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Food proteins from animals and plants: Differences in the nutritional and functional properties

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ABSTRACT

Background: Animals and plants are the main sources of dietary proteins, and there are important differences in the type of protein that they supply. The differences include molecular structure, amino acid profile, digestibility, and technical functionality in food, i.e. the ability to gel, emulsify, bind water etc. These inherent differences influence their bioavailability from a human nutrition perspective, as well as the sensory quality of foods containing animal or plant proteins. These fundamental differences mean that designing plant-based foods to mimic animal foods requires much more than simple substitution of one ingredient with another.

Scope and approach: We survey some of the nutritional and technological functionality data for animal- and plant-derived food proteins and discuss the nature and implications of the differences between them.

Key findings and conclusions: Plant-based foods typically provide less complete protein nutrition because of lower digestibility and source-specific deficiencies in essential amino acids, compared with animal proteins. Such differences may not be as essential for adults as they are for infants and young children, due to their developmental requirements. Plant proteins can be subjected to various processes to bring their functionality closer to that of animal proteins (e.g. hydrolysis to improve solubility), but some processes that improve functionality also diminish amino acid bioaccessibility or bioactivity, creating negative nutritional consequences. Much more research and innovation are required to enhance the potential of plant proteins. In the short to medium term, nutritional and functional synergies between plant and animal proteins may offer a path to creating nutritious and attractive foods.

1. Introduction

Proteins in the human diet vary in chemical, biological, functional, and nutritional characteristics depending on their source, molecular make-up and structures. Protein intake in our diet comes from whole foods (raw, cooked or processed) or formulated food products that contain fractionated protein ingredients derived from animal or plant sources.

Animal protein is broadly recognised as having higher nutritional quality than plant-based protein. This alludes to its amino acid composition, digestibility and ability to transport other important nutrients such as calcium and iron. In addition, its technological functionality such as gelling, emulsification, and foaming, which gives food its appealing texture and sensory attributes, is considered superior to plant-based protein (Kim, Wang, & Selomulya, 2020). Proteins from animal sources, particularly dairy proteins, are important for providing adequate nutrition for human, particularly infants for their cognitive and physical development. Numerous reports and recommendations support the use of animal protein sources in food aid products (Allen & Dror, 2011).

Proteins from plant sources have attracted increased interest. Consumers increasingly look for plant-based food options, either for sustainability, health or ethical reasons, and food companies are responding with many new plant-based alternatives. The early plant protein products had dissimilar textural and flavour characteristics compared to animal protein products. In general, plant proteins offer lower nutritional values due to unbalanced amino acid composition (e.g. lack of some Essential Amino Acids (EAAs), such as lysine), and slow or reduced digestibility due to their molecular structures, for example. However, they still provide a good protein source for humans and can contribute to a balanced diet.

The inherent structural differences between animal and plant proteins hamper direct substitution in many products including major impact on sensory properties. However, by discovering more about the

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characteristics of all types of proteins, modifying their attributes through processing, and maximising their function, we have the capability to design increasingly innovative plant protein solutions that are acceptable to the consumer.

The aim of this article is to provide up-to-date scientific information on the food proteins from major animal and plant sources, with a focus on differences in their nutritional and functional properties. This knowledge will facilitate exploration of emerging food protein sources and overall improvement of nutritional and technological functionality of food proteins for all stages of human life.

2. Major sources of food proteins

Many of the most commonly available and utilised proteins from animal and plant sources are presented in Fig. 1a and **1b.** Also included are emerging food protein sources such as insects, pseudocereals (quinoa and chia seeds) and hemp seeds. The data shown as percentages are protein concentrations in natural biological resources (i.e. per wet weight), except for various protein powder ingredients (i.e. per dry weight). These values were taken from major Encyclopaedia book series (Caballero, Finglas, & Toldrá, 2015; Dikeman & Devine, 2014; Fuquay, 2011; Melton, Varelis, & Shahidi, 2018; Wrigley, Corke, Seetharaman, & Faubion, 2015). Note that the protein content of a food is only one part of its nutritional value in a diet. The proteins in food can have different amino acid compositions and digestibility (see Section 4).

2.1. Proteins from animal sources

The major animal proteins in human foods (Fig. 1a) are from dairy, meat, seafood and eggs. Recently, protein from insects is attracting broader interest.

Dairy. Milk contains 3–7% protein, depending on the animal species. For instance, the total protein content in bovine drinking milk is typically 3.2%, whereas goat and camel are approximately 3% and up to 7% in sheep milk. Large variations exist due to the animal genetics, farming systems and seasonality. While bovine dairy provides the majority of global dairy protein consumption, the production of non-bovine milk and their dairy production are increasing steadily worldwide (Roy, Ye, Moughan, & Singh, 2020).

The principal dairy proteins fall into two groups: caseins and whey proteins at a ratio around 80%:20% of the total milk proteins from cow. The caseins, a family of phosphoproteins, are unique to milk and present

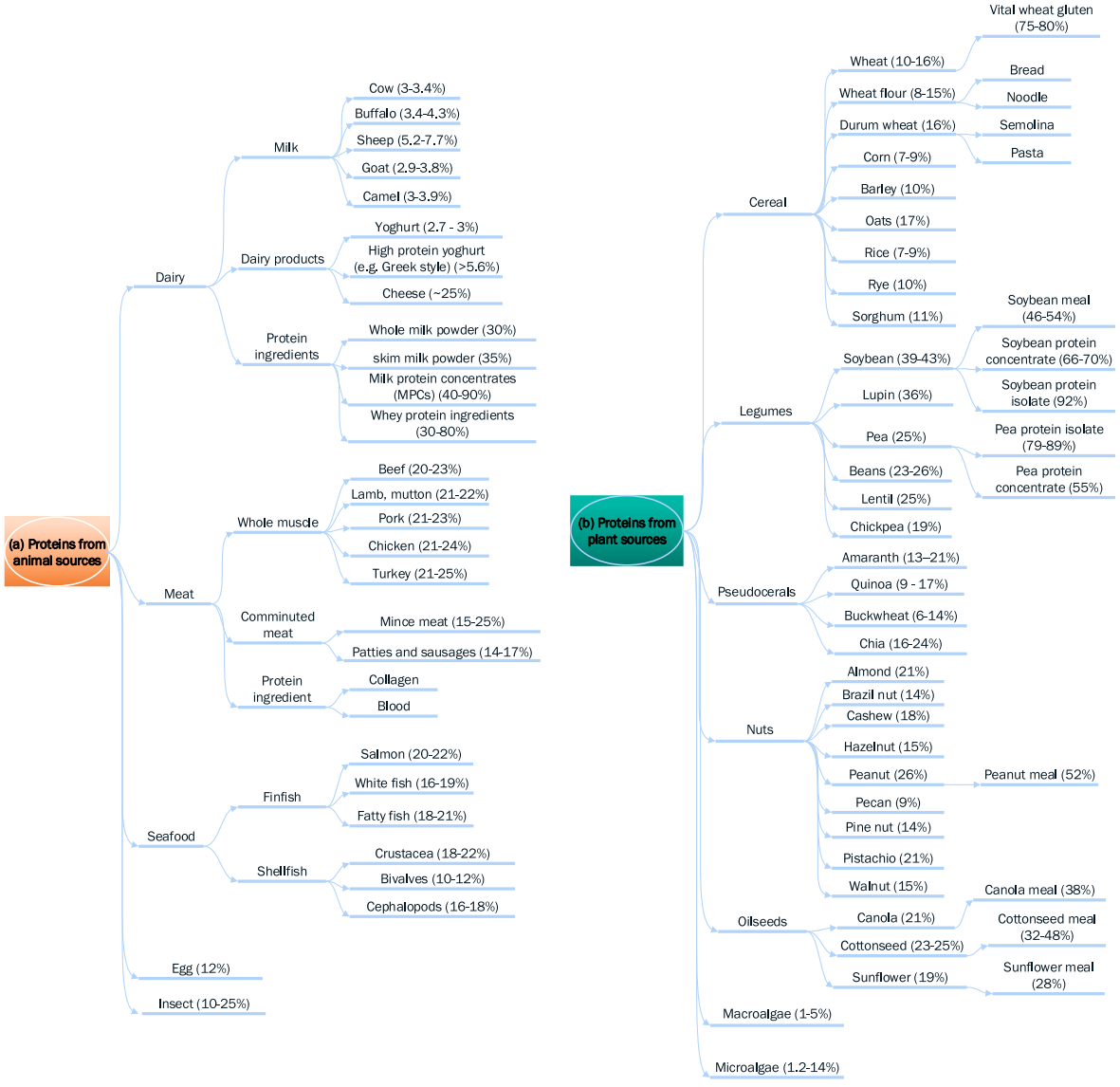

Fig. 1. Shows the protein contents from animal sources, protein ingredients and several food derived from them. (a) Animal sources; (b) plant sources. (Caballero et al., 2015; Dikeman & Devine, 2014; Fuquay, 2011; Melton et al., 2018; Wrigley et al., 2015).

as micelles in milk. One of the functions of casein micelles is to supply proteins, calcium, and phosphate in high concentrations that would otherwise be insoluble in water, to provide adequate nutrients to the neonate. The association between the mineral and protein components is also responsible for the functional properties that have been extensively exploited to produce dairy foods such as yogurts and cheeses. These unique nutritional and technological properties of caseins are difficult to replace with plant proteins.

