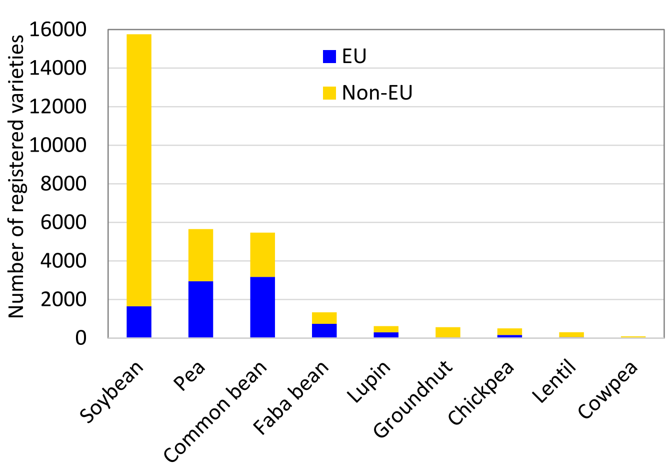

Fig. 3. Number of registered varieties[1] of grain legumes in EU and non-EU countries.
[1]Community plant variety office varieties database as per 2022-09-14 (https://cpvo.europa.eu).

Most grain legumes contain ANFs which are of proteinaceous (lectins, agglutinins, bioactive peptides and protein inhibitors) and non-proteinaceous (alkaloids, phytic acid, tannins and saponins) type (Sánchez-Chino et al., 2015). A negative effect on nutrient uptake in humans and animals have been reported for several ANFs, although some compounds reported as ANFs may also have health benefits if consumed in suitable amounts (Khazaei et al., 2019; Geraldo et al., 2022). The content of ANFs can be reduced by plant breeding assumed to contribute the most cost-effective reduction. For example, in soybean, lines have been developed with a decreased level of trypsin inhibitor (Kumar et al., 2015), while low levels of phytate is another breeding goal. Faba bean varieties are available with reduced tannin content, and also those with low levels of convicine and vicine (Khazaei et al., 2019). Furthermore, lupin varieties with low levels of alkaloids have been developed, and these are termed sweet lupins (Uauy et al., 1995). Although a reduced level of ANFs is a benefit for the consumer, acceptable levels of several ANFs in grain legume raw material for food use are not yet defined. However, reduced levels of ANFs might be associated with a decrease in yield for some crops due to the protective roles against abiotic and biotic stresses that they have in the plant.

As plant breeding efforts among the grain legumes have been focused on soybean (Fig. 3), there is an untapped potential to increase the genetic gains of the other grain legume crops by widening the genetic base of the cultivated gene pools (Pratap et al., 2021; Rubiales et al., 2021). Future breeding of those can to a higher extent be expected to target seed quality traits of importance for consumers. The increasing availability of genomic information and genetic markers for several of the legumes (Sahruzaini et al., 2020) in combination with molecular tools such as targeted mutagenesis can aid in this work.

4.2. Cereals, pseudocereals, oil crops and potatoes

Cereals as major crops, have been largely targeted by breeding efforts (Johansson et al., 2023a). Similar as for most other crops, the breeding activities have mainly been focusing on yield and resistance (Johansson et al., 2023b), although, for some cereals, protein content and composition have also been important traits (Johansson et al., 2023a). The most obvious case where protein content and composition have played a major role in breeding, is in wheat, highly consumed as bread, and bread-making quality is to a high degree determined by these traits (Johansson et al., 2020). A high loaf volume, perceived of importance by consumers, is correlated to the grain protein concentration while the ability of the proteins to aggregate and polymerise is linked to the gluten strength (Johansson et al., 2013; Markgren et al., 2022). Breeding to improve the nutritional quality of the wheat grain proteins has limited potential as all the storage proteins (ca 80 % of the wheat grain proteins) have low levels of essential amino acids, while the proteins with enzymatic function in the wheat grain are of the albumin and globulin type with more sufficient levels of lysine arginine, aspartic acid, threonine and tryptophan (Poutanen et al., 2022). Among the other cereals, protein content and composition are important characters for *e.g.* malt barley (*Hordeum vulgare* L.; around 10 % is preferable for beer production), which has resulted in breeding activities for these traits (Jaeger et al., 2021). However, with the exception of wheat and barley, breeding for improved grain protein content and composition has been limited in cereals as other yield and quality parameters have been of higher importance (Johansson et al., 2023a). Oats (*Avena sativa* L.) are diverging from the rest of the cereals as 80 % of its grain proteins are albumins and globulins, resulting in a high level of essential amino acids (Sterna et al., 2016).