With the advancement of processing technologies nearly half of the milk produced globally is now converted to dairy protein ingredients. Whole milk and skim milk are dried to produce milk powders. Skim milk powder usually contains 35% milk protein and whole milk powder is typically around 24% protein. Caseins and whey proteins are also commercially produced as high-protein ingredients through various processing steps such as separation, isoelectric precipitation, rennet coagulation and membrane filtration. The protein content of some of these ingredients (e.g. milk protein concentrates and whey protein isolates) are typically more than 80% and can be as high as >90%. Dairy protein ingredients are ubiquitous in beverages, confectionary, bakery products, meat and fish products, dietetic foods, infant formulae, foods for the elderly, and specialty products aimed at slimming, clinical and medical support, and sports nutrition (Harper, 2011).

Meat. The role of muscle meat as a food source is well established. Its protein content is relatively consistent across species, with an average near 22%. Comminuted and reformed foods comprised of muscle, organs or co-products, such as minced meat, burgers, sausages, and nuggets are common, although their protein content is generally lower than the muscle meat cuts (Fig. 1a). This is the category of animal protein-based products that potentially can be substituted by plant proteins, where the functionality of animal proteins (e.g. meat emulsion formation, water binding and fat binding capacity) may be matched by plant proteins. In addition, any negative flavour and taste notes from plant proteins can be more easily disguised in comminuted food products through formulation and the use of spices and flavouring agents.

In addition to the complete nutritional quality of its protein (i.e. all the EAA needed for growth and maintenance), meat provides other essential nutrients such as minerals (iron, zinc and selenium) and vitamins (D, B_6 and B_{12}) (Wyness et al., 2011). Iron in meat is mostly in the haem form, which is absorbed very efficiently. Moderate intake of lean meat is widely recognised to play an important part in a healthy balanced diet (Wyness et al., 2011).

Collagen is an abundant protein found only in the animal kingdom. It serves structural and connective roles in skin, bone, cartilage, tendon and blood vessels. When commercial collagen is partially hydrolysed or heat denatured, it forms gelatin, one of the most versatile meat protein ingredients. Gelatin is widely utilised as a food additive, such as stabiliser, thickener, gelling agent, film former, whipping agent, clarifying agent in various food products including confectionary and jelly desserts, ice cream, dairy product, meat product and beverages. Other applications include sauce, soup, frozen products, edible film, and coating, etc. The gelatin hydrolysate or collagen peptides are also manufactured on an industrial scale and are widely used as food ingredients.

Seafood is a diverse and valuable source of proteins. Edible fish muscle contains 16–21% protein. Fatty finfish and crustacea tend to have slightly higher protein contents. Fish is a prominent resource in many communities, and overall, provides about 16% of the animal proteins in the world. It is also a source of vitamins and minerals. Consumers have known for years that fish is a high-protein food with lower energy and total fat, particularly saturated fat, compared with other protein-rich animal foods.

One popular seafood product is surimi, which is made from a protein extract of fish meat and co-products. Different materials can be utilised in its production, such as underutilised species with low commercial value.

Egg proteins are recognised for their high nutritional quality, excellent digestibility, and complete provision of EAA. Avian eggs typically have 12% protein and 75% water. Approximately half of the protein in egg is in the albumen-rich white, 40% in egg yolk, and the remaining proteins are distributed in the eggshell and eggshell membrane. Proteins represent more than 90% of the egg white dry matter.

In addition to direct consumption, pasteurised whole egg, separated egg white, and egg yolk may be processed into liquid, frozen or powder forms. Processed egg products or egg powder ingredients are commonly incorporated into bakery, confectionery, and condiment products. Bakeries as a group are the largest users of whole eggs and separated yolks and whites. Manufacturers of mayonnaise and salad dressing rely on large quantities of salted yolks, and ice cream makers use sugared yolks. Plain yolks are also used for noodles and baby foods. Egg white products are primarily being used in cake pre-mix, sweets and meringue powders, etc. The function of egg white in these products is to provide the foam-forming capability and foam stability. Egg white is still considered as the reference for foaming properties, compared with other animal and plant protein ingredients.

Insects. The protein content of insects has been reported to be 19–24% (Lamsal, Wang, Pinsirodom, & Dossey, 2019). However, this is highly variable depending on the species, maturity stage, insect feed source and processing method. The protein is concentrated in muscles and cuticle layers covering the epidermis. Many insect-based protein ingredients for food or feed applications utilise drying and grinding of whole insects to powder. While insect consumption is common in some cultures in Asia, Oceania, Africa, and Latin America, it is unfamiliar to most Western populations. Therefore, the greater potential of insects will be as a processed protein ingredient (Gravel & Doyen, 2020).

2.2. Proteins from plant sources

The major source of plant proteins for human foods (Fig. 1b) are from grains, pulses, legumes, seeds, and nuts. Ancient grains, pseudocereals, and algae contribute relatively minor quantities to total global intake.

Wheat and cereal grains. Amongst all plant sources, wheat supplies the highest quantity of protein in the human diet (g/capita/day). Bread, breakfast foods, pasta and other wheat-based staples are consumed worldwide (Day, 2016). The protein content of cereal grains and the food prepared from them is in a range of 7–15%, and generally lower than animal protein foods on a dry matter basis.

Protein ingredients are also commercially produced from grains. For instance, 'vital wheat gluten' extracted from wheat as a co-product of starch production has a protein content as high as 75–80% and is added to a variety of manufactured food products (Day, 2011). Gluten serves to raise the protein content of flour-based products as well as increase water-binding capability, e.g. in processed meat products. One major issue associated with widespread utilisation of gluten from wheat (and similar proteins from barley and rye) is its link with celiac disease, which is characterised by inflammation of the small intestine resulting from an inappropriate immune response to the prolamin family of seed storage proteins.

Soy proteins. The overall contribution of soy protein in the average human diet is not as great as wheat protein. However, soy protein is the most popular plant protein source as an ingredient in formulated foods. Soybeans contain 35–40% of total protein, with a well-balanced amino acid composition, which makes soy protein an important source of plant protein, with the greatest potential to replace meat and dairy proteins in human diets.

A variety of soy protein derivatives are commercially produced, such as flour, protein concentrate, protein isolate, as well as texturised and hydrolysed proteins. Soy protein concentrate has >65% protein. Soy protein isolate is the most refined form of soy protein and has a protein content higher than 90%. They are used in a wide range of food products, chosen for their functional properties, such as water and fat binding, emulsification, foaming, and gelation.

Pea and other legumes. Pea is the second most important grain legume crop in the world and is used as a popular vegetable in human

food. The protein content of peas is typically about 25%, but is widely variable, depending on the genotype and growing conditions.

Chickpeas, lentils, and beans are other commonly consumed legumes. The protein content of these legumes is similar to peas, at around 20–36%. Lupins have a similar protein content to soybean, at about 40%. Despite the relatively high protein content in these legumes, the protein quality (i.e. amino acid profile and digestibility) is not as high as proteins of animal origin.

Legume seeds can be processed into flours, protein concentrates, or protein isolates to a protein content as high as 85–95%. These products can then be used in baking mixes, soup mixes, nutritional snack bars, pasta, meal replacement, beverages, baby food formulations, processed meat, and seafood products. Pea protein ingredients have good fat- and water-binding capabilities, emulsification properties, and can be used as an extender in emulsified meat products.

Pseudocereals (quinoa, buckwheat, amaranth, chia, etc.) are a current trend in human diets as they are gluten free grains with a good amino acid balance from a nutrition perspective. The protein content in pseudocereals, in general, are slightly higher than cereal grains (Fig. 1b), although they do vary greatly depending on the genotype and growing conditions.

Nuts and oil seeds. The protein content in nuts varies considerably. Peanuts, walnuts, almonds, pistachios, and cashews have the highest protein content at around 20% or higher, followed by Brazil nuts, hazelnuts, and pine nuts in the range of 11–15%. Pecan and macadamia nuts have the lowest protein content at below 10%. Nuts are most consumed as snacks or used in foods such as soups, cakes, pastries, cookies, bars and pasta sauces such as 'pesto.'