Breeding efforts for the pseudocereals have, due to their low production volumes, been limited and have mostly focused on agronomic traits to increase yield and yield stability (Joshi et al., 2018; López-Marqués et al., 2020; Chettry and Chrungoo, 2021). Thus, breeding of amaranth has been towards *e.g.* reduced seed shattering, reduced plant height, grain yield and colour (Joshi et al., 2018). For quinoa, which is a crop originally adapted to the Andean region, the development of day-neutral varieties has allowed cultivation in other parts of the world including Northern Europe (Jacobsen, 2017, López-Marqués et al., 2020). However, from a consumer and food industry perspective, there is an increased interest for the high-quality proteins from the pseudocereals, which are also contributing gluten-free alternative products (Janssen et al., 2017). This has resulted in studies on protein content and quality in *e.g.* buckwheat (Chettry and Chrungoo, 2021), and quinoa (Jacobsen, 2017, López-Marqués et al., 2020) with breeding activities targeting low saponin (an ANF) content in quinoa (López-Marqués et al., 2020). Furthermore, research is ongoing aiming to develop genetic markers for high protein content in quinoa (Grimberg et al., 2022).

Potato breeding has mainly targeted yield and resistance, but significant work has also been done on quality traits of importance for fresh consumtion, processed food products, and the starch and ethanol industry, *e.g.* targeting tuber size and shape, skin color, glycoalkaloid content, sugar content, and starch content and quality (Meenakshi et al., 2018). Breeding of oilseed rape has focused on yield, oil content, and oil quality, which are important traits for its use in food, feed and fuel (So and Duncan, 2021). Reduced levels of ANFs are important in both these crops for the protein to be useable in food applications, and directed mutagenesis breeding tools are being explored to reduce the glycoalkaloid levels in potato (Hussain et al., 2021; Zheng et al., 2021). The glucosinolate levels in oilseed rape has been reduced through breeding but there is a need to target a further reduction, and also for additional types of ANFs (Nour-Eldin et al., 2017; Östbring et al., 2020; So and Duncan, 2021).

4.3. Green biomass, cover crops, ley

Green biomass has mainly been used as a whole plant feed source for animals and thereby the breeding focus has been on biomass yield. When high yield is a breeding target, resistance to biotic stresses and tolerance/adaptation to abiotic stresses is always important, and therefore, such characters have also been taken into consideration (Capstaff and Miller, 2018). If green biomass, including cover crops, should be useful as a protein source for human consumption, additional breeding targets might be of relevance for the future. One such breeding goal might be the extractability of the proteins, as there is large variation for this trait among various green biomasses (Nynäs et al., 2021). Feasibility analyses of the protein fractionation from green biomass for human consumption have clearly demonstrated a higher protein extractability at fractionation as a major goal (Muneer et al., 2021; Prade et al., 2021). The genetic background of varietal and crop differences in protein extractability might be a major target in future breeding programs of green biomass as a protein source for consumers.

4.4. Contribution of plant breeding to tailor plant proteins for the consumer

The major opportunities to tailor plant proteins to suit the consumer through plant breeding is by the development of novel genotypes in current major and minor protein crops with i) high protein content, suitable protein composition and high protein extractability, and ii) low amount of ANF and other unwanted compounds. The consumer might be interested in novel plant-based protein sources that contribute taste, texture, nutrition etc to the plant-based food products simultaneously as the products have a low carbon footprint.

5. Processing of plant protein for human comsumption

Food has been processed as long as human cultivation has existed to satisfy consumers perceptions as regards food, utilizing traditional methods such as cooking, smoking and frying (Albuquerque et al., 2022). For the traditional consumption of seeds and tubers, soaking and cooking have been the most common processing methodologies, which have contributed to a deactivation of ANFs, inhibition of enzymes and binding proteins, reduction of the biogenic amine content, organic acids (*e.g.* phytic and oxalic), saponins, raffinose oligosaccharides etc. (Samtiya et al., 2020; Das et al., 2022). Additionally, these methods make nutritional compounds in the seeds and tubers more readily available for human digestion, contributing to human health and well-being (Gupta et al., 2015).

During the last century, processing has become increasingly sophisticated with a range of novel technologies emerging (Priyadarshini et al., 2019). The development of these new processing methods has contributed to paving the way for the wide range of novel plant-based high--protein products recently available commercially and highly requested by consumers (Alasi et al., 2024).

5.1. Modern processing methods to concentrate plant proteins

Currently, the market sees an increasing number of novel products and uses of plant proteins, *e.g.* these proteins are supposed to replace milk in milk-based products, egg in egg-based products and meat through meat analogues (Boukid, 2021). For such a utilization, a higher protein concentration is usually required in the source used for these products compared to what is present in the harvested protein crop. Applying processing methods to increase the protein content in the material compared to the harvested crop depends on the requirements and the value of the end product (Hewage et al., 2022; Chandran et al., 2023). The processes are also known to interact with cellular, structural and phytochemical aspects of the biomass used for protein fractionation (Pérez-Vila et al., 2022). The most commonly utilized modern methods to concentrate plant proteins are summarized in 5.1.1–5.2.2.

5.1.1. Air classification

Air classification has seen a rapid development in the commercial sphere for the production of protein concentrates. The method is performed dry and is therefore an efficient and low-cost process, resulting in no wet residual mass or whey to dispose of and no water consumption or product drying costs. Furthermore, the proteins are not denatured if the temperature is kept low, thus their functional properties are retained (Van Der Poel et al., 1990). In the process, particles within a milled flour are separated based on size using an air classifier into a fraction holding small particles, which are rich in protein, and another fraction holding larger particles, which are usually rich in starch. The purity of the obtained protein-rich fraction depends on the starch granule and protein body size distribution as well as the presence and composition of ANFs. ANFs are often enriched in the protein-rich fraction as has been shown for common bean, faba bean and pea (Van Der Poel et al., 1990; Coda et al., 2015; Wang and Maximiuk, 2019, De Angelis et al., 2021). Comparison of air classified protein concentrates from different yellow pea varieties revealed the presence of varietal differences in the composition of ANFs (Fenn et al., 2022) indicating breeding opportunities towards air classification adapted varieties. An issue with the air classification process is the exposure of a large surface area of the material to oxygen (air) which may activate lipoxygenases or non-enzymatic processes producing off flavours and odours (Wang et al., 2020; Sharan et al., 2021). Despite the mentioned drawbacks, the air classification methodology has been developed for a number of crops including grain legumes such as soybean, faba bean and pea, and cereals such as barley (Tabtabaei et al., 2023), with protein content of 30–60 g protein/100 g dry matter in the protein-rich fraction (Pelgrom et al., 2015; Tabtabaei et al., 2023). Both cultivation methodology and plant breeding could possibly be utilized to target improved air classification behaviour of various crops, thereby satisfying consumer perceptions of products, although limited emphasis has been directed towards such goals.

5.1.2. *Isoelectric precipitation*

Isoelectric precipitation of alkali extracted protein is the most well-established process to produce highly concentrated protein products, and has during the last 30 years been used on a wide array of seeds of legumes, cereals, oil crops, etc. (Mondor and Hernández-Álvarez, 2022). The advantages of this methodology are that it is easy to scale up into industrial processes with high productivity depending on the source material, although the use of harsh chemicals in the processes has a negative environmental impact and may negatively impact the functional properties of the proteins (Mondor and Hernández-Álvarez, 2022). In the process, mainly defatted plant material such as flakes, flour or protein-enriched fractions are treated with an alkaline solution to solubilise the protein, and thereafter the pH is adjusted to the isoelectric point resulting in protein precipitation. Mostly, an isoelectric point around 4.5 has been utilized to precipitate plant proteins (Mondor and Hernández-Álvarez, 2022). Also, different types of proteins in the same plant material may differ in isoelectric point, which might affect the protein recovery (Boye et al., 2010). For example the amount of the 12S globulin (cruciferin), and the 2S albumin (napin) in oilseed rape was found to be influenced by both cultivation conditions and genotype (Stolte et al., 2022), which would lead to varying effectiveness of isoelectric precipitation. Similar to air classification, several factors affect the quality of the produced protein, including the properties of the plant material such as the type and amount of protein and its ability to precipitate, the need to remove oil to avoid emulsion formation, and content and composition of ANFs and poor tasting compounds (Mondor and Hernández-Álvarez, 2022). Additionally, the alkaline pH utilized in this kind of processes possibly contributes to the protonation of lysine, which can result in covalent reactions with undesirable components, *e.g.* phenolic acids (Masoumi et al., 2024), resulting in nutritional and sensory quality degradation. For the production of potato protein, a specific isoelectric precipitation procedure has been developed that involves acidifying the process water to the isoelectric point of approximately pH 5, followed by heating to 120 °C with live steam to precipitate the protein (Strolle et al., 1973). However, this co-concentrates the protein and ANFs, namely glycoalkaloids and phenolics, making the protein product only suitable for animal feed and not human consumption.