The use of oilseeds (such as sunflower seeds or hemp) as a protein source for human food is very low. There is a renewed interest in industrial hemp for human and animal consumption. Currently it is grown for seed production, for oil, fibre production or as a dual-purpose crop. The hemp industry has grown rapidly worldwide in recent years, although it is not yet mainstream. Industrial hemp (*Cannabis sativa*) is a cannabis plant with naturally low levels (<1%) of the psychoactive component, tetrahydrocannabinol (THC) but also contains cannabidiol (CBD), which has therapeutic properties (House, Neufeld, & Leson, 2010). The seeds of hemp are typically 25% protein, 30% oil and 10–15% insoluble fibre, and do not contain THC or CBD. Hemp seeds (*Cannabis sativa* L.) are pressed to extract the oil, and the resulting hemp seed cake can be milled to make a powder as a source of vegetable protein and dietary fibre. The amino acid profile of hemp seed has a nutritional quality similar to soy with good digestibility but with lower lysine content (Herreman, Nommensen, Pennings, & Laus, 2020). The protein powder, and hemp flour is used in cooking, for shakes or drinks and may be used as a protein source for body building.

Macroalgae. Seaweeds have been consumed as sea vegetables in Far East countries, especially in Japan, for centuries. Some are also sources of hydrocolloids. Seaweeds have received a lot of attention recently in Western countries, with interest in exploring them as a sustainable, nutritious plant food. The main species used as foods belong to the brown, green, and red seaweed groups. The protein content in native seaweeds (80–90% water content) is relatively low (1–5% wet weight, and 6–30% dry weight), and it varies considerably depending on the species, season as well as the environmental conditions.

Microalgae are more commonly used as a source of food in Asian countries. Despite its high protein content (on average 1.2–14% wet weight based on 80% water content, and 6–70% dry weight) and being regarded as an alternative sustainable protein source, micro-algae have not gained significant importance as food protein (Geada et al., 2018; Stone & Nickerson, 2012). The major obstacles are its dark green colour and its slightly fishy smell, which limit the incorporation of the algal material into conventional food products. Currently, the production costs for microalgae are still too high to compete with conventional protein sources. Microalgae *Chlorella*, *Spirulina*, *Haematococcus* and *Dunaliella* represent the majority of the market, which can be commercialized in tablet, capsule, liquid and powder forms.

Analogues. Plant-based products to replace milks, yoghurts, cheeses and infant formulae (i.e. analogues) are becoming popular. Most plant-based drinks are manufactured by extracting plant material, such as soy, nut, or rice, and mixing into water. The plant materials are then homogenised and thermally treated [using ultra-high temperature (UHT) processing] to improve suspension of particles and to increase shelf life. The nutritional content of these plant-based drinks depends on the source, methods of processing, and whether the products are fortified (Makinen, Wanhalinna, Zannini, & Arendt, 2016). Products of the same 'type' but from different manufacturers have variable macro and micronutrient content (Cakebread, Wallace, Kruger, Vickers, & Hodgkinson, 2019; Singhal, Baker, & Baker, 2017) since the 'milk' analogue industry is not regulated in the same way as the dairy industry. The choice of mineral compounds used for fortification is important, for example, supplementation using different calcium forms can affect bioavailability (Shankar, Sakthibalan, Raizada, & Jain, 2018).

The production of meat analogues and edible insects as a replacement for traditional meat has gained traction. There are still challenges with palatability, appearance, and flavour. A step further from making analogues of meat using plant protein is the production of cultured meat, which is laboratory grown muscle cells producing an animal muscle-based meat. There are challenges with mass production and cost that has slowed commercialisation. There have been limited opportunity to study nutritional impacts of these products.

3. Differences in the structures of food proteins

In nature, proteins exist as well-defined three-dimensional structures (the tertiary structure) as a consequence of attractive and opposing molecular forces, including electrostatic forces, ion-pairing, van der Waals interactions, hydrogen bonding, the hydrophobic effect and conformational entropy. The hydrophobic effect is the dominant driving force in protein folding and leads to the compactness of a globular protein. Steric constraints and hydrogen bonding are largely responsible for the unique internal organisation of a protein comprising a combination of secondary structures such as α-helix, the β-sheet, and the β-turn.

The structures of proteins from animal and plant sources are inherently different because they have different polypeptide sequences and are within different native environments (Day, 2016). They contain different amounts of each of the secondary structures and subsequently have different tertiary structures. The dynamic conformation of a protein determines the performance of particular functional properties such as solubility, gelation, emulsification, and foaming properties. It also influences the nutritional function of the protein in a food, e.g. the accessibility to digestive enzyme attack, fragmentation into peptides, and availability of EAAs.

Each protein source contains several classes of proteins which are structurally different, for example, the two major groups of proteins in milk – caseins and whey proteins. The caseins are known as intrinsically disordered proteins due to the lack (or low numbers) of disulphide bonds and their open and flexible structures. Together, they (β-, α_{S1}-, α_{S2}- and κ-caseins) form a protein colloid system called a casein micelle in milk. On the other hand, whey protein β-lactoglobulin is a globular protein and naturally exists as a dimer at neutral pH and as tetramers and octamers at acidic or basic pHs.

Considering meat as a protein source: there are three major groups of muscle proteins: sarcoplasmic, stromal, and myofibrillar (Boland, Kaur, Chian, & Astruc, 2018). Most sarcoplasmic proteins have globular structure with a high density of exposed polar and charged side chains, so are therefore readily soluble in water and low ionic strength solutions. Collagen (e.g. of stromal protein) forms triple-helical structures consisting of three polypeptide chains. Myofibrillar proteins, the most abundant protein fraction in meat that makes up the myofibril, consist of primarily myosin and actin. Myosin is composed of approximately 4500

amino acids and has a fibrous structure. On the other hand, actin exists as a globulin protein. Bundles of elongated myofibrils form the basis of meat muscle fibres that provide the eating characteristics of meat or muscle foods. Such unique structures are hard to replace or imitate with other proteins. Even with sophisticated extrusion technology and creative formulations, meat analogues made from vegetable proteins have not yet been able to replicate the texture and mouthfeel of real muscle foods.

A fundamental difference between animal and plant proteins is that the plant proteins are mostly storage proteins with large and compact structures. Plant proteins can be divided into four major classes, known as "Osborne fractions" (Day, 2013). These are albumins, globulins, prolamins and glutelins, based on their solubility and extractability in various solvents. Whilst most plant proteins contain these four protein classes, the protein contents of each class and their molecular size can vary considerably depending on the plant source (Day, 2013). Plant proteins of each of these classes exhibit different functional properties for food applications due to the molecular structures of the proteins.

The major storage proteins in cereals are prolamins (about 50% of the total grain proteins, except rice), and glutelins (20–40% and 80% in rice). These proteins have high contents of proline and glutamine, and thus generally insoluble (Fig. 2). Plant storage globulins are the major protein fraction of legumes, accounting 50–70% of the total legume proteins. Albumins are generally more prevalent in oilseeds and legumes (~20–25%), and high in the sulphur containing amino acids, cysteine and methionine.

4. Differences in the nutritional quality of food proteins

The major factors contributing to the nutritional quality of a dietary protein source are:

1. Proportion of protein in the material
2. Abundance of EAAs in protein
3. Digestibility of the protein

The protein content from different sources is given in Fig. 1 and discussed in Section 2. The EAA profiles of proteins from animal and plant sources (mg/g protein) are provided Table 1. The digestibility of food proteins are commonly measured by the Protein Digestibility-Corrected Amino Acid Score (PDCAAS) and the Digestible Indispensable Amino Acid Score (DIAAS) using animal models, and available data in literature are summarised in Table 2. The sources of data in Tables 1 and 2 are listed in Supplementary Tables 1 and 2

4.1. Amino acid profile

Proteins in food are hydrolysed by digestive enzymes into small peptides and individual amino acids, which are absorbed for use by the body for the synthesis of tissue proteins (growth and repair), catabolised to meet energy needs or used to synthesise other nitrogen containing compounds including hormones and neurotransmitters (Atherton, Smith, Etheridge, Rankin, & Rennie, 2010).

Nine of the twenty amino acids cannot be synthesised by the human body and so are referred to as EAAs. They are histidine, lysine, isoleucine, leucine, methionine, phenylalanine, threonine, tryptophan, and valine. Other amino acids such as arginine, glutamine, glycine, ornithine, proline, and serine are considered as 'conditionally essential' as they are more important at certain times of life such as during early development and in times of illness or stress. The rest of amino acids are considered "non-essential" as they can be synthesised by the body. For this review, the aromatic amino acids, (phenylalanine and tyrosine), and the sulphur-containing amino acids (methionine and cysteine) are reported together.