Plant breeding can be used to address various properties affecting protein precipitation, although until now, breeding goals to change such properties of the seed have been limited. Upcoming novel plant breeding methodologies, *e.g.* gene editing, open opportunities to knock out genes encoding certain proteins, thereby increasing the proportion of other proteins while still exhibiting a normal phenotype (Nguyen et al., 2013), although the use of such techniques might impact the consumer perceptions of these products. Plant breeding to reduce the ANFs in starch potatoes is underway (Liu, 2024) using gene editing techniques, and the expected outcome is an enhanced value of the protein product that can be made suitable for human consumption. Thus, advanced breeding techniques may have the potential to increase the protein yield at precipitation and/or to increase the nutritional profile of the precipitate as the process efficiency and/or product quality is improved.

5.1.3. *Membrane processing*

Membrane technologies are considered most promising in an industrial context among the emerging technologies, although these techniques have already been used in various contexts over the last 30 years to separate proteins in legumes, cereals and oilseed crops (Mondor and Hernández-Álvarez, 2022). The membrane technologies are used to replace or to complement isoelectric precipitation and are advantageous as they decrease chemical use and improve the functionality of the proteins, although the lack of productivity still hampers their industrial applications (Mondor and Hernández-Álvarez, 2022). In membrane processes, proteins are concentrated from solution by the use of a pressure gradient across a membrane with a certain pore size, allowing only molecules below a certain particle size to pass (Mondor and Hernández-Álvarez, 2022). However, despite the fact that this concentrates the protein, similar to air classification, small molecules *e.g.* ANFs and other undesirable compounds, have the potential to stay associated with the protein as they are smaller than the molecular weight cut-off. The use of ultra- or diafiltration may in such cases contribute to the reduction of these substances, where positive effects have been shown for *e.g.* trypsin inhibitors, phytic acid, phenolic acids and condensed tannins in some legumes and oil crop seeds (Mondor and Hernández-Álvarez, 2022). However, the effects of these processes are highly impacted by the status of the starting material in filtration. Thus, a reduction of the unwanted compounds through cultivation methods or breeding would reduce/eliminate the need for ultra- or diafiltration which would be associated with a reduction in water and energy use.

5.2. *Special case proteins – the need for alternative processes to concentrate proteins*

For two of the most abundant plant proteins on Earth, the wheat storage proteins (gluten proteins) and the proteins in green biomass (of which 50 % is RuBisCO), the methods described in 5.1. do not work effectively as processes to concentrate the proteins. Thus, suitable methods fitting these proteins are described in 5.2.1–5.2.2.

5.2.1. *Wheat gluten proteins*

The separation of protein from wheat is a special case due to the specific properties of the wheat gluten proteins, which are able to form strong disulphide cross-links and form the largest protein network in nature (Markgren et al., 2022). Current processes mix wheat flour with water, apply mixing energy to generate a protein network, wash the starch out of this protein network, and thereafter the remaining gluten is dried (Van Der Borght et al., 2005). The final product contains approximately 80 % protein, while the remaining part are small amounts of lipids and starch. In the marketplace, this protein is referred to as “Vital Gluten”. Extracted gluten consists mainly of glutenin and gliadin proteins, and the type and proportion of these protein groups in the wheat seed is a result of both genetic and environmental factors (Johansson et al., 1999). The types and quantity of the proteins in the gluten affect the viscoelastic properties and the strength imparted to the wheat flours, *e.g.* in bread-making (Johansson et al., 2013).

5.2.2. *Green biomass*

Processes for the separation of protein from green biomass have been investigated since the 1940’s (Pirie, 1942) and have seen renewed interest as demand increases for new sources of plant protein (Nynäs, 2022). The protein production process consists of two or three main steps; juicing the leaves to obtain a green juice fraction, mildly heating the juice to receive a “green protein” and “white juice” fraction rich in water soluble protein, from which the "white protein" is then iso-electrically or heat-precipitated into a leaf protein concentrate (LPC) with good functional properties suitable for human consumption (Nynäs et al., 2023; Nynäs et al., 2024). Similar to the protein processing methods described above to concentrate plant proteins, ANFs and other unwanted compounds may travel together with the proteins when concentrated from green biomass. Amount and type of ANFs present in the protein concentrate depends on *e.g.* the biomass source and specific fractionation procedure. The harvest date of the green biomass is highly important for the protein fractionation as it impacts the lignin and starch/cellulose/hemicellulose (Godin et al., 2013) and phenolic (Kiskini et al., 2016) contents of the products. There is a general need to increase the process efficiency of the protein fractionation from green biomass (Tamayo Tenorio et al., 2018); around 50 % of the protein currently remains in the pulp after the juicing process (Nynäs et al., 2023), as a result of the limited protein extractability of non-soluble proteins from the fiber fraction (Tamayo Tenorio et al., 2016). Relatively low rates of protein recovery for human consumption have been reported, *e.g.* between 1 and 2 % of the initial crude protein content in broccoli, kale, white and red clover, lucerne and perennial ryegrass (Damborg et al., 2020; Prade et al., 2021). Opportunities to improve the protein extraction efficiency by changes in the processing methodology are obvious targets (Nynäs et al., 2023), but these characters can also be improved through cultivation practices, harvesting times and plant breeding activities. As green biomass crops are currently mainly used as animal feed, either directly, as ensiled, or dried, there should be room for improvement through breeding for the needs of green biomass extraction processes.

5.3. Contribution of processing to tailor plant proteins for the consumer

The major opportunities to tailor plant proteins to suit the consumer through processing is by i) refining existing, and ii) developing novel processing methods to harvest and produce the future high-quality plant-based products. The consumer might be interested in low- and highly processed plant-based products with a high quality in terms of attributes such as taste, texture, nutrition etc and with a low carbon footprint.

6. Economic feasibility and environmental effects - opportunities from plant protein for human consumption

6.1. Current food crops

The wide range of new high protein food products containing various plant proteins contribute novel opportunities, not least when it relates to economic and environmental effects from production, although they also present currently unknown risks in terms of allergens, contaminants and toxins (Loveday, 2019). Most of the protein sources currently used for the emerging high protein food products are based on production of crops already utilized as food crops (*e.g.* cereals, grain legumes). Thus, their production has been rationalized in industrialized countries to fit into a production system that is built on the use of fuels and mineral fertilizer manufactured from fossil sources, which have a large environmental impact in terms of GHG emissions. Besides this contribution to the global warming potential, use of fertilizers is also known to potentially contribute to nutrient emissions and an increase in acidification and eutrophication potentials. In an environmental context the production of plant protein to be used for high protein products may potentially be advantageous from nitrogen-fixing crops, i.e. forage and grain legumes, as compared to conventionally fertilized crops such as cereals, oilseed crops, potatoes etc. (Lötjönen and Ollikainen, 2017). However, significant reductions of the environmental impact of also non-leguminous crops such as cereals are possible using for example improved management practices such as precision farming to decrease the use of fertilizers and pesticides (Roy and George K, 2020). Furthermore, measures for decarbonization such as a switch to renewable fuels, *e.g.* biogas or HVO (hydrotreated vegetable oil), as well as the use of climate smart mineral fertilizers, may contribute to reduced negative environmental impact. Here, use of N_2O abatement technology and fossil-free mineral fertilizer can reduce GHG emissions with 50–60 % and 80–90 % (Fossum, 2014; Yara, 2022), respectively. Additional measures to reduce the negative environmental impact include an increase in biodiversity in the agricultural landscape, *e.g.* through the use of multifunctional buffer zones. These can be uncultivated plots to attract birds (Koleček et al., 2015) or flowering strips to attract beneficial insects for biological pest control (Raderschall et al., 2022), that may subsequently decrease the need for chemical insecticides.

Plant breeding efforts to reduce the environmental impact in crop production has been limited and the major focus has been on yield, resistance and in some crops on quality related traits (Mourad et al., 2019; Johansson et al., 2023b). However, yield-related genetic improvements of the plant material are usually positive from an environmental perspective, since the increase in yield is often a result of the diversion of efforts by the plant to produce storage products (*e.g.* more or larger grains, seeds etc. as well as higher content of proteins) and consequently might not require more production means such as fuel or fertilizer. On the other hand, an increase in the harvest index (the weight of harvested product per weight of total aboveground biomass production) may also reduce the aboveground amount of biomass of plant residues contributing to soil organic carbon (SOC), which increases GHG emissions. SOC contribution of aboveground biomass is, however, of lesser importance compared with the contribution from root biomass, especially on light soils (Kätterer et al., 2011). Another approach contributing significantly to the reduction of the negative environmental impact is to increase nitrogen use efficiency (NUE), i.e. the ratio of the crop nitrogen in the harvested products and the total input of nitrogen fertilizer (Johansson et al., 2023b). An increase in NUE leads to a reduction in fertilizer requirements (Mosleth et al., 2020) and, consequently, to lower emissions from fertilizer manufacture and use and associated environmental problems such as eutrophication and acidification.