The only source of EAAs is from diet. Dairy, soy, egg and meat are considered complete sources of protein, as they contain all nine of the EAAs in adequate proportions for human body needs. When one or more EAAs are deficient in a protein source, it can limit the capacity for protein synthesis in the human body. In Table 1, each EAA (mg/g protein) is ranked by colour according to the amount of EAA in the protein source compared to the other sources (dark green is highest and white lowest). Firstly, it is evident that proteins from animal sources are different to those of plant sources, and secondly there is great variation comparing animal to animal source, and also plant to plant source.

For example, the lysine and threonine contents in most plant proteins, particularly in grain-based proteins, are substantially lower than animal proteins except for quinoa. However, quinoa is low in isoleucine, leucine and valine compared to oat, hemp, pea or soy. (Table 1). Lysine helps the body absorb calcium, and it plays an important role in the formation of collagen which is important for bones and connective tissues (Civitelli et al., 1992).

The branched-chain amino acids, leucine, valine and isoleucine, are thought to boost muscle growth and enhance exercise performance, although their effects are likely to be dependent on the nutritional status of the person (Bifari & Nisoli, 2017). Leucine plays an important role in enhancing and maintaining muscle mass and promoting lean body growth. Some studies suggest it can stimulate muscle growth and mitochondrial biosynthesis, thus preventing deterioration of muscle with age (Sun & Zemel, 2009). Dairy protein ingredients and concentrates are all high-quality proteins that are rich in leucine (Table 1). However, some plant proteins (e.g. those from cornmeal and sorghum)

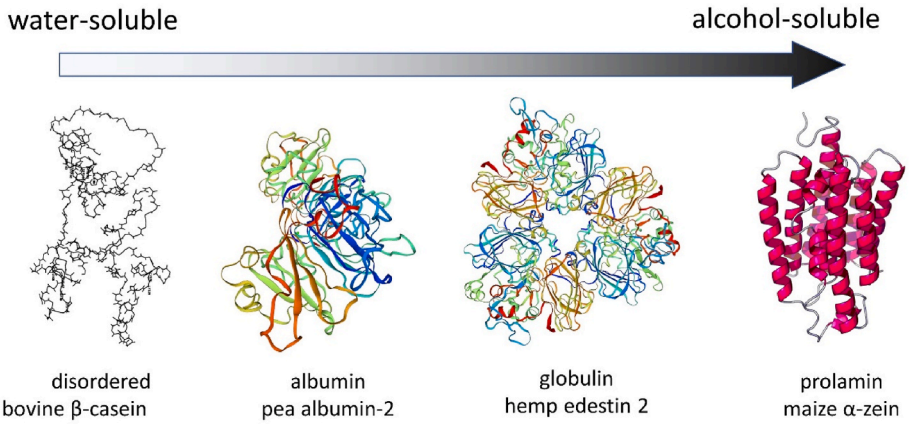

Fig. 2. The relationship between protein type and solubility (structures not to scale). The β-casein structure is from Kumosinski, Brown, and Farrell (1993), pea albumin-2 structure and hemp edestin 2 structures are from SWISS-MODEL entries ALB2_PEA and A0A090CXP8_CANSA, and the maize α-zein structure is from Díaz-Gómez, Castorena-Torres, Preciado-Ortiz, and García-Lara (2017).

Table 1
Essential Amino acid profiles of common protein sources. Each EAA (mg/g protein) is ranked by colour according to the amount of EAA in the protein source compared to the other sources (dark green is highest and white lowest). n.d. = not determined. Data sources are provided in Supplement Table 1.

Essential Amino acids	Basic		Neutral	Neutral (branched chain)			Aromatic		Sulphur AA
(mg/g protein)	Histidine	Lysine	Threonine	Isoleucine	Leucine	Valine	Phenylalanine + Tyrosine	Tryptophan	Methionine + Cysteine
Animal proteins									
Cow milk	28	84	47	53	99	65	95	14	30
Sheep milk	29	90	49	54	105	69	99	17	33
Goat milk	30	97	54	69	105	80	111	15	42
Caseins	31	85	46	59	102	76	114	14	33
Whey protein	16	109	88	74	121	69	75	17	52
Beef	31	70	36	40	65	46	61	10	35
Pork	37	76	40	39	71	47	68	11	30
Chicken	34	100	46	52	85	51	40	n.d.	31
Marine Fish	7	76	65	50	96	84	38	20	30
Freshwater Fish	33	33	38	38	57	44	52	6	14
Whole egg	25	78	51	57	91	64	98	12	47
Egg white (albumin)	17	62	36	46	68	49	77	10	38
Egg yolk	33	104	71	65	115	72	114	18	50
House cricket (adult)	24	55	37	47	74	54	83	7	24
Plant proteins									
Wheat flour	26	27	31	37	75	47	85	13	41
Durum wheat	23	24	30	26	70	44	73	13	36
Corn	27	29	36	39	128	51	100	8	44
Cornmeal	27	29	26	38	109	46	88	5	32
Oat	25	43	35	39	76	54	91	9	43
Rice	26	28	37	45	88	63	82	14	44
Rice protein concentrate	17	21	28	34	62	45	104	11	39
Rice protein isolate	17	23	29	34	64	44	86	12	40
Sorghum	18	16	29	34	127	43	76	n.d.	7
Soybean	28	73	47	54	90	55	99	16	31
Isolated soy protein	25	56	39	49	56	51	94	13	26
Soy protein concentrate	25	62	36	45	76	47	86	12	28
Pea protein concentrate	24	67	38	44	76	49	97	9	19
Fava beans	31	63	39	35	85	48	77	8	27
Chickpea	23	55	32	38	65	37	82	10	22
Lentil	29	69	44	35	71	46	71	5	26
Lupin	39	45	40	40	69	41	80	10	13
Amaranth	27	43	31	19	43	21	55	n.d.	41
Quinoa	19	24	67	8	24	9	27	10	6
Buckwheat protein	25	52	35	38	68	52	80	17	42
Hemp protein isolate	32	27	34	36	65	47	83	10	32
Hemp seed protein meal	33	39	38	36	69	47	77	11	38
Peanuts	25	39	22	35	70	40	88	7	16
Microalgae	26	66	52	45	93	61	98	n.d.	27
Microalgae cultured	28	72	53	44	92	62	101	n.d.	26
Microalgae products	22	70	49	51	91	62	96	n.d.	29

can also supply a similar level of leucine (mg/g protein) to animal proteins. It should be noted that although leucine is a high proportion of the protein in these sources, the protein content and digestibility are relatively low, therefore they are not considered to be the good sources of leucine.

Compared to animal sources, plant sources generally also have lower levels of tryptophan (Table 1). Tryptophan plays a role in the production of serotonin, melatonin, niacin and nicotinamide, with higher dietary intake leading to reduced depressive symptoms and anxiety (Lindseth, Helland, & Caspers, 2015). Methionine and cysteine levels in cereal proteins are similar to the animal proteins, however, they tend to be lower in legume proteins. Methionine is involved in cysteine synthesis via the transsulfuration pathway, which is rate limiting for the key antioxidant molecule, glutathione. Methionine is also the primary methyl donor in the body involved in the synthesis of several key metabolites including creatine and phosphatidylcholine, in times of active

Table 2
DIAAS and PDCAAS for common protein sources. PDCAAS-protein digestibility-corrected amino acid score, DIAAS- digestible indispensable amino acid score, LEAA-limiting essential amino acid, His-histidine, Lys-lysine, Thr-threonine, Leu leucine, Phe-phenylalanine, Tyr-tyrosine, Trp-tryptophan, Met-methionine, Cys cysteine, DM dry matter. Blank cells-data unavailable. *Truncated value. Columns are coloured according to the scores: highest scores are dark green signifying high quality EAA with good digestibility, pale green less so, and yellow or white signifies poor quality protein or poor digestibility. Blank cells signify absence of data. Data sources are provided in Supplement Table 2.

	0-6 month		LEAA	6 month - 3yr		3 yr-adult		LEAA
	PDCAAS	DIAAS	0-6 month	PDCAAS	DIAAS	PDCAAS	DIAAS	> 6month
Animal proteins								
Skimmed milk powder	88	81	Trp Thr	100*	105	100*	123	Met + Cys
Milk protein concentrate	85	85	Trp	100*	120	100*	141	Met + Cys
Casein				100	117			N/A
Whey protein isolate	66	67	Phe + Tyr	97	100	100*	125	His
Whey protein concentrate	72	71	Phe + Tyr	100*	107	100*	133	His
Pork					117			N/A
Beef cuts					97			N/A
Chicken				100*	108			
Whole egg					101			N/A
House cricket (Acheta domesticus-adult)				77				
Plant proteins								
Wheat	42	37	Lys	51	45	51	54	Lys
Corn (flour)					36			Lys
Rice				47	47			Lys
Sorghum				25	29			Lys
Oats					77			Lys
Oat protein concentrate	43	41	Phe + Tyr	58	56	69	67	Lys
Soy (flour)	72	73	Leu	93	89	100*	105	Met + Cys
Soy protein isolate	71	68	Met + Cys	86	84	100*	98	Met + Cys
Pea					70			Met + Cys
Pea protein concentrate	49	45	Trp	71	62	84	73	Met + Cys
Fava beans					55			Met + Cys
Quinoa				68				
Hemp seed cake					54			Lys
Lupin					68			Met + Cys

growth (Elango, 2020).