6.2. Green biomass

The fact that all crop parts are utilized when green biomass is used to produce protein for human consumption, results in a potential to increase the protein productivity per land area (Fig. 4). Current food crops such as peas, beans and barley typically produce 440–1090 kg of edible plant protein per hectare (Kaya et al., 2005; Neugschwandtner et al., 2015). Including also oat, soybean, faba bean and wheat in this comparison, this range broadens to 200–1840 kg of plant protein (Cazzato et al., 2012; Nadi et al., 2013; Neugschwandtner et al., 2015; Koppel et al., 2020). The potential of total crude protein in green biomass of grasses and forage legumes is 410–2900 kg of plant protein per hectare (Solati et al., 2018; Thers and Eriksen, 2021). For comparison, meat and milk/eggs have a considerably lower protein productivity of 20–570 and 100–730 kg plant protein per hectare, respectively, assuming a protein feed conversion efficiency of 4–20 % for meat and 24–25 % for milk and eggs (Alexander et al., 2016). As a consequence, the detour via animal production is less resource efficient by far (Sabaté et al., 2015).

However, recent feasibility studies (Muneer et al., 2021; Prade et al., 2021) show the lack of economic incentives to produce protein for human consumption from green biomass due to the low yield of the fractionation procedures presently used. Still, due to the high market prices for this kind of protein, a few percent-units increase in the protein yield of an LPC from green biomass for human consumption may result in sufficient economic benefits. The increasing refinements of the proteins might also result in increased digestibility and therefore increased nutritional value (Tomé, 2013) which might contribute economic value to the protein product. The low dry matter content of green biomass is another issue in terms of process cost, since approx. 600–900 kg of water

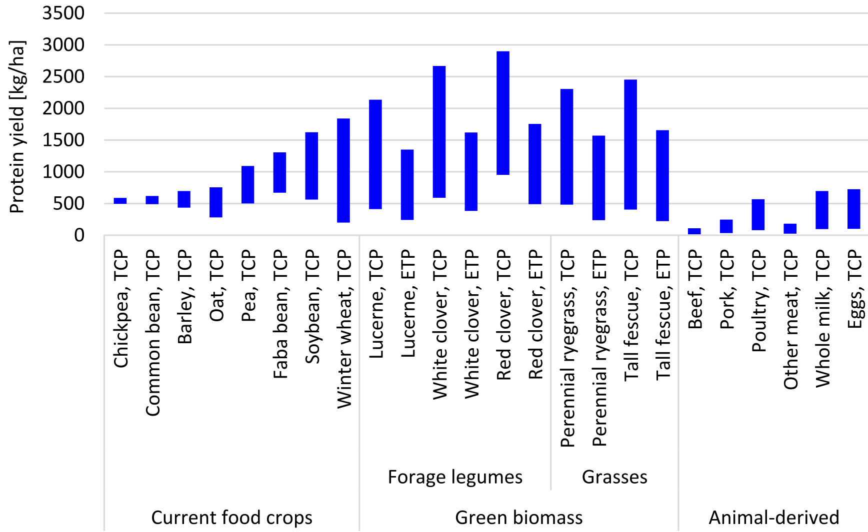

Fig. 4. Ranges of protein yields [kg/ha] from current food crops and green biomass based on published data (Kaya et al., 2005; Cazzato et al., 2012; Nadi et al., 2013; Peer et al., 2013; Neugschwandtner et al., 2015; Solati et al., 2018; Koppel et al., 2020; Sudár et al., 2021; Thers and Eriksen, 2021). Animal-derived protein yields based on protein yields of forage legumes and grasses and corresponding protein feed conversion efficiency as presented by (Alexander et al., 2016). TCP = total crude protein; ETP = extractable true protein.

have to be removed per ton of fresh biomass before a storable product can be obtained. This is especially significant in comparison to protein extraction from current food crops, which demonstrate much higher DM content for the crop parts that are harvested (Tamayo Tenorio et al., 2018). However, additional economic incentives from the fractionation of proteins from green biomass might be received by the production of high-value co-products. Studies have indicated opportunities to fractionate a co-protein stream suitable for animal feed purposes, *e.g.* monogastric animals such as pigs (Nynäs et al., 2023). Assuming average extractabilities of 55 % (32–73 %) for such feed protein (Solati et al., 2018; Thers and Eriksen, 2021), the yield range for grasses and forage legumes is 220–1750 kg extracted plant protein per hectare (Fig. 4), which is comparable to that of current food crops, only that this protein can be grown also on land not suited for current food production. As another co-product from this process, the fiber fraction containing most of the remaining share of proteins, is suitable as animal feed for ruminants (Nynäs et al., 2023). Fractionation of additional compounds (*e.g.* polyphenols or dietary fibers) suitable for food or medical products or to be used as biofertilizers or biostimulants, may also contribute to increased economic feasibility of LPC fractionation for human consumption from green biomass (Prade et al., 2021). In general, the potentially low environmental impact from feedstock supply, specifically emission of GHGs, make green biomass clearly interesting for supply of proteins for human consumption.