Nut proteins lack in some EAAs (Table 1, peanut as an example). Lysine (Brazil nut, cashew nut, hazelnut, pine nut, and walnut), sulphur amino acids methionine and cysteine (almond), tryptophan (macadamia, pecan), and threonine (peanut) are thought to be the first limiting amino acid for human (2–5 year old) requirements) (Venkatachalam & Sathe, 2006).

In summary, for the human body to make maximal use of dietary protein, there needs to be a readily available supply of all EAAs. The provision of EAA can be from plant or animal source. Where EAAs are lacking (limiting) complementary protein sources should be provided to ensure high quality protein and subsequent nutritional value.

4.2. *Protein digestibility*

Digestibility, or the measure of how well a human or animal can digest proteins and absorb amino acids, can be measured experimentally (Moughan, Gilani, Rutherfurd, & Tome, 2012). Methods include laboratory based *in vitro* protein digestibility assays (using acid and digestive enzymes), or *in vivo* feeding of animals then measuring unabsorbed amino acids in faeces and in the small intestine after a meal. The validity of extrapolating data from one species to another (e.g. animal trials to humans) depends on the similarity in metabolism and gut physiology, e.g. growing pigs are considered a good model for digestion in adult humans (FAO, 2013).

PDCAAS is a method of evaluating the quality of a protein based on both the amino acid requirements of humans (amino acid score, AAS) and their ability to digest it (Protein Digestibility-Corrected, PDC). In the literature PDCAAS values are often indicated as a fraction. In Table 2, we use a percentage for ease of comparison. A PDCAAS value can range from 0% to 100%. Values of >100 are truncated to 100. PDCAAS measures digestibility from faecal nitrogen. The microbiota, mostly present in the colon, also consume dietary and endogenous amino acids to produce cellular amino acids. These amino acids are not absorbed by humans in the colon and these bacterial cell amino acids are excreted in faeces. PDCAAS takes no account of amino acids produced from bacterial activity in the colon, with the net result that faecal digestibility almost always overestimates true digestibility.

PDCAAS was superseded in 2011 by DIAAS, which is considered a truer measure of protein nutritional quality since it accounts for ileal digestibility. DIAAS determines the digestibility of each individual amino acid, which is especially important in foods that have been processed or heated, or that have a high concentration of antinutritional factors, which can decrease the bioavailability or digestibility of different amino acids (Gilani, Tomé, Moughan, Burlingame, & Rutherford, 2012; Moughan, 2003). A DIAAS score of 100 means the quality of the test protein is equal to the quality of the reference protein. Proteins of animal origin tend to have better score of EAA and better digestibility than those of plant origin and so animal sources are used as reference proteins. The DIAAS methodology is now the recommended preferred method (FAO, 2013).

There is some concern that DIAAS has limitations for the assessment

of plant proteins (Craddock, Genoni, Strutt, & Goldman, 2021) and some protein sources have yet to be determined using DIAAS. For this reason, Table 2 shows both PCDAAS and DIAAS values, where available, and the limiting amino acids for each protein source for 0–6 months, 6 months - 3 years and over 3 years age groups. Also shown is the protein content (g/100g product) highlighting the amount of protein in the product that could be available for digestion. Columns are coloured according to the scores with highest scores coloured dark green signifying high quality EAA with good digestibility, pale green less so, and yellow or white signifying poor quality protein or poor digestibility. Many of the animal protein scores are around 100, whilst many of the plant proteins score less favourably. The exceptions are the mycoprotein, soy and pea proteins which score well, especially in the over 3 years age group (Table 2).

Digestibility is specific to a given food material or ingredient and cannot be generalised to other materials from a given source. This is complex because of variation in the physical and chemical availability of protein to digestive/absorptive processes, and the co-occurrence of substances that may inhibit digestion and/or absorption (Loveday, 2019). To be digestible, amino acids need to be released into the gut during digestion in the form of free amino acids or short peptides in which the sidechains of the amino acid are in their native form. There are several factors that can impact digestibility:

A. Limited bioaccessibility due to inherent or process-induced cross-linking or aggregation;
B. The chemical sidechain of one or more EAAs has reacted to produce nutritionally-inert (or even toxic) forms;
C. The food contains antinutritional factors that inhibit digestive enzymes and/or bind protein/amino acids;
D. Specific non-EAAs saturate the transporter enzyme complexes in gut tissue through which EAAs are also taken up, leading to competitive inhibition of EAA uptake.

Covalent crosslinks may be present within or between protein molecules, either natively or as a result of chemical, physical or biological processing. Protein crosslinking can decrease digestibility by inhibiting denaturation and obstructing enzyme access to peptide bonds in digestive conditions. For example, β-casein crosslinked with transglutaminase is more resistant to pepsinolysis (Monogioudi et al., 2011). Chemical crosslinking of egg protein with glutaraldehyde or methylglyoxal can inhibit hydrolysis by trypsin and chymotrypsin, as can Maillard reactions between proteins and sugars (Lassé et al., 2015). Heating can disrupt tertiary structure, rendering protein more digestible, but under some conditions amino acid side-chains are chemically modified (Lassé et al., 2015), which lowers the metabolic availability of EAAs (Elango, Ball, & Pencharz, 2009).

Strongly acidic, alkaline or oxidizing conditions can chemically modify lysine, serine, cysteine and methionine into derivatives such as lysinoalanine, cysteic acid and methionine sulphoxide. These derivatives are nutritionally unavailable and may in some cases be toxic (Gilani, Xiao, & Cockell, 2012). Analytical protocols for measuring these EAAs in food should account for possible process-induced derivatisation (Rutherfurd & Moughan, 2007, 2012).

Some protein sources contain proteins or carbohydrate polymers that block digestive enzymes, for example soy beans contain trypsin inhibitors, which inhibit digestion in the small intestine (Sathe, 2012). Polyphenols such as tannins can strongly bind proteins, making them unavailable for digestion (Stern, Hagerman, Steinberg, & Mason, 1996; Wong & Cheung, 2001). *In vitro* digestibility assays may not pick up the effects of digestion inhibitors, which need to be removed or inactivated for protein to be nutritionally available.

Lastly, competitive inhibition of the transporter enzyme complexes by non-essential AAs can reduce uptake of EAAs. Dietary amino acids are taken up into the body in the gut via several different transport systems that will take up only specific amino acids. These transporter complexes are also found in the brain, heart, kidneys and lungs, where they take up amino acids from the blood stream into tissues. Almost all neutral amino acids are taken up via the same transporter (B^0), so L-cysteine and L-leucine compete with L-glutamine (Fan, Adeola, McBurney, & Cheeseman, 1998). Anionic amino acids share a transport complex called the cystine/glutamate antiporter ($b^{0,+}$), which means that cysteine (in the form of cystine) and lysine compete with arginine (Bröer, 2008).

There is recent clinical evidence that a high oral intake of arginine inhibits lysine uptake (Schmidt, Murthy, Ennis, Stockler-Ipsiroglu, & Elango, 2020). This supports the findings of earlier human intestinal perfusion experiments with mixtures of amino acids (Matthews, 1972). For the dataset reported by Gorissen et al. (2018) (10 plant proteins, 5 animal proteins) the ratio of arginine to lysine is on average four times as high in plant proteins as in animal proteins (Supplementary Data). Competitive inhibition of uptake at the gut mucosa could conceivably diminish the bioavailability of lysine in plant-based foods, but the magnitude of this effect in free-living humans consuming normal diets is difficult to judge, in light of myriad other contributing factors (Matthews, 1972).

5. Technological functionality of food proteins

Technological functionality is defined as the effectiveness with which a protein-rich ingredient can fulfil a specific role in a food or beverage. In additional to their nutritional values, proteins also play important roles in the physicochemical properties and sensory quality in foods.

Comparing the technological functionality of proteins from animal and plant sources relies on the widespread use of standardised or comparable analytical methods, which is rare. In the case of solubility, emulsifying activity index, oil-holding and water-holding capacities, methods are sufficiently standardised to make meaningful comparisons, and we have compiled datasets for these functionalities. For other functionalities, a wide variety of equipment and methods are reported in literature, and we have not been able to make meaningful comparisons across a range of protein sources for emulsion stability, foaming capacity, foam stability, heat stability, thickening or gelling properties.

Published functionality data for proteins from both animal and plant sources are shown in Fig. 3 and spreadsheets in Supplementary Information. Fig. 3 shows a subset of data that represents the diversity of reported values; supplementary spreadsheets contain the full datasets. In some cases, data were extracted from graphs using WebPlotDigitizer (https://apps.automeris.io/wpd/).

There are physicochemical reasons why certain functionalities should be correlated with each other. Small amphiphilic proteins that can rapidly adsorb to air-water interfaces and stabilise them in foams often have some ability to stabilise oil-water interfaces in oil-in-water emulsions. Good solubility is a precursor of both functionalities. Surface charge enhances solubility, and gives a protein the ability to provide electrostatic stabilisation (or bridging) to emulsion droplets (Karaca, Low, & Nickerson, 2011). It has been reported that the emulsifying functionalities of several legume-derived proteins were correlated with solubility and surface charge, but interfacial tension and surface hydrophobicity were not correlated with other functionalities (Karaca et al., 2011).

Six functionalities for a range of plant-derived proteins, using consistent analytical methods were reported recently by a research group at the University of Saskatchewan (Lam, Warkentin, Tyler, & Nickerson, 2017; Shi et al., 2020; Stone, Avarmenko, Warkentin, & Nickerson, 2015; Stone, Karalash, Tyler, Warkentin, & Nickerson, 2015). We have sought correlations within this dataset (Supplementary Material), but among the pairs of functionality parameters, none showed particularly compelling relationships. This is partly because this dataset focuses on protein extracts from a few crops, especially peas. It may also be because empirical functionality measurements capture the influence of several physical or chemical phenomena simultaneously, as discussed below.

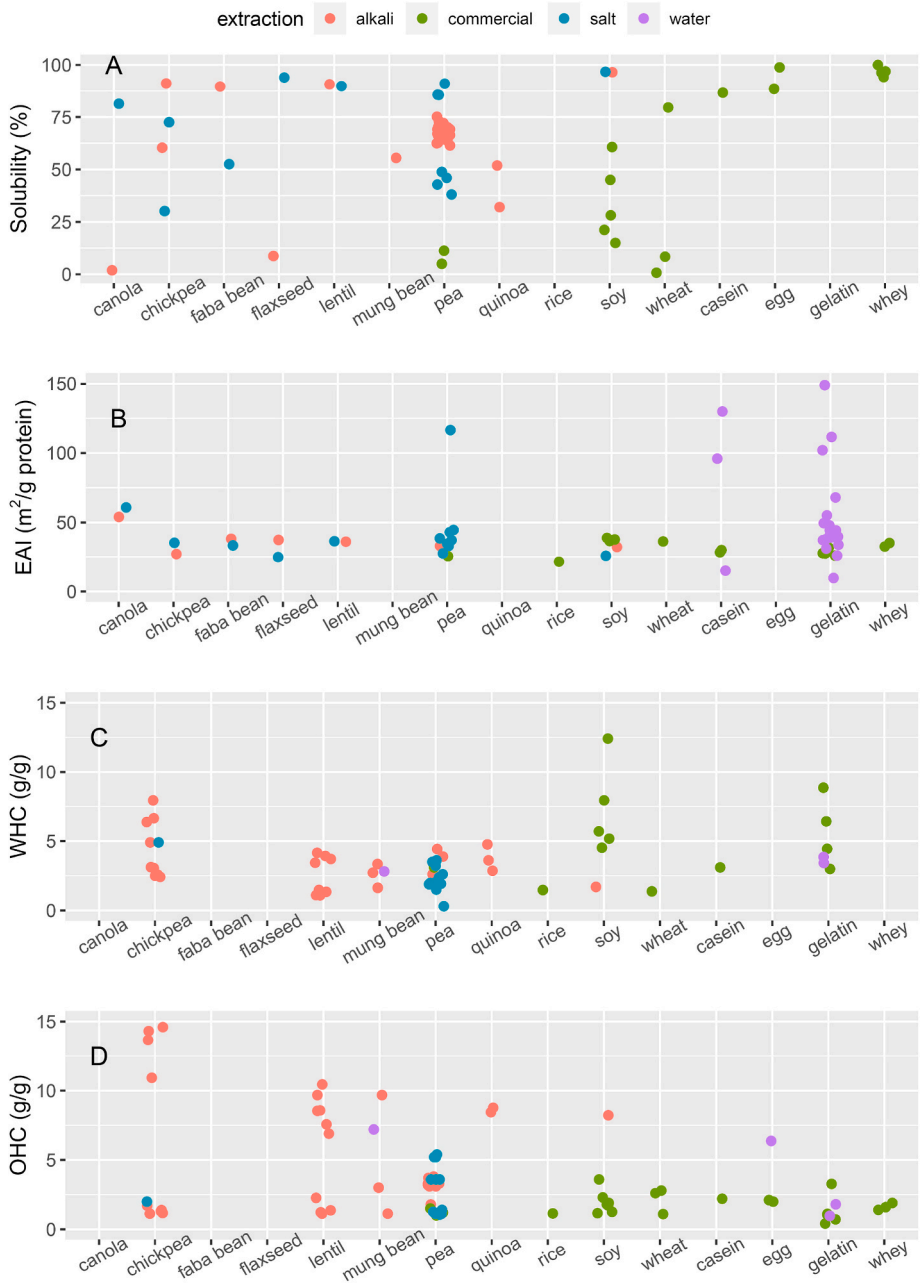

Fig. 3. Functionality of proteins from plant and animal sources. EAI, emulsifying activity index; WHC, water-holding capacity; OHC, oil-holding capacity. For complete dataset and references, see Supplementary Material.

5.1. Solubility

Most food protein ingredients are supplied as dry powders, and the ability to dissolve into water-based solutions is a key precursor of several other functionalities. Definitions of 'soluble' and 'insoluble' are not clear-cut, because the continuum between dry powder particles and a molecular solution of protein includes kinetically stable scenarios, such as suspended (but sedimentable) particles and thermodynamically stable states such as colloidally-stable micelles.

Fig. 3A shows the solubilities of food proteins extracted from a range of animal and plant sources, dissolved in water at neutral pH at a concentration of 1% w/w. The animal proteins (egg, whey, caseinate) all have solubilities >85%, whereas plant proteins span a much wider range of solubilities. Plant storage proteins are usually quite hydrophobic, as befits proteins designed to remain inert and compact in the seed. Milk and egg proteins are hydrophilic, which reflects their origin from aqueous systems.

Commercially extracted proteins are subject to harsher conditions than laboratory-extracted proteins, due to heat- and mass-transfer limitations at commercial scale. The commercially extracted plant proteins have poor solubility, however the commercial whey, egg and caseinate retained good solubility (Fig. 3A). This suggests that, potentially, there is a considerable room for optimising industrial processing of plant proteins. For laboratory-extracted proteins, the method of extraction often has a large influence on solubility, as seen by comparing alkali- and salt-extracted proteins in Fig. 3.

Proteins become soluble when their affinity for water is greater than their affinity for each other, and both are affected by the ionic environment – pH and salt concentration. Many proteins show a U-shaped curve of solubility vs. pH at low ionic strength (Fig. 4), reflecting poor solubility around the isoelectric point, where electrostatic repulsion is minimal and protein-protein aggregation occurs readily. The location

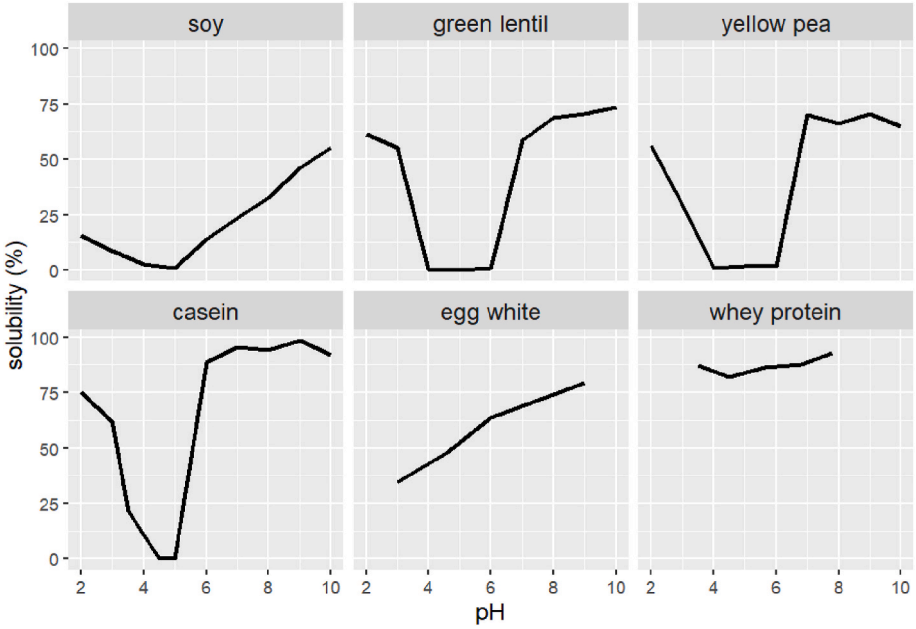

Fig. 4. The effect of pH on solubility for various food proteins. Data sources: Soy protein, Zhao, Shen, Wu, Zhang, and Xu (2020); green lentil and yellow pea, Boye, Aksay, et al. (2010); casein, Post, Arnold, Weiss, and Hinrichs (2012); egg white, Ferreira Machado et al. (2007); whey protein Pelegrine and Gasparetto (2005). For complete dataset see Supplementary Material.

and depth of the solubility minimum at low ionic strength depends on the source of the protein and the fraction, e.g. 7S pulse proteins are generally more soluble than 11S (Kimura et al., 2008).