6.3. Feasibility and environmental impact measures of the use of plant proteins in the food system

The global food system is known as a major driver of the negative environmental challenges including climate change (Vermeulen et al., 2012; Rosenzweig et al., 2020), biodiversity loss (Crist et al., 2017; Dudley and Alexander, 2017) and pollution and depletion of freshwater resources (Wallinga, 2009). An increased use of fractionated plant proteins in the human diet, not least from green biomass, has been suggested as potential production system that could contribute considerably to solving part of these challenges (Santamaría-Fernández and Lübeck, 2020). Within the food system, the product with the highest negative environmental impact is meat, while also production of other animal products such as milk and eggs contribute to the environmental burden. Indeed, many studies have shown that plant-based protein products have a lower carbon footprint, in most cases irrespective of what animal product they replace and how they are produced (Röös et al., 2018; Leinonen et al., 2020). To compare the environmental impact of different products, such as meat versus plant protein-based alternatives, life cycle assessments (LCAs) are commonly used. However, the choice of the LCA method has an impact on the outcome of the results, as shown in studies comparing the results of attributional LCA (describing flows attributed to delivery of an amount of the functional unit) with consequential LCA (describing flows attributed to a change in output of the functional unit; Thomassen et al. (2008); van Zanten et al. (2018)). To understand the environmental effect of the exchange of meat to plant-based alternatives, the use of consequential LCA is most logical, although an increase in consumption of plant protein-based alternatives has been shown to not be directly correlated to a decrease in meat consumption (Siegrist et al. (2024); Font-i-Furnols (2023)). In addition, it is not straight-forward which mass ratio for such a replacement should be assumed, since it is affected by factors such as protein digestibility, amino acid composition and energy content (Loveday, 2019). Also, different efficiency measures can be applied, *e.g.* the supply with essential amino acids. To complicate this situation, there are different ways of measuring digestibility and the methodologies used to determine protein quality have different advantages and drawbacks (Mansilla et al., 2020) which may influence the interpretation and subsequently the replacement ratio. In conclusion, content and quality of several components such as essential amino acids, fibers, phenolics, etc. may play an important role for the assessment of the impact of the replacement (Nadeeshani et al., 2022).

As for all assessment and impact studies on production and manufacturing process, the production system of the fresh biomass, i.e. the cultivation system for crops producing the plant proteins, and the co-products of the fractionation system, needs to be taken into account as well. The incorporation of a break crop (*e.g.* legume or forage) in the cropping system, may contribute both economic and environmental returns to the farmer and/or the environment (Liu et al., 2022). Additionally, a high resource use efficiency is a necessity for decreasing the environmental footprint of the main product, as well as for the co-products. In the case of plant proteins, that means that plant-protein production is integrated with co-product valorization, which can be realized in a biorefinery approach. The occurring co-products need to be valorized from a perspective of other product replacements or recovery of valuable compounds (*e.g.* bioactive molecules, plant nutrients) and energy. For the economic feasibility of the overall production process, valorization of side-streams is important (Møller et al., 2021). Additional product replacements with co-products may include fossil fuels or resources, *e.g.* bioactive molecules replacing fossil-based chemicals, biogas replacing fossil vehicle fuels or digestate replacing mineral fertilizer. Furthermore, feed products to ruminant and monogastric animals can be produced as co-products from the green biomass fiber and the green juice fractions, respectively, increasing protein feed volumes and potentially replacing imported soybean-based feed (Nadeeshani et al., 2022). Also, studies comparing the use of the plant proteins as replacers in feed products should be taken into consideration (Nynäs et al., 2024).

7. Synthesis

The synthesis of the knowledge gathered in the present review paper clearly show the need, opportunities and potentials of the use of a wide array of crop sources for the production of plant proteins for human consumption to benefit consumer needs and perceptions. The protein intake per capita does not need to be increased, instead there is most likely room for a small decrease, but the total global protein requirement for human consumption is increasing due to the global population increase. Furthermore, there are requirements for increase in protein intake in certain population segments (low-income countries, elderly and young people etc.), and of a shift of part of the protein intake from animal to plant derived sources mainly due to environmental reasons as plant proteins generally show a lower climate footprint than animal-based ones. Such a shift benefits from the intake of plant protein from various sources (*e.g.* a combination of cereals and grain legumes) for the consumer to receive a suitable combination of essential amino acids. Production of plant protein from various crop sources also reduces the negative environmental effect within the crop production systems, where a higher variability of crops in the system contribute to increased biodiversity and lower pest and disease pressures. Furthermore, legumes and forages contribute with nitrogen fixation, and as a result the need for chemical inputs are decreased with a more diverse cropping system. Challenges for such an increased diversity still remains though through the lack of economic incentives for farmers and under-developed processes and market chains for the products. Also, the cultivation practices seem to have limited impact on the protein content (except for N fertilization to non-legume crops), extractability (except for harvest time of certain green biomass crops) and presence of unwanted components such as ANFs in the crop protein sources, although protein polymerization of the gluten proteins in wheat has been shown to be largely influenced by environmental factors. There is a high potential for increased cultivation of grain legumes and use of them for human consumption to a much higher extent than at current, for example in Europe in which only a minor share of the arable land is used for growing these crops today. However, this requires the development of crop varieties with high and more stable yields. The plant protein with the highest potential as a source for human consumption in the long-term is that derived from the green biomass. This is the most abundant protein on Earth and an increase in the use of this protein for human consumption would contribute to an efficient protein production in the field through the use of the whole plant instead of only seeds or tubers. Furthermore, green biomass can be grown worldwide and on lands not used for food production today, and the protein from green biomass shows both nutritional and functional high-value properties. However, the protein yield from current processing technologies of green biomass is too low for economic and environmental sustainability of the protein use for human consumption. Other challenges are consumer acceptance of novel products, unwanted compounds (*i.e.* polyphenols, ANFs etc.), co-precipitating with the proteins and hampering *e.g.* taste and nutritive value, as well as food regulation policies hampering the use of non-food crops as human food items. Both novel and further developed processing and plant breeding methods have the potential to change the opportunities to use protein from green biomass as well as from other sources such as grain legumes, potatoes and oil crops in the future. Through plant breeding efforts it might be possible to increase the protein extractability in the crops and simultaneously decrease the level or the co-precipitation behavior of ANFs and other un-wanted components. Changes on a molecular level, increasing the opportunities for plant protein production and fractionation, simultaneously as levels of ANFs are decreased can potentially be carried out in cooperation between researchers and plant breeders. Upcoming processing methods including advanced filtration or other separation methods might thereafter contribute to further purification steps, resulting in opportunities for economic and environmental high-value, high-quality plant proteins of various types and from various crops combinations for human consumption, thereby satisfying the consumer both locally and globally. However, both local and global food security frames might be needed to be developed in order to create overlapping frames at a macro-scale to bridge the distance between consumers and experts for the plant-based protein shift (de Boer and Aiking, 2011).

8. Conclusions

Plant proteins need to be of increasing importance within human consumption in the future as their consumption contribute nutrition to the increasing global population and a reduced negative environmental footprint to food production and to the human food protein supply. Food based on plant proteins generally shows lower GHG emissions and land use than food based on animal-derived proteins which drives together with health concerns, the consumer interest, especially in certain segments (younger, female), for plant protein-based alternatives. The increased use of plant-based proteins for human consumption may contribute to a more diversified source supply, i.e. a mix of various plant proteins such as those from cereals and grain legumes, which improves the content of essential amino acids and simultaneously contributes benefits to the cropping system through increased agrobiodiversity, breaking monocultures and use of lands not cultivated today. Increased cultivation of diverse crops for plant-based protein food has the potential to contribute significantly to increased human consumption of plant protein, but a development is required all through the food value chain to secure increased economic incentives for producers. The use of proteins from green biomass for human consumption shows high potentials; green biomass constitutes the most abundant protein on Earth, it shows the highest protein production efficiency among the crops as whole plants can be used for protein production, and green biomass can be grown almost everywhere on Earth. However, the use of these proteins for human consumption is also the most challenging among the plant proteins, due to lack of incentives for the growers, low protein yield in fractionation processes, legislation procedures as related to novel food and consumer acceptance of novel products. In general, for all crops to be used to produce plant protein for human consumption, an increase in protein content and extractability and a decrease in the presence of unwanted compounds such as ANFs are important characters. To secure such changes in the crops, plant breeding will play a major role and breeding for these characters should be included in breeding programs. Suitable genotypes should then be combined with production in cropping systems that secure economically feasible plant protein sources with a low carbon footprint, and processing utilizing modern technologies with a low carbon footprint to secure high-quality products that satisfies the consumer.

CRediT authorship contribution statement

Eva Johansson: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Georg Carlsson:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Åsa Grimberg:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **William R. Newson:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Thomas Prade:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Sara Spendrup:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Sven-Erik Svensson:** Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Eva Johanssoon reports financial support was provided by Swedish Research Council Formas. Eva Johanssoon reports financial support was provided by Region Skåne. Thomas Prade reports financial support was provided by Swedish Energy Agency. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.clrc.2025.100319.

Data availability

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

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