The method of extraction also affects solubility, for example lentil protein concentrated by isoelectric precipitation has a wider and deeper solubility minimum than ultrafiltration-concentrated lentil protein (Boye, Aksay, et al., 2010). Alkali-extracted (pH 12) soy protein was more soluble than acid-extracted protein (pH 1.5) at pH above or below the isoelectric point (Jiang, Xiong, & Chen, 2010). On the other hand, alkali-extracted quinoa protein (pH 8–11) became less soluble as extraction pH increased (Ruiz, Xiao, Van Boekel, Minor, & Stieger, 2016)

The solubility of poorly-soluble proteins may be improved by hydrolysing protein with enzymes (Kankanamge et al., 2015; Wouters, Rombouts, Fierens, Brijs, & Delcour, 2016), but if hydrolysis creates small, hydrophobic peptides then hydrolysates have a bitter taste. Creating molecular complexes with polysaccharides can reduce allergenicity (Xu, Gong, Gern, Ikeda, & Lucey, 2018), and chaperone-like caseins can solubilise very hydrophobic proteins (Chuang, Wegrzyn, Anema, & Loveday, 2019). Deamidating wheat proteins (Webb, Naeem, & Schmidt, 2002) or caseinate (Yao & Zhao, 2015) with acid treatment can decrease hydrophobicity of the proteins, and thus improve their solubility.

5.2. *Emulsification*

Proteins that can adsorb to and stabilise oil-water interfaces are effective emulsifiers. Forming a protein-stabilised emulsion involves movement of a protein from the aqueous phase to a newly formed interface, adsorption at the interface and often unfolding, crosslinking or other conformational rearrangement over time. Proteins such as those from milk and egg, that are soluble, flexible, and amphiphilic make the best emulsifiers.

Small proteins tend to be more effective emulsifiers than large proteins or aggregates, due to higher molar concentration for a given mass, and therefore more effective stabilisation via the Gibbs-Marangoni effect (Van Vliet & Walstra, 2017). Plant globulin proteins occur natively as high molecular weight trimers (7S vicilins) or hexamers (11S legumins) (Boye, Zare, & Pletch, 2010), which detracts from their emulsification abilities. However, denaturation and/or limited hydrolysis can disrupt native structures and render plant globulins into effective emulsifiers (Wu, Hettiarachchy, & Qi, 1998).

The resistance of an emulsion to instability mechanisms such as coalescence, flocculation and Ostwald ripening depends on the characteristics of the interface: charge, thickness, permeability, steric barriers etc. Creaming resistance depends partly on the rheological properties of the continuous phase: a protein that enhances low-shear viscosity of the continuous phase can inhibit creaming. Typically, protein in an emulsion is located both in the continuous phase and at the interface. The balance depends on total protein concentration, water-to-oil ratio and whether the protein contains hydrophobic regions capable of adsorbing to an interface.

Various protocols exist for measuring both the ability of proteins to form emulsions and the stability of protein-stabilised emulsions. The diversity of methods makes comparisons problematic. Pearce and Kinsella (1978) developed the emulsifying activity index (EAI) to estimate the interfacial area per gram of protein, typically in m^2/gram. This method has been criticised as lacking relevance to food emulsions, for which the protein-to-oil ratio is typically higher than the ratio used for measuring EAI (Walstra & De Roos, 1993), but with few other standardised tests it is nevertheless useful for comparison.

Fig. 3B shows a compilation of EAI values for various protein materials, and data from a wide range of oilseeds can be found in Moure, Sineiro, Domínguez, and Parajó (2006). Protein concentration appears to affect EAI, e.g. increasing the casein concentration from 5 to 20 mg/mL decreased EAI from 130 to 68 m^2/g (Haque & Mozaffar, 1992), an effect attributed to aggregation of protein in solution and consequent thickening of interfaces. On the other hand, increasing the concentration of gelatin in emulsions (10–30 mg/mL) produced a modest increase in EAI (Jridi et al., 2013). The effect of concentration appears to be protein-specific, probably reflecting the propensity for self-aggregation in solution.

It is clear that wide ranges of EAI have been reported for several protein sources such as caseinate (49–149), soy protein (26–111) and whey protein (55–102). This reflects the variability in protein materials from a given source, which stems from seasonal and varietal differences,

but especially from different processing.

5.3. Water-holding capacity

The water holding capacity (WHC) is a measure of how much water a test material can chemically and physically bind. A high WHC is useful for maintaining juiciness and softness in intermediate- and high-moisture foods such as smallgoods (sausages, salami etc.), meat analogues and ready meals.

WHC is typically measured by adding water to a dry sample in a test tube, mixing and equilibrating for some time, then centrifuging at low speed and removing the supernatant. The pellet contains the test material solids and several populations of water molecules: a) strongly-interacting 'constitutional' water molecules with low molecular mobility, b) water molecules with intermediate mobility that are rapidly sampling hydration sites on the test material, and c) high-mobility water with properties similar to bulk water (Loveday, Huang, Reid, & Winger, 2012). High-mobility water may be retained in viscous gel phases formed by hydrated/dissolved biopolymers or held in pores and interstitial spaces by capillary forces.

For materials that may partially dissolve, a correction to the WHC can be made for the mass of dissolved material in the supernatant. Unfortunately, this correction is rarely included, and for that reason, uncorrected WHC values of partially soluble materials measured using excess water should be viewed with caution.

WHC values for protein-rich food materials are compiled in Fig. 3C. WHC is not suitable for highly soluble materials, such as caseinate, egg white and whey protein. As seen with other functional parameters, wide-ranging values have been reported for some proteins, e.g. soy (1.69–12.4) and bovine gelatin (2.99–6.42), reflecting how the diverse processing methods deliver diverse functionality.

Soy protein generally has high WHC, but other legumes (peas, lentils) have intermediate WHC, and the cereals (rice, wheat) have poor water-holding capacity. Cereal proteins are dominated by hydrophobic prolamins, whereas legume proteins are mainly water-soluble albumins and salt-soluble globulins (see section 3), which explains their WHC differences.

5.4. Oil-holding capacity

Oil-holding capacity (OHC) measures the affinity of a material for lipid, usually a vegetable oil. A high OHC is important for proteins used in batters and as binders in emulsion-based comminuted meat products or plant-based alternatives. Retained oil contributes to the juiciness and mouthfeel of the product and carries fat-soluble flavour compounds.

OHC is measured analogously to WHC – excess oil is mixed into a sample, free oil is removed by centrifuging at low speed and draining, and the mass of oil retained in the sample is calculated by difference then standardised to a 'per gram' basis.

The OHC of proteins is partly related to their intrinsic hydrophobicity. Proteins containing a greater proportion of hydrophobic amino acids, such as leucine, isoleucine, valine, and phenylalanine, can interact with nonpolar lipids via van der Waals forces. Blockwide distribution of hydrophobic amino acids, such as in caseins (Horne, 2009), gives rise to peptide regions that can enter lipid phases. Tertiary structure determines surface hydrophobicity, which is related to the distribution of hydrophobic amino acids between the interior and exterior of a folded peptide chain. Physical entrapment of lipids is also thought to contribute to oil holding, in that powders with a low bulk density (highly porous or convoluted shape) absorb more oil (Ma, 2016).

The relative range of OHC values is narrower than for other functional parameters (Fig. 3D). Animal proteins (e.g. casein, whey, gelatin) have moderate OHC, however, some of the plant proteins (e.g. pea, soy, wheat) are equivalent or slightly better at retaining oil than proteins from animal sources (Fig. 3d). Although extraction method has a relatively minor effect on OHC, concentrating alkali-extracted plant protein with ultrafiltration could give a slightly higher OHC than using isoelectric precipitation (Boye, Aksay, et al., 2010). Similarly salt extraction gives a high OHC than alkali extraction (Stone, Karalash, et al., 2015).

6. Discussion

6.1. Key differences between animal and plant proteins

Proteins fill different roles in animal bodies and plant tissues, and protein molecular structures and microstructures are correspondingly different. The nutritional and physicochemical functionalities of a protein-rich food or ingredient are determined by the protein source (animal tissue/biofluid and plant), but also the extraction/purification processes used to produce it, which fractionate proteins, modify structures and co-extract different non-protein materials.

Animal proteins supply EAAs more effectively than plant proteins, due to their amino acid composition and high digestibility. Two or more plant proteins can be consumed together to improve amino acid adequacy, but low digestibility remains a major problem with substantial impacts on human health and development, particularly for infants and young children. There is an urgent need for technologies to improve plant protein nutrition, e.g. through selective plant breeding or genetic modification, fortification with EAAs (van Vliet, Burd, & van Loon, 2015) or processing approaches that increase digestibility by addressing structural barriers to amino acid bioaccessibility and bioavailability (Salazar-Villanea, Hendriks, Bruininx, Gruppen, & Van Der Poel, 2016; Tamayo Tenorio, Kyriakopoulou, Suarez-Garcia, van den Berg, & van der Goot, 2018). However, blending plant proteins with animal proteins has more immediate potential to address these limitations (Rutherfurd, Fanning, Miller, & Moughan, 2015).

The physicochemical functionalities of animal and plant proteins are also very different. Plant proteins are typically more hydrophobic and aggregated (e.g. in oligomers), and less soluble and flexible than animal proteins, making it more challenging to use plant proteins in various food products without having negative impacts on sensory quality. However, protein functionality can be improved with various chemical and physical approaches. Care must be taken that processing for functionality improvements does not induce amino acid sidechain modifications or structural changes that subsequently diminish the amino acid bioavailability or bioactivity of plant proteins even further (Lassé et al., 2015; Rutherfurd, Montoya, & Moughan, 2014).

Food proteins are the major cause of allergy. Although allergens are distributed into few protein families, both plant and animal proteins alike have the potential to be allergenic (reviewed by Costa et al., 2020; Costa et al., 2021). Classification into families of the main (plant and animal) food allergens has identified some common structural, functional and biochemical properties that may contribute to allergenicity (Radauer, Bublin, Wagner, Mari, & Breiteneder, 2008). Food processing can change proteins in many ways including post-translational modification (glycosylation, phosphorylation), structural integrity (and position of the allergen within), stability (heat, pressure, light (radiation), mechanical and chemicals) which can influence allergenicity. For example, changing a protein's conformation can mask existing allergen epitopes resulting in complete or partial loss of allergenicity or conversely may reveal previously hidden epitopes, increasing allergenicity. Other process-induced changes, such as glycation or aggregation, can also have an impact, such as the protein aggregation of 2S albumins (seed storage protein) that can increase allergenicity, or aggregation of prolamins (legumes and cereal) that reduces it. New emerging food processing technologies, such as ohmic heating (OH), has been shown effective in changing the balance between monomeric and aggregated forms of β-lactoglobulin and physicochemical alterations of soybean proteins, thereby reducing their allergenic potentials (Pereira et al., 2020, 2021).

However, the clinical effects of process-induced modifications are

yet to be fully explored. There are significant knowledge gaps in our understanding of how the physicochemical parameters of process-modified proteins interact with the immune system to drive protein allergenicity both from animal and plant origin. Research in this area should be prioritised given the global appetite for protein.

6.2. Improving protein technological functionality

The restricted physicochemical functionalities of plant proteins typically limit their usage in food products, e.g. low solubility makes it difficult to include them in beverages, and the tendency to be compact, aggregated and inflexible limits their ability to stabilise interfaces. Protein functionality can be improved by physical, chemical and/or biochemical treatments, either of the protein alone or in combination with other components. The general principles of protein modification approaches are discussed below, and have been reviewed in detail elsewhere (Akharume, Aluko, & Adedeji, 2021; Burger & Zhang, 2019). Many plant protein food ingredients are relatively new, which means that there is little published information about modifying them to improve functionality, and strong potential for new developments in this respect.

Physical treatments include heating, static high-pressure treatment (Balasubramaniam, Martínez-Monteagudo, & Gupta, 2015) and shear-inducing processes such as ultrasonication (Gharibzahedi & Smith, 2020), ultra-high pressure homogenisation, pulsed electric fields (Zhang et al., 2021) or other shear treatments (Bekard, Asimakis, Bertolini, & Dunstan, 2011). Typically, physical treatments denature proteins, and can induce aggregation or crosslinking as a result of exposing hydrophobic residues that were buried in the interior of the protein. Denatured albumins and globulins (e.g. pea albumins and β-lactoglobulin from milk) are better able to adsorb to interfaces than native forms, and can form gels via disulphide bonds and hydrophobic interactions.

Chemical modifications may involve deamidating (Webb et al., 2002; Yao & Zhao, 2015), succinylating (Delahaije, Wierenga, Giuseppin, & Gruppen, 2014), acetylating (Yin, Tang, Wen, & Yang, 2009) or phosphorylating (Li, Enomoto, Hayashi, Zhao, & Aoki, 2010). Chemical modifications often change the charge and hydrophilicity of proteins, which affect pH- and salt-stability, as well as potential to crosslink. Complexing proteins with polysaccharides, dextrans or sugars can increase hydrophilicity, leading to enhanced emulsifying properties (Stone & Nickerson, 2012; Turgeon, Schmitt, & Sanchez, 2007) and increased solubility (Chuang, Ye, Anema, & Loveday, 2020). Non-covalently complexing hemp protein with casein can improve solubility and emulsifying properties (Chuang et al., 2020). A combination of hydrolysis and dextran grafting has been shown to decrease the allergenicity of whey proteins (Xu, Gong, Gern, & Lucey, 2020).

The most common biochemical modifications deliberately applied to proteins are enzymatic crosslinking or hydrolysis. Crosslinking enzymes include transglutaminase, laccase, and tyrosinase (Isaschar-Ovdat & Fishman, 2018; Loveday, Sarkar, & Singh, 2013; Selinheimo, 2008). Enzyme products for hydrolysing proteins are typically derived from conventional or genetically modified microbes, although some proteases can be sourced from fruit such as papaya (papain), pineapple (bromelain) and kiwifruit (actinidin). Hydrolysis of plant proteins can improve solubility, gelling and emulsifying properties (Wouters et al., 2016).

Some of the most reactive amino acids such as lysine, histidine, and tryptophan are also nutritionally essential, and their bioactivity can be diminished or eliminated by side-chain modifications. In some cases, side-chain modifications lead to toxic by-products. For example, under alkaline conditions, lysine, serine and cysteine can react to form lysinoalanine; this reaction renders them nutritionally unavailable but also creates reaction products that are toxic to the kidneys (Gilani, Xiao, & Cockell, 2012). In humans, methionine sulphoxide from dietary sources (oxidised proteins) is detected in blood plasma, indicating limited metabolic capacity to enzymatically reduce it to methionine (the biologically active form), and this may be especially true of young children (Kolpin & Hellwig, 2019). Therefore, one needs to be aware that some of the processes that improve physicochemical functionality can actually diminish nutritional quality.

Processes at moderate temperature and pH are the most promising for improving functionality without diminishing protein nutrition, e.g. enzymatic processes, and fermentation.

6.3. Future prospects

Plant proteins are important ingredients in the food industry given the global increase in demand for protein. Diversifying into plant food crops can add some resilience to the animal farming systems, balancing human nutrition needs with environment impact. Genetic modification for nutritional improvement of plant proteins may be more efficient in the long-term. Blending and co-processing animal and plant proteins together can also give rise to synergistic nutritional and technological functionality enhancement (Alves & Tavares, 2019; Nicolai, 2019). The design principles for blended-protein food systems are still under development, and there is much scope for innovation here.

This article has focused on proteins from established crops and livestock. New food protein sources from plant, animal, fungal and other kingdoms are being commercialized at a rapid pace. Cultured cell-based methods or synthetic biology approaches are emerging to create structured animal protein foods (i.e., meat analogues generated from cell cultures; shrimp made of algae, and vegan cheeses), however challenges remain on the viability and efficiency of the cultured cells impacting on the nutrition profile, flavour and taste (Lv et al., 2021; Rubio, Xiang, & Kaplan, 2020). Large scale manufacturing and food safety is another big hurdle to produce recombinant food. Currently there is still a lack of risk management and food safety standards.

Demonstration of equivalent or superior/new functions of novel protein sources compared to existing alternatives is essential for human nutrition and market success. Further, the basis of proteins in providing essential nutritional needs for humans at each different life stage cannot be ignored.

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Author contributions

L.D., Conceptualisation; L.D., J.C., S.M.L., writing—original draft, review and editing. All authors have read and agreed to the published version of the manuscript.

Declarations of competing interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.tifs.2021.12.020.

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